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The Dorsomedial Visual Area of Owl Monkeys: Connections, Myeloarchitecture, and Homologies in Other Primates

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ABSTRACT

Cortical connections of the dorsomedial visual area (DM) of owl monkeys were revealed with injections of the bidirectional tracer, wheatgerm agglutinin conjugated with horseradish peroxidase (WGA-HRP), or the retrograde fluorescent tracer, diamidino yellow. Microelectrode recordings in two cases identified DM as a systematic representation of the visual hemifield in a densely myelinated rectangle of cortex just rostral to the dorsomedial portion of the second visual area (V-II, or area 18). Cortex was flattened and cut parallel to the surface in all cases so that the myeloarchitectonic borders of DM and other areas such as the primary visual area (V-I or area 17), V-II or area 18, and the middle temporal visual area (MT) could be readily determined, and the surface view patterns of connections could be directly appreciated. The ipsilateral pattern of connections of DM were dense and visuotopically congruent with area 17, area 18, and MT, and moderate to dense connections were with the medial visual area (M), the rostral division of the dorsolateral visual area, the dorsointermediate area, the ventral posterior area, the caudal division of inferotemporal cortex (ITc), the ventral posterior parietal area, and visuomotor cortex of the frontal lobe. The connections of DM were concentrated in the cytochrome oxidase (CO)-dense blobs of area 17, the CO-dense bands of area 18, and the CO-dense regions of MT. Callosal connections of DM were with matched locations in DM in the opposite hemisphere, and with VPP.

The ipsilateral connections of DM with area 17 were confirmed by injecting WGA-HRP into area 17 in one owl monkey. In addition to labelled cells and terminals in area 18 and MT, bidirectionally transported tracer was also apparent in DM. Evidence for the existence of DM in other primates was obtained by injecting area 17 and examining the areal patterns of connections and myeloarchitecture in three species of Old World monkeys, two additional species of New World monkeys, and prosimian galagos. In all of these primates, one of three major targets of area 17 was a densely myelinated zone of cortex just rostral to dorsomedial area 18, in the location of DM in owl monkeys. Thus, it seems likely that DM is a visual area common to all primates.

Key words: visual cortex, posterior parietal cortex, frontal eye field, prosimians

Although the present investigation was an effort to determine the connections of a specific visual cortical field in primates, the dorsomedial visual area (DM), we also had a broader objective. This study is part of a series of studies in primates designed to determine which subdivisions of visual cortex are common to a range of primate taxa. Understanding what areas are homologous in different species is important because basic features or similarities found across taxonomic groups are most likely to be preserved or retained in humans. Even without access to the compelling direct evidence for the primary visual area (V-I or area 17), and the tantalising suggestions of a second visual area (V-II or area 18) and a middle temporal visual area, MT (see Kaas, '92), we can be reasonably confident of the existence of V-I, V-II, and MT in humans because these areas have been identified in all investigated primates (for review see Kaas and Krubitzer, '91). Indeed, a major strength of the comparative approach is that by assigning homologies in a variety of extant primates, and even in

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other mammals, we can make strong inferences about unstudied, or poorly understood species.

In view of the general agreement that at least three visual areas exist in all or most primates, it is logical to ask if there are other visual areas that exist in a range of primate species, and therefore are likely to exist in humans. Surprisingly, no other visual area is now widely recognised as a part of the basic primate or even simian plan, and even descriptions of Old World monkey visual cortex organisation have differed considerably (e.g., Boussaoud et al., '90; Felleman and Van Essen, '91). It seems as if the only thing investigators agree on is that primate visual cortex contains a large number of visual areas. Unfortunately, this alone does little to increase our understanding of visual processing strategies, the organisation of visual cortex in humans, or the evolution of sensory systems in mammals. Possibly, some of the disparities in proposals reflect species differences, but other differences may reflect the difficulty of interpreting ambiguous or sparse data, the procedural differences between investigators, and the technical difficulty of locating particular cortical fields in the complex fissures of some primates.

In attempting to investigate the organisation of visual and other areas of cortex, smaller New World monkeys, such as owl monkeys, offer considerable technical advantages. Most of the cortex of the relatively unfissured hemisphere is directly accessible for injections and electrophysiological recording, and some procedures, such as cutting sections of cortex parallel to the surface, are more easily accomplished. On the other hand, macaques and other Old World monkeys are often considered to be more relevant experimental animals, since they are more closely related to humans. However, the human visual system should not be treated simply as an expanded version of the macaque monkey visual system for several reasons. Most importantly, humans and Old World monkeys are not that closely related. Our closest relatives are the African apes, and the lineages leading to humans and extant Old World monkeys have been distinct for over 20–30 million years (e.g., Fleagle, '88; Martin, '90). We know from the astonishing changes that have occurred in the humanoid brain over the last 3 million years, where the human line went from the small, bipedal, tree climbing, australopithecine to the modern *Homo sapiens,* that brain evolution can be quite rapid. Second, the divergence of apes from Cercopithecoid (Old World) monkeys was not much more recent than the divergence of Old and New World simians (25–35 million years ago) or even the divergence of simian and prosimian lines (35–50 million years ago). Thus, humans are only distantly related to both Old World monkeys and New World monkeys. Given these relationships and time spans, it would seem that visual areas that can be demonstrated to be stable over a long period of time are more likely to also be present in humans, than visual areas that presumably did not exist at the time of simian divergence. Finally, existing Old World species are relatively closely related to each other, and do not have the long standing distinct lines of descent such as those that exist within the prosimian and the New World simian radiations. Thus, studies of only Old World monkeys might reveal recent specialisations that are not shared by other primates, including humans, and therefore inferences about human neural organisation and function based on direct extrapolation from macaque monkeys are problematic. Only comparative studies of a variety of primate taxa allow one to determine aspects of neural organisation that are common to most or all primates, and likely to be present in humans by virtue of common descent. Since attempts to investigate fully and compare a range of taxa can be difficult; a practical compromise is to investigate extensively a species or group with the major technical

Abbreviations

Owl Monkeys

AI	primary auditory area
DI	dorsointermediate visual area
DL	dorsolateral visual complex
DLc	caudal division of dorsolateral visual complex
DLr	rostral division of dorsolateral visual complex
DM	dorsomedial visual area
FEF	frontal eye field
FR	frontal rostral field
FST	fundal superior temporal area
FSTd	dorsal division of fundal superior temporal area
FSTv	ventral division of fundal superior temporal area
FV	frontal ventral eye movement field
IT	inferotemporal cortex
ITc	caudal division of inferotemporal cortex
ITr	rostral division of inferotemporal cortex
M	medial visual area
MI	primary motor area
MST	medial superior temporal area
MT	middle temporal visual area
MTc	crescent of middle temporal visual area
PP	posterior parietal cortex
PV	parietal ventral area
R	rostral auditory area
SII	second somatosensory area
SMA	supplementary motor area
VA	ventral anterior area
VP	ventral posterior area
VPP	ventral posterior parietal area
VS	ventral somatosensory area
1	somatosensory area 1
3a	somatosensory area 3a
3b	primary somatosensory area (SI)
2	somatosensory area 2
17	primary visual area (V-I)
18	second visual area (V-II)

Macaque Monkeys

LIP	lateral intraparietal area
PIP	posterior intraparietal area
PO	parietal occipital area
V-II/V2	second visual area
V-III/V3	third visual area
V3d	dorsal division of V3
V3v	ventral division of V3
V3A	visual area rostral to V3d
V4	fourth visual area
VIP	ventral intraparietal area

Other Terms

CO	cytochrome oxidase
DY	fluorescent tracer diamidino yellow
hm	horizontal meridian
lf	lower field
M	magnocellular channel
OD	optic disc
p	peripheral field
P	parvocellular channel
P-B	parvocellular blob channel
P-I	parvocellular interblob channel
uf	upper field
WGA-HRP	anatomical tracer wheatgerm agglutinin conjugated to horseradish peroxidase

advantages (such as a lissencephalic cortex) and then obtain relevant, but less complete, information from other taxa to be interpreted in the context of the more extensive information. This is the approach we took in the present study of DM of owl monkeys (Allman and Kaas, '75) and the DM region of cortex in other primates.

In this paper we consider the possibility that DM of owl monkeys (Allman and Kaas, '75) is an area common to all primates. This investigation is an extension of our previous comparative study of the connections of MT in three species of New World monkeys and prosimian galagos (Krubitzer and Kaas, '90b). The results from that study indicate that a field in the relative position, and with the dense myelination of DM is interconnected with MT in each of these primates, as is DM in owl monkeys (Weller et al., '84; Krubitzer and Kaas, '90b). However, in marmosets and galagos, these connections appeared to be inconsistent. In part, this may be a consequence of underestimating the size of DM and attributing connections to adjacent cortex rather than to DM. Furthermore, the dorsal division of the third visual area (V3d) and the visual area rostral to V3d (V3A) of macaque monkeys is in the relative position of DM, and has connections with MT (Maunsell and Van Essen, '83; Ungerleider and Desimone, '86). Thus, it is possible, based on relative position and connections with MT, that cortex in the V3d and V3A region of macaque monkeys is DM. An apparent difficulty with this proposal is that dorsal V3 is thought to represent only the lower visual quadrant (e.g., Gattass et al., '88), and therefore seems quite different from DM in owl monkeys, which represents the complete visual hemifield (Allman and Kaas, '75). However, there are upper quadrant representations in the adjoining field V3A, and we will explore the possibility that DM corresponds to both V3 and portions of V3A.

