Visual Neuroscience (1990), 5, 165–204. Printed in the USA.

Cortical connections of MT in four species of primates: Areal, modular, and retinotopic patterns

LEAH A. KRUBITZER AND JON H. KAAS
Department of Psychology, Vanderbilt University, Nashville

(RECEIVED January 24, 1990; ACCEPTED May 7, 1990)

Abstract

Cortical connections were investigated by restricting injections of WGA-HRP to different parts of the middle temporal visual area, MT, in squirrel monkeys, owl monkeys, marmosets, and galagos. Cortex was flattened and sectioned tangentially to facilitate an analysis of the areal patterns of connections. In the experimental cases, brain sections reacted for cytochrome oxidase (CO) or stained for myelin were used to delimit visual areas of occipital and temporal cortex and visuomotor areas of the frontal lobe. Major findings are as follows: (1) The architectonic analysis suggests that in addition to the commonly recognized visual fields, area 17 (V-I), area 18 (V-II), and MT, all three New World monkeys and prosimian galagos have visual areas DL, DI, DM, MST, and FST. (2) Measurements of the size of these areas indicate that about a third of the neocortex in these primates is occupied by the eight visual areas, but they occupy a somewhat larger proportion of neocortex in the diurnal marmosets and squirrel monkeys than the nocturnal owl monkeys and galagos. The diurnal primates also have proportionally more neocortex devoted to areas 17, 18, and DL and less to MT. These differences are compatible with the view that diurnal primates are more specialized for detailed object and color vision. (3) In all four primates, restricted locations in MT receive major inputs from short meandering rows of neurons in area 17 and several bands of neurons in area 18. (4) Major feedforward projections of MT are to two visual areas adjoining the rostral half of MT, areas MST and FST. Other ipsilateral connections are with DL, DI, and in some cases DM, parts of inferotemporal (IT) cortex, and posterior parietal cortex. (5) In squirrel monkeys, where injection sites varied from caudal to rostral MT, caudal parts of MT representing central vision connect more densely to DL and IT than other parts. Both DL and IT cortex emphasize central vision. (6) In the frontal lobe, MT has dense connections with the frontal ventral area (FV), but not with the frontal eye field (FEF). (7) Callosal connections of MT are most dense with matched locations in MT of the other hemisphere, rather than with the outer boundary of MT representing the vertical meridian. Targets of sparser callosal connections include FST, MST, and DL.

The results support the conclusions that (1) prosimian primates and New World monkeys have at least ten visual and visuomotor areas in common, (2) the connections of MT are remarkably consistent across four species of primates, (3) the anatomical segregation of visual subsystems in areas 17 and 18 is common to all primates, (4) connections from the part of MT representing central vision with visual areas emphasizing central vision are more dense, and (5) MT and the associated fields MST and FST occupy proportionally more cortex in nocturnal than diurnal primates.

Keywords: Area 17, Area 18, Visual cortex, Corpus callosum, Frontal lobe

INTRODUCTION

The middle temporal visual area, MT, in the upper temporal lobe of primates (Allman & Kaas, 1971*a*; Allman et al., 1973; Gattass & Gross, 1981; Van Essen et al., 1981) is an area important for visual tracking and the perception of motion (Newsome et al., 1985; Dürsteler et al., 1987; Newsome & Pare, 1988; Logothetis & Schall, 1989; Newsome et al., 1988). Cortical connections of MT include major inputs from both the first (V-I) and second (V-II) visual areas, and MT projects to adjoining visual areas FST, MST, and posterior parietal cortex (for review see, Van Essen, 1985; Maunsell & Newsome, 1987; & Kaas 1988). In the present study, we address two basic questions about the connections of MT. First, how do the connection patterns of MT compare across species of primates? We expect the connections of the same cortical area to be highly similar across species, yet striking species differences in connections have sometimes been demonstrated for areas of sensory and motor cortex. For example, the second somatosensory area, SII, receives major thalamic connections from the ventroposterior nucleus in at least some nonprimate mammals (e.g. Burton & Kopf, 1987; Krubitzer & Kaas, 1987*b*), but most of the projec-

Reprint requests to: Jon H. Kaas, 301 A & S Psychology Building, Department of Psychology, Vanderbilt University, Nashville, TN 37240, USA.

tions in monkeys originate in the ventroposterior inferior nucleus instead (Friedman & Murray, 1986; Krubitzer & Kaas, 1986). MT appears to exist in all primates, and MT can often be identified with certainty from myeloarchitecture. Thus, it is possible to compare connections across species using myeloachitectonic criteria to ensure that the injections are restricted to MT and do not involve adjacent fields.

A second important question is "Do parts of MT representing central vision have different connections than parts representing paracentral and peripheral vision?" Cortical areas are usually thought of as having similar connections throughout. However, only parts of V-I devoted to central vision appear to project to the cortex in the DL/V4 region of extrastriate visual cortex of macaque monkeys (Zeki, 1978*a*; Perkel et al., 1986; Van Essen et al., 1986; Cusick & Kaas, 1988*b*), and Ungerleider et al. (1986) concluded that parts of V4 representing central vision have different cortical connections than parts of V4 representing peripheral vision. Thus, we determined the connections of different parts of MT in squirrel monkeys where most of MT is accessible on the surface of the cortex.

Studies of MT connections to date have included marmosets (Spatz & Tigges, 1972), squirrel monkeys (Tigges et al., 1981), owl monkeys (Weller et al., 1984), galagos (Wall et al., 1982), and macaque monkeys (Maunsell & Van Essen, 1983; Ungerleider & Desimone, 1986*a*). Although somewhat different patterns of connections have been reported in these studies, the significance of the reported variations is difficult to evaluate since methods differed across studies, and there are uncertainties about the identities of target areas. The early studies were performed before the current, more comprehensive understanding of the organization of the extrastriate cortex developed, and more recent investigators have related results to somewhat different conceptual schemes of cortical organization. In addition, all of the major studies of MT connections were completed before it was appreciated that modular subdivisions of visual areas can have different connections. For example, neurons in specific cytochrome-oxidase dense bands in V-II of macaque monkeys (DeYoe & Van Essen, 1985; Shipp & Zeki, 1985, 1989*b*), squirrel monkeys (Krubitzer & Kaas, 1989*a*), and apparently owl monkeys (Shipp & Zeki, 1989*b*) project to MT, but it is not certain if this type of organization holds for other primates. More specifically, are modular connections of MT with V-I and V-II present in a wide range of primates, and can these modules be identified architectonically and anatomically in different lines of primate evolution? One difference in the connections of MT with modules in V-II has already been reported. CO thick bands in V-II project to MT in macaque monkeys (DeYoe & Van Essen, 1985; Shipp & Zeki, 1985, 1989*b*), whereas CO thin bands project to MT in squirrel monkeys (Krubitzer & Kaas, 1989*a*). Since CO thick and thin bands have been related to separate magnocellular and parvocellular subsystems, respectively (see DeYoe & Van Essen, 1988; Livingstone & Hubel, 1988), this reported difference in connections in squirrel and macaque monkeys is intriguing. Examining modular connections of MT with V-I and V-II in major lines of primate evolution may lead to a greater understanding of the development and evolution of cortical modules in the visual system. In the present investigation, detailed descriptions are given for four different primate species.

We addressed the question of how species of primates differ in visual cortical organization by injecting WGA-HRP into MT of owl monkeys, squirrel monkeys, marmosets, and galagos. Owl monkeys and squirrel monkeys make interesting comparisons in that they are New World Cebid monkeys adapted for nocturnal and diurnal vision, respectively (Hershkovitz, 1977). We would expect aspects of cortical organization and connections to reflect the behavioral adaptations of nocturnality and diurnality. Visual cortex appears to have two major hierarchies of processing stations, with one stream for object identification directed toward the inferior temporal lobe and the other for visual tracking and attention directed through MT to the posterior parietal cortex (Ungerleider & Mishkin, 1982; Mishkin et al., 1983). In dim light, a subsystem for detailed object vision may be less useful, while a subsystem for visual search may remain important. Thus, MT may be relatively more important in nocturnal primates.

Marmosets are of special interest as New World monkeys of the family *Callitricidae*, long regarded as the most primitive living monkeys (Beattie, 1927; Hershkovitz, 1977). Although it is important to recognize that living species typically contain a mixture of primitive, intermediate, and advanced features, primitive features may be more common in marmosets. Finally, galagos were included in these studies as an available prosimian primate. Since galagos are nocturnal (Hershkovitz, 1977), they might be expected to share some features of cortical organization with owl monkeys. However, as members of a separate branch of primate evolution, galagos could differ significantly from all New World monkeys. Because extant prosimians generally resemble early primates, results from galagos could help us achieve an understanding of the early stages of the evolution of visual cortex in primates.

In all species, we injected MT and, after perfusion, separated cortex from the rest of the brain, manually flattened cortex, and cut brain sections parallel to the surface. This allowed us to determine the details of surface-view patterns of connections without the difficulties and potential errors of laborious reconstructions. We used myelin stains and CO reactions to identify cortical areas, since these procedures have previously proven useful and accurate in identifying MT, VI, VII, and other subdivisions of cortex (e.g. Luethke et al., 1989; Tootell et al., 1985; Allman & Kaas, 1971*a*; Allman & Kaas, 1975). Myelin stains and CO reactions also identify bands in V-II and blobs in V-I (see Wong-Riley & Carroll, 1984; DeYoe & Van Essen, 1985; Shipp & Zeki, 1985, 1989*a*, *b*; Tootell et al., 1985; Livingstone & Hubel, 1987; Krubitzer & Kaas, 1989*a*) and allow connection patterns in V-II and V-I to be related to patterns of bands and blobs.

Some of these results have been briefly presented elsewhere (Krubitzer & Kaas, 1987*a*, 1988*a*, 1989*a*, Kaas & Krubitzer, 1988).

Methods

The cortical connections of the middle temporal visual area, MT, were investigated in six squirrel monkeys (*Saimiri sciureus*), three owl monkeys (*Aotus trivirgatus*), two marmosets (*Callithrix jacchus*), and three galagos (*Galago senegalensis*) by injecting small amounts of wheatgerm agglutinin conjugated to horseradish peroxidase (WGA-HRP) or other anatomical tracers into the cortex in the expected location of MT. After appropriate survival periods, the animals were perfused, and the brains removed. The cortex was separated from the deep structures, manually flattened, and cut parallel to the surface. Some sections were reacted to reveal the WGA-HRP and other sec-

tions were stained for myelin or reacted for cytochrome oxidase (CO). Injection sites and connection patterns were later related to subdivisions of the cortex identified by differences in CO or myelin. The basic procedures closely follow those used previously in this laboratory (e.g. Cusick & Kaas, 1988*a*; Kaas et al., 1989; Krubitzer & Kaas, 1989*a*).

At the beginning of each experiment, each animal was anesthetized with initial injections of ketamine hydrochloride (30–50 mg/kg; White et al., 1982) and acepromazine maleate (1 mg/kg). Supplemental injections of one-tenth of the original injection were given as needed to maintain surgical levels of anesthesia. In addition, a local anesthetic, 2% xylocaine hydrochloride, was infused along the incision line. Using standard sterile surgical procedures, the skin was cut and retracted, and a small amount of bone was removed over cortex in the region of MT in the upper temporal lobe. A small slit was placed in the dura to admit the injecting micropipette coupled to a 10-μl Hamilton syringe. Injections were 0.05–0.08 μl of 0.1% WGA-HRP, except for one squirrel monkey where the anatomical tracer was tritiated WGA-HRP, and one owl monkey, where the tracers were separate injections of 0.2 μl of 2% of the fluorescent tracers, fast blue, and diamidino yellow. After injections in each case, the opening in the skull was covered by a cap of dental acrylic, the skin was sutured, and animals were allowed to recover from anesthesia. Antibiotics were given, and after survival periods of 2 days for the WGA-HRP injections or 5 days for the fast blue injection, each animal was given a lethal dose of barbiturate (pentobarbital sodium) and, when areflexive, perfused transcardially with 0.9% saline followed by fixative (2% buffered paraformaldahyde) and then fixative with 10% sucrose.

In preparation for histology, each brain was removed immediately after perfusion, and the cortex was separated from the brain stem. Next, sulci were opened by blunt dissection, and the cortex was separated from the underlying white matter and manually flattened with the aid of several cuts. The flattened cortex was submerged in 30% sucrose in phosphate buffer under a lightly weighted glass plate. This procedure allowed all or nearly all of the neocortex to be retained in one or two large flat pieces (Fig. 1). After about 15 h in the buffered sucrose solution, the flattened pieces were cut parallel to the cortical surface into 40-μm sections. Every third section was reacted for HRP with tetramethylbenzadine (TMB) following the procedures of Mesulam (1978) as modified by Gibson et al. (1984), or mounted for autoradiography (1 case) or for fluorescence (1 case). A second series of every third section was reacted for cytochrome oxidase (Wong-Riley, 1979*a*), and the remaining sections were stained for myelin with the Gallyas (1979) silver procedure.

A drawing tube connected to a microscope was used to produce detailed drawings of WGA-HRP label within individual brain sections at high magnification. Fluorescent label was illustrated using a fluorescent microscope coupled to an *X–Y* plotter. Other drawings of brain sections included myeloarchitectonic boundaries, or CO patterns. Local landmarks such as blood vessels and artifacts in the tissue that crossed the depth of cortex were used to align parts of drawings of adjacent sections so that label at different cortical depths could be summarized in a single surface view of the flattened cortex, and architectonic and CO boundaries could be superimposed.

For all sectioned cerebral hemispheres, the drawings included the total extent of neocortex and the myeloarchitectonic boundaries of visual areas. The total surface area of neocortex and the surface areas of cortical fields were measured from these drawings using an image analysis system (Bioquant, R & M Biometrics). Subdivisions of somatosensory, motor, and visuomotor fields were identified in the sections stained for myelin, and these fields were added as useful references to the summary drawings.

Laminar patterns of connections were determined by evaluating the depths of label relative to the reconstructed depth of the cortex and relative to layer IV, which was typically denser in CO preparations. Laminar patterns of MT connections for New World monkeys and galagos are more fully described elsewhere (Weller et al., 1984; Wall et al., 1982).

Results

Surface-view distributions of cortical label transported from injection sites in MT were determined for galagos, marmosets, owl monkeys, and squirrel monkeys. Results are presented in three main parts. First, we describe architectonic features of subdivisions of visual cortex in myelin-stained or CO-reacted brain sections cut parallel to the surface of manually flattened cortex. Identifying subdivisions of visual cortex across species of primates by myeloarchitecture and CO reactivity was important in the interpretation of the connection patterns. In addition, we provide measurements of the surface areas of the well-defined visual areas. Second, we relate injection sites to MT, as defined by myeloarchitecture, and describe ipsilateral connection patterns of MT relative to myeloarchitectonic fields and substructures within area 17 and 18 that are revealed by CO and myelin preparations. Third, we describe patterns of label in the contralateral cerebral hemisphere after MT injections.

Subdivisions of visual cortex

A number of visual areas were apparent in the sections from flattened cortex stained for myelin. Some of these same fields were also obvious in brain sections reacted for CO, but in general, the myelin-stained sections were more informative. However, the CO preparations revealed CO blobs in area 17 and CO bands in area 18. Cortical borders were determined by examining sections at several depths from the surface.

Area 17

Area 17 or V-I was easily identified in myelin or CO preparations, and the border between areas 17 and 18 was sharp. However, the appearance of the field varied with the depth of the brain section. In superficial sections reacted for CO, an array of evenly spaced CO-dense dots of blobs (see Horton, 1984 for review) was obvious in squirrel monkeys (Fig. 4A), owl monkeys (Fig. 2E), marmosets and galagos (Fig. 2D). In superficial sections, area 17 was lightly and heterogeneously myelinated (Fig. 2B, squirrel monkey and Fig. 4H, galago). Close inspection revealed a scattering of holes in the myelin pattern that formed a complimentary pattern to the CO-dense blobs (Fig. 3; see Krubitzer & Kaas, 1989*a* for details). Deeper layers of area 17, particularly layer 3C of Hassler (1966) (4B of Brodmann, 1909), were densely myelinated (Fig. 4D, 4G, and 4H: see Allman & Kaas, 1974*a*). Layer IV (4C of Brodmann, 1909) was very dark in CO preparations (Fig. 2A and 2C, also see Wong-Riley & Carroll, 1984).

The surface-view preparations of area 17 allowed regions devoted to central and peripheral vision to be identified. In

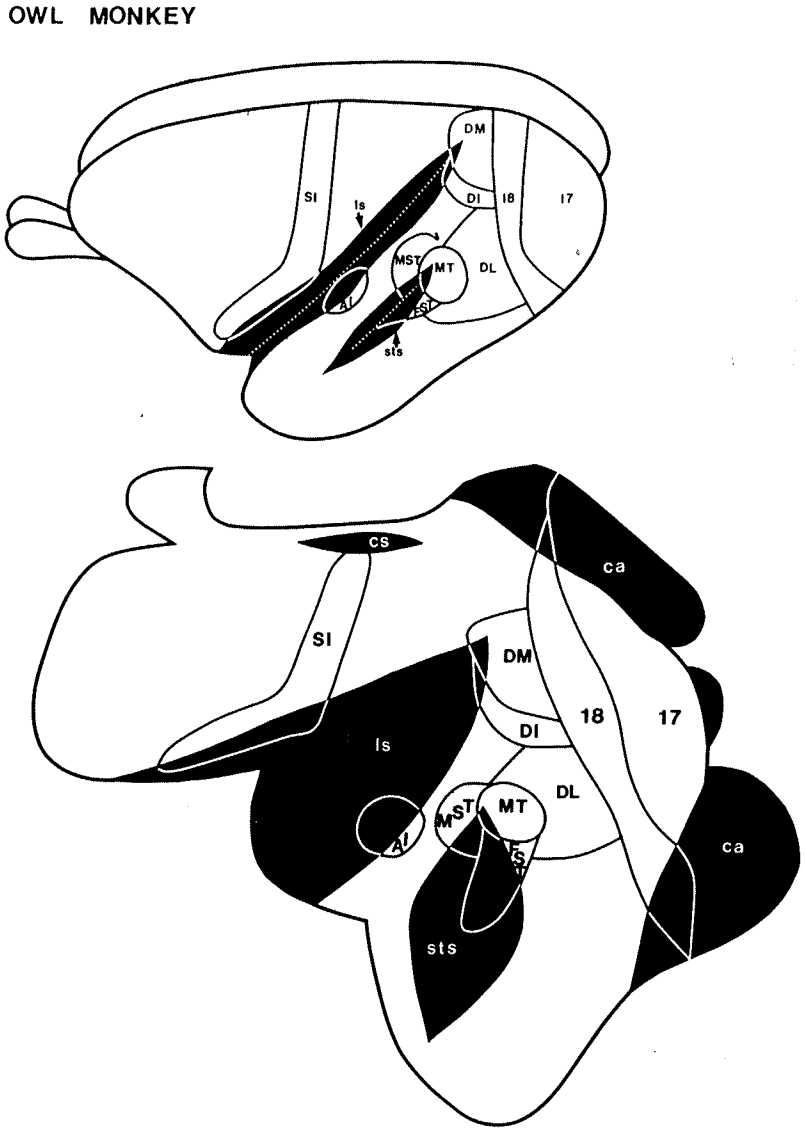

Fig. 1. Flattened neocortex in an owl monkey. A dorsolateral view of an owl monkey brain (above) depicts sulci and some of the cortical visual, auditory, and somatosensory areas. The sulci are slightly opened (solid black). The neocortex is shown below after it has been separated from the brain and manually flattened. Sulci are completely opened. Previously buried cortex is depicted in solid black. Solid lines mark architectonic boundaries, while the dotted lines indicate the fundus of the sulci. SI: primary somatosensory cortex; AI: primary auditory cortex; DM: dorsomedial visual area; DL: dorsolateral visual area; DI: dorsointermediate visual area; MT: middle temporal visual area; FST: fundal superior temporal area; MST: middle superior temporal area; 17: primary visual area; 18: second visual area; ls: lateral sulcus; sts: superior temporal sulcus; cs: cingulate sulcus; ca: calcarine sulcus; see Heurta et al. (1987) for details of the flattening procedure.

squirrel monkeys, the dorsolateral portion of area 17 representing central vision (Cowey, 1964) bulged rostrally into area 18 (Figs. 2A, 2B and 4A, 4B). A similar bulge was distinct in marmosets (Figs. 2C and 4G), but was less pronounced in owl monkeys (Fig. 2E) and galagos (Figs. 2D and 4H), which have less cortex devoted to central vision (Allman & Kaas, 1971*b*; Weller & Kaas, 1982). The representation of the temporal periphery of the visual hemifield (60–90 deg from fixation) is in the part of area 17 in the calcarine fissure that is bordered by architectonic field prostriata rather than area 18 (see Allman & Kaas, 1971*b*). In our preparations, the cortex at the rostral end of the calcarine fissure was typically split so that a portion was ventral and a portion dorsal in the flattened preparations (e.g. Fig. 12). In these locations, the cortex bordering area 17, without the banded appearance of area 18, was judged to be area prostriata. Thus, the dorsal and ventral extremes of area 17 in the flattened preparations represent peripheral vision, with the dorsal cortex devoted to the lower visual hemifield and ventral cortex devoted to the upper visual hemifield (e.g. Allman & Kaas, 1971*b*).

Area 18

In previous descriptions of CO preparations of flattened cortex, area 18 has been characterized as having a series of alternating dense and light bands that cross the width of the field (see Tootell et al., 1983; Livingstone & Hubel, 1987; Cusick &

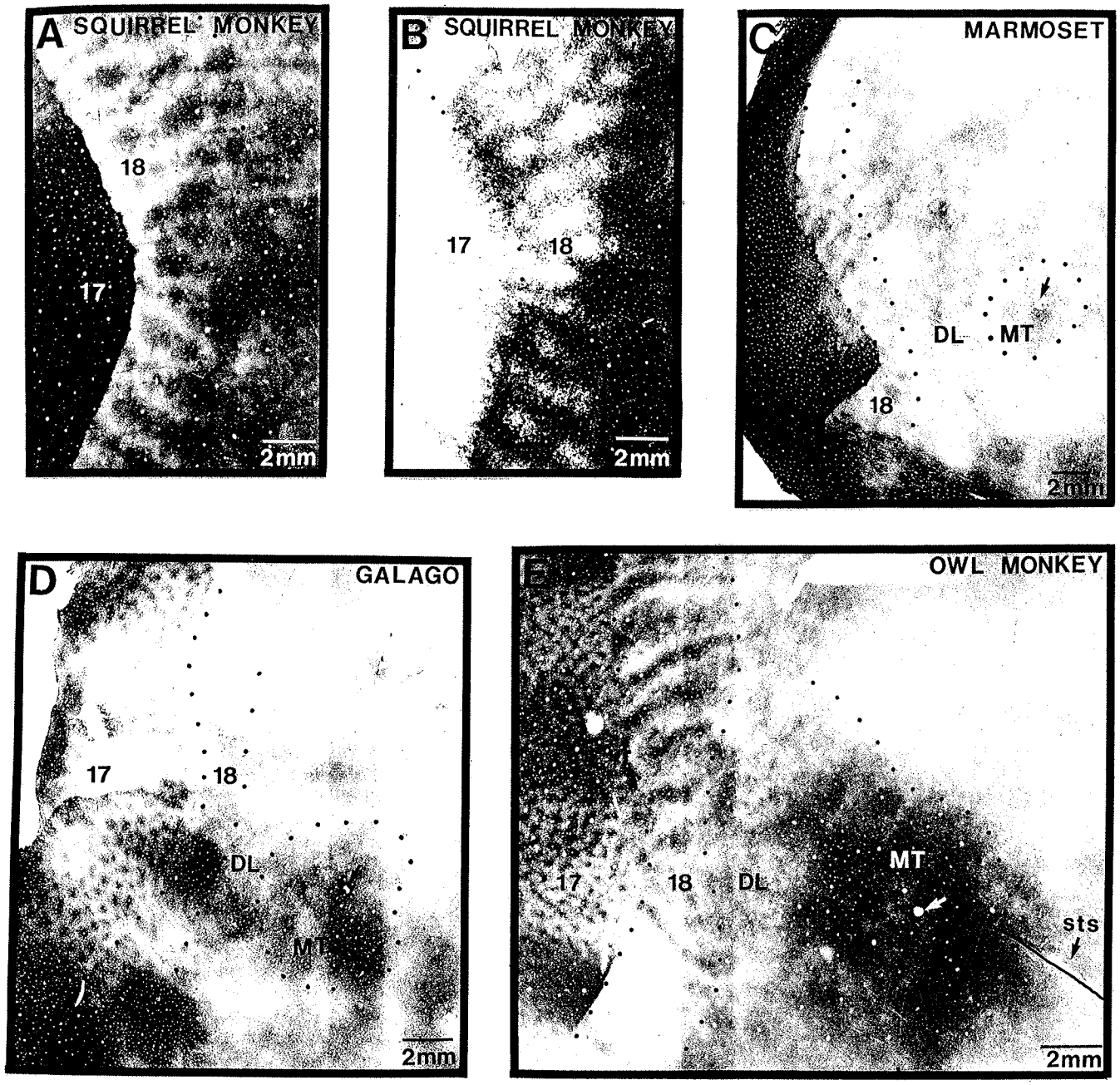

Fig. 2. Light-field photomicrographs of cortex that has been flattened, cut parallel to the surface, and reacted for cytochrome oxidase (A and C–E) or stained for myelin (B) in a squirrel monkey (A and B), marmoset (C), galago (D), and owl monkey (E). A lattice-like pattern of dense myelination can be identified in area 17 (B). In CO preparations, area 17 contains cytochrome-oxidase dark blobs and CO light interblob regions (D and E). In area 18, the alterations of CO dark and light bands are most distinct in squirrel monkeys and owl monkeys (A and E), less distinct in marmosets (C), and indistinct in galagos (D). In some portions of area 18 of squirrel monkeys (A) and owl monkeys (E), CO dark bands alternate between thick and thin, while in marmosets bands appear to be of equal thickness (C). In cortex stained for myelin, banding is also apparent (B); myelin-dense bands are CO light. Finally, a CO-dense oval of cortex is coextensive with the middle temporal visual area (C–E). Arrows in C–E in MT point to a micropipette puncture from an injection of WGA-HRP. Black dots mark architectonic boundaries. Rostral is right and dorsal is up in all figures. Other conventions are as in Fig. 1.

Kaas, 1988*a*; Krubitzer & Kaas, 1989*a* for squirrel monkeys; Hubel & Livingstone, 1987; Tootell & Hamilton, 1989, for macaque monkeys). The CO-dense bands have been described as alternating from thick to thin. In the present cases, the CO banding pattern was especially obvious in squirrel monkeys (Figs. 2A and 4A) and owl monkeys (Fig. 2E), where thicker and thinner bands often appeared to alternate. The CO banding pattern was less distinct in marmosets, and adjoining bands generally appeared to be of similar widths (Fig. 2C). In galagos, the banding pattern was weak and inconsistent.

Fig. 3. A graphic reconstruction of CO-dense regions (stipple) and myelin-dense regions (solid black) in areas 17 and 18 of squirrel monkeys. In both of these visual cortical fields, myelin-dense regions interdigitate with cytochrome-oxidase dense regions so that CO interblobs in area 17 (left) and interbands in area 18 (right) are myelin dense.

The myelin stains also revealed a banding pattern in area 18, where densely myelinated bands crossing area 18 alternate with poorly myelinated bands (also see Tootell et al., 1983). Such myelin dense bands were found in the middle layers of area 18 of squirrel monkeys (Fig. 2B), owl monkeys, and marmosets. This pattern is less obvious in galagos, where the bands of denser myelin are broader and fuse in deeper layers (Fig. 4H). A careful matching of myelin-stained and CO-reacted sections revealed that the CO light bands are myelin dense (Fig. 3). In area 18 of all of these primates, the most superficial cortex was more lightly myelinated, while the deeper cortex was more uniformly and densely myelinated. Together, the CO and myelin preparations allowed us to reliably identify most of all of the rostral border of area 18. Typically, the rostral border or area 18 was most obvious in the dorsolateral cortex, and less obvious in the cortex unfolded from the calcarine fissure. The junction of area 18 with prostriata was identified by a change to cortex that is poorly myelinated (see Allman & Kaas, 1971*b*).

Subdivisions of dorsolateral occipital cortex

The dorsolateral (DL), dorsointermediate (DI), and dorsomedial (DM) visual areas have been previously defined in owl monkeys (Allman & Kaas, 1974*b*, 1975). Parts of DL have been delimited recently in squirrel monkeys (Cusick & Kaas, 1988*a*), but DL, DI, and DM have not been identified in primates other than owl monkeys. DL is in the general location of the V4 complex of macaque monkeys, and DI and DM are in the regions of dorsal V3 and V3a of macaque monkeys (see Discussion).