Our approach to the issue of identifying DM across species is twofold. First, we attempted to further characterise DM in owl monkeys. Could the electrophysiological studies (Allman and Kaas, '75) of 15 years ago, showing the representation of both upper and lower visual quadrants in DM, be confirmed? Is this map, as previously reported, coextensive with a densely myelinated zone on the border of V-II? And, most importantly, what are the connections of DM? Although the connections of DM have been described briefly after lesions or injections of tritiated proline (^{3}H-proline) (Wagor et al., '75), there have been no further studies. In addition, in previous studies, cortex was cut in standard planes of section so that the modules within a field, shapes of fields, and spatial relationships of fields were more difficult to determine. In the present investigation, the manually flattened cortex cut parallel to the surface can be used effectively to show the details of the areal and modular connection patterns in cortex, as well as the spatial relationships of fields (e.g., Krubitzer and Kaas, '90a,b). We investigated the visuotopic organisation of DM in owl monkeys using microelectrode mapping procedures, and placed injections of wheatgerm agglutinin conjugated to horseradish peroxidase (WGA-HRP) into DM. These results were then related to myelin and cytochrome oxidase (CO) patterns in sections cut from the flattened brains.

Our second step in this investigation was to see whether two robust and easily identified features of DM of owl monkeys exist for cortex in the expected location of DM of other primates. One obvious feature of DM is its dense myelination. We have already noted that an area in the relative position of DM is densely myelinated in prosimians and New World monkeys (Krubitzer and Kaas, '90b), and the comparable region, "dorsal V3," in Old World monkeys has also been described as densely myelinated (Burkhalter et al., '86; Gattass et al., '88; Girard et al., '91). Another feature of DM is that it is one of only three areas with major, direct projections from all of striate cortex (Lin et al., '82), although DL/V4 receives sparse projections from the central field representation of V-I. We compared connection patterns in manually flattened cortex after area 17 injections in prosimians and New and Old World monkeys to see if the projection zones of area 17 included the densely myelinated DM or presumptive DM region. Preliminary reports of some of these results have been published elsewhere (Krubitzer and Kaas, '89a, '90a).

MATERIALS AND METHODS

This study consists of two separate groups of experiments. In the first set of experiments, the connections of DM were investigated in four New World owl monkeys (*Aotus trivirgatus*) by placing small injections of WGA-HRP, and in one case diamidino yellow (DY), into different locations in DM. In two of these animals, DM was mapped using multiunit recording techniques similar to those used in the initial studies on DM by Allman and Kaas ('75). However, unlike the cases in the initial recording experiments, cortex in our experiments was manually flattened and cut parallel to the cortical surface so that the microelectrode map, injection sites, and patterns of transported tracer could be related to myeloarchitectonic boundaries of DM and other fields. In this group of experiments, the areal and modular connections of DM were determined.

In the second set of experiments, we investigated the possibility that DM is an extrastriate visual cortical area common to a wide range of primates by injecting the primary visual cortical area in one owl monkey (*Aotus trivirgatus*), two galagos (*Galago senegalensis*), one marmoset (*Callithrix jacchus*), two squirrel monkeys (*Saimiri sciureus*), two Old World talapoin monkeys (*Miopithecus talapoin*), one Old World patas monkey (*Erythrocebus patas*), and two macaque monkeys (*Macaca fascicularis*) to see whether, in these primates, a densely myelinated field, similar in appearance and location to DM in owl monkeys (Krubitzer and Kaas, '90b), also receives inputs from area 17 as it does in owl monkeys (Lin et al., '82). In this second group of experiments, neocortex was again completely flattened and sectioned parallel to the cortical surface so that connection patterns could be related to myeloarchitectonic boundaries.

Surgical procedures and injections of anatomical tracers

At the beginning of all experiments, the animal was anaesthetised with ketamine hydrochloride (30 mg/kg) and xylazine (3 mg/kg) i.m. (Krubitzer et al., '93). To maintain a surgical level of anaesthesia, 10% of the original dose of ketamine and xylazine was administered as needed throughout the experiments. With standard sterile surgical procedures, the scalp was cut, the skull above either DM or area 17 was removed, the dura was reflected, and a small injection of 0.1% (0.03–0.05 μl) WGA-HRP, or 3 small injections of 3% (0.2 μl) DY was made with a micropipette

coupled to a Hamilton syringe. At the time of the injection, area 17 was localised as the most posterior region of cortex in all primates, and DM was localised as the cortex just caudal to the caudal tip of the lateral sulcus in owl monkeys. Injection sites were later verified by means of architectonic criteria (see below).

After injections were complete, the opening in the skull was closed, the scalp was sutured, and the animal was allowed to recover for two days (four days for DY). At this time, the animal was administered a lethal dose of sodium pentobarbitone and when areflexive, was perfused transcardially with 0.9% saline followed by 2% paraformaldehyde in phosphate buffer and then 2% paraformaldehyde in 10% sucrose phosphate buffer. Immediately following perfusion, the brain was removed from the cranium, the cortex was separated from the brainstem and thalamus, sulci were gently pried apart and the total neocortex was completely flattened (Fig. 1). The cortex was placed between lightly weighted glass slides and left to soak for approximately 15 hours in 30% sucrose phosphate buffer. The procedures follow those described previously (Krubitzer and Kaas, '90b).

Electrophysiological recording procedures

In two of the owl monkeys in which DM was injected, microelectrode recordings were made in DM on the day of perfusion. These animals were anaesthetized with 25% urethane in 0.9% saline (125 mg/100 g) i.p. (Allman and Kaas, '71a). Supplementary doses were given as needed throughout the experiment. After the animal was anaesthetised, the skull above DM in the hemisphere contralateral to the injection was removed using surgical procedures described above. A large acrylic well was built around the opening in the skull and filled with silicone fluid to reduce pulsation and prevent desiccation. The skull was then cemented to a bar held in a vice so that the visual field contralateral to the opening was unobstructed. The pupil contralateral to the cortical opening was dilated with cyclopentolate hydrochloride, and a thin layer of silicone fluid was spread over the cornea to prevent desiccation and clouding. A metal eye ring was sutured to the sclera of the contralateral eye and was cemented to the acrylic well on the skull. A translucent hemisphere (60 cm diameter), which served as the visual field, was centred around the fixed eye, and the optic disc and retinal blood vessels were projected onto the surface of the hemisphere by directing a beam of high intensity light into the eye with a fibre optic illuminator (see Fernald and Chase, '71). This was done before electrophysiological recordings commenced, and several times during the recording session to check eye position.

Recordings from small neural clusters were made with low impedance (0.9–1.2 MΩ at 1,000 Hz) glass insulated, tungsten microelectrodes. The microelectrode carrier was attached to a micromanipulator and electrodes were advanced with a stepping microdrive. Recording depths were from 500 to 1,000 μm below the pial surface. Neural activity was amplified, heard on a loudspeaker, and displayed on an oscilloscope. An enlarged photograph of the cortical surface was used to locate the position of each electrode penetration relative to vascular patterns.

Visual stimuli consisted of moving, small bars of projected light, back-lit dark bars, and full field flashes of light. Receptive fields were plotted directly on the hemisphere and defined as that area which produced an obvious neural response when visually stimulated. Most neurons were responsive to small bars of light, approximately 5° in length and 0.5° in diameter, moving through the receptive field. After receptive fields for multiple, closely spaced electrode penetrations in DM were plotted, lesions were placed at physiological boundaries by passing small currents (10 μA for 6 seconds) through the electrode. Electrophysiological experiments were terminated by injecting the animal with a lethal dose of sodium pentobarbitone and perfusing the brain as in the other experiments.

Histological procedures and data analysis

The flattened cortex was cut into 40 μm sections on a freezing microtome and alternate sections were processed for horseradish peroxidase (HRP) with tetramethylbenzidine (Mesulum, '78, modified by Gibson et al., '84), processed for CO (Carroll and Wong-Riley, '84) and stained for myelin with the Gallyas ('79) silver stain. In the DY-injected brain, sections were mounted for fluorescence microscopy rather than processed for HRP. All sections containing labelled cell bodies and axon terminals were reconstructed with the aid of a camera lucida, and superimposed upon sections processed for CO or stained for myelin. By matching local blood vessel patterns and tissue artifacts (e.g., Fig. 7), the total pattern of connections could be related to architectonic boundaries of fields. In three owl monkeys, injections in DM were completely confined to the architectonic boundaries of the field. In the two cases in which electrophysiological recordings were made, electrolytic lesions were identified and combined with reconstructions of connections and architecture. Cortical modules in areas 17 and 18 were easily identified in CO-processed sections, and labelled cells and axon terminals in areas 17 and 18 were related to these modules in all cases.

RESULTS

We describe the areal patterns of connections of the dorsomedial visual area, DM, in owl monkeys and provide evidence that DM is an extrastriate cortical area common to a wide range of primates. Results are presented in three parts. In the first part, we describe the topographic organisation of DM as revealed by microelectrode recordings in owl monkeys. In the second part, overall connection patterns produced by injections of WGA-HRP into DM are described. Also in this section, modular connections of DM with areas 17, 18, and MT are related. Finally, we describe the myeloarchitecture of DM and surrounding fields and the connections of DM with area 17 in New World owl monkeys, marmosets, squirrel monkeys, prosimian galagos, and three species of Old World monkeys.

The organisation of visual cortex in owl monkeys: architectonic fields and visuotopic organisation of DM and M

Figure 1 indicates the locations and aspects of the retinotopic organisation for some of the proposed areas of visual cortex of owl monkeys. The fields are depicted on cortex that has been separated from the rest of the brain and flattened as a single sheet (with the aid of cuts in cortex of the lateral sulcus, area 17, and parts of frontomedial cortex). How this cortex is flattened, and what portions are buried in the lateral, superior temporal, and calcarine fissures is shown in Figure 1 of Krubitzer and Kaas ('90b). The architectonic features of most of these fields in flat-

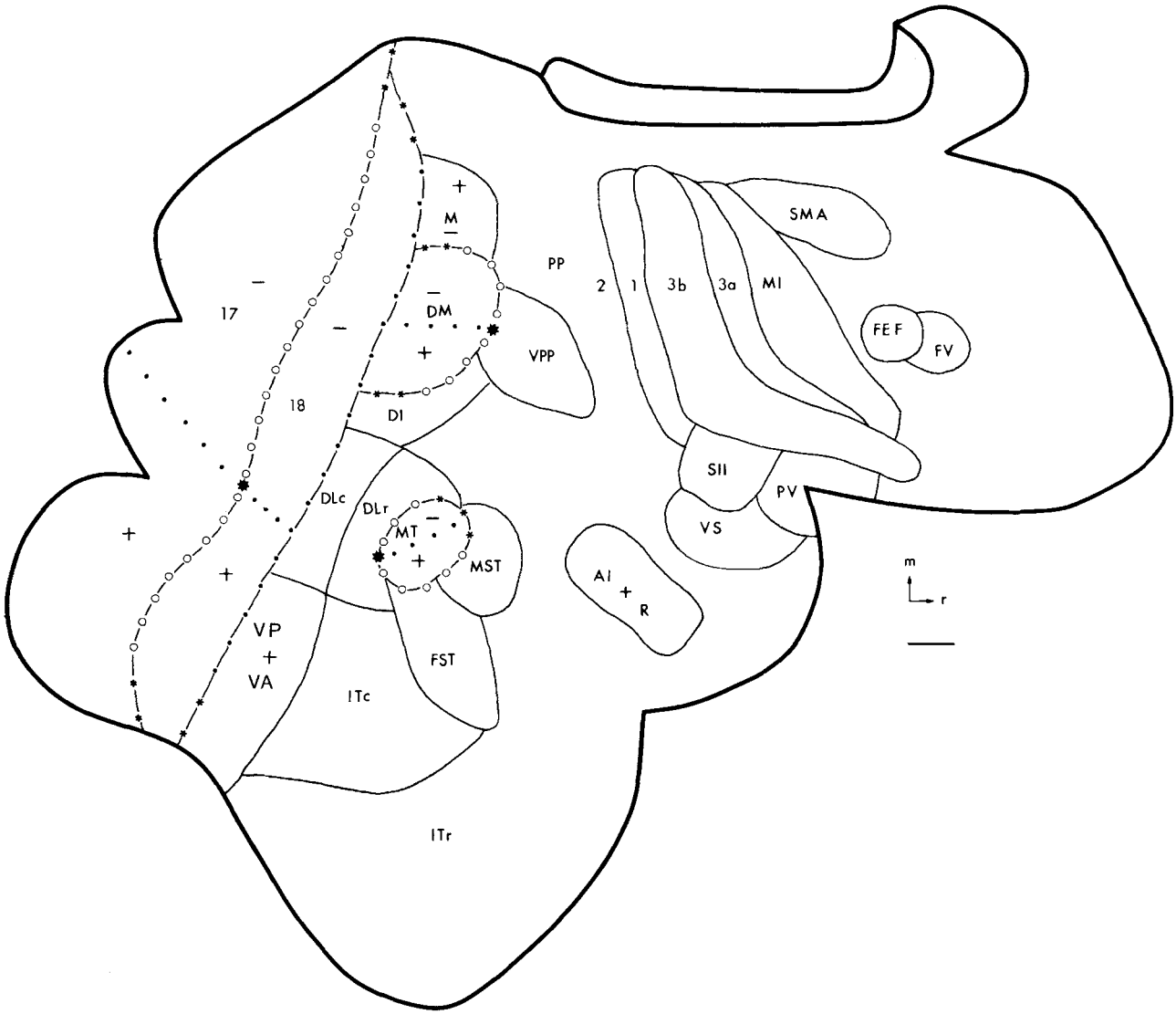

Fig. 1. The location and retinotopic organisation of some of the visual areas proposed for owl monkeys in cortex separated from the rest of the brain and flattened into a sheet. The representation in area 17 is a *first order,* or continuous, transformation of the visual hemifield (Allman and Kaas, '74a,b). Like area 17, MT is also a *first order* transformation. Other fields such as area 18, M, and DM are *second order,* or split transformations of the visual hemifield, so that adjacent points in visual space are not always represented as adjacent points in cortex. +, upper quadrants; −, lower quadrants; large stars, centre of vision; open circles, vertical meridian; dots, horizontal meridian; asterisks, peripheral fields. Thin solid lines mark architectonic boundaries. Somatosensory fields, auditory fields, and eye movement fields of frontal cortex are added so that the relative positions of sensory and motor fields can be appreciated. The arrows indicate medial and rostral. Scale bar = 2 mm.

tened cortex have been described elsewhere (Tootell et al., '85; Krubitzer and Kaas, '90b). Detailed descriptions of retinotopic organisation have been published for area 17, V-I, (Allman and Kaas, '71b), area 18, V-II, (Allman and Kaas, '74a), MT (Allman and Kaas, '71a), the dorsolateral visual area, DL (Allman and Kaas, '74b), which is now recognised as containing separate rostral (DLr) and caudal (DLc) areas with parallel retinotopic organisations (see Cusick and Kaas, '88b; Krubitzer and Kaas, '90b), DM (Allman and Kaas, '75) and the medial visual area (M) (Allman and Kaas, '76). The medial superior temporal area (MST) and the fundal superior temporal area (FST) were first described in macaque monkeys (Ungerleider and Desimone, '86), and are projection targets of MT (Weller et al., '84; Krubitzer and Kaas, '90b; Kaas and Morel, '93). We now have evidence that FST has dorsal (FSTd) and ventral (FSTv) subdivisions with different connections (Kaas and Morel, '93), but no distinction is attempted here. In addition, MT has recently been shown to contain an MT centre as well as an MT crescent (MTc; Kaas and Morel, '93). MT in the present investigation contains both MT proper and MTc. The dorsointermediate area (DI) is a poorly defined field (Allman and Kaas, '75) that we have modified using architectonic criteria to define and extend the rostral border (Krubitzer and Kaas, '90b). The caudal division of inferotemporal cortex (ITc) is from Weller and Kaas ('87), and the ventral posterior area + the ventral anterior area (VP + VA) is based on Newsome and Allman ('80) and

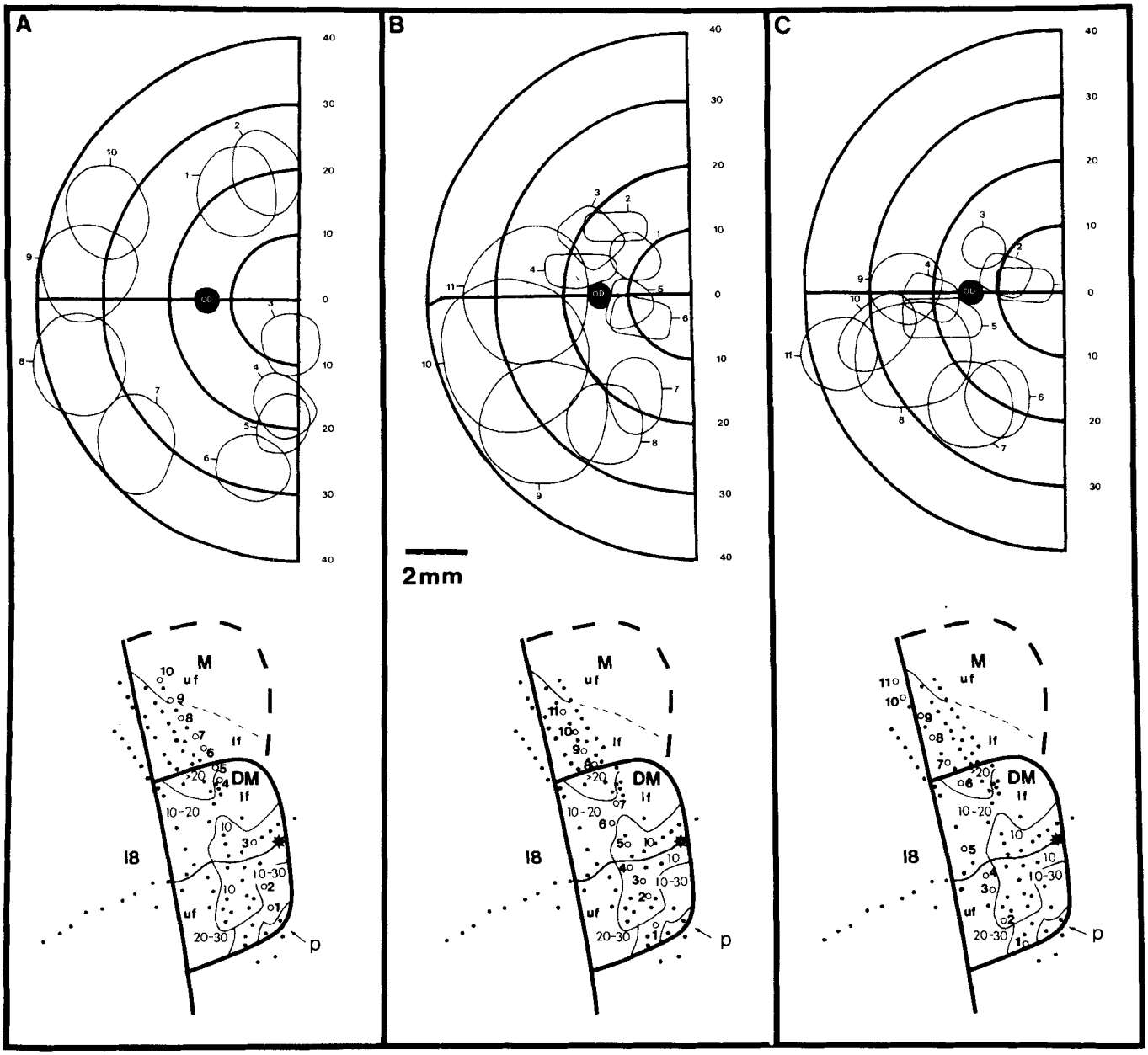

Fig. 2. Progressions of receptive fields (**upper figures**) for rows of recording sites crossing DM and M of an owl monkey. In **A, B,** and **C,** receptive fields for progressively more caudal rows of recording sites are shown on the flattened cortex (numbered open circles). Other recording sites are indicated by black dots. Although the recordings were actually from the left side of the brain and the receptive fields from the right visual hemifield, they are illustrated in reverse for consistency across illustrations. Thick lines denote architectonic boundaries, and thin lines indicate receptive field eccentricities for neurons in DM. In M, dashed lines indicate the approximate location of the horizontal meridian representations. See Abbreviations list for other conventions.