In owl monkeys, DM contains a systematic representation of the contralateral hemifield that is coextensive with a densely myelinated rectangle of cortex located between area 18 and the caudal tip of the lateral sulcus (Allman & Kaas, 1975). DM has direct inputs from area 17 (Lin et al., 1982). In our preparations of flattened cortex in owl monkeys, a densely myelinated zone was obvious in the expected location of DM (Fig. 4C). The shape, size, and location of this field closely correspond with DM as previously reconstructed from parasagittal brain sections (Allman & Kaas, 1975). We have also recorded from this field and found that it contains a representation similar to that reported by Allman and Kaas (1975), is coextensive with the myelin-dense region in sections from flattened cortex, and is also characterized by inputs from area 17 (Krubitzer & Kaas, 1989*b*, 1990). Thus, the field undoubtedly is DM. However, sections from the flattened cortex indicate the shape of DM more accurately, and the lateral border of DM is slanted caudomedially so that the field is less rectangular than previously illustrated. In CO preparations, DM is lighter than the surrounding cortex, but myelin stains are much more useful in defining the field.

In the present preparations, the cortex in a comparable position to DM in owl monkeys was densely myelinated in squirrel monkeys (Fig. 4B) and marmosets (Fig. 4D and 4G). In galagos, a DM-like region was apparent as a moderately dense wedge in some cases, while in other cases, a distinction between DM and the less densely myelinated DI (see below) was not obvious. DM, as so defined in marmosets, squirrel monkeys, and galagos, was more elongated and wedge-shaped than DM in owl monkeys. Typically, DM was not distinct in CO preparations. However, in squirrel monkeys, DM was notably lighter than the surrounding cortex, and a faint banding pattern, reminiscent of that in area 18, was often apparent (Fig. 4A).

DI is a narrow, less-myelinated strip of cortex just lateral to DM that has been described as responsive to visual stimuli (Allman & Kaas, 1975). A retinotopic organization and a rostral border has not been determined for this field. Thus, DI is not a well-characterized visual area. In our myelin-stained sections, a strip of cortex in the region of DI was less myelinated than DM. DI, defined as a less-myelinated field rostrolateral to DM, was especially distinct in marmosets and squirrel monkeys (Fig. 4B and 4D), but was less easily defined in galagos (Fig. 4H). DI usually was not obvious in CO preparations, but in squirrel monkeys DI was somewhat darker than bordering fields (Fig. 4A).

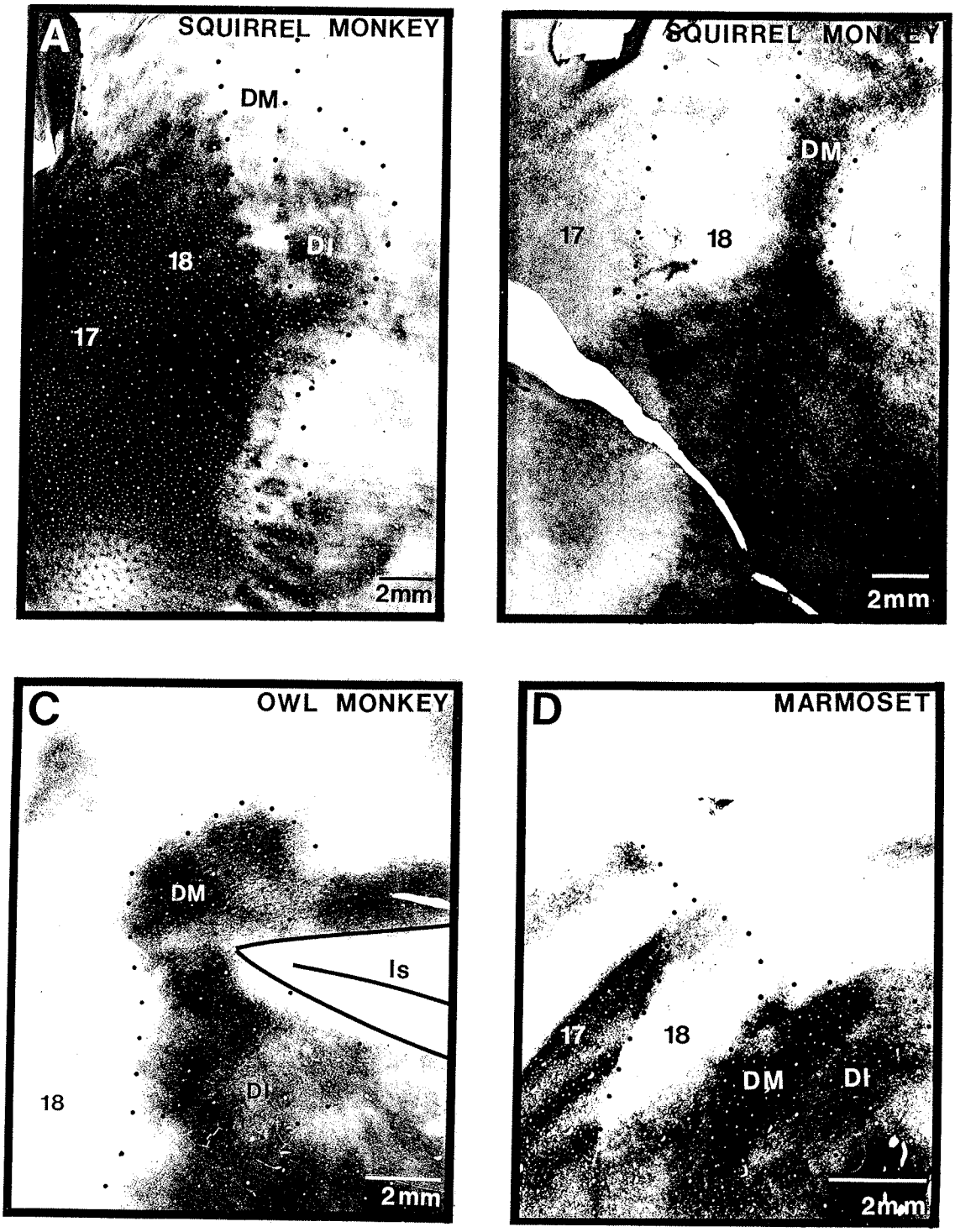

Fig. 4. Subdivisions of visual cortex in light-field photomicrographs of cortex that has been flattened, sectioned parallel to the surface, and stained for myelin (B–H) or reacted for cytochrome oxidase (A). The dorsomedial visual area, DM, is a myelin-dense field just rostral to the medial portion of area 18 (B–D and G). DM is long and narrow in squirrel monkeys (B), rectangular in owl monkeys (C), and wedge-shaped in marmosets (D). DM reacts lightly for CO (A). Just rostral to DM, the dorsal intermediate area, DI, stains somewhat less densely for myelin (C and D) and reacts darkly for CO (A). Lateral to DM and DI, the dorsolateral area, DL, stains moderately for myelin (E–H). The middle temporal visual area, MT, is an oval of heavily myelinated cortex just rostral to DL (E–H). The fundal superior temporal area, FST, ventral and slightly rostral to MT, stains less densely for myelin than MT. In all figures, rostral is right and dorsal is to the top. Conventions as in previous figures. Arrows in MT in parts G and H point to micropipette punctures from WGA-HRP injections. (*Figure continued on next page.*)

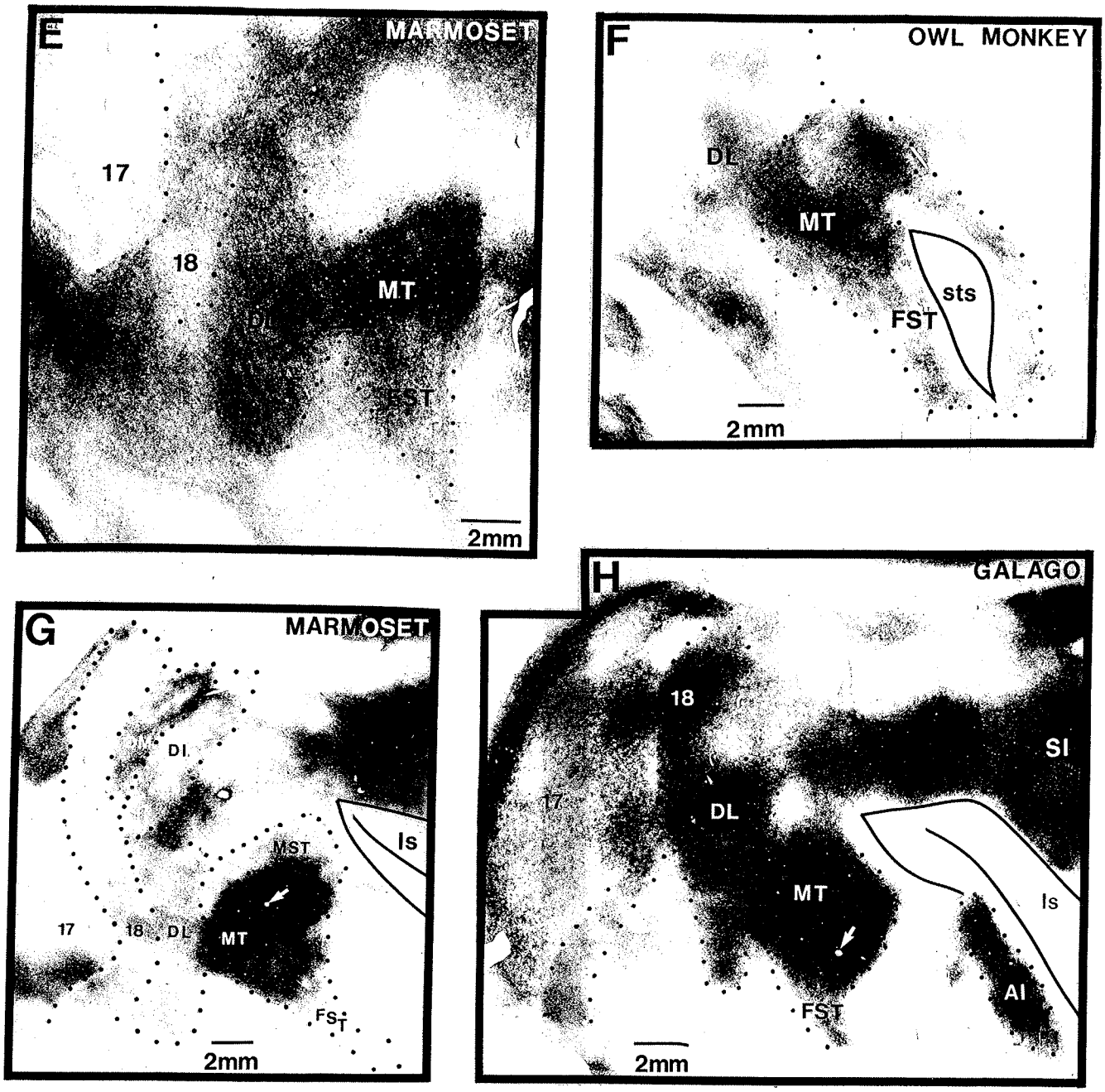

Fig. 4 continued.

DL was orginally defined as a systematic representation of the visual hemifield in the cortex between area 18 and MT of owl monkeys (Allman & Kaas, 1974*b*). More recent evidence from squirrel monkeys indicates that DL contains at least two subdivisions, a more caudal field with major inputs from area 18 and a more rostral field without major connections with area 18 (Cusick & Kaas, 1988*a*). Recent microelectrode-mapping data from owl monkeys (Sereno et al., 1986) are consistent with the conclusion that separate but parallel representations of the visual hemifield exist caudally and rostrally in DL. In sections from flattened cortex, DL was characterized by moderately dense myelination in owl monkeys (Fig. 4F), squirrel monkeys, marmosets (Fig. 4E and 4G), and galagos (Fig. 4H). In CO preparations, DL often was distinguished as a moderately dark field (Fig. 2E). So defined, DL did not appear to wrap as far around MT as suggested by electrophysiological data in owl monkeys (Allman & Kaas, 1974*b*). In addition, in favorable myelin stains and CO reactions, the caudal half of DL was darker than the rostral half in squirrel monkeys (see Fig. 3 of Cusick & Kaas, 1988*a*). Thus, in squirrel and owl monkeys there was architectonic evidence for caudal and rostral subdivisions, DLc and DLr.

Subdivisions of the upper temporal lobe

MT is a visual area that was first described in owl monkeys as a systematic representation of the contralateral visual

hemifield within a deeply myelinated oval of cortex in the upper temporal lobe (Allman & Kaas, 1971*a*). The dense myelination makes MT one of the most easily identified cortical areas. MT has subsequently has been defined in marmosets (Spatz & Tigges, 1972; Spatz, 1977), squirrel monkeys (Tigges et al., 1981), galagos (Allman et al., 1973; Symonds & Kaas, 1978; Wall et al., 1982), and macaque monkeys (Gattass & Gross, 1981; Van Essen et al., 1981; Desimone & Ungerleider, 1986; Ungerleider & Desimone, 1986*a*). In sections cut parallel to the surface and stained for myelin, the boundaries and shape of MT were quite obvious (Fig. 4E–4H). In addition, some unevenness of myelin staining occurred within MT of marmosets suggesting functional heterogeneity, but this unevenness was not apparent in the other primates studied. In CO preparations, MT was darker than surrounding cortex (Fig. 2C–2E).

Two fields adjoining MT were also densely myelinated. A superior temporal area, ST, was defined as an adjoining projection field of MT in owl monkeys (Weller et al., 1984), and corresponds to the medial superior temporal area, MST, of macaque monkeys as defined by Maunsell and Van Essen (1983). Ungerleider and Desimone (1986*b*) later concluded that the projection pattern of MT in macaque monkeys demonstrates two adjoining projection fields, one defining a more restricted MST and the other denoting an area in the fundus of the superior temporal sulcus, FST (the possibility of two fields was also suggested by Weller et al., 1984). The architectonic features of these two targets of MT have been noted only for macaque monkeys. Both MST and FST have been described as densely myelinated (Maunsell & Van Essen, 1983; Ungerleider & Desimone, 1986*a*,*b*).

In the present cases, two fields along the MT border can be distinguished by their shapes and partial discontinuity even though they are similar in myeloarchitecture and CO reactivity. We retain the terms, FST and MST, for these areas, even though the term FST is confusing when applied to species without a superior temporal sulcus. In our myelin-stained sections, FST was identified as a wedge-shaped area that narrowed ventrally from the border of MT (Fig. 4E–4H), while MST was a densely myelinated semicircular area immediately dorsal and slightly rostral to MT (Fig. 4G). Both FST and MST were somewhat less densely myelinated than MT, and both FST and MST were only moderately dense in CO preparations. Because of less myelination in superficial layers and an uneven plane of section, especially for unfolded cortex in fissures, MST and FST were not always distinct on the same sections.

Other fields

Our major concern in defining cortical fields was to characterize subdivisions with connections with MT. All of the areas described above have such connections (see below). MT also has connections with other portions of the temporal lobe and the parietal lobe (see below) where we were unable to identify the relevant fields. However, other connections of MT were with a subdivision of the frontal lobe that we refer to as the frontal ventral area (FV) (see Huerta et al., 1987). FV is a moderately myelinated oval of cortex just ventral to the electrophysiologically defined frontal eye field (FEF). Both fields have been briefly described for galagos and New World monkeys (Kaas & Krubitzer, 1988).

In addition to visual and visuomotor fields, we have identified auditory, somatosensory, and motor fields in some of the illustrations. Primary auditory cortex (Fig. 7 of Luethke et al., 1989) and area 3b or S-I of somatosensory cortex (see Krubitzer & Kaas, 1988*b*, 1990) can be quite distinct as densely myelinated fields (they are also obvious in CO preparations; see Tootell et al., 1985), while the second somatosensory area, SII, and a parietal ventral area (PV), are often apparent as moderately myelinated ovals of cortex (Krubitzer & Kaas, 1990).

Sizes of myelorarchitectonic fields

By careful dissection, it was possible to preserve and flatten most or all of the neocortex (Fig. 1). The flattening process involved splitting parts of area 17 that are located in the calcarine fissure which altered the shape of area 17. Other regions in the temporal lobe were typically cut so the tissue could be flattened, but we did not attempt to delimit visual areas in the lower temporal lobe (see Weller & Kaas, 1987). Stresses in the tissue were largely relieved by such cuts, but local tears also occurred. Local damage to specific sections was compensated by transposing boundaries from drawings of different sections using local landmarks. The flattening process did not obviously distort the surface areas of subdivisions of cortex. This observation is consistent with the results of studies that indicate that little distortion of surface areas occurs in the flattening cortex (Olavarria & Van Sluyters, 1985). Thus, inaccuracies in the measurements of fields would largely stem from uncertainties of borders or parts of borders (see above), rather than tissue distortion.

The surface areas of cortical fields for different species were compared by measuring areas in individual cases and converting measurements to percentages of total neocortex to facilitate comparisons within and across species, while allowing for individual and species differences in brain sizes (Fig. 5). In all four primate species, area 17 occupied a large proportion of the neocortex (16–19%). However, the percentages of neocortex occupied by area 17 was somewhat smaller in nocturnal (galagos and owl monkeys) than diurnal (marmosets and squirrel monkeys) primates. Across these species, area 18 appeared to be less than half the size of area 17. Area MT is roughly one-tenth the size of area 17, but there is some variability with MT being proportionately somewhat larger in galagos than squirrel monkeys (Table 1). DL, in contrast, was proportionately larger in the diurnal primates (Table 1). Proportions of area 17, DL, MT, and MST were significantly different ($P<0.01$, Student's t test) in the comparisons of nocturnal and diurnal primates.

Ipsilateral cortical connections of MT

Connection patterns were determined for injections that were within MT, defined by myeloarchitecture, in six squirrel monkeys, three owl monkeys, three marmosets, and three galagos. In all cases, the effective injection site appeared to be completely within MT (see Fig. 6A–6D for photomicrographs of injection sites and Figs. 12–24). The locations of injections varied in MT, allowing us to study topographic patterns of connections of MT with other fields, and compare connection patterns and densities of connections for injections in different parts of MT.

Area 17

The injections in MT led to three major conclusions about connections with area 17. First, in all cases, labeled neurons in area 17 were in the middle and deep layers of the cortex, while

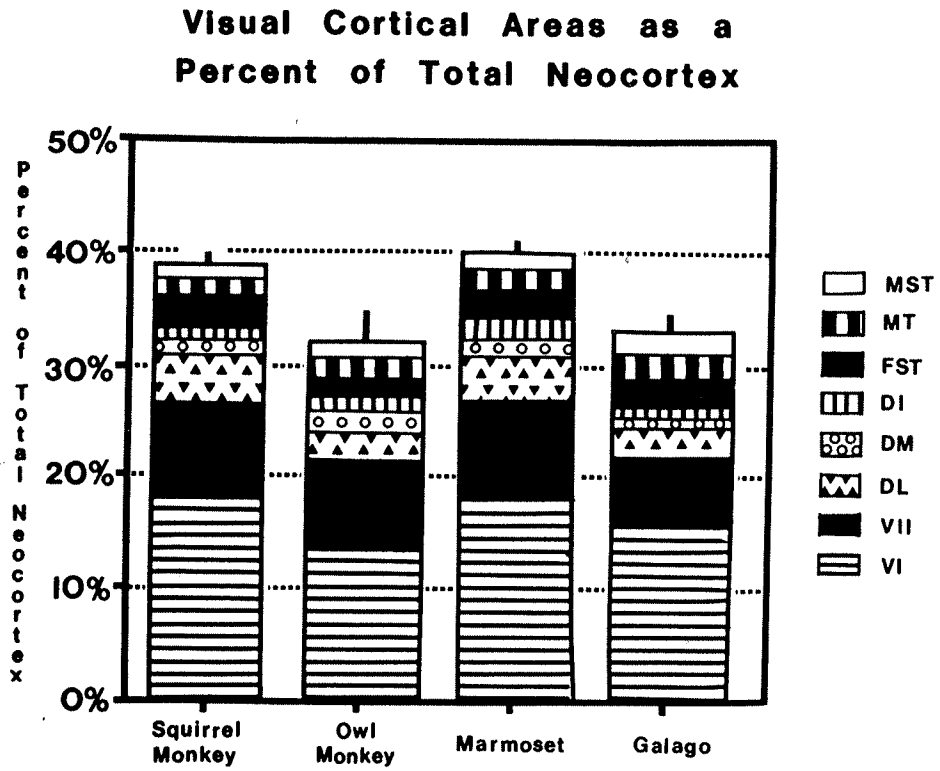

Fig. 5. Histograms of the surface areas of eight architectonically defined cortical fields relative to the total neocortex in four species of primates. The proportion of neocortex assumed by the eight visual areas is significantly larger in diurnal species. Codes for visual areas are on the right. Abbreviations are as in Fig. 1.

label in fine processes representing feedback projections from MT was most dense in the superficial cortical layers. In brain sections cut parallel to the cortical surface, layer IV of Hassler (1966) was easily recognized in the CO sections as a very dark layer (layer IVc of Brodmann, 1909), and most labeled neurons were just superficial to layer IV. These observations are consistent with the considerable evidence from other studies that neurons in layer IIIc of Hassler (1966) and deeper neurons near the junction of layer V with layer VI project to MT, and projections from MT to area 17 terminate most densely in superficial layers (for review see Weller & Kaas, 1981; Tigges et al., 1981).

A second conclusion is that labeled neurons and labeled terminals in area 17 have somewhat different distributions tangential to the surface. Injections in MT typically produced a region where labeled neurons were aligned in short merging and diverging rows (Figs. 7B–7D and 8C–8E) although this was less apparent in some cases (Fig. 7E). Within rows, labeled neurons sometimes were distributed in closely spaced clumps (Figs. 7C and 7D). The more superficial label consisting of fine processes was rather evenly distributed both over and between the rows (Figs. 7A, 8A, and 8B). However, the superficial label was less dense in small ovals that were over the CO blobs. These differences in the distributions of feedforward and feedback connections in area 17 were apparent in squirrel monkeys (also see Krubitzer & Kaas, 1989*a*), owl monkeys, marmosets, and to a lesser extent, in galagos.

The third conclusion supported by the present results is that the connections between MT and area 17 form a topological pattern. Furthermore, when the retinotopic maps in MT of galagos (Allman et al., 1973) and owl monkeys (Allman & Kaas, 1971*a*) and area 17 of galagos (Krubitzer et al., unpublished experiments) and owl monkeys (Allman & Kaas, 1971*a*) are considered, it is clear that the connections are between retinotopically matched locations. In addition, the electrophysiological data on the retinotopic organization of dorsolateral area 17 in squirrel monkeys (Cowey, 1964), in conjunction with the connection pattern, provide evidence that MT has a similar retinotopic organization in squirrel monkeys as in owl monkeys and galagos. Finally, if the bulge in dorsolateral area 17 of marmosets corresponds to central vision, as it does in squirrel monkeys, then the connection patterns indicate features of retinotopic organization in MT of marmosets as well.

The topographical pattern of connections of MT with area 17 is apparent from the variations in the locations of injection sites in MT and the corresponding label in area 17 for the individual cases (squirrel monkeys, Figs. 12–16; owl monkeys, Figs. 17–19; marmosets, Figs. 20 and 21; and galagos, Figs. 22–24). These results indicate that caudal or caudoventral MT, representing central vision, connects with the rostral portion of dorsolateral (in the intact brain) area 17, and that more rostral locations in MT, representing paracentral and peripheral vision, connect with parts of area 17 folded into the calcarine fissure (as a result of cuts during flattening, area 17 has a strip-like shape, and calcarine cortex is upper and lower in the strip). The results also show that medial (dorsal) MT (lower visual quadrant) connects with medial area 17 and lateral MT connects with lateral area 17.

Area 18

In all cases, the injections in MT labeled neurons and fine processes in area 18. Observations were made on the laminar distributions of label, the relationships of label to the CO

Table 1. *Surface areas of cortical fields as a percentage of the total surface of neocortex (See Fig. 1 for visual areas).*

Case number	17	18	DL	DM	DI	FST	MT	MST	Total
				Squirrel monkey					
1	19.5	7.6	4.4	1.8	1.0	2.7	1.3	1.4	39.7
2	19.9	8.9	4.7	1.4	1.0	3.1	1.1	1.1	41.2
3	17.4	8.7	4.2	1.2	.9	3.0	1.6	1.2	38.2
4	19.7	6.5	3.4	1.2	1.0	2.6	1.3	1.4	37.1
5	19.1	9.4	4.0	1.3	1.3	2.4	1.4	1.1	40.0
6	13.7	7.1	5.7	1.4	1.4	3.2	1.6	1.8	35.9
Mean %	18.2	8.0	4.4	1.4	1.1	2.8	1.4	1.3	38.7
Std Dev	2.4	1.1	.8	.2	.2	.3	.2	.3	2.0
				Owl monkey					
1	14.6	9.2	3.5	1.7	1.5	2.0	2.1	1.7	36.3
2	18.4	8.8	3.3	2.4	1.8	1.2	1.8	1.1	38.8
3	15.0	5.0	2.2	1.5	1.6	1.5	1.3	1.3	29.4
4	6.7	7.5	4.2	1.7	1.3	2.1	1.8	1.8	27.1
Mean %	13.7	7.6	3.3	1.8	1.6	1.7	1.8	1.5	32.9
Std Dev	4.9	1.9	.8	.4	.2	.4	.3	.3	6.3
				Marmoset					
1	16.1	8.2	4.0	1.8	2.8	2.5	1.5	1.1	38.0
2	16.9	8.8	3.5	1.5	2.2	2.7	2.3	1.6	39.5
3	20.0	8.8	3.7	1.1	1.9	2.4	2.0	1.5	41.4
4	15.7	7.5	4.1	1.3	1.7	2.5	1.9	1.7	36.4
5	22.3	9.6	3.1	1.4	2.0	1.7	1.7	1.3	43.1
6	18.5	9.3	4.4	1.3	2.2	2.0	1.6	1.1	40.4
Mean %	18.3	8.7	3.8	1.4	2.1	2.3	1.8	1.4	39.8
Std Dev	2.5	.8	.5	.2	.4	.4	.3	.3	2.4
				Galago					
1	19.6	6.8	2.9	.6	.7	2.2	2.3	2.2	37.4
2	15.9	4.6	2.0	.8	1.0	2.7	1.9	1.4	30.3
3	13.5	8.0	2.5	1.2	1.3	2.7	2.5	1.9	33.6
4	16.0	4.4	2.6	.8	1.4	1.8	2.0	2.1	31.1
Mean %	16.3	6.0	2.5	.9	1.1	2.4	2.2	1.9	33.1
Std Dev	2.5	1.7	.4	.2	.3	.4	.2	.4	3.2

and myelin bands in area 18, and on topographic patterns of connections.

After MT injections, the labeled neurons were almost all located in the middle layers of area 18, presumably in layer III as previously reported for squirrel monkeys (Tigges et al., 1981), owl monkeys (Weller et al., 1984), and macaque monkeys (Maunsell & Van Essen, 1983; DeYoe & Van Essen, 1985; Ungerleider & Desimone, 1986*a*). Fine, scattered label, representing terminations in area 18, was most dense in more superficial sections including those through superficial parts of layer III as previously reported for owl monkeys (Weller et al., 1984), marmosets (Spatz & Tigges, 1972), squirrel monkeys (Tigges et al., 1981; Krubitzer & Kaas, 1989*a*), macaque monkeys (Maunsell & Van Essen, 1983; Ungerleider & Desimone, 1986*a*), and galagos (Wall et al., 1982).

In New World monkeys, the distributions of label in area 18 were related to the patterns of the CO-dense bands. In squirrel monkeys, labeled neurons projecting to MT were largely confined to every other CO-dense band, while more superficial label in fine processes was dense in the same bands, but was also present in the other set of CO-dense bands (Fig. 9A, 9B, 9E, and 9F). Little label was in the CO light, myelin-dense interbands (Fig. 9C and 9D). Concentrations of label within the CO-dense bands in squirrel monkeys are also indicated in Fig. 12–16. Although the figures include both retrogradely and anterogradely transported label, the label in the thin bands (Figs. 12 and 13) appears somewhat denser due to the superimposition of both types of label (also see Fig. 3 of Krubitzer & Kaas, 1989*a*). Thus, projections from area 18 to MT appear to originate in the thin set of alternating CO-dense bands, while the feedback projections from MT to area 18 appear to terminate in both the thick and thin bands.

In owl monkeys, we obtained less extensive data on the relationship of CO-dense bands to connection patterns. However, results were consistent with those in squirrel monkeys. In owl monkeys 88-16 (Fig. 9G), the fluorescent dye, fast blue (FB), was injected into MT, while another fluorescent dye, diamadino yellow (DY), was injected in DL. Neurons labeled with FB were found most densely in two thin CO bands. The neurons labeled by the injection of DY in DL, on the other hand, were in both thick bands and interbands in area 18. In two other owl monkeys, where WGA-HRP was injected in MT, label was concentrated into band-like strips in area 18 and in one case the labeled neurons were generally in alternate bands while the labeled terminals were more broadly distributed in both sets of CO-dense bands.

In marmosets, label in area 18 after MT injections was concentrated in band-like regions (Figs. 10, 20, and 21). In one of these marmosets, the CO reactions revealed some of the CO-dense bands, and the dense retrograde label was largely confined to three alternating CO bands (Figs. 10E and 20). These bands were thin, but adjacent bands also appeared to be thin. Thus, it appears that in at least parts of area 18 of marmosets, adjacent CO-dense bands are of the same width. As in the squirrel and owl monkeys, anterograde label was in every CO-dense band, all of equal width (Fig. 10D). Although we were unable to identify the CO banding in area 18 of marmoset 87-51, label in area 18 was in bands and anterograde label was more broadly distributed.

In galagos, the CO reactions did not distinguish CO-dense bands and interband regions. Nevertheless, in each of three cases with an injection in MT, and one case with an injection in DL, label was concentrated in band-like regions of area 18 (Figs. 11A–11D and 22–24). As in the other primates studied, superficial anterograde label was dense in retrogradely labeled bands and between them and was thus more broadly distributed.

The injections in MT also revealed topographic patterns of connections with area 18. In each of the six squirrel monkeys, labeled regions in area 18 extended from the caudal border of area 18, representing the zero vertical meridian, to the rostral border of area 18, representing the horizontal meridian (Figs. 12–16). Typically, these labeled regions occupied less than one-fifth the length of area 18, although as much as two-fifths of the length was labeled in one case (Fig. 12). Since the effective injection sites appeared to occupy less than one-fifth of MT, the labeled regions in area 18 and the injection sites in MT were roughly proportional. In addition, all of the injections were in the caudomedial half of MT, representing the lower visual quadrant, and all of the labeled regions were in the medial half of area 18, also representing the lower visual quadrant (Fig. 12–24). The more caudal injections in MT, in the portion representing central vision, produced label in more laterally in medial area 18, while the more rostromedial injections produced label in more medial regions of area 18, demonstrating interconnections between parts of area 18 and MT representing paracentral and peripheral vision. Thus, connections were topographic and retinotopically matched.

In owl monkeys (Figs. 17–19), the two WGA-HRP injections

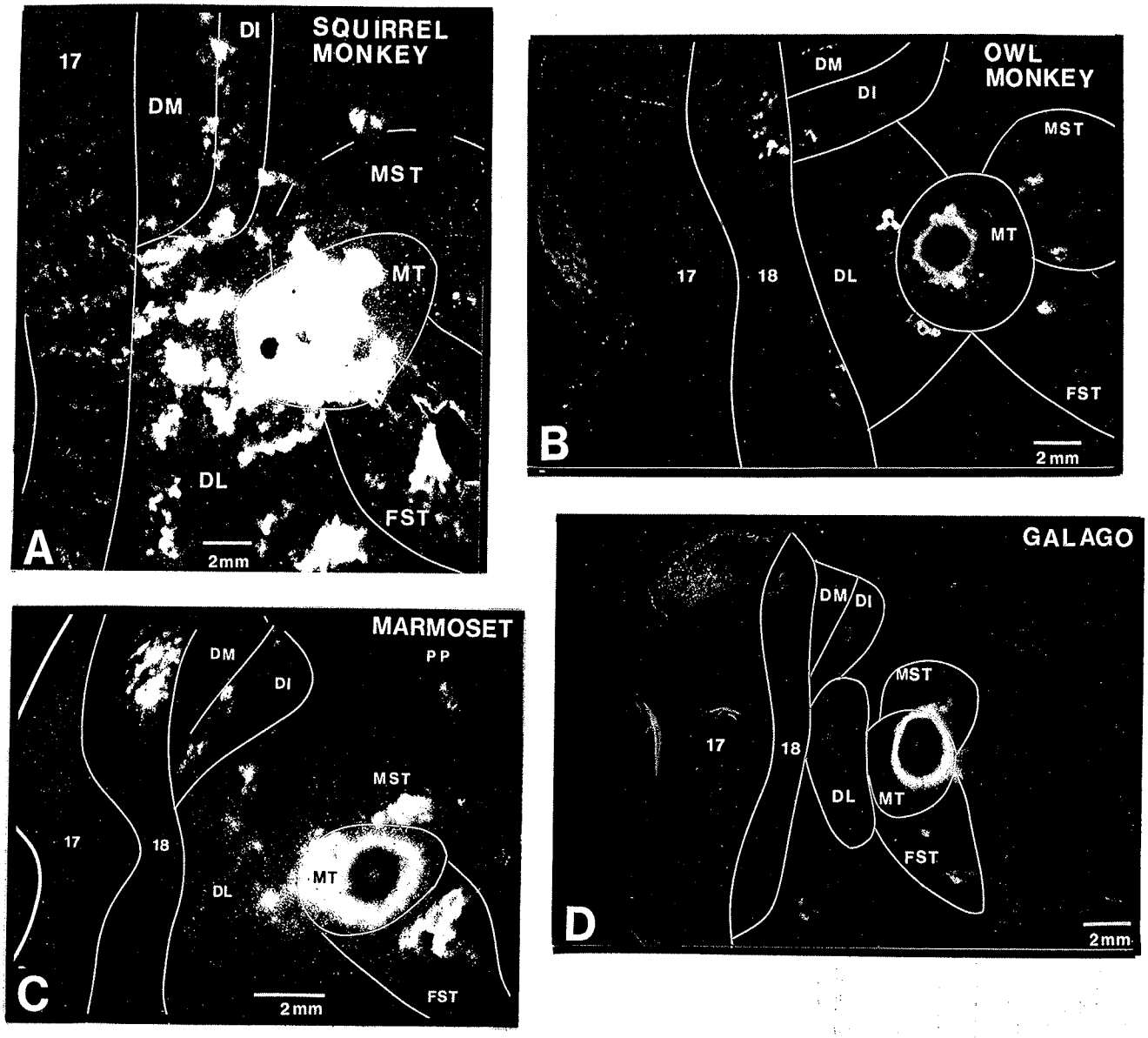

Fig. 6. Dark-field photomicrographs of flattened cortex showing the areal distributions of label resulting from injections of WGA-HRP in MT. In all species examined, areas 17 and 18 contain dense patches of both anterograde and retrograde label (B and D). Label is also apparent in areas DL, DM, DI, MST, and FST. Note the similarity in the distribution of label in all four species. Solid white lines mark architectonic boundaries. In all figures, rostral is right and dorsal is to the top. Conventions are as in previous figures.

labeled regions roughly one-third to one-fifth the size of area 18, while the one FB injection labeled only a restricted part of area 18. The WGA-HRP injections were well-centered in MT in portions related to the horizontal meridian, and the resulting label in each case was concentrated along the rostral border of area 18, which represents the horizontal meridian, and was located in separate medial and lateral locations in area 18, which represent the lower and upper visual quadrants. Also in correspondence with expected retinotopic relationships, the more rostral injection resulted in label displaced more toward the medial and lateral ends of area 18, while the injection of FB in medial MT produced label only in medial area 18.

In the two marmosets, the transported label crossed much (Fig. 21) or all (Fig. 20) of area 18 and extended over about one-fourth of the field. A caudolateral injection labeled the mid-portion of area 18, devoted to central vision, while an injection centered in MT labeled separate regions displaced towards the ends of area 18 related to paracentral and peripheral vision.

In galagos, injections in MT produced band-like arrays of label that partly crossed the width of area 18 (Figs. 22–24). The labeled regions occupied one-fourth of area 18 or less. An injection near the rostrolateral border of MT produced label near the ends of the area 18 belt with more label at the lateral end (Fig. 22). This pattern is consistent with label resulting from an injection in the cortex representing peripheral vision along the horizontal meridian, with more of the injection site in the representation of the upper than the lower visual quadrant. An injection in rostromedial MT resulted in label only in the medial end of area 18 (Fig. 24), suggesting that the injection site was confined to the representation of peripheral vision in

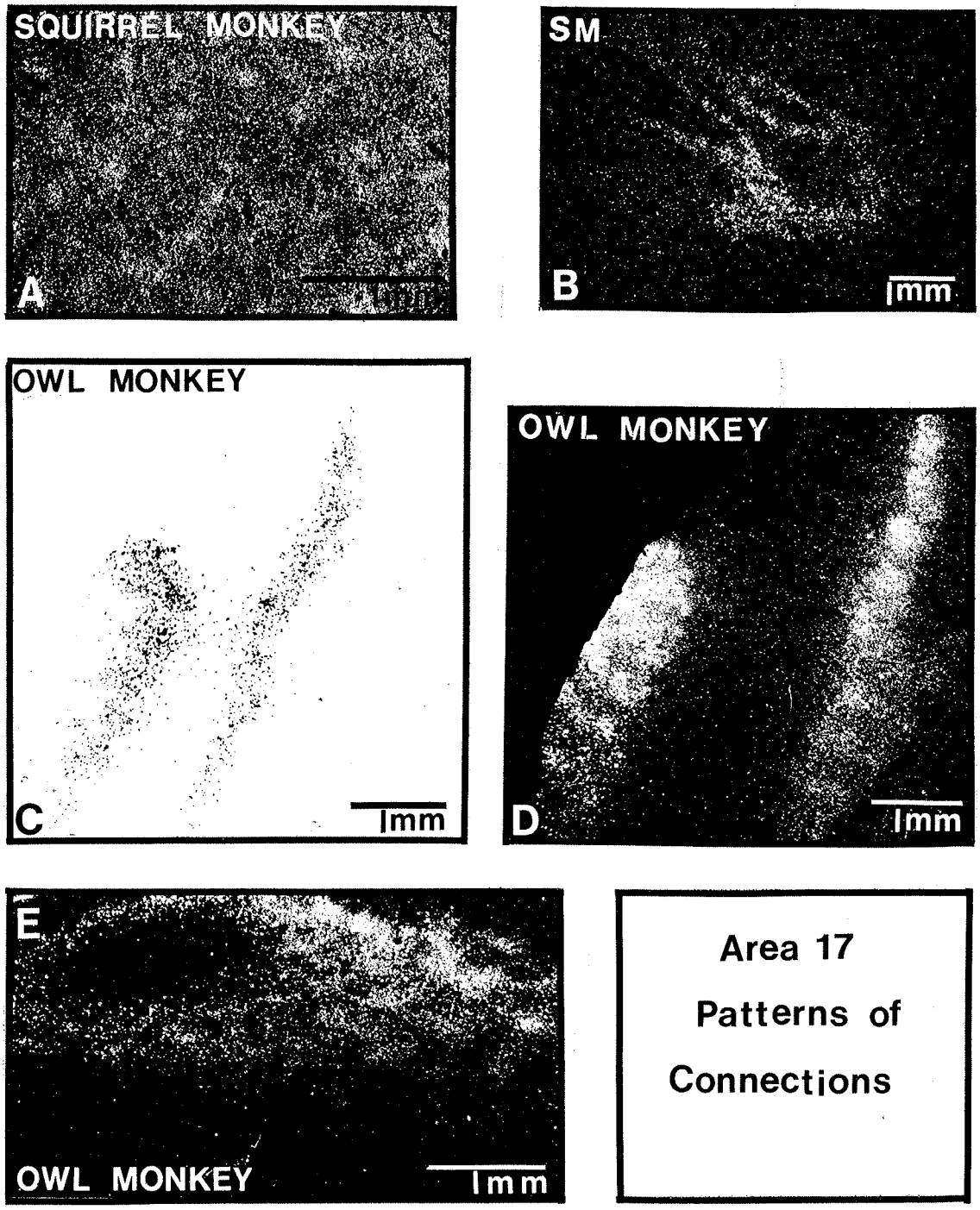

Fig. 7. Dark-field and light-field photomicrographs of patterns of anterograde (A) and retrograde (B–E) label in area 17 after injections of WGA-HRP in MT in squirrel monkeys and owl monkeys. Anterograde label (A) forms a broadly distributed lattice-like network that relates to the CO interblob regions. In squirrel monkeys (B) and owl monkeys (C and D), retrograde label in area 17 generally forms several meandering rows. Note that the density of label in these bands is not homogeneous. An intricate pattern of combined anterograde and retrograde label is apparent in superficial layers of area 17. SM: Squirrel monkeys. Other conventions are as in previous figures.

the lower quadrant. An injection centered in MT produced label displaced slightly into the medial half of area 18 (Fig. 23). From the location of the injection site, label was expected in a location equally displaced into the lateral half of area 18, but such label was not noted (however, label was present in lateral area 17).

The dorsolateral area (DL) of the occipital cortex

DL is a subdivision of the visual cortex that disproportionately represents central vision (Allman & Kaas, 1974*b*). The caudal part of DL, DLc, is strongly interconnected with area 18 and the rostral part of DL, DLr, has few or no connections with area 18 (Cusick & Kaas, 1988*a*). Our injections in MT indicate

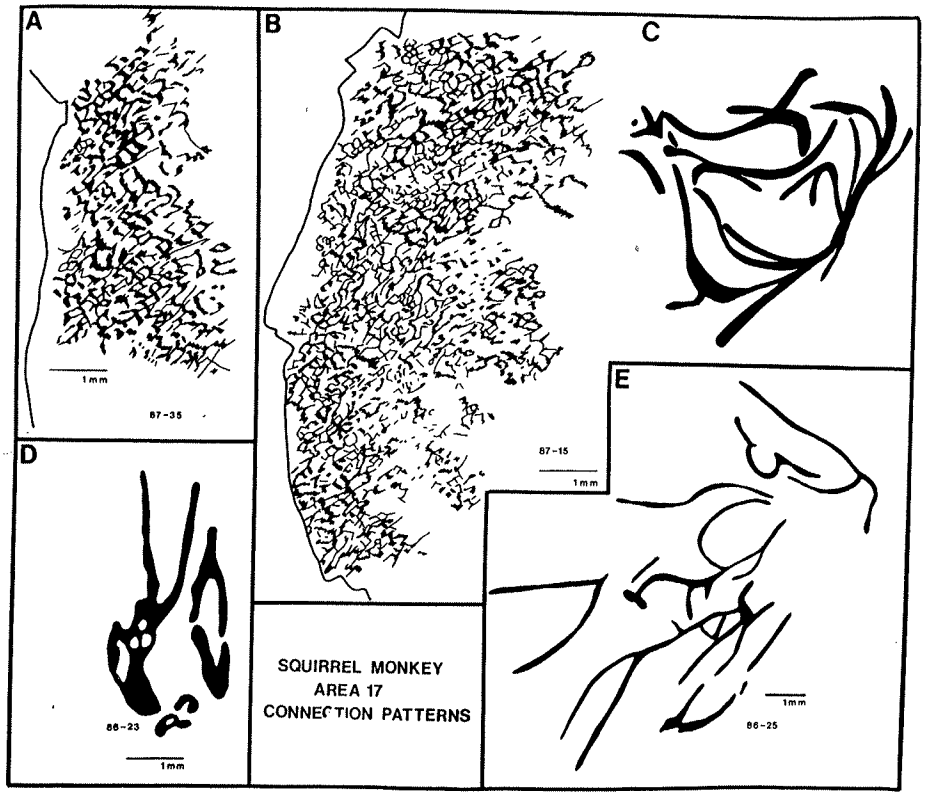

Fig. 8. Graphic reconstructions of patterns of anterograde (A and B) and retrograde (C–E) label in area 17 of squirrel monkeys after injections of WGA-HRP or tritiated WGA-HRP (E) in MT. The pattern of anterograde label (A and B) is lattice-like in appearance and more broadly distributed than retrograde label (compare areal extents of B and C). Retrogradely labeled neurons in area 17 after injections in MT form intricate banding patterns. Conventions are as in previous figures.

that DL is interconnected with MT in both New World monkeys and galagos, and the connections are denser with DLr. The part of MT representing central vision has the most dense connections with DL, and the differences in the density of connections related to central vision are more pronounced in the diurnal squirrel monkeys and marmosets, where central vision is emphasized.

The relationship between the location of the injection site and the density and distribution of label in DL was most apparent in squirrel monkeys where six injections ranged in location from caudal to rostral MT. The injection in squirrel monkey 87-35 (Fig. 12) was near the caudal margin of MT. The transported label in dorsolateral portions of areas 17 and 18 indicated that the injection was in part of MT representing central vision and spread slightly into the representation of the lower visual quadrant. The injection produced scattered clumps of labeled neurons and fine processes over much of DL. The labeled neurons were largely in the deeper half of layer III, while the fine label was more broadly distributed across layers. The clumps of label were concentrated in rostral DL, and, more noticeably, in the medial half of DL, which is devoted to the lower visual quadrant. Nevertheless, major clumps of label were in lateral DL, which represents the upper visual quadrant. Thus, the label was dense, discontinuously distributed, and concentrated in part of DL that retinotopically matched the injection site.

The injection sites in the other five squirrel monkeys were placed in more rostral locations in MT, and were progressively more displaced from the representation of central vision. The progression also formed a series of cases with less and less label in DL, and label more and more restricted in rostromedial DL. (1) The injection in case 87-16 (Fig. 13) was only slightly displaced from the caudal border of MT. The label in areas 17 and 18 indicate that the injection was in part of MT representing parafoveal vision just a few degrees (see Cowey, 1964) into the lower visual quadrant. Scattered clumps of label were observed again across much of DL, especially caudally and dorsally in DL. However, the label was less dense than in the previous case involving central vision, and the label in lateral DL was especially reduced. (2) A slightly more caudal injection in MT involving vision just a few degrees further in the lower visual quadrant produced less label in DL, and the label was largely restricted to caudomedial DL (Fig. 14). (3) An injection somewhat more rostral in MT involving slightly more paracentral vision resulted in only sparse label in DL. This label was restricted to rostral DL, and practically no label was in lateral DL (Fig. 15). (4) Two other cases with more rostral injections in MT involving more peripheral vision (87-25, Fig. 16; 86-61, not shown) resulted in very sparse label that was largely confined to the rostromedial section of DL.

Injections in the other primates provided further information on the relationship of the location of the injection site in MT to the amount and distribution of label in DL. In owl monkeys, all three injections in MT involved paracentral vision (Figs. 17–19). The resulting label in DL was roughly comparable to that following injections involving paracentral vision in MT of squirrel monkeys. Thus, the label was relatively sparse, dis-

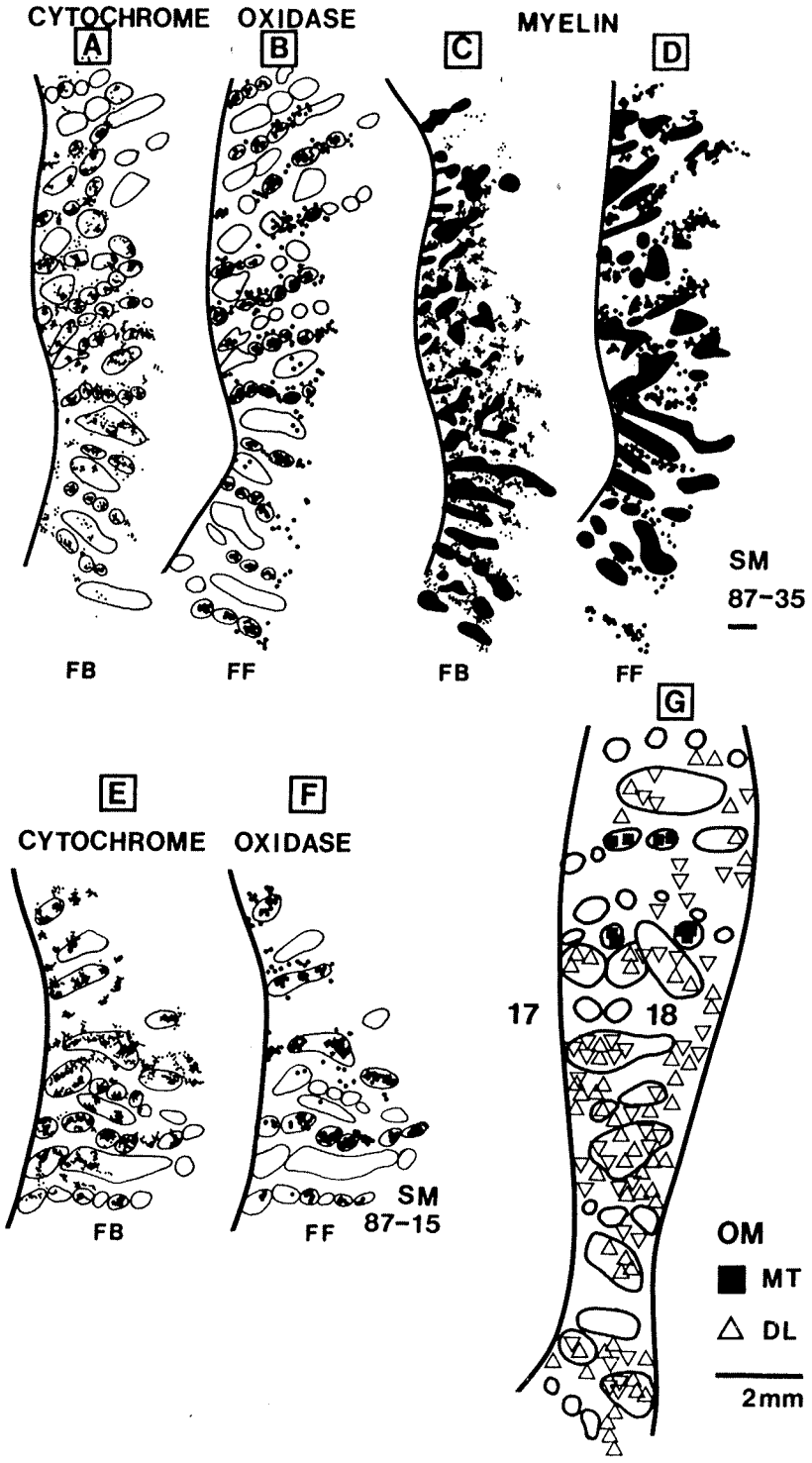

Fig. 9. Patterns of anterograde (A, C, and E) and retrograde (B, D, F, and G) label in area 18 after injections in MT in squirrel monkeys and owl monkeys. These patterns of label have been related to both myelin and CO stains (A–D) or to CO stains (E–F) in squirrel monkeys and in owl monkeys (G). Note that retrograde or feedforward (FF) label is in every other CO-dense band (B, F, and G), while anterograde or feedback (FB) label is in every cytochrome-oxidase rich band (A and E). In one owl monkey (G), an injection of fast blue was placed in MT while an injection of diamidino yellow was placed in DL. The retrogradely labeled cells in area 18 are nonoverlapping; injections in MT label neurons in CO thin bands while injections in DL label neurons in both thick and interbands. Finally, after MT injections, both feedforward and feedback patterns of connections are found outside of myelin-dense bands (CO interbands) in area 18 (C and D). Conventions are as in previous figures.

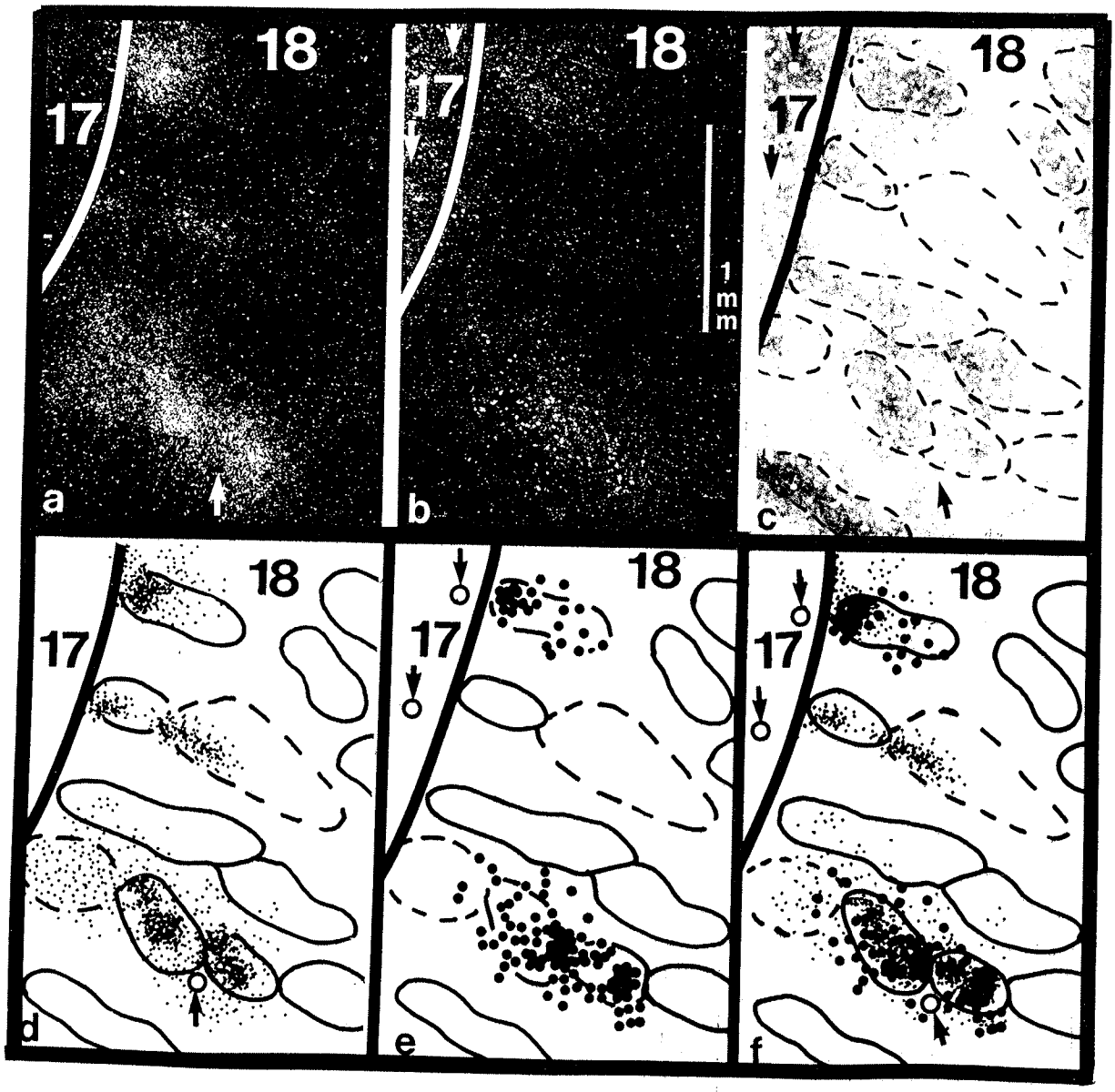

Fig. 10. Dark-field photomicrographs of anterograde (A) and retrograde (B) label in area 18 in marmoset 87-53 resulting from an injection of WGA-HRP in MT. The adjacent light-field photomicrograph (top right) indicates CO-dense regions in area 18 in relation to this label. The bottom row of figures graphically depicts patterns of anterograde and retrograde label in relation to CO-dense bands (outlined in solid black lines; dashed lines mark less dense parts of the CO bands) in area 18. The anterograde label (A and D) is more broadly distributed than retrograde label (B and E). Also, the CO bands are of nearly equal thickness. Scale bar applies to all figures. Small arrows in all figures mark some of the blood vessels (small circles in bottom figures) used to align sections.

tributed in clumps, and largely confined to rostral DL. Injections involving the horizontal meridian in MT, judging by the split location of label in area 18, resulted in label in both lateral and medial locations in DL (Figs. 17 and 18). Since DL (Allman & Kaas, 1974*b*), similar to V-II (Allman & Kaas, 1974*a*), has a split representation of most of the horizontal meridian, separate medial and lateral locations of label were expected in these cases. In marmosets, the case with the injection in the part of MT representing central vision produced somewhat more label in DL (Fig. 20) than in the injection in part of MT representing paracentral vision (Fig. 21). Because of the location of the injection site on the representation of the horizontal meridian in marmoset 87-51 (Fig. 21), a separate region of dense label was expected but not observed in the lateral DL. In galagos, two cases with injections in parts of MT representing paracentral (88-10; Fig. 23) and peripheral vision (88-11, Fig. 24) resulted in notable amounts of label in DL. However, DL was nearly free of label after an injection into rostrolateral MT representing extreme peripheral vision (Fig. 22).

The dorsointermediate (DI) and dorsomedial (DM) areas of the occipital cortex

After MT injections, sparse-to-moderate amounts of label were observed in DI of all four species of primates. Label was also observed in DM of squirrel monkeys and owl monkeys, but not galagos and marmosets.