Sereno and Allman ('91). In this paper, we define the ventral posterior parietal area (VPP) as the ventral portion of posterior parietal cortex (PP of earlier reports, e.g., Kaas et al., '77) that receives dense inputs from DM and is more densely myelinated than surrounding cortex. A list of these fields and other fields described in primates is given in the Abbreviations list.

Most of the visual fields of owl monkeys have also been described in terms of myeloarchitectonic, cytoarchitectonic, and to a lesser extent, CO patterns (see Krubitzer and Kaas, '90b for review). In particular, DM has been characterised as densely myelinated (Allman and Kaas, '75; Wagor et al., '75), and in sections from flattened cortex, DM of owl monkeys is roughly rectangular (Fig. 12B; and see Krubitzer and Kaas, '90b). In the present investigation, we found that the representation of the visual hemifield in DM (Fig. 2) is coextensive with this densely myelinated rectangle (Fig. 12B). VPP is a densely myelinated oval of cortex occupying part of the banks of the superior temporal sulcus, which extends from the rostromedial border of DM

to near the caudal border of somatosensory area 2. Immediately caudal to DM, area 18 stains heterogeneously for myelin with myelin dark and light bands running across its rostrocaudal extent (see Krubitzer and Kaas, '89b, '90b), but at the laminar level shown in this investigation these bands are not apparent. MT is distinct as a darkly myelinated oval of cortex at the caudal tip of the superior temporal sulcus. A moderately myelinated medial superior temporal field, MST, is located just rostral and slightly dorsal to MT.

Although divisions of inferotemporal cortex (IT) have not been described in cortex that has been flattened and cut tangentially, the relative locations of labelled cell bodies and terminals in the present investigation can be easily related to general locations in IT cortex. Within IT cortex, architecture and patterns of connections from area 18, MT, DL, and DM suggest at least two divisions, caudal IT (ITc), and rostral IT (ITr). The rostral field is located just lateral to ITc and caudolateral to FST, and the caudal field is just rostral to VP and lateral to DL. The present VP may include both VP and more anterior cortex, VA (Newsome and Allman, '80; Sereno and Allman, '91). Although electrophysiological mapping of the VP + VA region has not been done in owl monkeys, we know from connectional studies in a number of New World monkeys (including owl monkeys) and prosimian galagos, that both upper and lower field information reaches this area (e.g., Weller and Kaas, '85; Krubitzer and Kaas, '90b; Weller et al., '91; present investigation). Figure 1 provides an overview of most of these subdivisions, and some of these subdivisions are shown architectonically in Figures 12 and 13.

Finally, several ovals of densely myelinated cortex have been described in the frontal cortex in a variety of primates (Kaas and Krubitzer, '88; Krubitzer and Kaas, '90b). These fields are coextensive with the physiologically defined frontal eye field (FEF) and the frontal ventral field (FV). In the present investigation, these fields were identified architectonically and related to connections from DM. An additional field, just rostral to FV, was also defined based on its moderately myelinated appearance and its connections from DM. We term this presumptive field the frontal rostral area (FR).

Sections processed for cytochrome oxidase were generally not as useful in defining DM as sections stained for myelin. However, in favourable CO preparations, DM was moderately dark. The CO preparations were much more useful for identifying modules in areas 17, 18, and MT (also see Tootell et al., '85). CO-dense blobs surrounded by CO-sparse interblobs were distinct in area 17, and the characteristic CO-dense bands interdigitated by CO-sparse bands were observed in area 18 (Fig. 7B and E). CO stains in MT produced a mottled appearance of CO-dense and sparse regions in some animals, as previously described by Tootell et al. ('85).

Electrophysiological results. Because the retinotopic organisation of DM has been described in detail previously, we did not attempt to map this field extensively. Instead, our goals were to see if the general organisation could be confirmed, and if the physiologically defined DM matched the densely myelinated rectangle observed in flattened cortex. As in previous reports (Allman and Kaas, '75; Baker et al., '81), receptive fields were quite large in DM (of the order of 5–10° for central fields and 10–15° for peripheral fields; see Fig. 2). Neurons responded best to small bars of light moving in particular directions, and most of the recording sites in DM contained neurons that were highly direction selective. However, direction selectivity was not systematically investigated. Representative results from one of the two cases are shown in Figure 2. The upper visual quadrant was represented laterally and the lower visual quadrant medially in DM. Thus, receptive field sequences for lateromedial rows of recording sites (e.g., Fig. 2, r.f. 1–5A, 1–8B and 1–6C) progress from upper to lower visual quadrants. Receptive fields for more rostral recording sites in DM tended to be closer to the zero vertical meridian (line of decussation) than receptive fields for more caudal recording sites (compare receptive fields for rows A, B and C in Fig. 2). In the case illustrated in Figure 2, only a few recording sites encountered neurons (Fig. 2, p; not shown) with receptive fields with eccentricities greater than 30°. However, the peripheral representation in DM occupies only a small rostromedial and rostrolateral portion of the field (Allman and Kaas, '75), and our recording sites did not include portions of rostromedial DM. Overall, the results were consistent with the concept of a complete or nearly complete representation of the contralateral hemifield, with the representation of zero vertical meridian along the rostral border, the representation of zero horizontal meridian bisecting the area into a lower quadrant medially and an upper quadrant laterally, and a partial splitting of the representation of the horizontal meridian to form at least part of the caudal border of DM, as previously reported (Allman and Kaas, '75). There was some scatter in receptive field positions around values predicted from summary maps. For example, receptive field 1 for row A (Fig. 2A) would be expected to be superior rather than inferior to receptive field 2. Such scatter could reflect some sort of modular organisation in DM or indicate that the overall retinotopic organisation is not precise. Nevertheless, it is clear that DM does represent both upper and lower quadrants, and that the overall organisation corresponds to that previously reported.

Electrophysiological recordings also provided information on the organisation of areas surrounding DM. Recording sites in the part of area 18 (V-II) just caudal to DM had neurons with receptive fields in the lower visual quadrant, with neurons more caudal in area 18 having receptive fields closer to the zero vertical meridian and neurons more rostral in area 18 having receptive fields closer to the zero horizontal meridian. Rows of recording sites progressing across area 18 and into DM produced sequences of receptive fields that progressed from the lower visual quadrant at the vertical meridian at the 17/18 border to the horizontal meridian at the 18/DM border, and then back toward the vertical meridian, with a sudden displacement into the upper quadrant for progressions into lateral DM. The line of change corresponded to the architectonic border. There was no evidence for any other area interposed between DM and area 18.

Recordings extending from the medial border of DM, in cortex of the medial wall of the cerebral hemisphere, produced sequences of receptive fields that reflected the previously reported retinotopic organisation of M. Similar to previous descriptions (Allman and Kaas, '76), large portions of M were devoted to the peripheral visual field (Fig. 2). Also, the sizes of receptive fields in M were even larger than those found in DM, ranging from 15 to 25°. As our electrode went from DM into M, receptive fields progressed from the peripheral lower visual field in DM to the peripheral lower visual field in M, to the horizontal meridian, then to the peripheral upper field. At the physiological

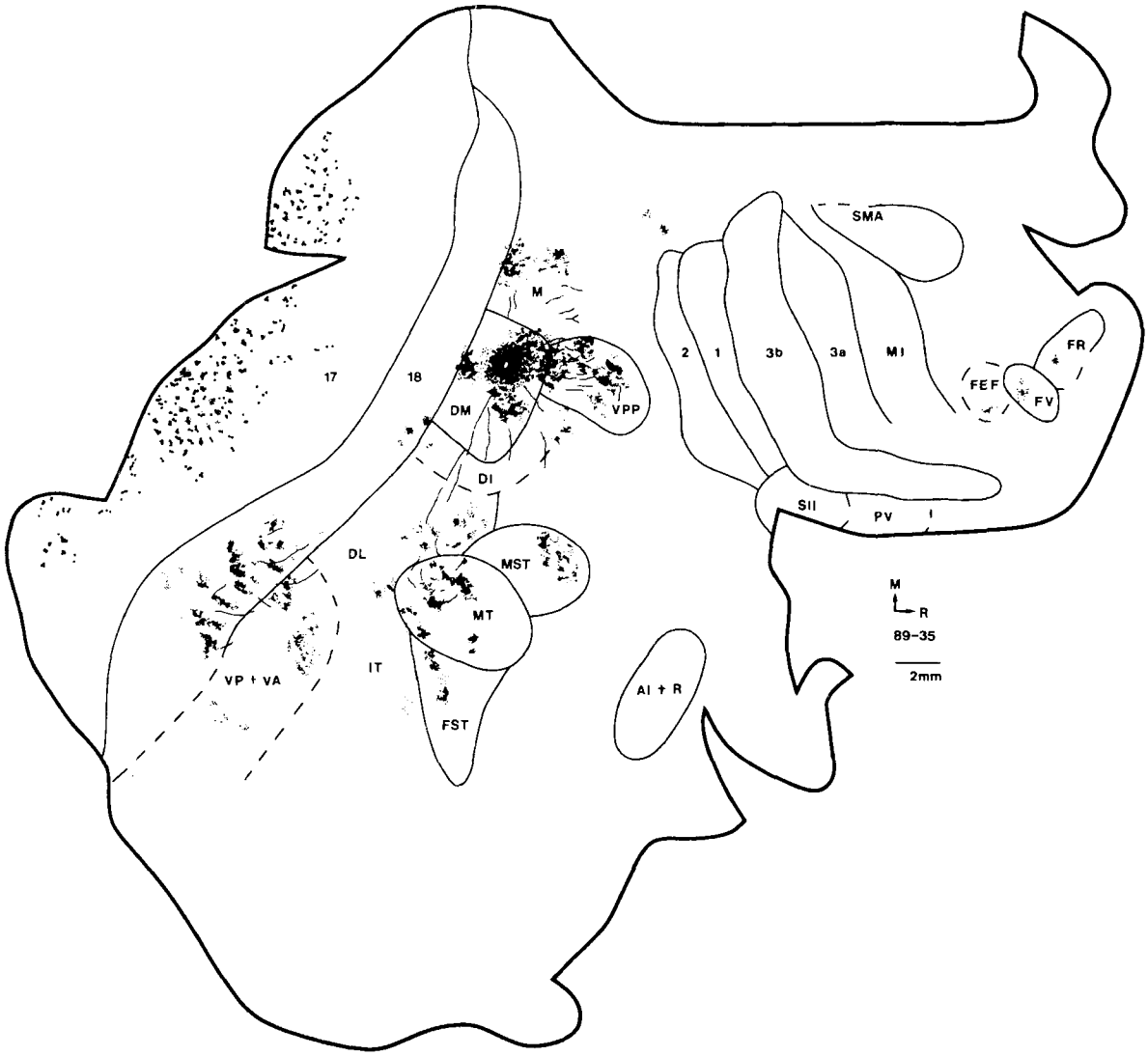

Fig. 3. The connections of DM in owl monkey 89-35. The injection site (black oval) and transported label (dots) are shown on a representative section cut parallel to the flattened surface of the cortex. Large dots denote retrogradely labelled cell bodies and small dots represent anterogradely labelled axon terminals. The distribution of axon terminal labelling in area 17 reflected that of retrograde labelling but is not shown here. Solid lines mark architectonic boundaries and dashed lines are approximated boundaries. Although the injection in DM is quite small, the extent of cortex containing labelled neurons and terminations in area 17 is large. Bands of labelled neurons and axon terminals are found in area 18, and foci of anterograde and retrograde are in MT, MST, FST, M, VPP, DLr, IT, VP, DI and several fields of the frontal cortex. The ventral posterior region may include the ventral anterior area and is therefore termed VP + VA. AI + R is the densely myelinated region that includes both auditory fields.

boundary of DM and M, receptive fields reversed away from the vertical meridian back towards the horizontal meridian (Fig. 2A–C). Cortex rostral and lateral to DM was visually responsive, but less so than DM, and we did not attempt to map these regions.

Cortical connections of DM

Small injections of WGA-HRP restricted to DM in three owl monkeys, and injections of DY in one monkey, resulted in remarkably similar patterns of connections with a number of visual cortical areas. Because cortex was completely flattened and sectioned parallel to the cortical surface, the distribution of label could be readily appreciated, often in a single section (Fig. 4). Fields interconnected with DM included areas 17 and 18, DLr, MT, FST, MST, VPP, M, VP, IT, and eye movement fields of frontal cortex. Patterns of labelled cells and axon terminals were consistent with the topographic organisation of DM and connected fields (see Fig. 1). Contralateral connections of DM were most dense with DM, but they also included VPP.

Intrinsic connections of DM. In all cases, injections of WGA-HRP in DM resulted in patches of labelled cell bodies and axon terminals in adjacent portions of DM. The intrinsic connections of this field were of three types. First, patchy protrusions of connections were observed extending from the injection site. For instance, in case 89-35 (Fig. 3), patches of labelled neurons and terminals were distributed immediately around the injection core. Likewise, in case

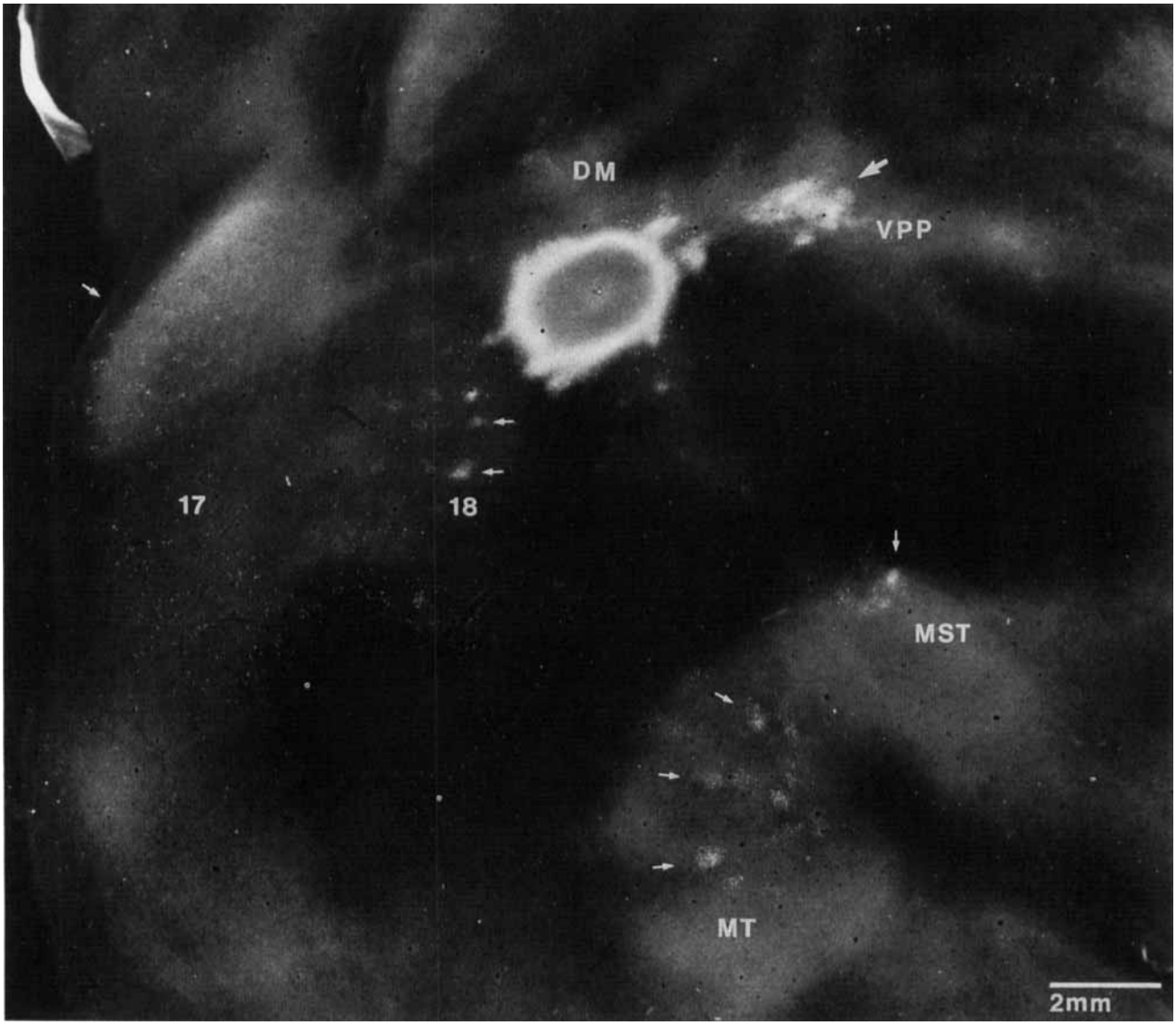

Fig. 4. A darkfield photomicrograph of an injection of WGA-HRP in DM in owl monkey 88-32. This section was cut tangential to the flattened cortex and processed for HRP. The core of the injection in DM is dark. Transported tracer immediately around the core forms a white halo. Other transported tracer is seen as white puffs throughout the section. Local transport in DM, further from the injection, is in several small clumps. Transported tracer to other visual cortical areas such as 17, 18, MT, MST, and VPP can also be identified at this laminar level. Although this section has not been stained for myelin, heavily myelinated areas such as MT and MST appear grey compared to the deep black of surrounding fields. Small arrows point to puffs of label in area 17, bands of label in area 18, and patches of labelled cells and terminations in MT and MST; and the large white arrow points to the dense forward projection to VPP. Conventions as in previous figures.

89-58 (Fig. 6), local transport surrounding the injection core was evenly distributed. Second, numerous labelled cells and terminals were observed approximately 1–1.5 mm from the injection site (Figs. 3–6). Third, sparse connections were also observed as far as 3 mm from the injection site (e.g., Fig. 6). Similar results were obtained with DY injections in caudal DM. Labelled neurons were scattered over DM, but they were most dense around the injections sites. These results suggest that intrinsic connections of DM are between both retinotopically similar and mismatched portions of the representation.