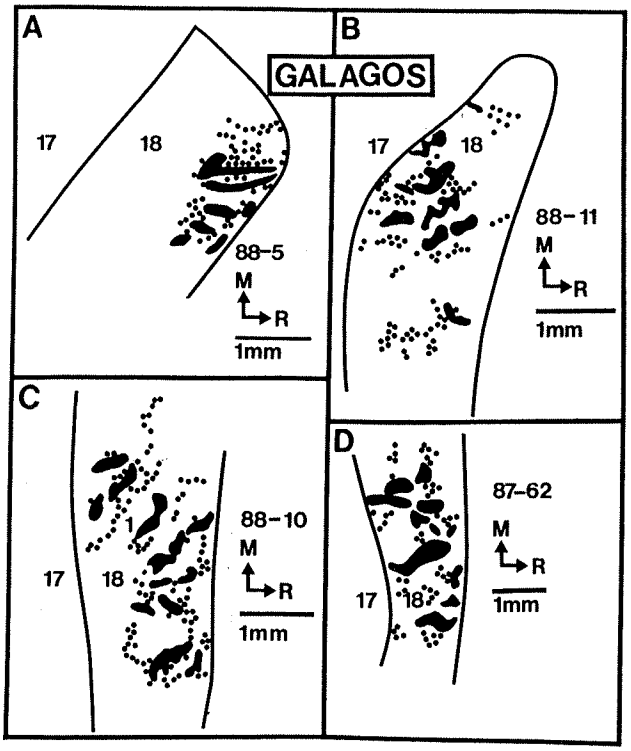

Fig. 11. Graphic reconstructions of anterograde (dots) and anterograde and retrograde (solid black) label in area 18 after injections of WGA-HRP in MT of galagos (A–C) and DL (D). As in the other species (Figs. 8–10), anterograde label is more broadly distributed than retrograde label and is found both in regions where retrogradely labeled neurons are located, and in regions between retrogradely labeled neurons. After injections in MT, label in area 18 is in small clumps of neurons that form bands across the field. Other bands of labeled neurons result from injections in DL. Conventions are as in previous figures.

In owl monkeys, where the locations of architectonic features of DM and DI have been established in previous studies (e.g. Allman & Kaas, 1975), connections with the DM/DI region were revealed in all three cases with MT injections. The labeled cells in these three cases were at the level of inner layer III, while labeled fine processes were more widely distributed. The scattered foci of label roughly, although not precisely, corresponded to expected retinotopic relationships. In owl monkey 88-7 (Fig. 17), the injection was in part of MT representing the horizontal meridian a few degrees from fixation. Label was scattered in clumps in rostrolateral DM, a portion devoted to central and paracentral vision. In another case where FB was injected into part of MT representing paracentral vision in the lower quadrant, labeled neurons were found in the mid-portion of DM (central to paracentral vision). An injection of WGA-HRP in part of MT representing more peripheral vision (Fig. 18) produced scattered clumps of label over more of DM, with concentrations near the lateral and medial borders of DM where peripheral vision is represented.

In owl monkeys, DI occupies the cortex between DM and DL. The myeloarchitectonic patterns in the present cases suggest that DI also extends rostromedially to partly border rostrolateral DM. In all three owl monkeys with MT injections, labeled neurons and, in two cases, processes, were found in DI (Figs. 17–19). The label was scattered in clumps over much of DI in the two cases with WGA-HRP injections, but was restricted to a few cells in rostral DI in the case with the FB injection.

In squirrel monkeys, DM and DI appear to have slightly different shapes and positions than in owl monkeys. DM is longer and narrower and DI extends medially along the rostral border of DM. Injections in the caudal part of MT representing central vision produced scattered clumps of label over much of DM and DI (Figs. 12 and 13), suggesting central vision is emphasized in these fields. More rostral injections in parts of MT representing paracentral vision resulted in less label in DI and little label in DM (Figs. 14 and 15). An injection in rostral MT related to more peripheral vision produced relatively sparse label in DI and DM. In marmosets, injections of WGA-HRP into parts of MT devoted to central (Fig. 20) and paracentral (Fig. 21) vision resulted in scattered label in DI, but not in DM. Similar results were obtained in galagos, where injections placed in the representations of paracentral (Fig. 23) and peripheral (Fig. 24) vision in MT produced scattered clumps of labeled neurons and processes in DI but not in DM. No label was found in DM or DI after an injection in the rostrolateral pole of MT (Fig. 22), which represents extreme peripheral vision.

Superior temporal areas (MST and FST)

Dense foci of transported tracer were observed in FST and MST in all species. The connections of MT with these fields were of the "feedforward" type (Rockland & Pandya, 1979; Maunsell & Van Essen, 1983; Van Essen & Maunsell, 1983; Weller et al., 1984). Thus, labeled cell bodies were both in supragranular and infragranular layers of MST and FST, while labeled axon terminals were most dense in the middle cortical layers. In general, FST was more densely interconnected than MST with MT. However, the locations of label and the amounts of label in these fields varied from case to case.

In squirrel monkeys, the two cases with injections related to central vision produced scattered foci of label over much of FST, but little label in MST (Figs. 12 and 13). More label was apparent in MST of other cases with injections involving paracentral and peripheral vision (Figs. 14–16). Thus, there was a suggestion that paracentral and peripheral vision are emphasized in MST.

Connections between MT and both MST and FST were also demonstrated in owl monkeys, marmosets, and galagos. In owl monkeys (Figs. 17 and 18) and marmosets (Figs. 20 and 21) with WGA-HRP injections in MT, dense patches of label were scattered within MST and FST. For uncertain reasons, the FB injection in MT of another owl monkey labeled groups of neurons in MST but not FST (Fig. 19). In all three galagos, injections in MT produced scattered foci of dense label in both MST and FST (Figs. 22–24). The scattering of foci of label over large portions of MST and FST after restricted injections in MT suggests that retinotopic organization, if present, is not as orderly in these fields as in MT.

The frontal ventral area (FV)

After MT injections, dense foci of labeled neurons and processes were consistently found in the frontal visual area, FV, of the frontal lobe. FV is a visual or visuomotor area just ventral to the frontal eye field with connections with the frontal eye field (Huerta et al., 1987). In some of the cases (e.g. Figs. 12, 18, 20, and 22), the frontal eye field was identified by low levels of electrical stimulation (see Kaas & Krubitzer, 1988), and marker lesions were placed near the borders of the field. These

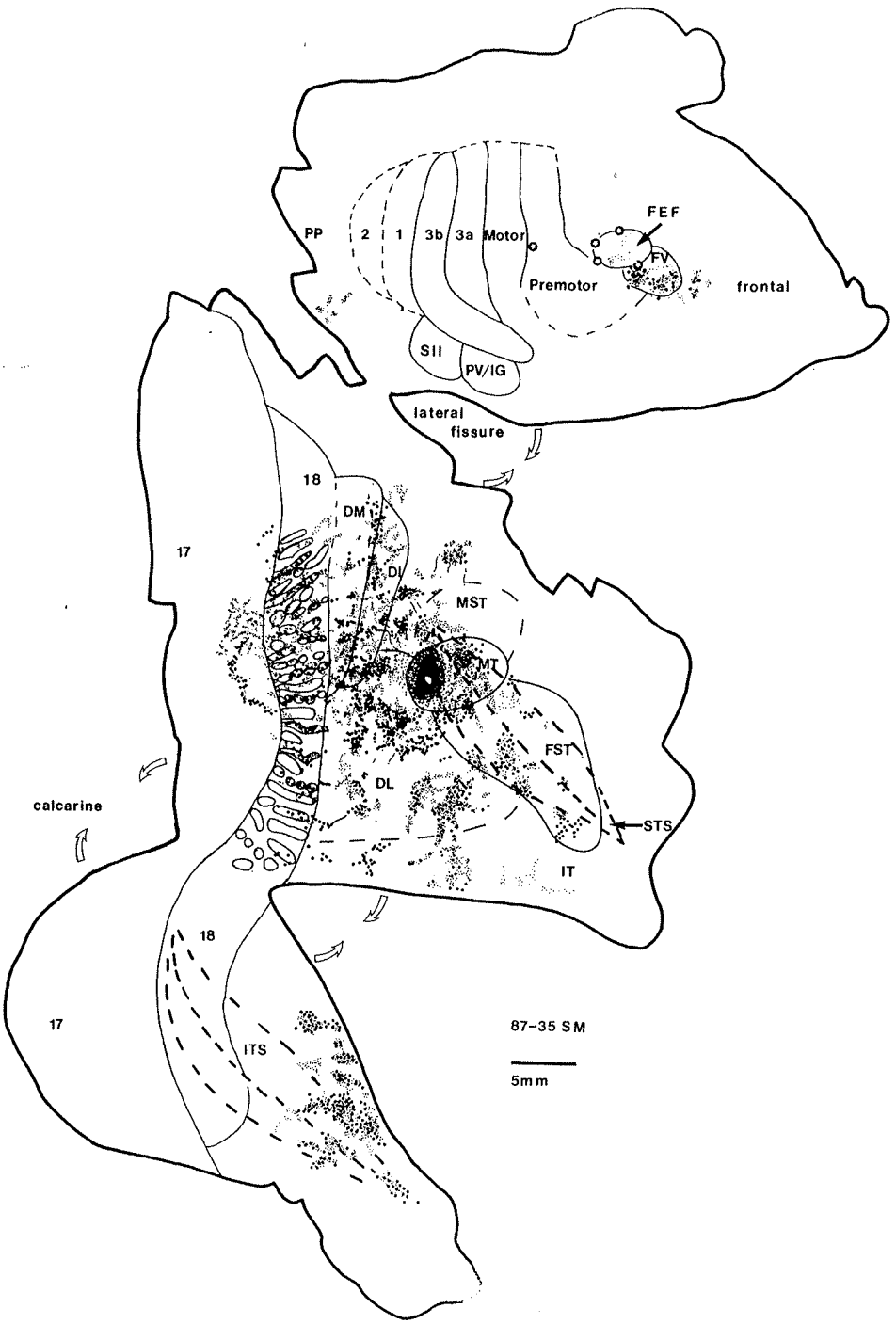

Fig. 12. Transported label (dots) after an injection of WGA-HRP in caudal MT in squirrel monkey 87-35. Results are shown on a representative brain section from the flattened cortex (see Fig. 1). Transported tracer is in areas 17 and 18, MST and FST, and in the posterior parietal cortex and the ventral temporal lobe. In the frontal cortex, labeled cell bodies and axon terminals are abundant in the frontal ventral area (FV, see text), but not in the physiologically defined frontal eye field, FEF. Large dots represent labeled cell bodies and small dots represent labeled axon terminals. Solid black lines mark architectonic boundaries. Thin dashed lines mark approximated borders, and thick dashed lines indicate major sulci. Stars in frontal cortex mark lesions placed at physiological boundaries of FEF, and at the junction of motor and premotor cortex. Arrows mark cuts where the cortex was joined. Abbreviations for visual areas are as in Fig. 1. Areas 3b (S-I), 3a, 1, and 2 are conventional architectonic subdivisions of the somatosensory cortex. See Krubitzer and Kaas (1990) for the second (S-II) and parietal ventral (PV) somatosensory areas. PV is in the cortex identified as insular granular (IG).

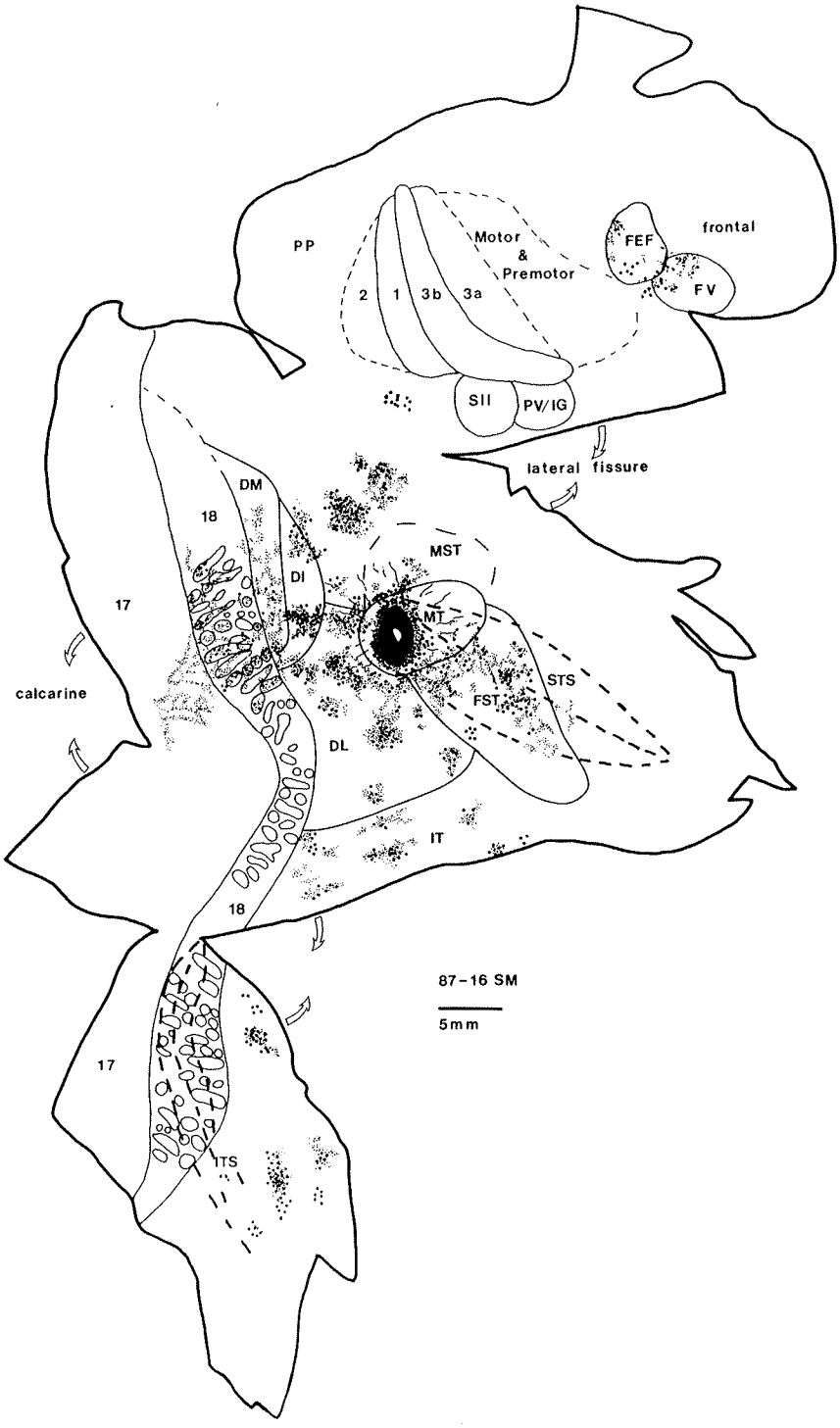

Fig. 13. Transported label after an injection of WGA-HRP in MT just caudal to the representation of central vision in squirrel monkey 87-16. Label in areas 17 and 18 is located medial to the representation of central vision. Label in DL is quite dense. Conventions are as in Fig. 12.

marker lesions were later found along the borders of an oval of dense myelination. In addition, an adjoining oval of less dense myelination, FV, was noted in these cases, and the dense label resulting from the MT injections was within this oval. Single injections in MT typically produced several foci of label in FV and little or no label if FEF (Figs. 12-19).

Other ipsilateral cortical connections

In some cases, MT injections produced label in portions of the inferior temporal cortex and posterior parietal cortex. In galagos, MT injections also labeled cortex in the lateral sulcus.

In squirrel monkeys, injections in the portion of MT representing central vision resulted in scattered label in the inferior

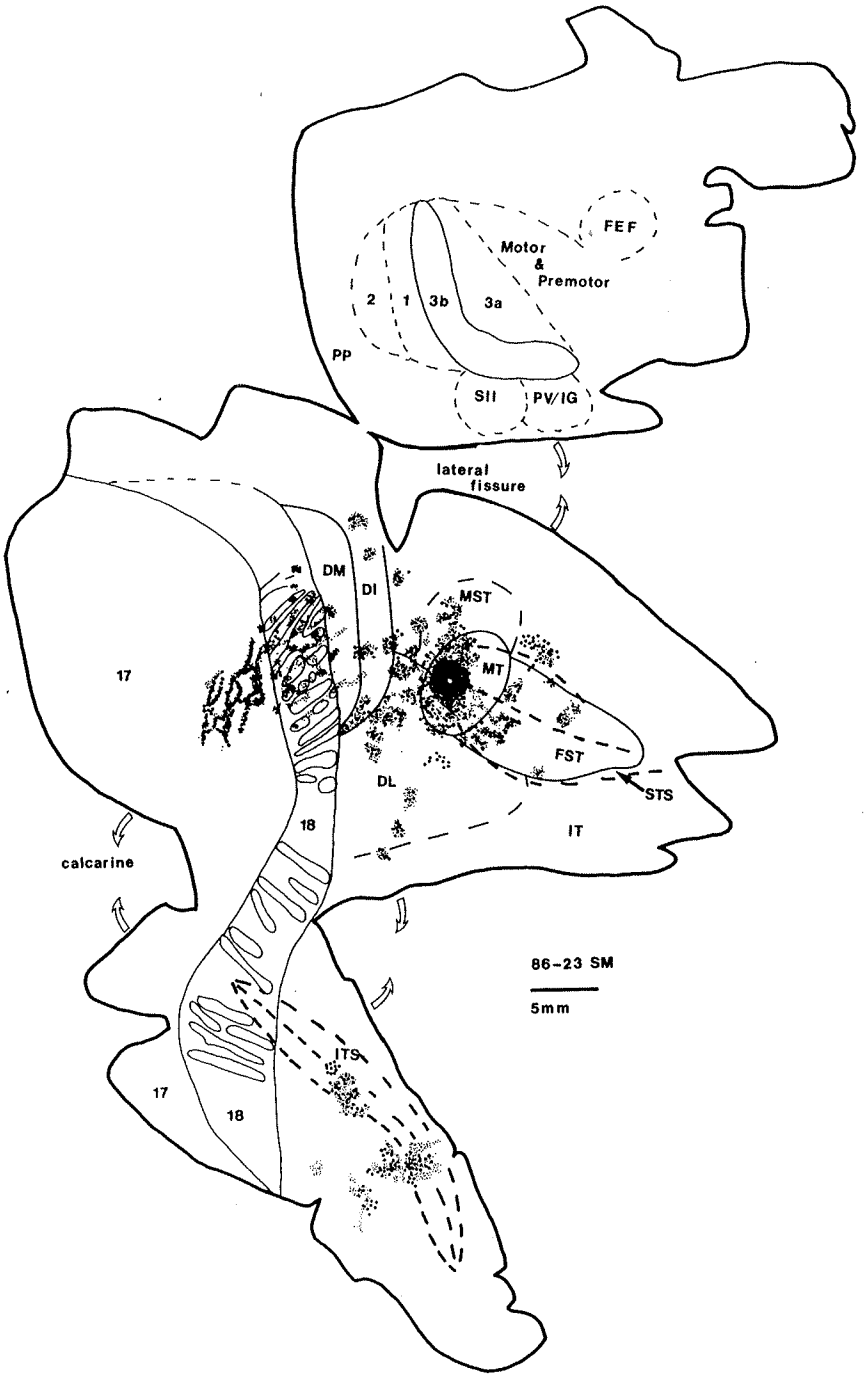

Fig. 14. Transported label after an injection of WGA-HRP in part of MT representing the paracentral lower visual field in squirrel monkey 86-23. Transported tracer in areas 17 and 18 is in corresponding parts of the visual-field representations. Conventions are as in Fig. 12.

temporal cortex that was most dense near or in the inferior temporal sulcus (Figs. 12 and 13). Injections in parts of MT related to paracentral vision produced less label in the inferior temporal sulcus, ITS (Figs. 14 and 15). The most rostral injections in MT in parts related to more peripheral vision produced little or no label in the inferior temporal cortex or in the ITS. Thus, there was evidence that the parts of MT representing central vision project most strongly to the ITS and inferior temporal cortex (IT). Label patterns in IT varied in the other primates as well. In owl monkeys, WGA-HRP injections labeled clusters of neurons and processes in the inferior temporal cortex, but the label was sparse (Figs. 17 and 18), and a FB injection labeled no neurons in IT. In contrast, a restricted DY injection in DL labeled many neurons in IT. In marmosets, the most widespread label in IT followed an injection in the part of MT representing central vision, while other parts of MT demonstrated more restricted connections with IT. In all three galagos, the MT injections produced considerable label in IT (Figs. 22–24), but less label was apparent in the case with the injection involving peripheral vision.

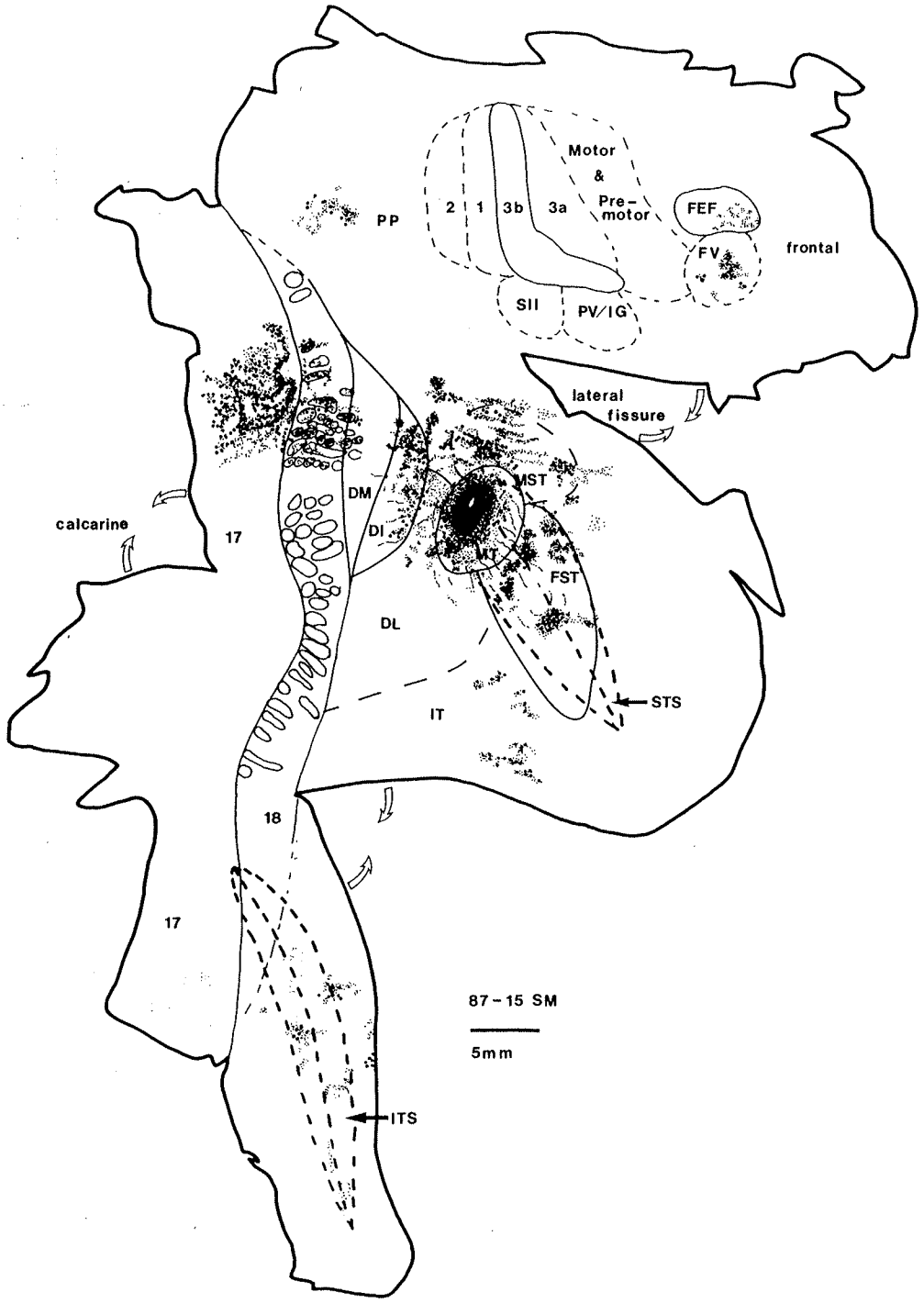

Fig. 15. Transported label after an injection in the lower visual-hemifield representation in MT in squirrel monkey 87-15. Labeled cell bodies and axon terminals in areas 17 and 18 are in corresponding parts of the lower visual-hemifield representation. Label in DL, ITS, and IT is much sparser than in previous cases (Figs. 12 and 14). Conventions are as in Fig. 12.

After MT injections, scattered foci of label were commonly observed in the posterior parietal cortex. In squirrel monkeys, this label was most notable in the ventral posterior parietal cortex, just medial of MST (Figs. 12–15). However, more medial label in the posterior parietal cortex was apparent in two cases (Figs. 12 and 15). Evidence for connection with portions of the posterior parietal cortex was also obtained in one of three owl monkeys (Fig. 18) and both marmosets (Figs. 20 and 21). In galagos, label was observed in the cortex medial to MST in all three cases. Finally, injections in MT of galagos, but not monkeys, labeled scattered regions in the cortex of the lateral sulcus (Figs. 22–24).

Callosal connections

Injections in MT in all four species of primates labeled fibers that coursed rostrally and then medially in the white matter to cross to the opposite cerebral hemisphere in the caudal third of the corpus callosum (also see Weller et al., 1984). Labeled neu-

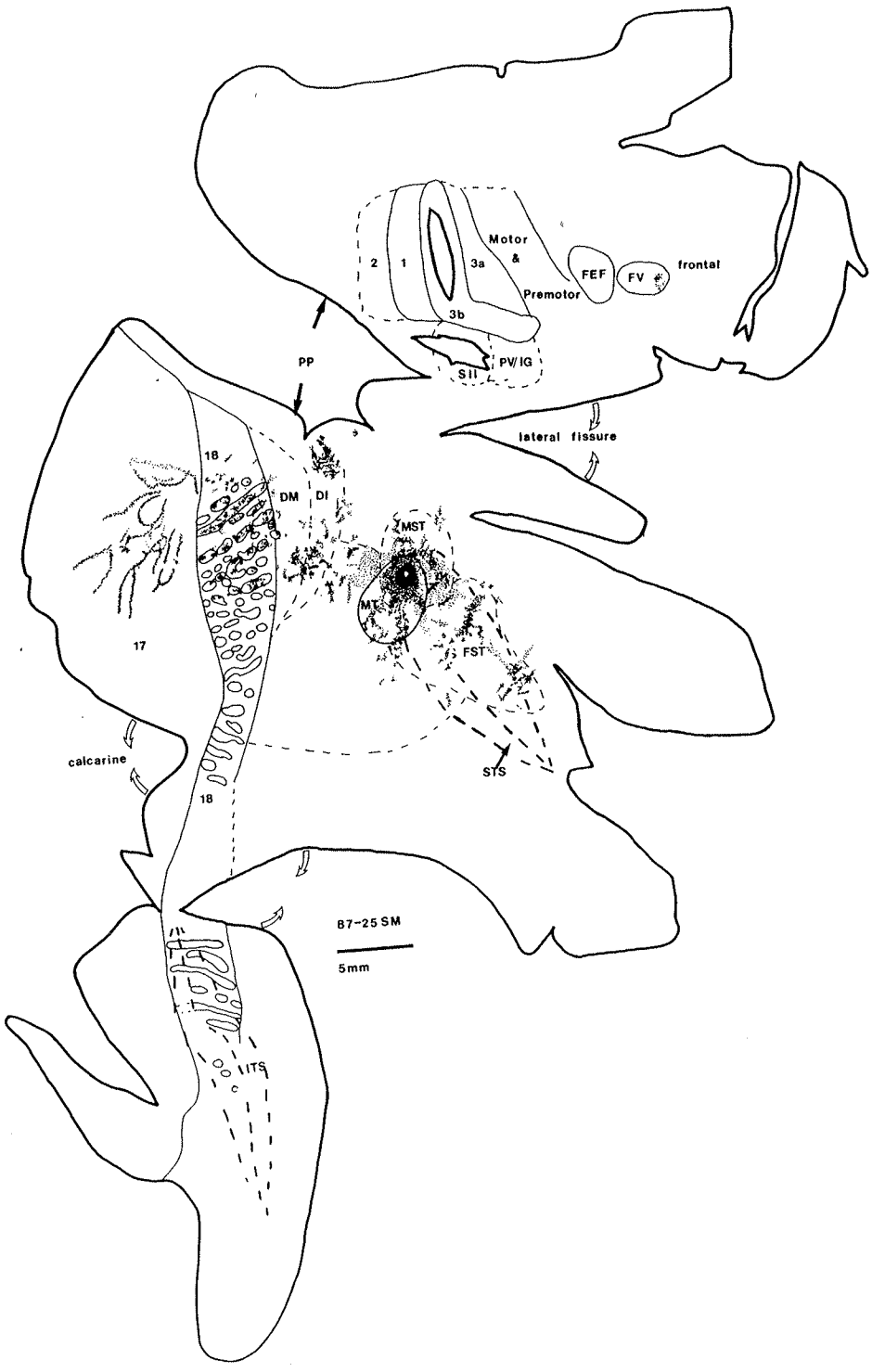

Fig. 16. Transported label after injections of tritiated WGA and proline in the peripheral lower field representation in MT in squirrel monkey 87-25. The locations of label in areas 17 and 18 are in the representation of the peripheral lower field. Only a small amount of label is in DL, and no label is in ITS or IT. Label in the frontal cortex is in FV only. Conventions are as in Fig. 12.

rons and processes were observed in MT, and less densely in DL, FST, and MST.

Each injection in MT produced a zone of label that typically contained several distinct foci in the contralateral MT. The location of the zone of dense label often closely matched that of the injection site. This was most obvious in squirrel monkeys. Thus, a caudorostral sequence of injection sites labeled a caudorostral sequence of regions in contralateral MT (Figs. 25A–

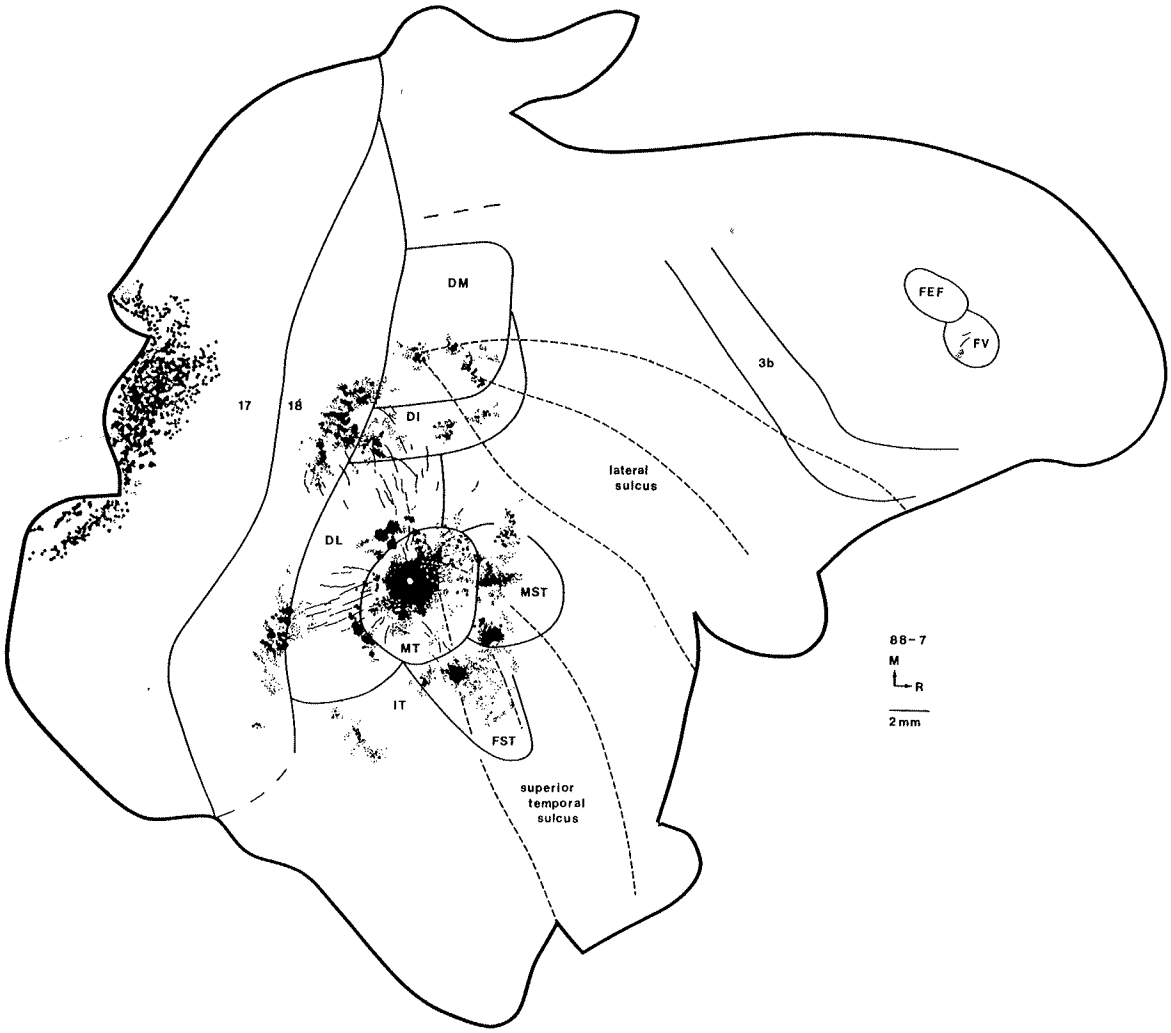

Fig. 17. Transported WGA-HRP after an injection in a representation of the paracentral visual field in MT in owl monkey 88-7. Label in area 18 is split into medial and lateral foci indicating that the injection in MT was on the representation of the horizontal meridian. In DL, label is also split medially and laterally. A very sparse patch of label is in FV. Conventions are as in Fig. 12.

25E). The connections related locations in the two hemifield representations that are roughly mirror symmetric about the zero vertical meridian. In owl monkeys, callosal connections were studied only in one case. Although transported label was scattered over much of contralateral MT (Fig. 26A), the callosally transported label was more concentrated in rostral MT, corresponding to the injection in rostral MT. Scattered callosally transported label was also found in MT of marmosets (Fig. 26C and 26D). An injection in rostroventral MT of a galago produced foci of label in rostroventral MT of the opposite hemisphere (Fig. 26B). Although this label was along the outer border of MT, injections more typically produced label that was scattered within MT, and there was no obvious tendency for callosally transported label to be concentrated along the outer border of MT.

In marmosets, an uneven distribution of myelin was observed in MT of some cases. Results from one of these cases suggest that callosal connections preferentially relate to the myelin-dense portions of MT (Fig. 26D).

Callosally transported label from MT injections was observed in DL of only a few cases. In squirrel monkeys, injections in caudal MT, representing central vision, produced notable amounts of label in contralateral DL (Fig. 25A and 25B) while more rostral injections in MT produced little or no label in contralateral DL (Fig. 25C–25E). Sparse label was noted in contralateral DL of two marmosets (Fig. 26C) but not in the one owl monkey and the one galago studied.

Foci of sparse callosally transported label were usually apparent in FST of squirrel monkeys (Fig. 25A–25E). The callosally transported label in FST was denser in an owl monkey (Fig. 26A), marmosets (Fig. 26C), and a galago (Fig. 26B). Although label in the contralateral MST was noted in only one squirrel monkey (Fig. 25D), such label was prominent in an owl monkey (Fig. 26A), galago (Fig. 26B), and marmosets (Fig. 26C). Finally, in one squirrel monkey, some label was found in IT contralateral to the MT injection (Fig. 25A).

Discussion

The present study provides evidence that at least ten visual and visuomotor areas are common to squirrel monkeys, owl mon-

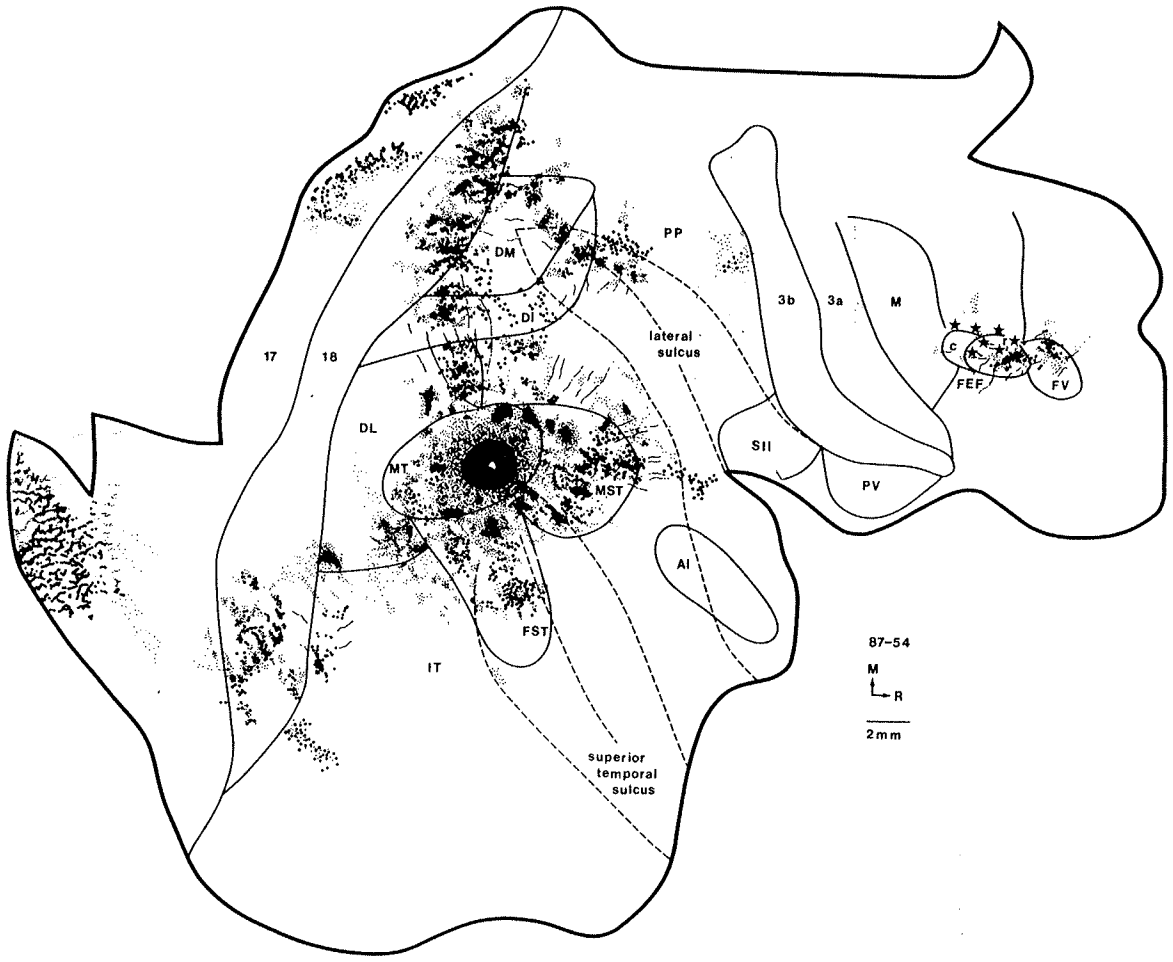

Fig. 18. Transported label after an injection of WGA-HRP in rostral MT in owl monkey 87-54. The injection was in the representation of the peripheral field along the horizontal meridian. Label is in the visuotopic register in areas 17 and 18. Label in DL is medial and lateral. Stars mark microlesions placed in and around physiologically defined FEF. The region marked C also produced eye movements. Conventions are as in Fig. 12.

keys, marmosets, and galagos. These areas include area 17 (V-I); area 18 (V-II); the dorsolateral (DL), dorsointermediate (DI), and dorsomedial (DM) visual areas; the middle temporal (MT), middle superior temporal (MST), and "fundal" superior temporal (FST) visual areas; and the frontal eye field (FEF) and frontal visual area (FV) (Fig. 27). All of these fields are interconnected with MT, a visual area thought to have a critical role in visual tracking, motion perception, and visuospatial attention (e.g. Ungerleider, 1985; Newsome et al., 1985; Siegel & Anderson, 1986; Dürsterler et al., 1987; Newsome & Pare, 1988). MT has additional connections with visual cortex in subdivisions of the temporal lobe that we did not attempt to define, suggesting that the examined primates share even more viusal areas with an MT influence. The network of interconnected areas is similar in a member of the prosimian radiation and in members of the two major branches of the platyrrhine radiation, and is little changed by adaptations for diurnal or nocturnal niches. Furthermore, evidence for most of these areas, defined by connections with MT, exists for Old World macaque monkeys (Fig. 28). In addition, this study demonstrates that the segregation of visual modules in areas 17 and 18, associated with MT and the magnocellular processing streams, is present in all four species of primates (Fig. 29). Thus, at least some of the anatomical connections of the magnocellular subsystem exist in a range of primate species, and may have originated early in primate evolution and be a common feature of all primates including humans.

The major implication from this study is that an interconnected array of roughly 12–15 visual and visuomotor areas arose early in primate or pre-primate evolution and have been retained, with elaborations and additions, in most or all extant primates. The significance of MT, as a critical area in this array, is the suggestion that, from the beginning of primate evolution, an emphasis was placed on detecting and localizing stimulus change, in addition to evaluating the static properties of objects. Finally, the results provide further evidence that MT is not isolated within a single processing stream directed to attention and detection centers in the parietal cortex, but is also related to the color and form stream directed to the inferior temporal cortex (see Ungerleider & Mishkin, 1982; Mishkin et al., 1983; Livingstone & Hubel, 1987). Because object vision is highly dependent on central vision, the present evidence that parts of MT devoted to central vision are more densely interconnected with the stream for object vision is not surprising.

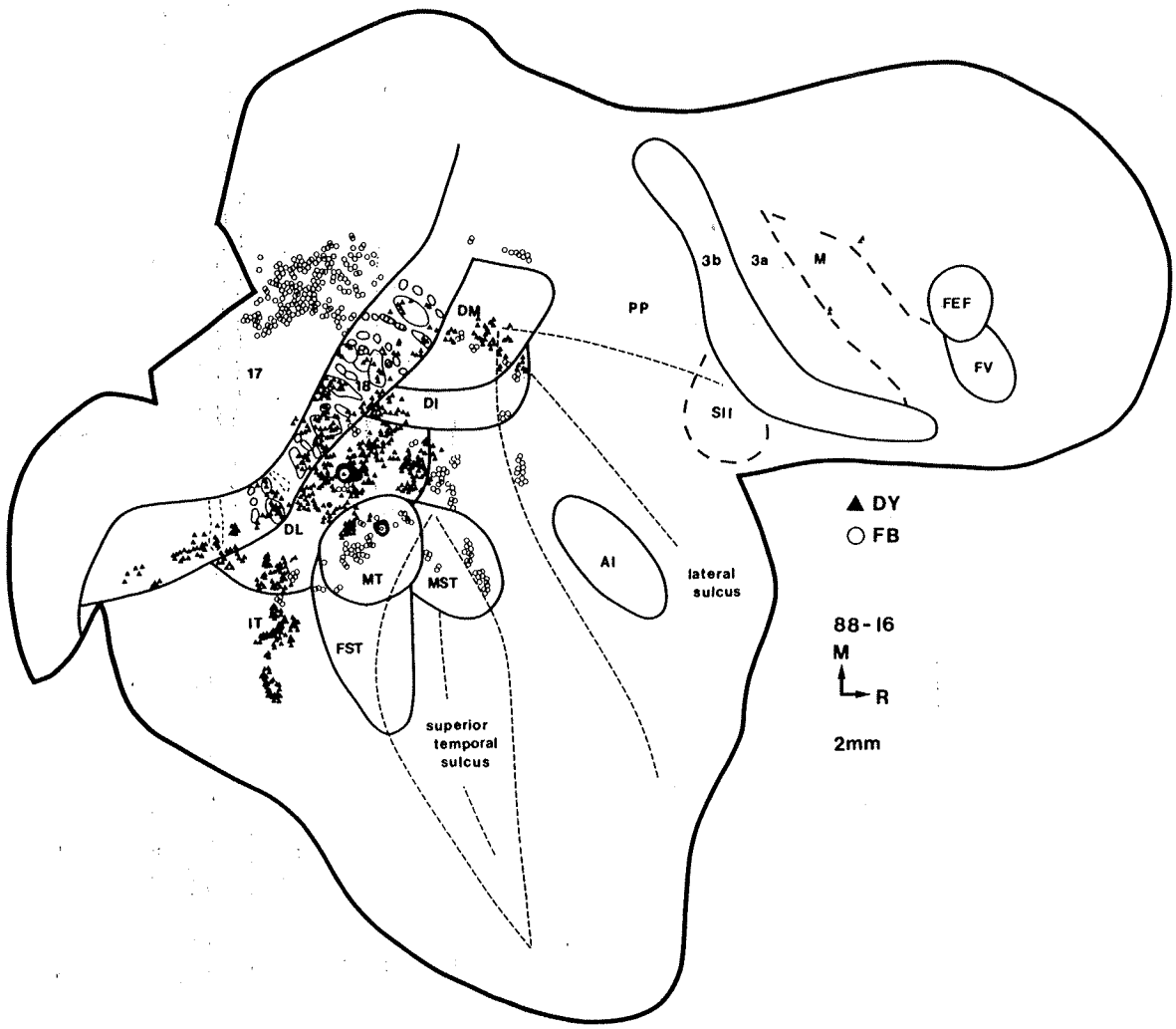

Fig. 19. Transported fast blue (open circles) after an injection in the paracentral lower visual-field representation in MT and diamidino yellow (filled triangles) after an injection in DL of owl monkey 88-16. In areas 17 and 18, fast blue label is dorsal in paracentral lower hemifield representations. The injection in DL labeled a broader extent of area 18 and DM, and strongly labeled IT. Conventions are as in Fig. 12.

Subdivisions of the visual cortex in primates

Several architectonically distinct visual cortical fields were identified by architecture, location, and connections with MT in each of four species of primates. In each species, the total areal extent of these fields was measured and compared to the total extent of the neocortex.

Most of the visual fields considered in the present investigation have been described previously both physiologically and architectonically in owl monkeys (Allman & Kaas, 1971*a*,*b*, 1974*a*,*b*, 1975; Tootell et al., 1985). Our descriptions of these fields in owl monkeys are in good agreement with previous reports. Areas 17 and 18 closely correspond to the descriptions of Allman and Kaas (1971*b*, 1974*a*). However, in cortex that has been flattened and stained for myelin or reacted for CO, a slight bulge in the middle of area 17 representing central vision is apparent (also see Tootell et al., 1985). In addition, the width of area 18 varies so that the central portion is quite narrow and the medial and lateral portions of this field are somewhat wider. In previous physiological studies, DL was reported to wrap around both the dorsal and ventral portions of MT (Allman & Kaas, 1974*b*). However, the present architectonic results in owl monkeys suggest that DL surrounds the caudal half of MT while MST and FST border MT rostromedially and ventrally, respectively.

DM was first described in owl monkeys as a densely myelinated rectangle of cortex with a systematic representation of the visual field (Allman & Kaas, 1975). Our present estimation of the shape and size of DM in sections cut parallel to the brain surface is very similar to earlier descriptions, although the present size may be somewhat smaller. DI appears to wrap around the ventral and rostral portions of DM. Earlier physiological studies described DI as located predominantly ventral to DM (Allman & Kaas, 1974*b*, 1975). However, the rostral boundary of DI was not determined in this study. In flattened cortex, Tootell et al. (1985) described a darkly CO-staining region they called DX, because they were uncertain if this field was DM or DI. DX is in the same relative location and stains similarly for CO as does DI in the present study. Thus, it is likely that DX described by Tootell et al. (1985) is DI.

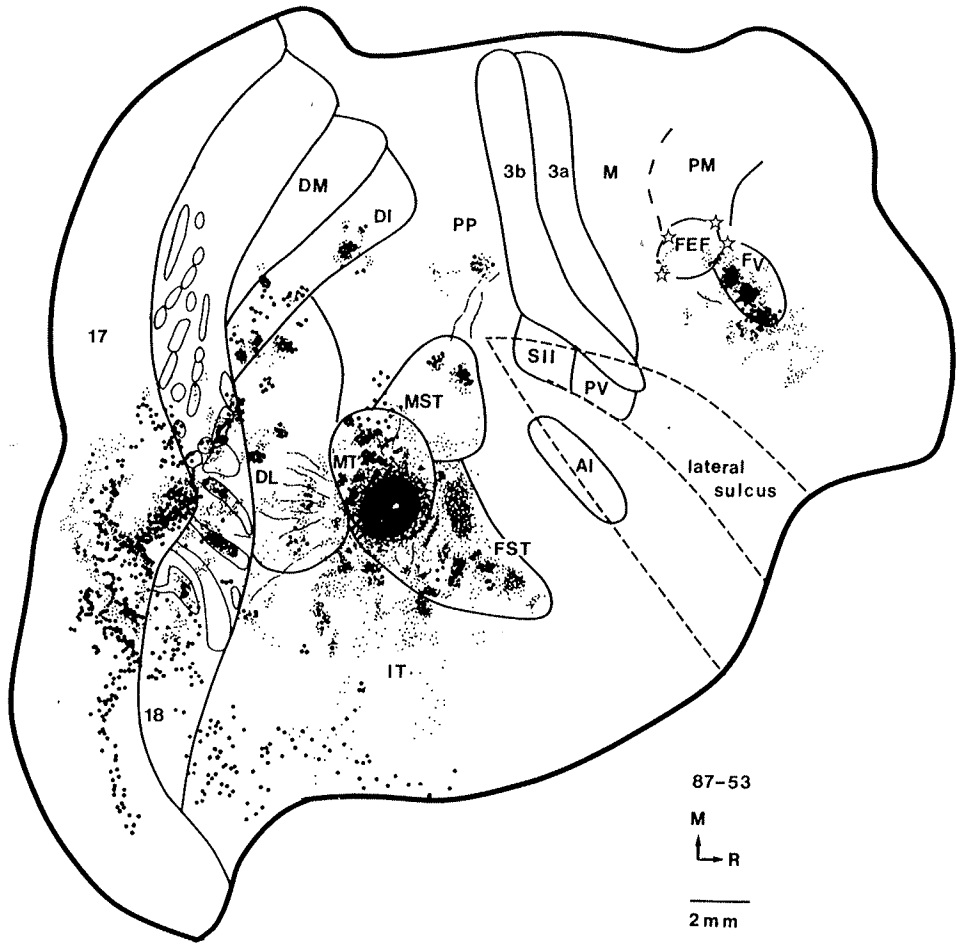

Fig. 20. Label after an injection of WGA-HRP in MT in marmoset 87-53. Label is in parts of areas 17 and 18 that represent central vision. Moderately dense patches of label are in DI but not in DM, and only sparse label is found in PP. In the frontal cortex, dense patches of label are in FV but not in the physiologically defined FEF. Stars mark microlesions placed at physiological boundaries. Conventions are as in Fig. 12.

In the region of the superior temporal sulcus of owl monkeys, areas MT and MST have been identified in previous physiological (Allman & Kaas, 1971*a*) and connectional studies (Weller et al., 1984). In these and other studies, MT was shown to be densely myelinated, and Tootell et al. (1985) have demonstrated that MT reacts darkly for CO. In the present investigation, MST is identified as an oval of dense myelination immediately rostral and slightly dorsal to MT. In earlier studies in owl monkeys, MST was shown as partly separated from MT by an extension of DL (Weller et al., 1984). However, connections from MT to the MST–DL region are found immediately adjacent to the rostral boundary of MT and in a separate location displaced more caudally from the MT border. The adjacent projection is located in the more myelinated MST region and the caudal location is in DL.

Except for V-I, V-II, and MT, different names have been assigned to visual areas in macaque monkeys (see Fig. 28; Maunsell & Newsome, 1987; Van Essen, 1985). However, several additional homologies appear to be likely. For instance, V4 of macaques resembles DL in New World monkeys in relative location, architecture, and retinotopic organization (Van Essen & Zeki, 1978; Gattass et al., 1988). Both DL in New World monkeys (Kaas & Lin, 1977; Tigges et al., 1974; Weller & Kaas, 1985; Cusick & Kaas, 1988*a*) and V4 in macaques (Zeki, 1971; Felleman & Van Essen, 1983; DeYoe & Van Essen, 1985; Shipp & Zeki, 1985, 1989*b*) are characterized by major inputs from V-II and dense connections with the inferotemporal cortex. Given these similarities, V4 and DL are probably homologous (see Weller & Kaas, 1985 for review). Homologies of other dorsal areas are less certain. Dorsal V3 or V3d (Zeki, 1978*b*; Burkhalter et al., 1986; Gattass et al., 1988) lies immediately rostral to area 18 and somewhat dorsal to V4. This field is in the same relative location, appears to be architectonically similar, and is the same shape as DM in squirrel monkeys. In addition, dorsal V3 or a field in the approximate location of dorsal V3 receives direct input from area 17 (Cragg, 1969; Zeki, 1969, 1971, 1978*b*; Rockland & Pandya, 1981; Weller & Kaas, 1983; Perkel et al., 1986; Van Essen et al., 1986) as does DM in owl monkeys, galagos, marmosets, and squirrel monkeys (Lin et al., 1982; Cusick & Kaas, 1988*b*; Krubitzer & Kaas, 1989*b*). We have recently demonstrated such connections in Old World talapoin monkeys (Kaas & Krubitzer, 1990). In addition, the dorsal V3 region is interconnected with MT in Old World monkeys (Maunsell & Van Essen, 1983; Ungerleider & Desimone,

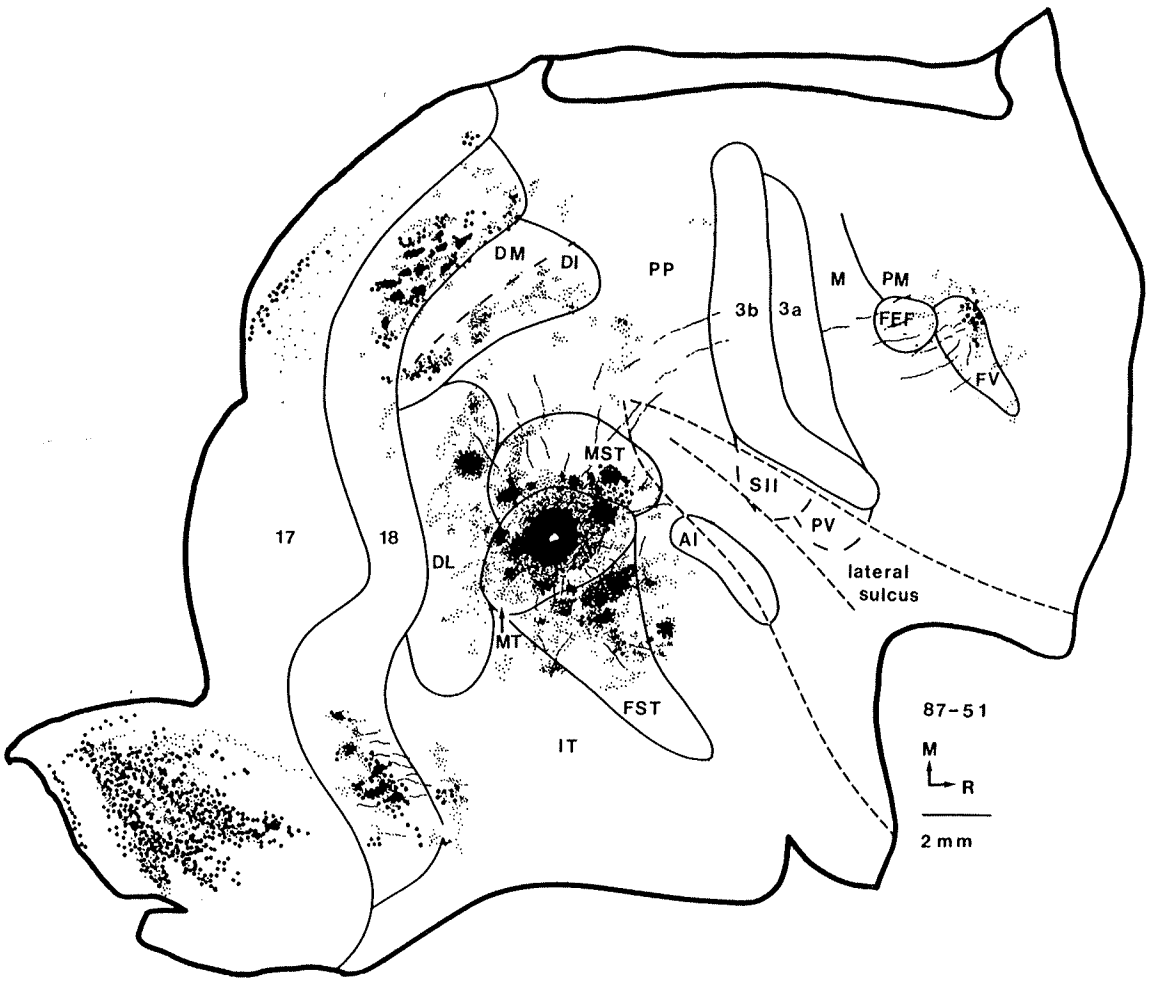

Fig. 21. Transported label after an injection in the representation of paracentral vision along the horizontal meridian in MT of marmoset 87-51. Label is in corresponding parts of representations in areas 17 and 18. Conventions are as in Fig. 12.

1986*a*) as is DM in New World monkeys (Spatz & Tigges, 1972; Wagor et al., 1975; Weller et al., 1984; present study). Thus, it is possible that the dorsal V3 region is DM. Evidence against this hypothesis is that DM contains a complete representation of the visual hemifield (Allman & Kaas, 1975), while only a lower field representation has been demonstrated in V3d (Gattass et al., 1988).

A field immediately rostral to V3 in macaque monkeys has been termed V3a (Van Essen & Zeki, 1978; Zeki, 1978*b*; Maguire & Baizer, 1984; Gattass et al., 1988). This field is architectonically similar to V3, and contains a representation of the contralateral visual hemifield (Gattass et al., 1988). It is possible that this field is homologous with either part of DM or DI in New World species since similarities in relative location, architectonic appearance, and connections exist.