Area 17. Injections in DM produced foci of labelled cell bodies and axon terminals in area 17 in all four cases. In two WGA-HRP cases, the bidirectionally transported tracer was rather broadly distributed over large extents of area 17 (Figs. 3 and 5). In the third WGA-HRP case (Fig. 6), for uncertain reasons, there was relatively little transported tracer in area 17. However, in the case with three small DY injections in caudal DM, a broad expanse of area 17 possessed labelled neurons (not shown). In most cases, the injections were made in central portions of DM near the region representing the horizontal meridian, and they probably involved parts of DM representing the upper and the lower visual quadrants. As expected, the zones of bidirectionally transported tracer included medial and lateral parts of area 17 devoted to the lower and upper quadrants, respectively. Most of the transported tracer in area 17 was in cortex that is relatively close to the represen-

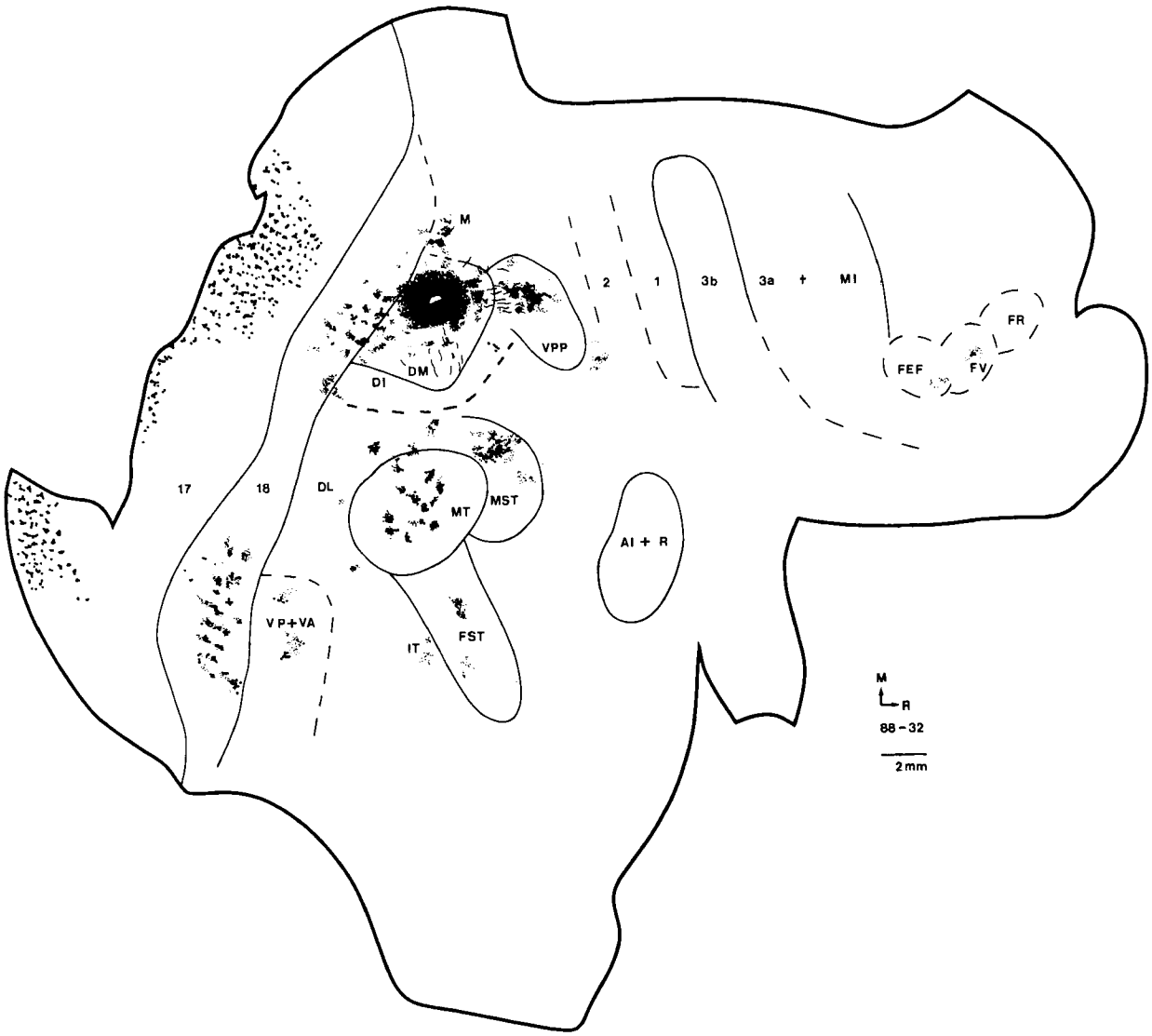

Fig. 5. A reconstruction of labelled cell bodies and axon terminals in cortical fields resulting from an injection of WGA-HRP in DM of owl monkey 88-32. The pattern of connections of DM in this case is remarkably similar to the previous case (Fig. 3). Only the distribution of labelled cells is illustrated for area 17 in this figure, but the anterograde pattern of label reflected the retrograde pattern of label. Conventions as in previous figures. Modified from Krubitzer and Kaas ('90a).

tation of the horizontal meridian (in flattening, area 17 was split, and thus lateral and medial extensions of the zones of label would adjoin in the intact brain). The extensions of the zones of labelled cell bodies and axon terminals well into parts of area 17 representing the upper visual quadrant indicate that information from the upper visual quadrant, as well as the lower visual quadrant, reaches DM. This anatomical result supports the contention, based on electrophysiological recordings, that DM represents both the upper and lower quadrants.

Although the retrogradely labelled cell bodies and anterogradely labelled axon terminals in area 17, at any given location, were sparse, they were distributed over a large extent of area 17 (e.g., Figs. 3 and 5). In one case 89-35 (Fig. 3), the zone in area 17 containing labelled cell bodies and terminals encompassed 22 mm of cortex, while the injection core in DM was only about 1 mm in diameter. Because area 17 is ten times the size of DM (Krubitzer and Kaas, '90b), neurons in DM have access to information, via area 17, over large parts of the visual field. As noted above, receptive fields for neurons in DM are much larger than for neurons in area 17.

Area 18. In all three WGA-HRP cases, parts of area 18 contained labelled cell bodies and axon terminals from the injections in DM (the DY case only had labelled cell bodies). The largest injection, centred in DM (Figs. 4 and 5), produced band-like arrays of labelled neurons and terminals both medially, in part of area 18 representing the visual space about 20–30° into the lower visual quadrant, and laterally, in a portion of area 18 devoted to the comparable region of the upper visual quadrant (see Allman and Kaas, '74a). A smaller and more rostral injection produced bands of labelled neurons and terminals in lateral area 18 in a slightly more central location corresponding to

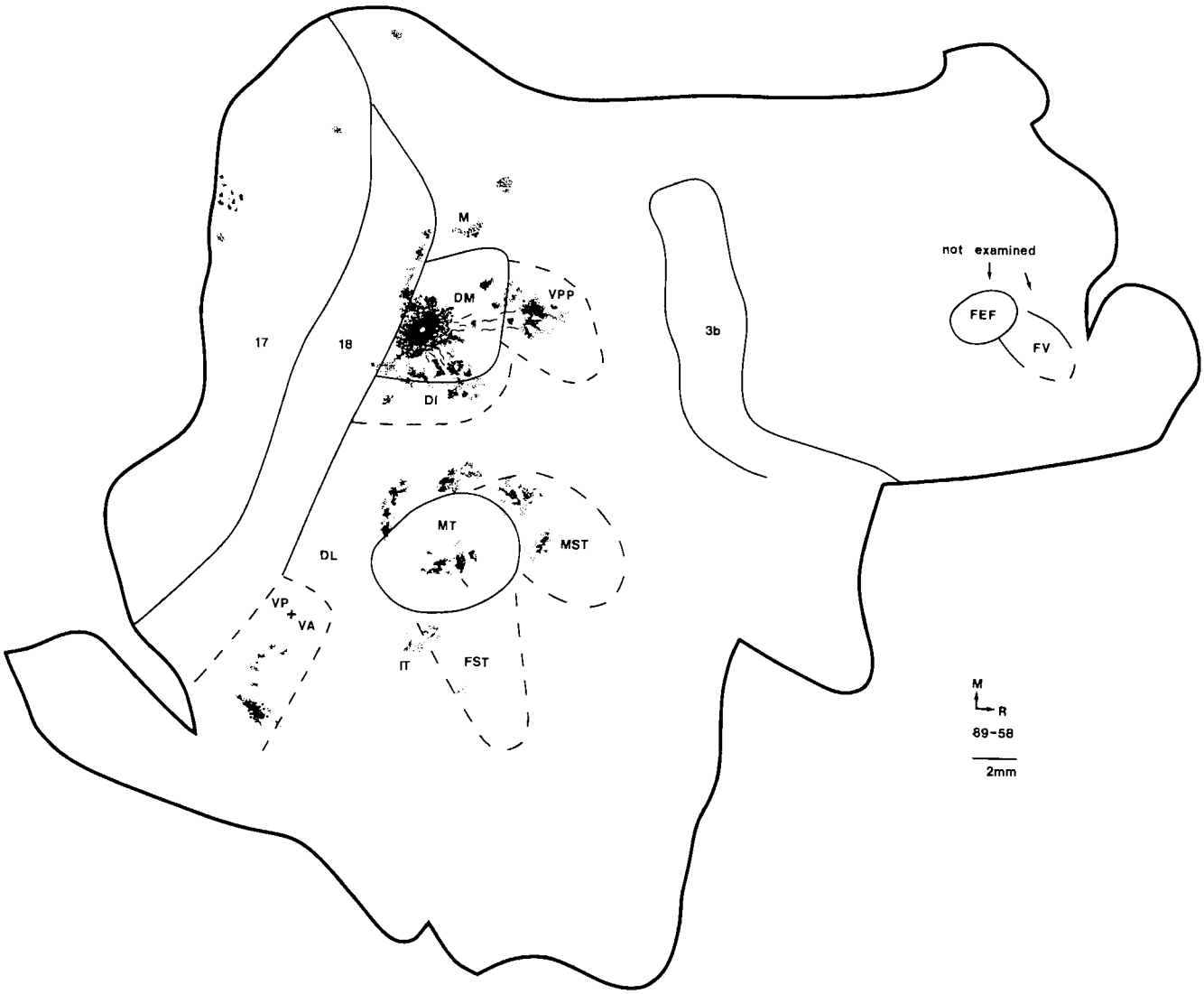

Fig. 6. A reconstruction of labelled cell bodies and axon terminals in cortical fields resulting from an injection of WGA-HRP in DM in owl monkey 89-58. Patterns of connections are similar to those illustrated in previous cases (Figs. 3 and 5). Conventions as in previous figures.

5–20° into the lower quadrant, but only sparse labelled cell bodies and axon terminals were found medially in area 18 (Fig. 3). In the third WGA-HRP case (Fig. 6), only small amounts of bidirectionally transported tracer were found in area 18 in the representation of the lower visual quadrant near the horizontal meridian. The case with the DY injections in DM resulted in labelled cell bodies in adjoining parts of area 18 devoted to the representation of the lower visual quadrant, but some labelled neurons were also in lateral portions of area 18. The two WGA-HRP cases with substantial amounts of bidirectionally transported tracer were in lateral as well as medial area 18, and provide further evidence that DM represents the upper as well as the lower visual quadrant, and indicate that the connections of DM with area 18 are with clumps of neurons that are arranged in regularly spaced rows.