We identified three fields in the superior temporal sulcus, MT, MST, and FST. MT has been identified in the superior temporal sulcus in owl monkeys (Allman & Kaas, 1971*a*; Weller et al., 1984; Felleman & Kaas, 1984), squirrel monkeys (Tigges et al., 1981), marmosets (Spatz & Tigges, 1972; Spatz, 1977), cebus monkeys (Fiorani et al., 1989), and macaque monkeys (Ungerleider & Mishkin, 1979; Montero, 1980; Gattas & Gross, 1981; Maunsell & Van Essen, 1983; Albright et al., 1984; Maioli et al., 1983; Desimone & Ungerleider, 1986; Ungerleider & Desimone, 1986*a*,*b*). MST is part of superior temporal (ST) cortex, a previously demonstrated projection zone of MT in owl monkeys (Weller et al., 1984). In macaque monkeys, an equivalent part of this projection zone is termed MST (Maunsell & Van Essen, 1983; Desimone & Ungerleider, 1986; Ungerleider & Desimone, 1986*a*), and this term is used here. FST has previously been identified only in macaque monkeys (Desimone & Ungerleider, 1986; Ungerleider & Desimone, 1986). However, similarities in relative location, architectonic appearance, and connections suggest that the FST described here corresponds to FST in macaques.

Relatively little is known about extrastriate visual cortical organization in prosimian primates. Although the connections and visuotopic organization of MT have been described in galagos (Allman et al., 1973; Wall et al., 1982) there has been little progress in defining additional extrastriate visual cortical areas (however, see Allman et al., 1979). The present investigation provides both architectonic and connectional evidence that at least some extrastriate cortical areas described above in New and Old World simians exist in prosimian galagos as well. The

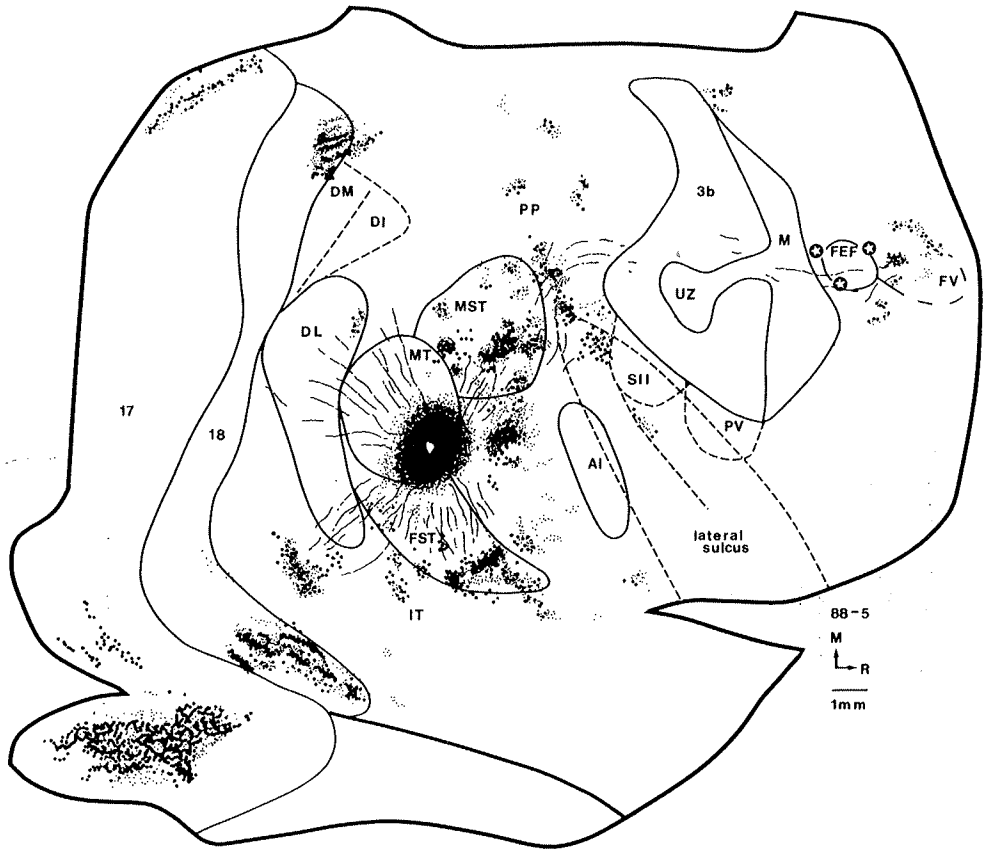

Fig. 22. Transported label after an injection in rostral MT in galago 88-5. The injection is in the representation of peripheral vision on the horizontal meridian. Resulting label in parts of areas 17 and 18 is also in the representations of peripheral vision. Stars mark microlesions placed at physiologically defined borders of the FEF. Conventions are as in Fig. 12.

dorsal visual areas, DL, DM, and DI, are architectonically distinct, in the same relative positions, and relate in a similar manner to patterns of connections from MT (Wall et al., 1982; present study). We are presently uncertain how the proposed subdivisions, DM and DI, relate to the dorsal area in galagos of Allman et al. (1979). The dorsal area was described as having a retinotopic organization similar to that of the medial area of owl monkeys (Allman & Kaas, 1976) just medial to DM. By position, the dorsal area appears to be at least partly medial to the present DM. Areas in the superior temporal sulcus such as MT, FST, and MST were also identified in galagos. Again, these fields are architectonically and connectionally similar to those fields in monkeys.

By flattening and sectioning all neocortex in each of the experimental cases, we were able to compare the sizes of areas to the total extent of neocortex. Areas varied in architectonic distinctiveness, and thus measurements for some areas should be interpreted with caution. However, the flattening process appears to introduce little distortion (Olavarria & Van Sluyters, 1985; Tootell & Silverman, 1985; Lowell et al., 1987), and there was little variability in proportional sizes of areas. Most values were highly similar although values from some cases were deviant (Table 1). Measurement errors may have contributed to these deviant values, or they may be true differences. Our measurements (except for one monkey) of the proportion of neocortex occupied by area 17 in owl monkeys are in good agreement with previous measurements in owl monkeys (17%, Tootell et al., 1985). In owl monkeys, Tootell et al. (1985) found MT to be about 37 mm^2 or 1.5% of neocortex while we found MT of owl monkey to be 25.75 mm^2 or 1.8% of neocortex. Previous measurements of MT in macaques (e.g. Albright & Desimone, 1987), although absolutely larger, are relatively smaller than our measurements of MT in diurnal monkeys. Area 18 (V-II) in owl monkeys in the present study is comparable in size ($X = 93.6$ mm^2; 7.6% of neocortex) to that estimated in owl monkeys (~100 mm^2; ~5% of neocortex) by Tootell et al. (1985). The percent of neocortex that area 18 occupies is slightly larger in diurnal (8–8.7%) than nocturnal (6–7.6%) species examined in this study. Estimates of the surface area of area 18 in *Cebus appella* (Rosa et al., 1988) of 819–883 mm^2 were approximately four times larger than measurements in the squirrel monkeys in the present investigation (186–294 mm^2).

Previous studies suggest that there may be considerable individual variability in the sizes of visual areas. In macaque monkeys, Van Essen et al. (1984) report that measurements of the surface areas of striate cortex varied from 690–1560 mm^2. Likewise, estimates of the size of MT in macaque monkeys have ranged from 33–110 mm^2 (see Erickson et al., 1989 for review). Our results show similar variability in the absolute size of fields within the same species. For example, in six squirrel monkeys, estimates of area 17 varied from 378–653 mm^2. Similar variation occurred for other areas in the same species and for area 17 and other fields in other primates. Yet, most of this

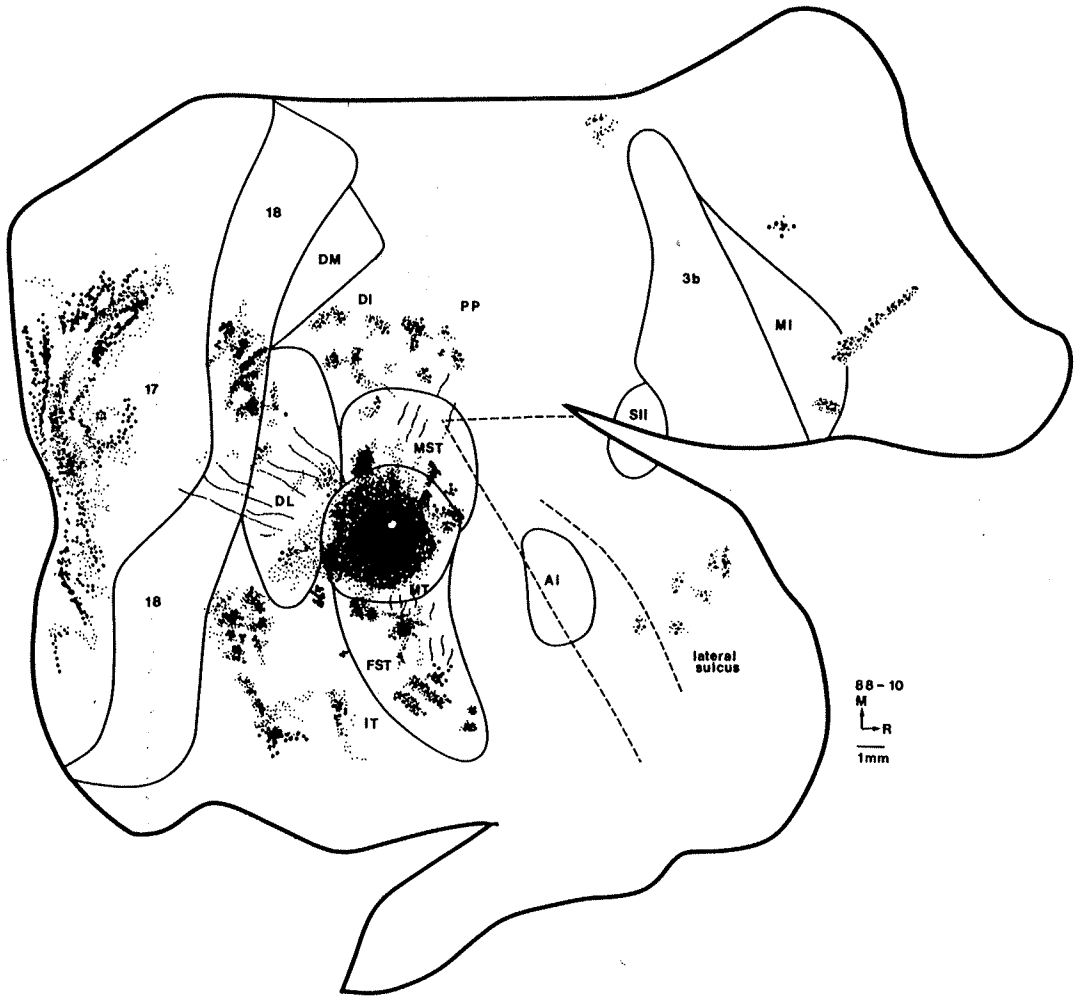

Fig. 23. Label after an injection of WGA-HRP in the representation of the paracentral vision MT in galago 88-10. Conventions are as in Fig. 12.

variability appears to relate to overall differences in brain sizes in the measured individuals. In agreement with the evidence that variations in the sizes of visual areas are related to differences in brain sizes, striate cortex measurements from the two hemispheres of the same macaque monkeys are highly similar (Van Essen et al., 1984). In addition, MT measurements are strongly correlated with body weight (Ungerleider & Desimone, 1986*b*; Maunsell & Van Essen, 1987), which is closely related to brain size. Furthermore, measurements across primate species show a close correlation of area 17 size with brain size (Frahm et al., 1984).

The differences in the sizes of areas in diurnal and nocturnal primates noted in the present investigation are consistent with previous comparisons in the visual system of nocturnal and diurnal primates. In the lateral geniculate nucleus (LGN), diurnal primates have relatively more neural tissue devoted to parvocellular than magnocellular layers (Hassler, 1966; Stephan et al., 1988). Our results extend this idea of parvocellular emphasis in diurnal primates by demonstrating a relative enlargement of cortical areas assoicated with the parvocellular pathway, such as area 17, area 18, and DL, in diurnal primates (Fig. 6). The nocturnal primates, owl monkeys and galagos, had somewhat less visual cortex relative to the total neocortex (Fig. 5; Table 1), and they had somewhat more emphasis on the "attention and visual tracking" stream (areas MT and MST). However, given the divergence of the four species in evolution and the different behavioral adaptations, the similarities in proportional sizes of all eight measured fields seem remarkable.

Connections

The connection patterns of MT were highly consistent across species. Thus, MT had strong connections with areas 17, 18, MST, and FST and moderate-to-sparse connections with DM, DI, IT, ITS, and posterior parietal (PP) cortex. Connections with all fields were discontinuous and patchy, suggesting that all fields are modularly organized. Differences in the densities of connections of central and peripheral portions of MT with extrastriate cortical areas DL, IT, ITS, and MST were noted. Finally, the connections of MT with areas 17 and 18 were topographically organized in a similar manner across species.

Area 17

The injections in MT demonstrated interconnections with area 17 in all cases. The labeled portions of area 17 varied in location with the injection site in MT in a pattern that indicates

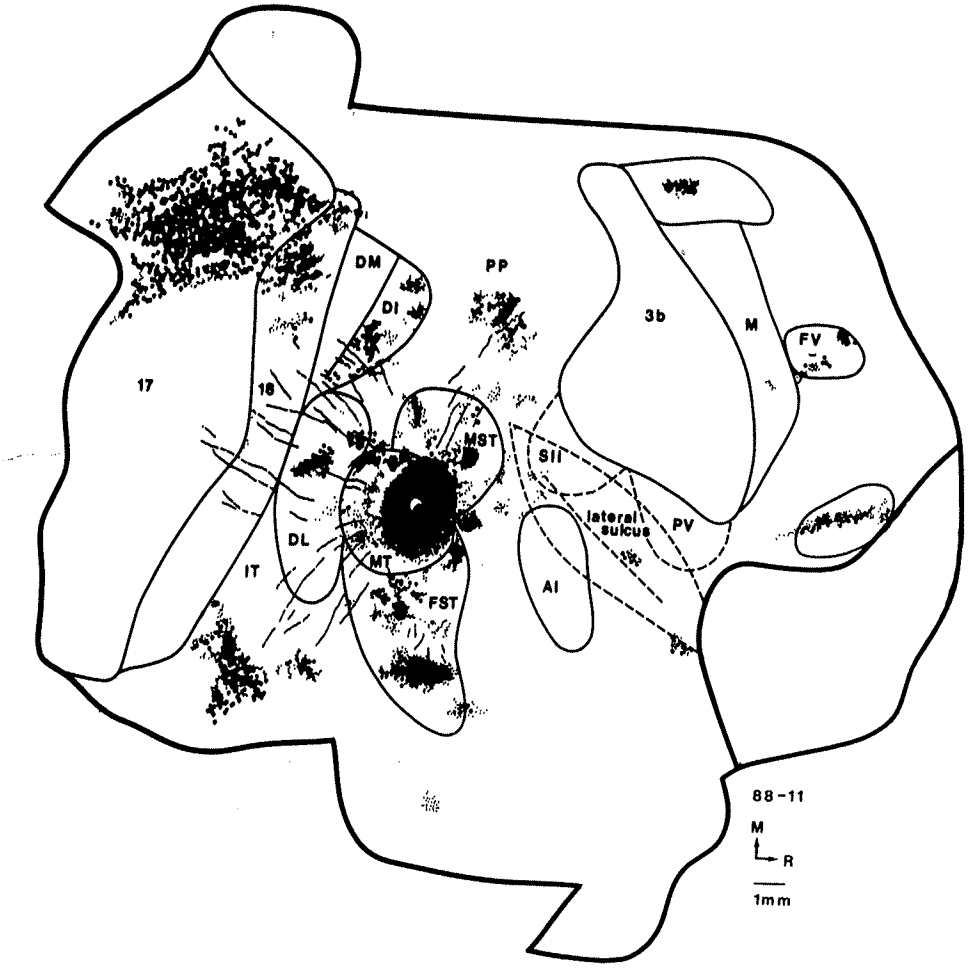

Fig. 24. Label after an injection in the representation of the peripheral lower field in MT in galago 88-11. Label is in medial parts of areas 17 and 18 that also represents the peripheral lower field. Conventions are as in Fig. 12.

that retinotopic locations in the two representations are interconnected. The neurons projecting to MT from area 17 often appeared to form several short, meandering rows with a spacing reminiscent of orientation columns. Return projections were more broadly distributed across rows.

The existence of projections from area 17 to cortex in the region of MT were first established by Kuypers et al. (1965), and now the existence of such interconnections is well-established for a range of primate species (Cragg, 1969; Zeki, 1969; Spatz et al., 1970; Tigges et al., 1981; Spatz & Tigges, 1972; Spatz, 1975, 1977; Martinez-Millán & Holländer, 1975; Wall et al., 1982; Cusick & Kaas, 1988*b*; Symonds & Kaas, 1978; Weller & Kaas, 1983; Montero, 1980; Ungerleider & Mishkin, 1979: Maunsell & Van Essen, 1983; Van Essen et al., 1986; Ungerleider & Desimone, 1986*a*,*b*). However, most of these studies were based on injections centered in MT or placed in the most accessible part of area 17 on the dorsolateral surface of the brain, and thus, little information was obtained on topographic patterns of connections. Yet, a number of investigators demonstrated enough of the topographic pattern of projections to MT from area 17 to reveal at least partial retinotopic matching (e.g. Ungerleider & Mishkin, 1979; Spatz, 1977; Symonds & Kaas, 1978; Ungerleider & Desimone, 1986*a*). In particular, Spatz (1977) varied injection sites from central vision in caudolateral MT to peripheral vision in rostromedial MT of marmosets and found a topographic pattern of connections with area 17 that closely corresponds to the patterns revealed in the present study. In both studies, injections in caudolateral MT labeled dorsolateral portions of area 17 while progressively more rostromedial injections labeled regions of area 17 progressively displaced onto the medial wall and into the calcarine fissure.

After MT injections, most labeled neurons in area 17 were in supragranular layers while fewer labeled neurons were in infragranular layers. Fine label, suggestive of projections terminating in area 17, was largely in the superficial layers. These results are consistent with the more detailed descriptions of laminar patterns of connections (e.g. Tigges et al., 1981; Rockland & Pandya, 1981; Wong-Riley, 1979*b*; Maunsell & Van Essen, 1983; Shipp & Zeki, 1989*a*) demonstrating that neurons projecting to MT are located in layer IIIc of Hassler (1966) and at the layer V/VI junction (Meynert cells), while return terminations are densest in layers I, II, and upper III. However, in the surface-view preparations, it often appeared that labeled cells in area 17 formed 2–5 short, parallel meandering rows, while superficial label was more evenly distributed, but less dense over the CO puffs (also see Krubitzer & Kaas, 1989*a*). The conver-

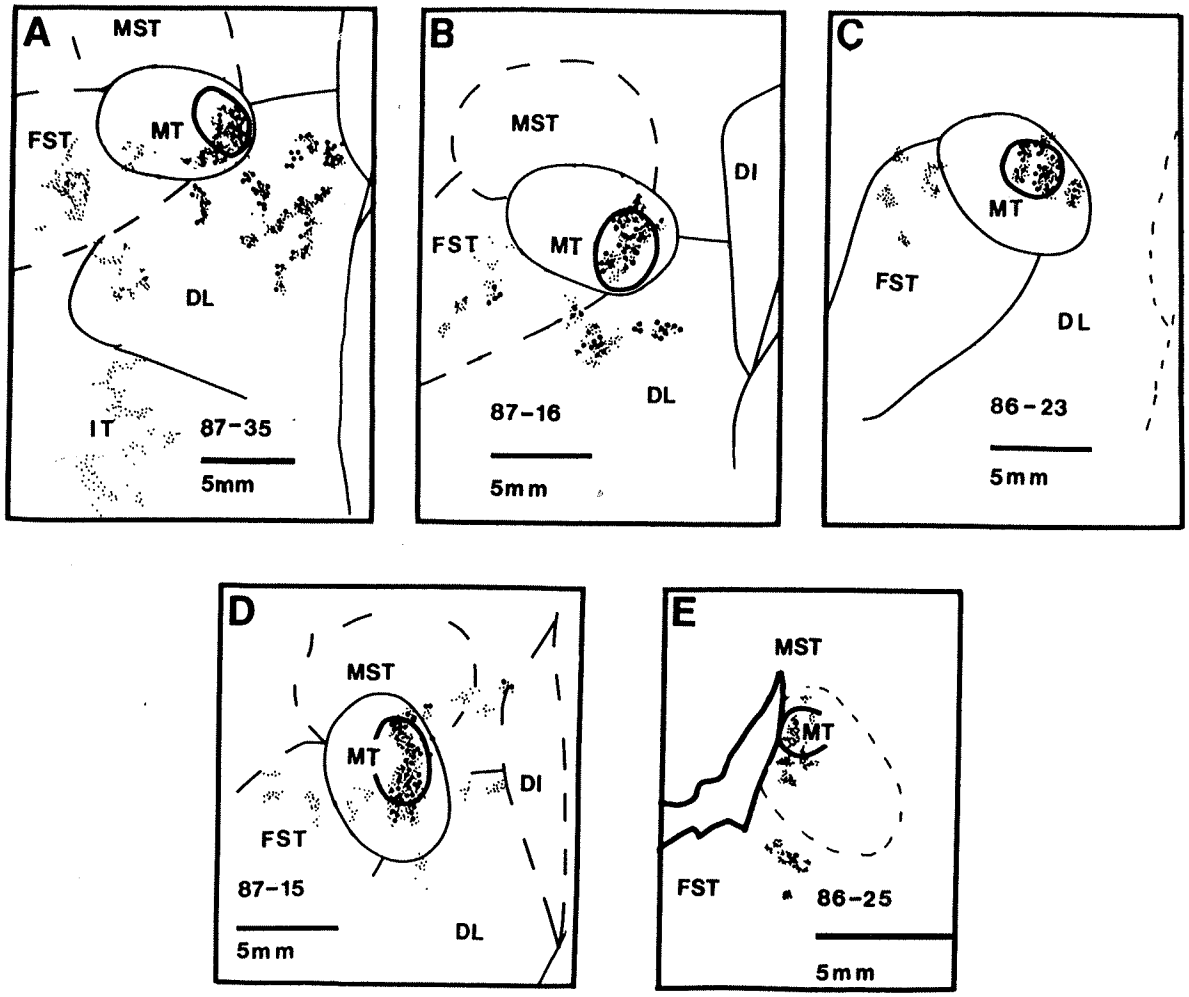

Fig. 25. Callosally transported label after injections in MT in the opposite hemisphere in squirrel monkeys 87-35 (A), 87-16 (B), 86-23 (C), 87-15 (D), and 86-25 (E). The locations of the injection in the corresponding part of the contralateral MT are outlined in thick black lines. Regardless of the part of MT injected, the resulting callosal label is largely in a corresponding part of MT and is not concentrated on the representation of the vertical meridian on the perimeter of MT. Sparser amounts of label were also in FST, DL (A, B, and D), IT (A), and just dorsal to DL (D). Conventions are as in previous figures.

gence of projections from a small region of area 17 to a restricted location in MT has been most clearly demonstrated with multiple tracers by Perkel et al. (1986). The present results indicate that this convergence can be from discontinuously distributed groups of neurons. Since both area 17 (Hubel & Wiesel, 1974; Hubel et al., 1978; Blasdel & Salama, 1986) and MT (Albright, 1984; Albright et al., 1984) have systematic spacings of orientation-selective neurons, separate rows of labeled neurons in area 17 could result from an injection largely within a specific orientation-selective group in MT, if the larger receptive fields of the MT neurons reflect inputs from several matched orientation-selective bands of neurons in area 17 (see Kaas, 1986; Krubitzer & Kaas, 1989*a*). In macaque monkeys, however, Shipp and Zeki (1989*a*) found patchy distributions of cells in area 17 projecting to MT rather than rows.

It is not clear if feedback to area 17 is to dendrites of neurons projecting to MT or separate neurons located more superficially. Since many of the area 17 neurons of layer IIIc of Hassler (1966) that project to MT have dendrites in superficial layers (Lund & Boothe, 1975), the feedback could include projection neurons. Feedback terminations may contribute to the complex pattern of orientation columns in area 17 described by Blasdel and Salama (1986) using voltage-sensitive dyes. Since voltage-sensitive dyes are effectively visualized only within 300 μm of the pial surface, they may demonstrate orientation-specific activation patterns related to both feedback patterns in superficial layers and intrinsic mechanisms, while the activation pattern in deeper layers could largely reflect intrinsic processing.

Area 18 (V-II)

Injections in MT revealed retinotopically matched interconnections with area 18 in all four primate species. Projecting cells originated in band-like strips across the width of area 18. In the three species of monkeys, where the CO-dense bands were obvious, the projecting cells were concentrated in every other band, and often these were clearly the thinner bands. Return projections were to every CO-dense band.

The observation that the neurons projecting to MT are lo-

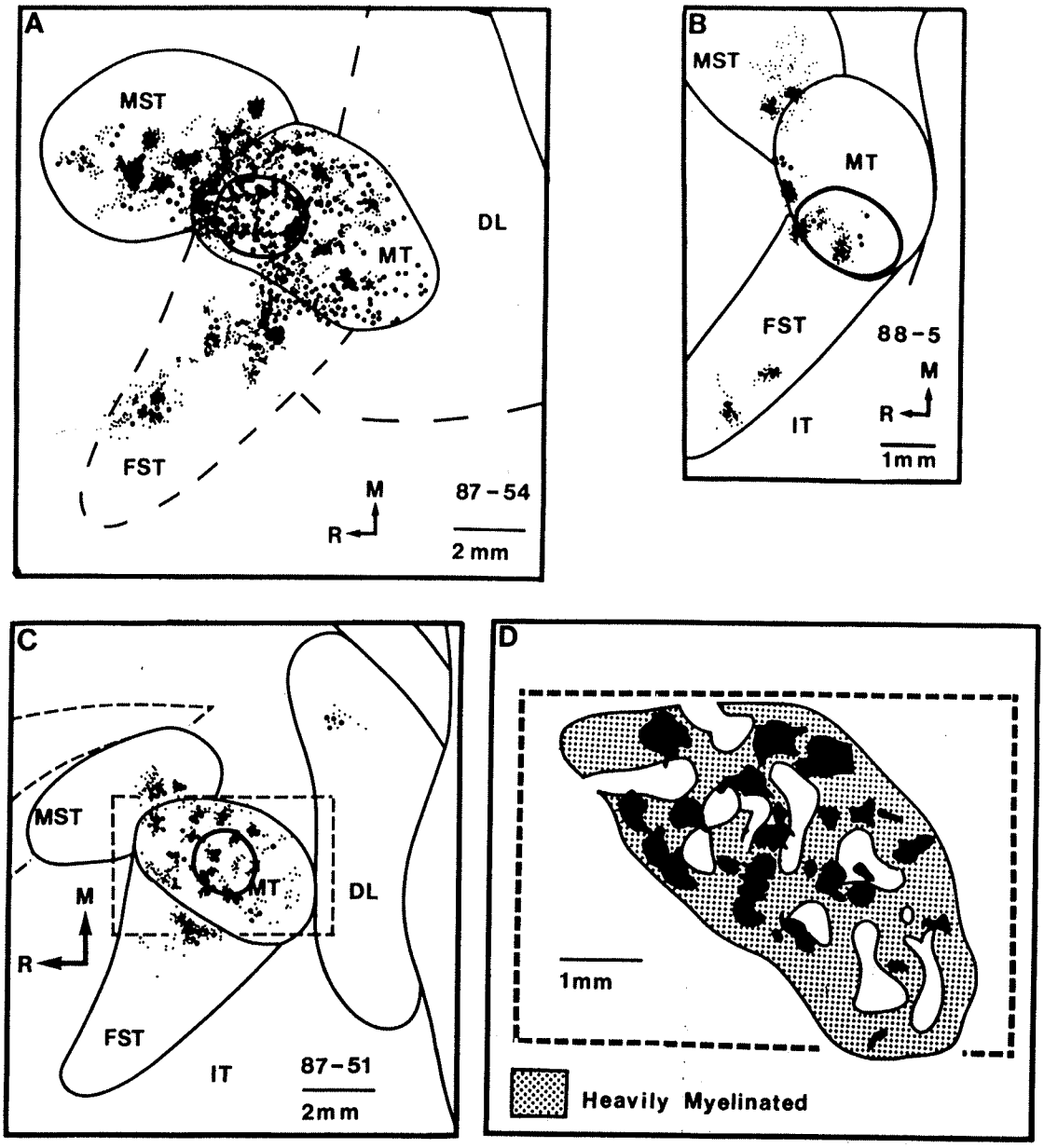

Fig. 26. Callosally transported label after injections in MT in the opposite hemisphere in owl monkey 87-54 (A), galago 88-5 (B), and marmoset 87-51 (C and D). The corresponding locations of injections in MT of the contralateral hemisphere are denoted by thick black lines. Dense label is in parts of MT matching the injection in MT in the opposite hemisphere. Label is also found in FST and ST. MT of marmoset 87-51 (C and D) had regions of heavy and less heavy mylelination and the label was in the regions of dense mylelination (D).

cated in CO-dense bands in New World monkeys corresponds with the findings of DeYoe and Van Essen (1985) and Shipp and Zeki (1985, 1989*b*) that one set of CO-dense bands, the thicker bands, projects to MT in macaque monkeys. However, in the New World monkeys, when differences in band thickness are apparent, the thinner bands appear to project to MT. We previously reported this result for squirrel monkeys (Krubitzer & Kaas, 1989*a*). Recently, Shipp & Zeki (1989*b*) noted that injections in MT of owl monkeys labeled CO-dense bands in area 18, but there were uncertainties about the thickness of the labeled bands and even if all or only alternate bands were labeled. Since the thicker bands in area 18 in both macaque and squirrel monkeys (Livingstone & Hubel, 1984, 1987, 1988) are thought to receive inputs from the magnocellular stream of area 17 and relay to MT, this apparent difference in results is puzzling. However, these investigators report that the functional role of thick and thin bands in area 18 are sometimes reversed (see Fig. 18 of Hubel & Livingstone, 1987). Furthermore, in some monkeys such as marmosets, bands are of equal thickness, and a difference in thickness of adjoining bands in area 18 is not always apparent in owl, squirrel, and macaque monkeys. The most salient feature across species is that sets of alternating bands have different connections.

Previously, connections of MT with area 18 have been demonstrated in macaque monkeys (e.g. Maunsell & Van Essen, 1983; Ungerleider & Desimone, 1986*a*), owl monkeys (Weller

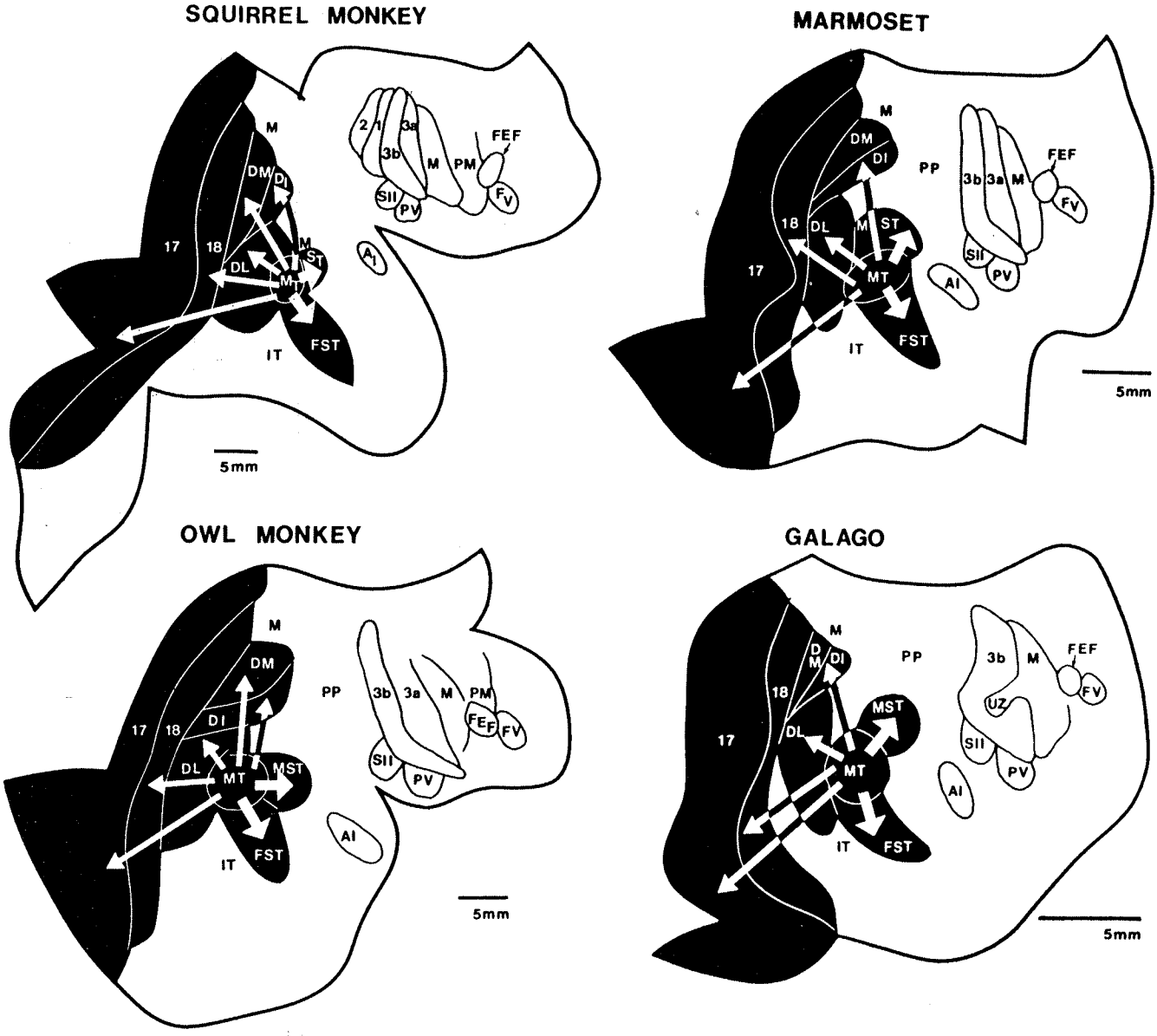

Fig. 27. Visual cortical areas (solid black) and the patterns of connections with MT (arrows) in the four species of primates investigated. M is the medial visual area (Allman & Kaas, 1976). Other abbreviations are as in Figs. 1 and 12.

et al., 1984), squirrel monkeys (Tigges et al., 1974; Cusick & Kaas, 1988*a*), and galagos (Wall et al., 1982). Although injections in MT or V-II were not systematically varied in these studies, the illustrated connection patterns demonstrate at least some degree of retinotopic matching. The retinotopic organization of V-II has been described physiologically in macaques (Gattass et al., 1981), *Cebus appella* (Rosa et al., 1988), and owl monkeys (Allman & Kaas, 1974*a*), and our results provide evidence for similar retinotopic organization of V-II in galagos, marmosets, and squirrel monkeys.

Connections with occipital fields DL, DM, and DI

Several fields immediately rostral to area 18 on the dorsal surface of the cortex have connections with MT. These fields include the dorsolateral, DL, the dorsointermediate, DI, and the dorsomedial, DM, visual areas. Evidence for these connections also exists in previous reports. However, a contribution of the present study is that we relate connections to areas defined architectonically rather than by position alone. Thus, in all species, we specifically relate connections of MT to areas DL, DM, and DI, rather than to general regions of the dorsal cortex. In addition, the flattened preparations show the patchy distribution of the connections accurately.

Connections between MT and cortex in the location of DL have been described for owl monkeys (Weller et al., 1984), squirrel monkeys (Tigges et al., 1981; Cusick & Kaas, 1988*a*), marmosets (Spatz & Tigges, 1972), and galagos (Wall et al., 1982). In Old World monkeys, the region of DL, termed V4 (Zeki, 1971*a*), also has connections with MT (Maunsell & Van Essen, 1983; Ungerleider & Desimone, 1986*a*). Connections between MT and cortex in the region of DM and DI have been reported for New World monkeys (Weller et al., 1984; Wagor et al.,

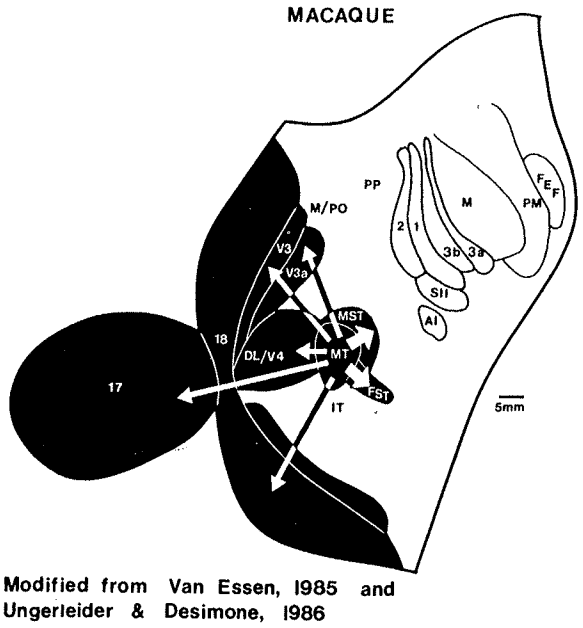

Fig. 28. Visual areas and connections of MT in macaque monkeys. V3 and V3a may correspond to DM and DI, while V4 appears to be DL. Relative positions, architectonic appearances, electrophysiological recordings for some areas, and connections with the middle temporal visual area all support the contention that there are at least eight visual areas common to all primates. The parieto-occipital area (PO) of macaques may correspond to the medial area (M) of owl monkeys.

1975; Spatz & Tigges, 1972), prosimians (Wall et al., 1982), and Old World macaques (Maunsell & Van Essen, 1983; Ungerleider & Desimone, 1986*a*; also see Fig. 28). In macaque monkeys, the region termed dorsal V3 appears to have connections with MT (Maunsell & Van Essen, 1983; Ungerleider & Desimone, 1986*a*). However, V3a (Zeki, 1980; Van Essen et al., 1986; Gattass et al., 1988) may be part of the region that projects to MT since there are uncertainities about extents and boundaries of these fields.

Temporal areas FST and MST

In the present investigation, MT has major projections to two adjoining cortical areas in the temporal lobe, the middle superior temporal area, MST, and the fundal superior temporal area, FST. These two fields were first defined by projections from MT in macaque monkeys by Maunsell and Van Essen (1983) and Ungerleider and Desimone (1986*a*), and we use these terms here (see Boussard et al., 1990 for review). Feedforward connections from MT to two locations in the superior temporal cortex have also been reported for owl monkeys (Weller et al., 1984) and to the general location of MST in New World marmosets (Spatz & Tigges, 1972) and prosimian galagos (Wall et al., 1982). Present results, together with those from previous investigations, indicate that MST and FST are characterized by strong feedforward projections from MT in a wide range of primate species.

Connections with the frontal lobe

An unexpected result of the present investigation is that MT does not project primarily to the frontal eye field of the frontal lobe as has been previously reported in a variety of primates (e.g. Spatz & Tigges, 1972; Maioli et al., 1983; Ungerleider & Desimone, 1986*a*). Rather, the major frontal target of MT is to an eye-movement field (see Kaas & Krubitzer, 1988 for a previous report) just ventral to the FEF, which we define as the frontal ventral area, FV (Huerta et al., 1987). Both the FEF and FV were identified in the present study using microstimulation procedures in which physiological boundaries of these fields were marked and related to myeloarchitecture.

In agreement with our results, Leichnetz (1989) reported that injections of HRP in the cortex just ventral to the FEF densely labeled cortex in the region of MT. However, we did note sparse and variable connections of MT with the FEF, and other investigators have described such connections as sparse (Ungerleider & Desimone, 1986*a*; Huerta et al., 1987). Recently, detailed physiological recordings in the region ventral to the FEF have shown that neurons in this region are responsive to smooth-pursuit eye movements rather than saccadic eye movements like the FEF (MacAvoy et al., 1988). In addition, the ventral eye-movement field has connections with the FEF (Huerta et al., 1987) and the supplementary eye field (Huerta & Kaas, 1990). The connections of MT and FV, and interconnections of FV with the FEF and the supplementary eye field, are compatible with the proposed role of MT in smooth-pursuit eye movements, suggested by behavioral impairments after MT lesions (Newsome et al., 1985; Dürsteler et al., 1987).

Interhemispheric connections

In the present investigation, interhemispheric connections were densest with the matched or homoregional (see Weller & Kaas, 1981) location in MT in the contralateral hemisphere, regardless of the eccentricity of the injected location in MT. Other connections were with FST and MST. In other investigations of MT connections, callosally transported tracer was found predominantly in MT in New World monkeys (Weller et al., 1984; Spatz & Tigges, 1972), Old World monkeys (Maunsell & Van Essen, 1983; Ungerleider & Desimone, 1986*a*), and prosimian galagos (Wall et al., 1982). Label was also noted in the location of MST in several studies (Spatz & Tigges, 1972; Weller et al., 1984; Maunsell & Van Essen, 1983). Previous studies of total patterns of interhemispheric connections have also demonstrated that all parts of MT have callosal connections, and that the connections are not restricted to the outer boundary of MT (Newsome & Allman, 1980; Van Essen et al., 1981, 1982; Cusick et al., 1984; Gould et al., 1987) which represents the zero vertical meridian (e.g. Allman & Kaas, 1971*a*). Because injections in different animals were distributed across the representation of the visual hemifield in MT in the present investigation, we were able to clearly demonstrate that the dominant interhemispheric connections are mirror symmetric.

In the present study, we provide anatomical evidence for modular organization in MT. The coincidence of callosal connections with myelin-dense regions in MT of marmosets is the only demonstration of an anatomical segregation related to an architectonic distinction in a visual area other than V-I and V-II. The function of this modular segregation of callosal connections in MT is unknown. Since both ipsilateral and contralateral inputs to MT are spaced in dense patches, it is possible that ipsilateral and callosal recipient zones in MT are segregated and related to differences in myelin density in MT.

DL connections

As part of our effort to reveal modular connections of area 18, different fluorescent tracers were injected in DL and MT

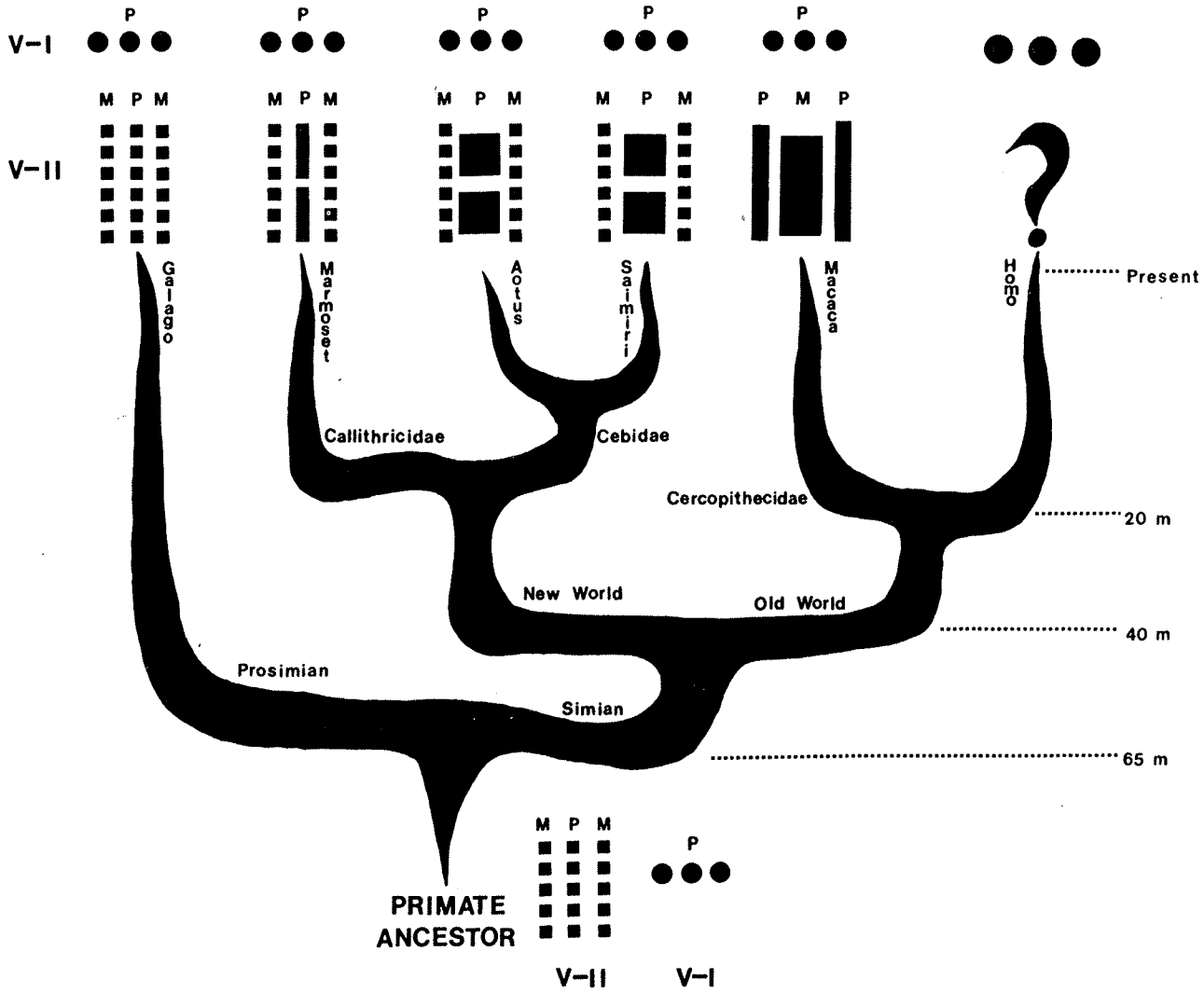

Fig. 29. The evolution of modules in areas 17 and 18 of primates (see text for discussion). Dots for V-I indicate CO blobs associated with the parvocellular (P) system. Although connections of modules are not known for humans, they do have CO blobs in area 17 (Horton & Hedley-Whyte, 1984). Bands of neurons in V-II associated with the parvocellular or magnocellular (M) systems may be of equal or different thicknesses. The bands are composed of group neurons (squares) that in some primates fuse to form bands (bars). We propose that the common ancestor of all primates possessed modules related to the magnocellular (M) and parvocellular (P) pathways in the visual system. Millions of years is denoted as "m."

of one owl monkey and one galago. Besides indicating the separateness of the band-like arrays of neurons in area 18 that project to DL or MT in these primates, the injections in DL also revealed dense connections with the inferior temporal cortex, as well as sparser connections with DM, DI, and MT.

The connections of DL have been more fully described for owl monkeys (Weller & Kaas, 1985) and squirrel monkeys (Cusick & Kaas, 1988*a*). The similarities of DL connections in galagos and New World monkeys with those described for V4 of macaque monkeys (see Desimone & Ungerleider, 1989 for review) provide part of the evidence that DL, which contains at least two subdivisions (Cusick & Kaas, 1988*a*), is an area common to all primates.

Variations in the density of connections of parts of MT representing central, paracentral, and peripheral vision

The caudolateral part of MT representing central vision has denser connections with DL, IT, and ITS in squirrel monkeys and marmosets. As injections were placed more rostromedially in MT, further from the representation of central vision, connections with these fields became sparse or no longer apparent. This variation was less obvious in owl monkeys and galagos. However, the rostromedial part of MT representing peripheral vision projected more densely to the posterior parietal cortex in galagos.

Differences in the connections of parts of MT representing central and peripheral vision have not been reported previously. However, there is evidence that parts of other visual areas differ in connections. For instance, only parts of area 17 devoted to central vision project densely to DL/V4 in a variety of primates (Cusick & Kaas, 1988*b*; Zeki, 1978*a*; Van Essen et al., 1986), while area V3a and the parieto-occipital area (PO) of macaque monkeys are thought to receive inputs predominantly from the parts of V-I and V-II representing peripheral vision (Zeki, 1980; Ungerleider, 1985; Colby et al., 1988). In addition, injections placed in parts of V4 representing central vision demonstrate

stronger connections with the inferotemporal cortex, while injections in dorsal portions of V4 representing more peripheral visual fields demonstrate denser connections with the posterior parietal cortex (Ungerleider et al., 1986). Thus, our results of differential connections of parts of MT representing central and peripheral vision are consistent with the notion that connections of a single cortical area may not be uniform throughout the field.

Results from such studies raise several issues about visual cortical organization. First, although one of the criteria of defining an area is by its unique set of connections, it is necessary to allow that different parts can have different connections. However, this clearly complicates the problem of subdividing the cortex. Thus, we stress the usefulness of multiple criteria in defining cortical fields (see Kaas, 1982). Second, these studies suggest that some of the variability in results often seen in studies of connections of cortical fields may be a consequence of different placement of injections within a field. Finally, the differential connections of central and peripheral field representations in MT indicate that MT is functionally heterogeneous with the central representation contributing more to the inferotemporal pathway for object recognition and the peripheral representation contributing more to the posterior parietal pathway for visual attention and tracking.

The evolution of cortical modules in V-I and V-II in primates

The present experiments provide evidence for the existence of similar modules in V-I and V–II of four species of primates. Cytochrome-oxidase blobs exist in area 17 of all these primates, and the sparseness of feedback projections from MT to these blobs implicates that they are related to the parvocellular rather than the magnocellular stream. Band-like distributions of neurons projecting to restricted locations in MT also suggest a modular component in area 17 of primates, perhaps one related to orientation-specific bands. Finally, all these primates have band-like arrangements of cells in area 18 that project to MT. This evidence, together with previously reported evidence that CO blobs are widespread in primates (e.g. Horton, 1984; Horton & Hedley-Whyte, 1984; Cusick & Kaas, 1988*a*; Condo & Casagrande, 1990; however, see McGuinness et al., 1986), and that thick, thin and pale bands exist in V-II of macaque monkeys, allow inferences to be made about the evolution of modular organization in V-I and V-II of primates (Fig. 29). Since all primates have magnocellular and parvocellular layers in the lateral geniculate nucleus (e.g. Kaas et al., 1978), the potential for the segregation of "M" and "P" streams exists in the cortex of all primates. Most primates, at least, also have CO blobs in area 17, which are assoicated with the "P" stream (e.g. Livingstone & Hubel, 1987; DeYoe & Van Essen, 1988). No non-primate mammal has been shown to have CO blobs or magnocellular and parvocellular geniculate layers, including tree shrews as the most available of the close relatives (*Archonta*) of primates. Thus, it is reasonable to assume that CO blobs, as modules in the P stream, arose early in primate or pre-primate evolution (hence their wide distribution), but after the divergence from *Archonta* (hence absence from tree shrews and other non-primates). The presence of bands of orientation-selective neurons in area 17 of tree shrews (Humphrey et al., 1980) suggests the even earlier evolution of such modules.

All higher primates appear to have CO-dense and CO-pale bands in V-II, and a hint of such segregation exists in prosimian primates. All primates also appear to have band-like arrays of neurons projecting to MT, and in simian primates these projection bands can be associated with every other CO-dense band (Fig. 29). Thus, one set of alternating CO-dense bands are part of the M stream. The alternate CO-dense bands project to DL (V4) as part of the P stream. In galagos, bands of neurons projecting to DL alternate with those projecting to MT. This suggests that the modular organization of M and P bands in V-II arose early in primate evolution, accounting for the wide distribution, but the conspicuous CO-dense bands that are associated with these modules probably evolved later, after the prosimian and simian divergence. That some modular segregation evolved even earlier in V-II is suggested by the banding pattern of projections of V-I to V-II projections in tree shrews (Sesma et al., 1984) and squirrels (Kaas et al., 1989), but we do not know if this banding relates to M and P streams. The connection patterns and CO patterns indicate that the shapes of P and M bands in V-II are variable in primates, with the bands being more like arrays of patches in some primates, and P and M bands vary in thickness. We propose that the P and M bands were equally thin early in simian evolution, and that bands related to P or M subsystems thickened later in evolution in different primates.

Another feature of visual connections common to all primates investigated in this study is the broad distribution of feedback connections from MT to V-I and V-II. In V-I, intricate patterns of meandering rows of neurons project to MT, while feedback is clearly more extensive and related to CO interblob regions of cortex. In V-II, feedforward connections to MT were from every other CO-rich band while feedback was to every CO-rich band. Thus, in both fields, feedback connections from MT are more broadly distributed, and at least in V-II, clearly relate to visual subsystems outside the M. Feedback may serve to modulate or provide cross talk between visual subsystems. Although "association" centers are generally thought to exist at higher stages of visual processing, we demonstrate here that associations between subsystems occur at elementary stages of processing in V-II and possibly in V-I. The broader distribution of feedback is likely to be a feature of all primates and possibly other mammals as well.

Summary and conclusions

The present study is unusual in several respects. First, the connections of visual area MT were studied in brain sections cut parallel to the surface of flattened cortex. Individual sections contained all or most of the neocortex of a single hemisphere, and for most cases, both the injected and the contralateral hemispheres were studied. These procedures allowed the total cortical projection pattern to be evaluated, and the densities of connections in different regions to be accurately appreciated. In addition, for any given region, the sections precisely revealed the patchy or modular nature of connection patterns. Second, the sections from the flattened cortex, when stained for myelin or reacted for cytochrome oxidase, allowed the total extent of a number of visual and other sensory areas to be sharply defined and measured. Furthermore, within area 18, the band-like modules that selectively project to MT could be identified in all simian species. Third, one of the potential targets of MT projections, the frontal eye field, was electrophysiologically identified and related to myeloarchitecture in some cases. This

allowed us to clearly distinguish projections to the FEF from those to the adjoining frontal ventral region. Fourth, the possibility that different parts of MT have different connection targets or densities of connections and that connections with other representations are visuotopic was investigated by systematically varying injection sites from caudolateral MT, representing central vision, to rostromedial MT, representing peripheral vision. Fifth, the same methods were applied to four species of primates, allowing the most accurate comparisons across species.

The results demonstrate that many features of visual cortex organization are highly similar across the investigated prosimian and simian primate species, and therefore are likely components of the visual system of all or most primates. We suggest that visual areas V-I, V-II, MT, MST, FST, DL, DM, and DI and visuomotor areas FEF and FV, all parts of an interconnected network, are basic components of the primate visual system. These fields constitute about the same proportion of neocortex in all four primates species, although areas in the object vision pathway tended to be somewhat larger in the diurnal primates. All of the fields have patchy or modular interconnections with MT and, in particular, separate band-like arrays of cells projecting to MT exist in V-II of all studied primates. Connections with at least V-I and V–II are visuotopic, and only the part of MT representing central vision relates significantly to areas in the object vision pathway in the inferotemporal cortex. Callosal connections tend to be roughly matched for location in MT, and therefore are visuotopically mismatched (except for the MT border), and most of the interhemispheric connections are with MT. Connections in the frontal lobe are ipsilateral and largely with FV rather than FEF. Results are consistent with those previously reported for MT connections in primates, but they also allow accurate statements about what areas and parts of areas interconnect with MT across species of primates.

Acknowledgments

We thank Chia-Cheng Lin, Anne Morel, Maureen Powers, and Jeff Schall for their helpful comments on this manuscript. Research was supported by NEI Grant EY-02686.

References

ALBRIGHT, T.D. (1984). Direction and orientation selectivity of neurons in visual area MT of the macaque. *Journal of Neurophysiology* **52**, 1106–1130.

ALBRIGHT, T.D. & DESIMONE, R. (1987). Local precision of visuotopic organization in the middle temporal visual area (MT) of the macaque. *Experimental Brain Research* **65**, 582–592.

ALBRIGHT, T.D., DESIMONE, R., & GROSS, C.G. (1984). Columnar organization of directionally selective cells in visual area MT of the macaque. *Journal of Neurophysiology* **51**, 16–31.

ALLMAN, J.M. & KAAS, J.H. (1971*a*). A representation of the visual field in the caudal third of the middle temporal gyrus of the owl monkeys (*Aotus trivirgatus*). *Brain Research* **31**, 85–105.

ALLMAN, J.M. & KAAS, J.H. (1971*b*). Representation of the visual field in striate and adjoining cortex of the owl monkey (*Aotus trivirgatus*). *Brain Research* **35** 89–106.

ALLMAN, J.M., KAAS, J.H. & LANE, R.H. (1973). The middle temporal visual area (MT) in the bushbaby (*Galago senegalensis*) *Brain Research* **57**, 197–202.

ALLMAN, J.M. & KAAS, J.H. (1974*a*). The organization of the second visual area (VII) in the owl monkey: a second transformation of the visual hemifield. *Brain Research* **76**, 247–265.

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

ALLMAN, J.M. & KAAS, J.H. (1975). The dorsomedial cortical visual area: a third tier area in the occipital lobe of the owl monkeys (*Aotus trivirgatus*). *Brain Research* **100**, 473–487.

ALLMAN, J.M. & KAAS, J.H. (1976). Representation of the visual field on the medial wall of occipital-parietal cortex in the owl monkey. *Science* **191**, 572–576.

ALLMAN, J.M., MIEZIN, F. & MCGUINNESS, E. (1985). Stimulus-specific responses from beyond the classical receptive field: neurophysiological mechanisms for local-global comparisons. *Annual Review of Neuroscience* **8**, 407–430.