The temporal areas: MT, FST, and MST. DM had dense, patchy connections with three areas in the superior temporal sulcus, the middle temporal visual area, MT, the medial superior temporal area, MST, and the dorsal division of the fundal superior temporal complex (FST). Connections with MT were clearly topographic. Injections in a paracentral upper field representation in DM, which spread slightly into lower field representations (Fig. 3, case 89-35), resulted in densely labelled neurons and terminals in the caudal portion of MT in the representation of paracentral upper and lower fields. A larger injection in the part of DM representing more peripheral vision along the horizontal meridian (hm) (Figs. 4 and 5, case 88-32) resulted in labelled cell bodies and axon terminals in the central portion of MT devoted to more peripheral vision along the horizontal meridian. Transported tracer in this case was further from the caudal border of MT representing central vision. A very small injection in a paracentral horizontal meridian representation in DM labelled cell bodies and axon terminals in the middle of MT, at the representation of the horizontal meridian away from the central field representation (Fig. 6). Finally, the DY injections in caudal DM labelled a broad

middle portion of MT that was in a more rostral location than the previous case.

Connections of DM with MST and dorsal FST also appeared to be topographic. The paracentral upper field representation in DM (Fig. 3, case 89-35) was connected with the most rostral portion of MST and a dorsal portion of dorsal FST adjacent to MT. An injection in a paracentral representation on the horizontal meridian of DM (Figs. 4 and 5, case 88-32) labelled neurons and terminals in MST in a more mediocaudal position than the previous case, and resulted in labelled cell bodies and terminals in a portion of dorsal FST further from the ventral border of MT. An injection centred in a more peripheral field representation in DM (Fig. 6, case 89-58) labelled neurons and axon terminals in MST in a caudal location, close to the rostromedial boundary of MT, and labelled neurons and terminals in FSTd in a caudodorsal location. The DY injections produced only a few labelled neurons in the caudal portion of MST and no labelled neurons were observed in FST.

Our results indicate that MST may be a mirror reversal representation of MT. The peripheral lower visual field representation in the rostral portion of MT is adjacent to a similar representation in the caudal portion of MST and a lateral portion of FST. With a progression caudolaterally in MT, rostromedially in MST, and caudomedially in FST, more central fields are represented. The topographic relationship of these three fields to each other was best demonstrated in case 89-35 (Fig. 3) where foci of labelled cell bodies and axon terminals in MT and FST were adjacent, and labelled cell bodies and terminals in MT and MST were at opposite poles in each field. The labelled neurons were largely in supragranular layers, but some deeper neurons were also labelled.

DLr and DI. Sparse, patchy connections were found in the region of the dorsal intermediate area (DI) and in the region of the rostral division of the dorsolateral area (DLr). Evidence for the existence of DI is not as compelling as the evidence for MT (Allman and Kaas, '75; Krubitzer and Kaas, '90b). However, the present results provide additional support for a dorsal intermediate region interposed between DM and DL. Bidirectionally transported tracer, distant from the location of tracer in DLr and adjacent to the ventral and rostral boundaries of DM, was found in the location of DI. Labelled cell bodies and axon terminals in this region were split into two separate locations in all cases (Figs. 3–6). In two cases (Figs. 3 and 5), a sparse patch of bidirectionally transported tracer was found just rostral to area 18 and lateral to DM, and a separate patch of anterograde and retrograde label was found just rostral to DM and lateral to VPP. In another case (89-58, Fig. 6), labelled neurons and terminals in DI were in two distinct foci. The injections of DY in DM resulted in several clumps of labelled cells in DI. The separate locations of transported tracer suggest that the topography of DI may be complex with discontinuities or splits in the representation of the visual hemifield, or that the DI region contains more than one field.

All three WGA-HRP cases had sparse but obvious patches of anterograde and retrograde label in rostral portions of DL, in DLr. The patches of labelled cell bodies and terminals were in the central to medial portions of DLr, which are devoted to central vision and the paracentral lower quadrant representations, respectively. In addition, patches of labelled neurons and terminals were present more laterally in DLr in case 89-35 (Fig. 3), in a portion related to paracentral vision in the upper quadrant (see Allman and Kaas, '74b). The restriction of labelled cell bodies and axon terminals to the rostral part of the DL complex in these cases provides further support for the distinction between the rostral and caudal subdivisions, and the proposal that they are separate visual areas (see Cusick and Kaas, '88b).

M and VPP. Two fields adjacent to DM, M and VPP, have very dense interconnections with DM in all cases. Although the boundaries of M were often difficult to define, several dense patches of bidirectionally transported tracer could clearly be attributed to the region immediately adjacent to the medial portion of DM in all of the WGA-HRP cases (Figs. 3–6). Densely labelled cell bodies and terminals in M were in either one or two large clumps. The DY injections also labelled a large number of cells in M.

In all cases, we were able to recognise VPP as a densely myelinated oval of cortex just rostral to DM on the banks of the superior temporal sulcus (Fig. 1). VPP appears to be the major output target of DM. Labelled axon terminals and cell bodies in VPP formed a tightly packed cluster in two cases (Figs. 4–6), and were somewhat more broadly distributed, but in dense foci in the third case (Fig. 3). The DY injections also labelled neurons in VPP. Terminations were dense in middle cortical layers, while labelled neurons were in both supragranular and infragranular layers.

VP + VA and ITc. Transported tracer was consistently observed in two separate locations in the lower temporal lobe. Immediately rostral to the lateral portion of area 18, clumps of labelled cell bodies and axon terminal were observed in the VP + VA region after injections in DM (Figs. 3–6). In two of the three WGA-HRP cases, the transported tracer was in one clump or two closely spaced clumps (Figs. 5 and 6), and in one case (89-35, Fig. 3), transported tracer was in several clumps that spread across approximately 5 mm of cortex. In the DY case, most of the labelled neurons in VP + VA were in a single, large clump.

Sparsely labelled axon terminals were observed in the rostral half of ITc in three of the four cases. Although only anterograde label was found in ITc in the WGA-HRP cases, a few labelled cell bodies were found in the DY case. This result suggests that information flow from DM to ITc is largely unidirectional so that DM sends information to ITc but receives little direct information back.

FEF, FV, and FR. In the three cases where the frontal lobe was examined, transported tracer was observed in several locations. In a previous investigation, the frontal eye field (FEF) and frontal ventral visual area (FV) were electrophysiologically defined and found to be coextensive with two darkly myelinated ovals of cortex just rostral to the primary motor area, (M-I) in squirrel monkeys, owl monkeys, marmosets, and galagos (Kaas and Krubitzer, '88). A third myelinated oval was identified in the present study and was tentatively termed the frontal rostral field (FR) (Figs. 3 and 5). Bidirectionally transported tracer from injections in DM were consistently noted in FEF, FV, and in one case, FR. Transported tracer was within small clumps, and it appeared to be largely in axon terminals. However, in one WGA-HRP case (88-32), three labelled neurons were observed in FV, and several labelled neurons were in the same region in the DY case.

Other ipsilateral cortical connections. A few additional connections were observed in cortex other than the connections just described. However, these connections were not observed in all cases. In one case (89-35; Fig. 3), we noted labelled terminals and cell bodies in cortex immediately

medial to somatosensory area 2, and in another case (89-32; Fig. 5), labelled terminals were in two sparse clumps immediately caudal to area 2. One very small patch of anterograde label was noted in case 89-58 (Fig. 6), just rostral to the medial most portion of area 17 and ventral to the splenium of the corpus callosum.

Modular connections of DM with areas 17, 18 and MT

Area 17. A conspicuous feature of the zone containing transported tracer in area 17 was that the concentration of labelled neurons and terminal endings were in distinct foci that were highly regular in size and spacing (Figs. 3, 5, 7A, C). Since the CO blobs in area 17 have a similar distribution, it was natural to see whether the two patterns were related. We did this by using blood vessels and other tissue features to locally align regions of area 17 containing foci of labelled neurons and axon terminals with adjacent sections processed to reveal CO blobs (arrows in Fig. 7A and B). As shown in Figures 7A, B; 8A; 10A, almost all of the label in area 17 overlapped the CO blobs. Only a few scattered labelled neurons appeared to be outside of the blobs. The number of blobs containing labelled neurons varied from 184 (case 88-32, Fig. 4) to 11 (case 89-58; Fig. 6). Blobs generally contained 4–7 labelled neurons, but as many as 19 labelled neurons were found within a single blob (Figs. 8A and 10A). Blobs on the fringe of the labelled zone tended to have fewer labelled neurons than blobs in the centre of the labelled zone.

The laminar distribution of labelled cell bodies and presumptive axon terminals in area 17 was examined in one case where the cortical layers could be distinguished at the margin of the flattened cortex, where cortex curved and was cut nearly perpendicular to the layers (Fig. 9). Labelled neurons were predominantly in the superficial portions of layer III of Hassler ('67) and only a few neurons were as deep as the superficial part of layer IIIC (Layer IVb of Brodmann, '09). Thus, most of the labelled neurons were in the outer part of layer III where the CO blobs are found (for owl monkeys, see Horton, '84), rather than in layer IIIC, which is the major output layer to MT (see Weller et al., '84 for owl monkeys). The labelled processes that appear to indicate axon terminations were concentrated in layers I and II. Labelled terminations were more broadly distributed in area 17 and spread somewhat beyond the borders of individual blobs. The laminar distribution of labelled cell bodies and axon terminals was characteristic of a feedforward pattern from area 17 to DM, and a feedback pattern from DM to area 17 (Rockland and Pandya, '79).