ALLMAN, J.M., CAMPBELL, C.B.G. & MCGUINNESS, E. (1979). The dorsal third tier area in *Galago senegalensis*. *Brain Research* **179**, 355-361.

BEATTIE, J. (1927). The anatomy of the common marmoset (*Hapole jacchus Kuhl*). *Proceedings of the Zoological Society of London* **1927**, 593–718.

BLASDEL, G.G. & SALAMA, G. (1986). Voltage-sensitive dyes reveal a modular organization in monkey striate cortex. *Nature* **321**, 597–585.

BOUSSARD, D., UNGERLEIDER, L.G. & DESIMONE, R. (1990). Pathway for motion analysis: cortical connections of visual areas MST and FST in the macaque. *Journal of Comparative Neurology* **296**, 462–495.

BRODMANN, K. (1909). *Vergleichende Lokalisationslehre der Groshirnrinde*, Leipzig: Barth.

BURKHALTER, A., FELLEMAN, D.J., NEWSOME, W.T. & VAN ESSEN, D.C. (1986). Anatomical and physiological asymmetries related to visual area V3 and VP in macaque extrastriate cortex. *Vision Research* **26**, 63–80.

BURTON, H. & KOPF, E.M. (1984). Connections between the thalamus and somatosensory areas of the anterior extosylvian gyrus in the cat. *Journal of Comparative Neurology* **244**, 173–205.

COLBY, C.L., GATTASS, R., OLSON, C.R. & GROSS, C.G. (1988). Topographical organization of cortical afferents to extrastriate visual area PO in the macaque: a dual tracer study. *Journal of Comparative Neurology* **269**, 392–314.

CONDO, G.J. & CASAGRANDE, V.A. (1990). Organization of cytochrome-oxidase staining in the visual cortex of nocturnal primates (*Galago crassicaudatus* and *Galago senegalensis*, I: Adult patterns. *Journal of Comparative Neurology* **293**, 632–645.

COWEY, A. (1964). Projection of the retina on to striate and prestriate cortex in the squirrel monkey (*Saimiri sciureus*). *Journal of Neurophysiology* **27**, 366–396.

CRAGG, B.G. (1969). The topography of the afferent projections in the circumstriate visual cortex of the monkey studied by the Nauta method. *Vision Research* **9**, 733–747.

CUSICK, C.G., GOULD, H.J., III & KAAS, J.H. (1984). Interhemispheric connections of visual cortex of owl monkeys (*Aotus trivirgatus*), marmosets (*Callithrix jacchus*), and galagos (*Galago crassicaudatus*). *Journal Comparative Neurology* **230**, 311–336.

CUSICK, C.G. & KAAS, J.H. (1988*a*). Cortical connections of area 18 and dorsolateral visual cortex in squirrel monkeys. *Visual Neuroscience* **1**, 211–237.

CUSICK, C.G. & KAAS, J.H. (1988*b*). Surface-view patterns of intrinsic and extrinsic cortical connections of area 17 in a prosimian primate. *Brain Research* **458**, 383–388.

DESIMONE, R. & UNGERLEIDER, L.G. (1986). Multiple visual areas in the caudal superior temporal sulcus of the macaque. *Journal of Comparative Neurology* **248**, 164–189.

DESIMONE, R. & UNGERLEIDER, L.G. (1989). Neural mechanisms of visual processing in monkeys. In *Handbook of Neuropsychology, Vol. 2*, ed. BOLLER, F. & GRAFMAN, J., pp. 267–299. Amsterdam: Elsevier Press.

DEYOE, E.A. & VAN ESSEN, D.C. (1985). Segregation of efferent connections and receptive-field properties in visual area V2 of the macaque. *Nature* **317**, 58–61.

DEYOE, E.A. & VAN ESSEN, D.C. (1988). Concurrent processing streams in monkey visual cortex. *Trends in Neuroscience* **11**, 219–226.

DÜRSTELER, M.R., WURTZ, R.H. & NEWSOME, W.T. (1987). Directional-pursuit deficits following lesions of the foveal representation within the superior temporal sulcus of the macaque monkey. *Journal of Neurophysiology* **57**, 1262–1287.

ERICKSON, R.G., DOW, B.M. & SNYDER, A.E. (1989). Representation of the fovea in the superior temporal sulcus of the macaque monkey. *Journal of Exploratory Brain Research* **78**, 90–112.

FELLEMAN, D.J. & KAAS, J.H. (1984). Receptive field properties of neurons in the middle temporal visual area (MT) of owl monkeys. *Journal of Neurophysiology* **52**, 488–513.

FELLEMAN, D.J. & VAN ESSEN, D.J. (1983). V4 of macaque monkey extrastriate cortex. *Society for Neuroscience Abstracts* **9**, 153.

FIORANI, M., FATTASS, R., ROSA, M.G.P. & SOUSA, A.P.B. (1989). Visual area MT in the *Cebus* monkey: Location, visuotopic organization, and variability. *Journal of Comparative Neurology* **287**, 98–118.

FRAHM, H.D., STEPHAN, H. & BARON, G. (1984). Comparison of brain structure volumes in insectivora and primates, V: Area striata (AS). *Journal Hinforsch* **25**, 537–557.

FRIEDMAN, D.P. & MURRAY, E.A. (1986). Thalamic connectivity of the second somatosensory area and neighboring somatosensory fields of the lateral sulcus of the macaque. *Journal of Comparative Neurology* **252**, 348–373.

GALLYAS, F. (1979). Silver staining of myelin by means of physical development. *Neurology Research* **1**, 203–209.

GATTASS, R. & GROSS, C.G. (1981). Visual topography of striate projections zone (MT) in posterior superior temporal sulcus of the macaque. *Journal of Neurophysiology* **46**, 621–638.

GATTASS, R., GROSS, C.G. & SANDELL, J.H. (1981). Visual topography of V2 in the macaque. *Journal of Comparative Neurology* **201**, 519–539.

GATTASS, R., SOUSA, A.P. & GROSS, C.G. (1988). Visuotopic organization and extent of V3 and V4 of the macaque. *Journal of Neuroscience* **8**, 1831–1845.

GIBSON, A.R., HANSMA, J.C., HOUK, J.C. & ROBINSON, F.R. (1984). A sensitive low artifact TMB procedure for the demonstration of WGA-HRP in the CNS. *Brain Research* **298**, 235–241.

GOULD, H.U., WEBER, J.T. & RIECK, R.W. (1987). Interhemispheric connections in the visual cortex of the squirrel monkey (*Saimiri sciureus*). *Journal of Comparative Neurology* **256**, 14–28.

HASSLER, R. (1966). Comparative anatomy of the central visual systems in day- and night-active primates. *In Evolution of the Forebrain*, eds. HASSLER, R. & STEPHAN, H., pp. 419–434. Stuttgart, West Germany: Thiem Verlay.

HERSHKOVITZ, P. (1977). *Living New World Monkeys (Platyrrhini), Vol. 1*, Chicago, Illinois: University of Chicago Press.

HORTON, J.C. (1984). Cytochrome-oxidase patches. A new cytoarchitectonic feature of monkey visual cortex. *Philosophical Transactions of the Royal Society B* (London) **304**, 199–253.

HORTON, J.C. & HEDLEY-WHYTE, E.T. (1984). Mapping of cytochrome-oxidase patches and ocular-dominance columns in neurons in human visual cortex. *Philosophical Transactions of the Royal Society B* (London) **304**, 255–272.

HUBEL, D.H. & LIVINGSTONE, M.S. (1987). Segregation of form, color, and stereopsis in primate area 18. *Journal of Neuroscience* **7**, 3378–3415.

HUBEL, D.H. & WIESEL, T.N. (1974). Sequence regularity and geometry of orientation columns in the monkey striate cortex. *Journal of Comparative Neurology* **158**, 267–294.

HUBEL, D.H., WIESEL, T.N. & STRYKER, M.P. (1978). Anatomical demonstration of orientation of columns in macaque monkey. *Journal of Comparative Neurology* **177**, 361–380.

HUERTA, M.F., KRUBITZER, L.A. & KAAS, J.H. (1987). Frontal eye field as defined by intracortical microstimulation in squirrel monkeys, owl monkeys, and macaque monkeys, II: Cortical connections. *Journal of Comparative Neurology* **265**, 332–361.

HUERTA, M.F. & KAAS, J.H. (1990). Supplementary eye field as defined by intracortical microstimulation: connections in macaques. *Journal of Comparative Neurology* **293**, 299-330.

HUMPHREY, A.L., SKEEN, L.C. & NORTON, T.T. (1980). Topographic organization of the orientation-column system in the striate cortex of the tree shrew (*Tupaia glis*), II: Deoxyglucose mapping. *Journal of Comparative Neurology* **192**, 544–566.

KAAS, J.H. (1982). The segregation of function in the nervous system. *Contributions to Sensory Physiology* **7**, 201–240.

KAAS, J.H. (1986). The structural basis for information processing in the primate visual system. In *Visual Neuroscience*, ed. PETTIGREW, J.P., SANDERSON, K.J. & LEVICK. W.R., pp. 315–340. Cambridge: Cambridge University Press.

KAAS, J.H.(1988). Why does the brain have so many visual areas? *Journal of Cognitive Neuroscience* **1**, 121–135.

KAAS, J.H. & KRUBITZER, L.A. (1988). Subdivisions of visuomotor and visual cortex in the frontal lobe of primates: the frontal eye field and the target of the middle temporal visual area. *Society for Neuroscience Abstracts* **14**, 820.

KAAS, J.H. & KRUBITZER, L.A. (1990). The organization of visual cortex in Old World monkeys: studies on the miniature species (*Miopithecus talapoin*). *Investigative Ophthalmology and Visual Science* (Suppl.) **31**, 398.

KAAS, J.H. & LIN, C.H. (1977). Cortical projections in area 18 in owl monkeys. *Vision Research* **17**, 739–741.

KAAS, J.H., HUERTA, M.F., WEBER, J.T. & HARTING, J.K. (1978). Patterns of retinal terminations and laminar organization of the lateral geniculate nucleus of primates. *Journal of Comparative Neurology* **182**, 517–554.

KAAS, J.H., KRUBITZER, L.A. & JOHANSON, K.L. (1989). Cortical connections of areas 17 (V-I) and 18 (V-II) of squirrels. *Journal of Comparative Neurology* **281**, 426–446.

KRUBITZER, L.A. & KAAS, J.H. (1986). The second somatosensory area in primates: somatotopic organization, architecture, and connections in marmosets (*Callithrix jacchus*). *Society for Neuroscience Abstracts* **12**, 798.

KRUBITZER, L.A. & KAAS, J.H. (1987*a*). Connections of modular subdivisions of cortical visual areas 17 and 18 with the middle temporal area, MT, in squirrel monkeys. *Society for Neuroscience Abstracts* **13**, 3.

KRUBITZER, L.A. & KAAS, J.H. (1987*b*). Thalamic connections of three representation of the body surface in somatosensory cortex of gray squirrels. *Journal of Comparative Neurology* **265**, 549–580.

KRUBITZER, L.A. & KAAS, J.H. (1988*a*). Cortical connections of MT and DL in the prosimian galago: evidence that modular segregation of parallel pathways is a primitive feature in primates. *Society for Neuroscience Abstracts* **14**, 602.

KRUBITZER, L.A. & KAAS, J.H. (1988*b*). Responsiveness and somatotopic organization of anterior parietal field 3b and adjoining cortex in newborn and infant monkeys. *Somatosensory and Motor Research* **6**, 176–205.

KRUBITZER, L.A. & KAAS, J.H. (1989*a*). Cortical integration of parallel pathways in the visual system of primates. *Brain Research* **478**, 161–165.

KRUBITZER, L.A. & KAAS, J.H. (1989*b*). Modular connections of extrastriate visual area DM with areas 17, 18, and MT in monkeys. *Society for Neuroscience Abstracts* **15**, 1108.

KRUBITZER, L.A. & KAAS, J.H. (1990). The organization and connections of somatosensory cortex in marmosets. *Journal of Neuroscience* **10**, 952–974.

KUYPERS, H.G.J.M., SZWARCBART, M.K., MISHKIN, M. & ROSVOLD, H.E. (1965). Occipitotemporal cortico-cortical connections in the rhesus monkey. *Experimental Neurology* **11**, 245–262.

LEICHNITZ, G.R. (1989). Inferior frontal eye-field projections to the pursuit-related dorsolateral pontine neucleus and middle temporal area (MT) in the monkey. *Visual Neuroscience* **3**, 171–180.

LIN, C.S., WELLER, R.E. & KAAS, J.H. (1982). Cortical connections of striate cortex in the owl monkey. *Journal of Comparative Neurology* **211**, 165–176.

LIVINGSTONE, M. & HUBEL, D. (1984). Anatomy and physiology of a color system in the primate visual cortex. *Journal of Neuroscience* **4**, 309–356.

LIVINGSTONE, M. & HUBEL, D. (1987). Connections between layer 4B of area 17 and the thick cytochrome-oxidase stripes of area 18 in the squirrel monkey. *Journal of Neuroscience* **7**, 3371–3377.

LIVINGSTONE, M. & HUBEL, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science* **240**, 740–749.

LOGOTHETIS, N.K. & SCHALL, J.D. (1989). Neuronal correlates of subjective visual perception. *Science* **245**, 761–763.

LOWELL, S., FREEMAN, B. & SINGER, W. (1987). Topographic organization of the orientation-column system in large flat-mounts of the cat visual cortex. A 2-deoxyglucose study. *Journal of Comparative Neurology* **255**, 401–415.

LUETHKE, L.E., KRUBITZER, L.A. & KAAS, J.H. (1989). Connections of the primary auditory cortex in the New World monkey (*saguinus*). *Journal of Comparative Neurology* **285**, 487–513.

LUND, J.S. & BOOTHE, R.G. (1975). Interlaminar connections and pyrmidal neuron organization in the visual cortex, area 17, of the macaque monkey. *Journal of Comparative Neurology* **159**, 305–334.

MACAVOY, M.C., BRUCE, C.J. & GOTTLIEB, J. (1988). Smooth-pursuit

eye movements elicited by microstimulation in the frontal eye fields region of alert macaque monkeys. *Society for Neuroscience Abstracts* **14**, 956.

MAGUIRE, W.M. & BAIZER, J.S. (1984). Visuotopic organization of the prelunate gyrus in rhesus monkey. *Journal of Neuroscience* **4**, 1690–1704.

MAIOLI, M.G., SQUATRITO, S., GALLETTI, C., BATTAGLINI, P.P. & SANSEVERINO, E.R. (1983). Cortico-cortical connections from the visual region of the superior temporal sulcus to frontal eye field in the macaque. *Brain Research* **265**, 294–299.

MARTINEZ-MILLÁN, L. & HOLLÄNDER, H. (1975). Cortico-cortical projections from striate cortex of the squirrel monkey (*Saimiri sciureus*). A radioautographic study. *Brain Research* **83**, 405–417.

MAUNSELL, J.H.R. & NEWSOME, W.T. (1987). Visual processing in monkey extrastriate cortex. *Annual Review of Neuroscience* **10**, 363–401.

MAUNSELL, J.H.R. & VAN ESSEN, D.C. (1983). The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey. *Journal of Neuroscience* **3**, 2563–2586.

MAUNSELL, J.H.R. & VAN ESSEN, D.C. (1987). Topographic organization of the middle temporal visual area in the macaque monkey: representational biases and the relationship to callosal connections and myeloarchitectonic boundaries. *Journal of Comparative Neurology* **266**, 535–555.

MCGUINNESS, E., MCDONALD, C., SERENO, M. & ALLMAN, J. (1986). Primates without blobs: the distribution of cytochrome-oxidase activity in striate cortex in *tarsius*, hapalemur, *cheirogaleus*. *Society for Neuroscience Abstracts* **12**, 130.

MESULAM, M.M. (1978). Tetramethylbenzidine for horseradish peroxidase neurohistochemistry: a non-carcinogenic blue reaction product with superior sensitivity for visualizing neural afferents and efferents. *Journal of Histochemistry and Cytochemistry* **26**, 106–117.

MIKAMI, A., NEWSOME, W.T. & WURTZ, R.H. (1986*a*). Motion selectivity in macaque visual cortex, I: Mechanisms of direction and speed selectivity in extrastriate area MT. *Journal of Neurophysiology* **55**, 1308–1327.

MIKAMI, A., NEWSOME, W.T. & WURTZ, R.H. (1986*b*). Motion selectivity in macaque visual cortex, II: Spatiotemporal range of directional interactions in MT and V1. *Journal of Neurophysiology* **55**, 1328–1339.

MISHKIN, M., UNGERLEIDER, L.G. & MACKO, K.A. (1983). Object vision and spatial vision: two cortical pathways. *Trends in Neuroscience* **6**, 414–417.

MONTERO, V.M. (1980). Patterns of connections from the striate cortex to cortical visual areas in superior temporal sulcus of macaque and middle temporal gyrus of owl monkey. *Journal of Comparative Neurology* **189**, 45–59.

NEWSOME, W.T. & ALLMAN, J.M. (1980). Interhemispheric connections of visual cortex in the owl monkey. *Aotus trivirgatus*, and the bushbaby, *Galago senegalensis*. *Journal of Comparative Neurology* **194**, 209–233.

NEWSOME, W.T. & PARE, E.B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *Journal of Neuroscience* **8**, 2201–2211.

NEWSOME, W.T., WURTZ, R.H., DÜRSTELER, M.R. & MIKAMI, A. (1985). Deficits in visual-motion processing following ibotenic acid lesions of the middle temporal visual area of the macaque monkey. *Journal of Neuroscience* **5**, 825–840.

NEWSOME, W.T., WURTZ, R.H. & KOMATSU, H. (1988). Relation of cortical areas MT and MST to pursuit eye movements, II: Differentiation of retinal from extraretinal inputs. *Journal of Neurophysiology* **60**, 604–620.

OLAVARRIA, J. & VAN SLUYTERS, R.C. (1985). Unfolding and flattening the cortex of gyrencephalic brains. *Journal of Neuroscience Methods* **15**, 191–202.

PANDYA, D.N. & SELTZER, B. (1982). Association areas of the cerebral cortex. *Trends in Neuroscience* **5**, 386–390.

PERKEL, D.J., BULLIER, J. & KENNEDY, H. (1986). Topography of the afferent connectivity of area 17 in the macaque monkey: a double-labelling study. *Journal of Comparative Neurology* **253**, 374–402.

ROCKLAND, K.S. & PANDYA, D.N. (1979). Laminar orgins and terminations of cortical connections of the occipital lobe in the rhesus monkey. *Brain Research* **179**, 3–20.

ROCKLAND, K.S. & PANDYA, D.N. (1981). Cortical connections of the occipital lobe in the rhesus monkey: interconnections between areas 17, 18, 19, and the superior temporal sulcus. *Brain Research* **212**, 249–270.

ROSA, M.G.P., SOUSA, A.P.B. & GATTASS, R. (1988). Representation of the visual field in the second visual area in the cebus monkey. *Journal of Comparative Neurology* **275**, 326–345.

SERENO, M.I., MCDONALD, C.T. & ALLMAN, J.M. (1986). Organization of extrastriate cortex in the owl monkey. *Society for Neuroscience Abstracts* **12**, 1181.

SESMA, M.A., CASAGRANDE, V.A. & KAAS, J.H. (1984). Cortical connections of area 17 in tree shrews. *Journal of Comparative Neurology* **230**, 337–351.

SHIPP, S. & ZEKI, S. (1985). Segregation of pathways leading from area V2 to areas V4 and V5 of macaque monkey visual cortex. *Nature* **315**, 322–324.

SHIPP, S. & ZEKI, S. (1989*a*). The organization of connections between areas VI and V5 of macaque monkey visual cortex. *European Journal of Neuroscience* **1**, 309–322.

SHIPP, S. & ZEKI, S. (1989*b*). The organization of connections between areas V2 and V5 of macaque monkey visual cortex. *European Journal of Neuroscience* **1**, 333–354.

SIEGEL, R.M. & ANDERSON, R.A. (1986). Motion perceptual deficits following ibotenic acid lesions of the middle temporal visual area (MT) in the behaving rhesus monkey. *Society for Neuroscience Abstracts* **12**, 1183.

SPATZ, W.B. (1975). An efferent connection of the solitary cells of Meynert. A study with horseradish peroxidase in the marmoset *Callithrix*. *Brain Research* **92**, 450–455.

SPATZ, W.B. (1977). Topographically organized reciprocal connections between areas 17 and MT (visual area of the superior temporal sulcus) in the marmoset (*Callithrix jacchus*). *Experimental Brain Research* **27**, 559–572.

SPATZ, W.B. & TIGGES, J. (1972). Experimental-anatomical studies on the "middle temporal visual area (MT)" in primates. *Journal of Comparative Neurology* **146**, 451–464.

SPATZ, W.B., TIGGES, J. & TIGGES, M. (1970). Subcortical projections, cortical associations, and some intrinsic interlaminar connections of the striate cortex in the squirrel monkey (*Saimiri*). *Journal of Comparative Neurology* **140**, 155–174.

STEPHAN, H., BARON, G. & FRAHM, H.D. (1988). Comparative size of brains and brain components. *Comparative Primate Biology* **4**, 1–38.

SYMONDS, L.L. & KAAS, J.H. (Connections of striate cortex in the prosimian (*Galago senegalensis*). *Journal of Comparative Neurology* **181**, 477–512.

TIGGES, J., SPATZ, W.B. & TIGGES, M. (1974). Efferent cortico-cortical fiber connections of area 18 in the squirrel monkey (*Saimiri*). *Journal of Comparative Neurology* **158**, 219–136.

TIGGES, J., TIGGES, M., ANSCHEL, S., CROSS, N.A., LETBETTER, W.D. & MCBRIDE, R.L. (1981). Areal and laminar distribution of neurons interconnecting the central visual cortical areas 17, 18, 19, and MT in squirrel monkey (*Saimiri*). *Journal of Comparative Neurology* **202**, 539–560.

TOOTELL, R.B.H., HAMILTON, S.L. & SILVERMAN, M.S. (1985). Topography of cytochrome-oxidase activity in owl monkey cortex. *Journal of Neuroscience* **5**, 2786–2800.

TOOTELL, R.B.H. & SILVERMAN, M.S. (1985). Two methods for flat mounting cortical tissue. *Journal of Neuroscience Methods* **15**, 177–190.

TOOTELL, R.B.H., SILVERMAN, M.S., DE VALOIS, R.L. & JACOBS, G.H. (1983). Functional organization of the second cortical visual area in primates. *Science* **220**, 737–739.

TOOTELL, R.B.H. & HAMILTON S.L. (1989). Functional anatomy of the second visual area (V2) in the macaque. *Journal of Neuroscience* **9**, 2620–2644.

UNGERLEIDER, L.G. (1985). The corticocortical pathways for object recognition and spatial perception. In *Pattern Recognition Mechanisms*, ed. CHAGAS, C., GATTASS, R. & GROSS, C., pp. 21–37. Vatican City: Pontifical Academy of Sciences.

UNGERLEIDER, L.G. & MISHKIN, M. (1979). The striate projection zone in the superior temporal sulcus of *Macaca mulatta:* location and topographic organization. *Journal of Comparative Neurology* **188**, 347–366.

UNGERLEIDER, L.G. & MISHKIN, M. (1982). Two cortical visual systems. In *Analysis of Visual Behavior*, ed. INGLE, J.D., GOODALE, M.A. &

MANSFIELD, R.J.W., pp. 549–586. Cambridge, Massachusetts: MIT Press.

UNGERLEIDER, L.G. & DESIMONE (1986*a*). Cortical connections of visual area MT in the macaque. *Journal of Comparative Neurology* **348**, 190-222.

UNGERLEIDER, L.G. & DESIMONE (1986*b*). Projections to the superior temporal sulcus from the central and peripheral field representations of V1 and V1. *Journal of Comparative Neurology* **248**, 147–163.

UNGERLEIDER, L.G., DESIMONE, R. & MORAN, J. (1986). Asymmetry of central and peripheral field inputs from area V4 into the temporal and parietal lobes of the macaque. *Society for Neuroscience Abstracts* **12**, 1182.

VAN ESSEN, D.C. (1980). Functional organization of primate visual cortex. In *Cerebral Cortex, Vol. 3*, ed. PETERS, A. & JONES, E.G., pp. 259–329. New York: Plenum Press.

VAN ESSEN, D.C. (1985). Visual areas of the mammalian cerebral cortex. *Annual Review of Neuroscience* **2**, 227–263.

VAN ESSEN, D.C. & ZEKI, S.M. (1978). The topographic organization of rhesus monkey prestriate cortex. *Journal of Physiology* **277**, 193–226.

VAN ESSEN, D.C., MAUNSELL, J.H.R. & BIXBY, J.L. (1981). The middle temporal visual area in the macaque: myeloarchitecture, connections, functional properties, and topographic organization. *Journal of Comparative Neurology* **199**, 293–326.

VAN ESSEN, D.C., NEWSOME, W.T. & BIXBY, J.L. (1982). The pattern of interhemispheric connections and its relationship to extrastriate visual areas in the macaque monkey. *Journal of Neuroscience* **2**, 265–283.

VAN ESSEN, D.C. & MAUNSELL, J.H.R. (1983). Hierarchical organization and functional streams in the visual cortex. *Trends in Neuroscience* **6**, 370–375.

VAN ESSEN, D.C., NEWSOME, W.T. & MAUNSELL, J.H.R. (1984). The visual-field representation in striate cortex of the macaque monkey: asymmetries, anisotropies, and individual variability. *Vision Research* **24**, 529–448.

VAN ESSEN, D.C., NEWSOME, W.T., MAUNSELL J.H.R. & BIXBY, J.L. (1986). The projections from striate cortex (V1) to areas V2 and V3 in the macaque monkey: asymmetries, areal boundaries, and patchy connections. *Journal of Comparative Neurology* **244**, 451–480.

WAGOR, E., LIN, C.S. & KAAS, J.H. (1975). Some cortical projections of the dorsomedial visual area (DM) of association cortex in the owl monkey (*Aotus trivirgatus*). *Journal of Comparative Neurology* **163**, 227–250.

WALL, J.T., SYMONDS, L.L. & KAAS, J.H. (1982). Cortical and subcortical projections of the middle temporal area (MT) and adjacent cortex in galagos. *Journal of Comparative Neurology* **211**, 193–214.

WELLER, R.E. & KAAS, J.H. (1981). Cortical and subcortical connections of visual cortex in primates. In *Cortical Sensory Organization, Vol. 2*, ed. WOOLSEY, C.N., pp. 121–155. Clifton, NJ: The Humana Press.

WELLER, R.E. & KAAS, J.H. (1982). The organization of the visual system in galago: comparisons with monkeys. In *The Lesser Bush Baby (Galago) as an Animal Model: Selected Topics*. ed. HAINES, P.E., pp. 107–135. Boca Raton, Florida: CAC Press.

WELLER, R.E. & KAAS, J.H. (1983). Retinotopic patterns of connections of 17 with visual areas V-II and MT in macaque monkeys. *Journal of Comparative Neurology* **220**, 253–279.

WELLER, R.E., WALL, J.T. & KAAS, J.H. (1984). Cortical connections of the middle temporal visual area (MT) and the superior temporal cortex in owl monkeys. *Journal of Comparative Neurology* **228**, 81–104.

WELLER, R.E. & KAAS, J.H. (1985). Cortical projections of the dorsolateral visual area in owl monkeys: the prestriate relay to inferior temporal cortex. *Journal of Comparative Neurology* **234**, 35–59.

WELLER, R.E. & KAAS, J.H. (1987). Subdivisions and connections of inferior temporal cortex in owl monkeys. *Journal of Comparative Neurology* **256**, 137–172.

WHITE, P.F., WAY, W.L. & TREVOR, A.J. (1982). Ketamine—its pharmacology and therapeutic uses. *Anesthesiology* **56**, 119–136.

WONG-RILEY, M. (1979*a*). Changes in the visual system of monocularly sutured or enucleated cats demonstrable with cytochrome-oxidase histochemistry. *Brain Research* **171**, 11–28.

WONG-RILEY, M. (1979*b*). Columnar cortico-cortical interconnections within the visual system of the squirrel and macaque monkey. *Brain Research* **162**, 210–217.

WONG-RILEY, M. & CARROLL, E.W. (1984). Quantitative light- and electron-microscopic analysis of cytochrome-oxidase rich zones in V-II prestriate cortex of the squirrel monkey. *Journal of Comparative Neurology* **222**, 18–37.

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

ZEKI, S.M. (1971). Cortical projections from two prestriate areas in the monkey. *Brain Research* **34**, 19–35.

ZEKI, S.M. (1978*a*). The cortical projections of foveal striate cortex in the rhesus monkey. *Journal of Physiology* (London) **277**, 227–244.

ZEKI, S.M. (1978*b*). The third visual complex of rhesus monkey prestriate cortex. *Journal of Physiology* **177**, 245–272.

ZEKI, S.M. (1980). A direct projection from area V1 to area V3a of rhesus monkey visual cortex. *Proceedings of the Royal Society* (London) **207**, 499–506.