Area 18. The spacing of rows of labelled neurons and axon terminals in area 18 suggested a possible relationship with the CO-dense bands and CO-sparse interbands that have been associated with three types of processing streams in primate vision (see DeYoe and Van Essen, '88 for review). Alternate sections processed for CO or HRP are shown for case 89-35 in Figure 7D and E. By using common blood vessels to align the two sections, it was apparent that labelled cell bodies and terminations in this case overlaid four consecutive CO-dense bands, including both the thin and thick bands. The CO-sparse interband regions were almost free of transported tracer. Reconstructions of patterns of transported tracer from all cases support conclusions that neurons in all CO-dense bands project to DM. The number of bands containing labelled neurons and axon terminals in area 18 was dependent on the size of the injection in DM. Thus, a small injection in DM resulted in transported tracer in only the rostral part of three bands in the medial portion of area 18 (Fig. 6). A larger injection in DM resulted in transported tracer in five bands in the lateral portion of area 18, and 3 bands in the medial portion of area 18 (Figs. 3 and 8B, case 89-35), and a very large injection in DM (Figs. 5 and 10B, case 88-32) labelled neurons and axon terminals in fifteen bands in area 18. As in area 17, the distribution of axon terminals was also restricted to the CO-dense bands, although the labelled terminals were more broadly distributed and included more of the CO bands than the labelled cell bodies. The anterograde label was noted mostly in superficial layers, while labelled cell bodies were in supragranular layers. This pattern is indicative of a feedforward projection from area 18 to DM.

MT. In all cases, both anterograde and retrograde label in MT was patchy and discontinuous. Because discontinuities in MT have been demonstrated in myelin (Krubitzer and Kaas, '90b) and CO (Tootell et al., '85) stains, we tried to match our label to these architectonic distinctions. In one case in which the CO preparation was favourable, CO-dense regions surrounded by CO-sparse regions could be readily identified. When CO stains were matched with sections containing labelled cell bodies and axon terminals, both labelled cell bodies and axon terminals were coextensive with the CO-dense regions and avoided the CO-sparse regions in MT (Fig. 10C).

Callosal connections of DM

The callosal connections of DM were investigated in two owl monkeys. In both cases, injections in DM produced dense clusters of labelled neurons and terminals in DM of the opposite hemisphere in roughly a location homotopic to the injection site (Fig. 11A and B). Less dense foci of labelled cell bodies and terminals were located just rostral to DM in VPP in both cases. Examination of the corpus callosum in these two cases indicated that the interhemispheric axons course through the caudal fourth of the corpus callosum.

Evidence for DM in other primates

Myeloarchitecture. While DM has been fully demonstrated only in owl monkeys, a region resembling DM in position, myeloarchitecture, and connections with MT has been described in squirrel monkeys, marmosets, and galagos (Krubitzer and Kaas, '90b). In owl monkeys, DM is a densely myelinated rectangle of cortex on the rostral border of dorsomedial area 18 (Fig. 12B). A densely myelinated wedge of cortex in the relative position of DM is also obvious in other primates and some of these are depicted in Figures 12A (galago) and C (talapoin) and 13 (marmoset). The major difference in DM across primates is the shape. DM is more elongated along the area 18 border in squirrel monkeys and Old World monkeys than in owl monkeys, galagos and marmosets.

In addition to DM, a number of cortical fields are distinct in our preparations (e.g., Fig. 13; also see Krubitzer and Kaas, '90b). First, area 17 has a lattice-like appearance in superficial layers with myelin-light regions surrounded by myelin-dense regions (not shown). These myelin patterns in superficial layers are the negative of CO blob and interblob regions (see Fig. 1 of Krubitzer and Kaas, '89b). In middle and deeper cortical layers, area 17 stains more densely and homogeneously for myelin. Area 18 also stains heterogeneously for myelin, with myelin-dense and light

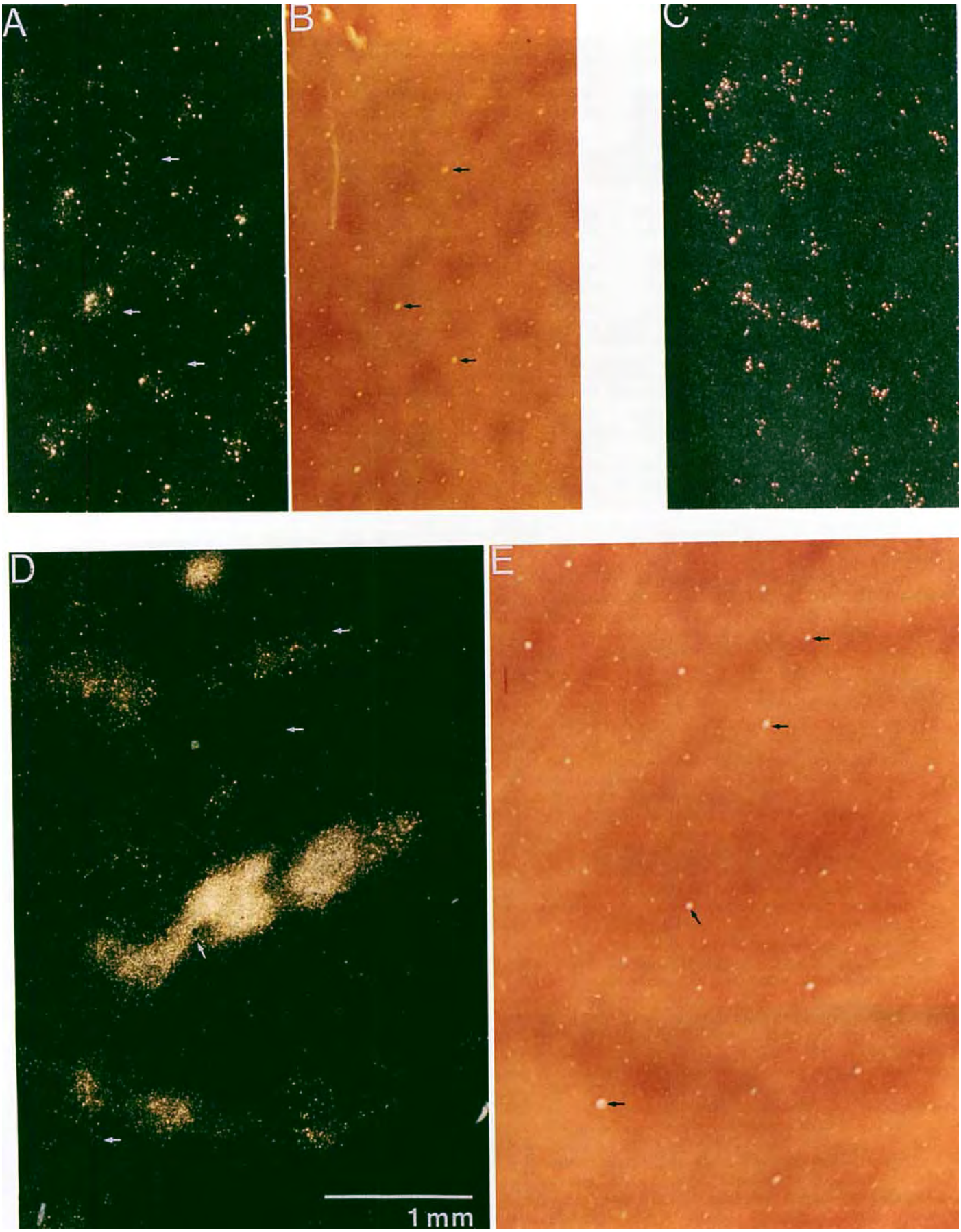

Figure 7

bands running the entire rostrocaudal width of the field (not shown here, but see Krubitzer and Kaas, '89b, '90b). Again, myelin dark regions in area 18 correspond to CO-sparse interband regions. Another area that stains consistently across primates is MT. MT stains very densely for myelin in most cortical layers (Fig. 13). However, in favourable preparations, myelin-dense regions appear mottled and interdigitate with myelin-light regions (see Krubitzer and Kaas, '90b). In all primates examined, FST is in the same relative position and stains moderately for myelin.

Connections with area 17. Another feature of DM in owl monkeys is connections with area 17. Present results indicate that injections of WGA-HRP in DM label neurons and terminals in area 17 (Figs. 3–6). Connections between DM and area 17 have also been demonstrated by injections of ^{3}H-proline and HRP into area 17 of owl monkeys (Lin et al., '82). In this section of the paper, we describe the cortical connections of area 17 in flattened cortex in an owl monkey, so that results can be directly compared with our owl monkey cases with DM injections. Then we describe patterns of connections of area 17 in other species of New World monkeys, prosimian primates, and Old World monkeys. The results suggest that the entire representation in area 17 has three major targets in all primates, area 18, MT, and DM. An additional connection with DL is also found when the part of area 17 representing central vision is injected.

Owl monkey. In one owl monkey, a large injection of WGA-HRP was placed in the caudal pole of the hemisphere in a dorsolateral portion of area 17, representing central vision along the horizontal meridian (Allman and Kaas, '71). The pattern and the relative densities of labelled cells and axon terminals are readily appreciated in the flattened preparation (Fig. 14). Patches of local, intrinsic connections, similar to those previously described in squirrel monkeys (Rockland and Lund, '83), were apparent around the injection site, which was split by the flattening procedure. In addition, patches of bidirectionally transported tracer were found in both medial and lateral locations in area 18 in portions representing paracentral vision some 10° from the centre of gaze along the horizontal meridian, and extending into both the lower and upper quadrant representations (see Allman and Kaas, '74a). Another zone of transported tracer was in caudal MT in a representation that is devoted to paracentral vision at the horizontal meridian. The third zone of transported tracer was less dense, and in the midportion of caudal DM which represents paracentral vision near the horizontal meridian some 10–15° from gaze. Thus, as expected (Lin et al., '82), connections were retinotopically matched with three targets, and more dense with area 18 and MT than with DM.

Marmoset. In one marmoset, an injection of WGA-HRP was placed in area 17 in the expected location of the representation of the horizontal meridian several degrees from the centre of gaze (Fig. 15). Again there was evidence for patchy, local intrinsic connections, and patchy connections both medially and laterally along the rostral border of

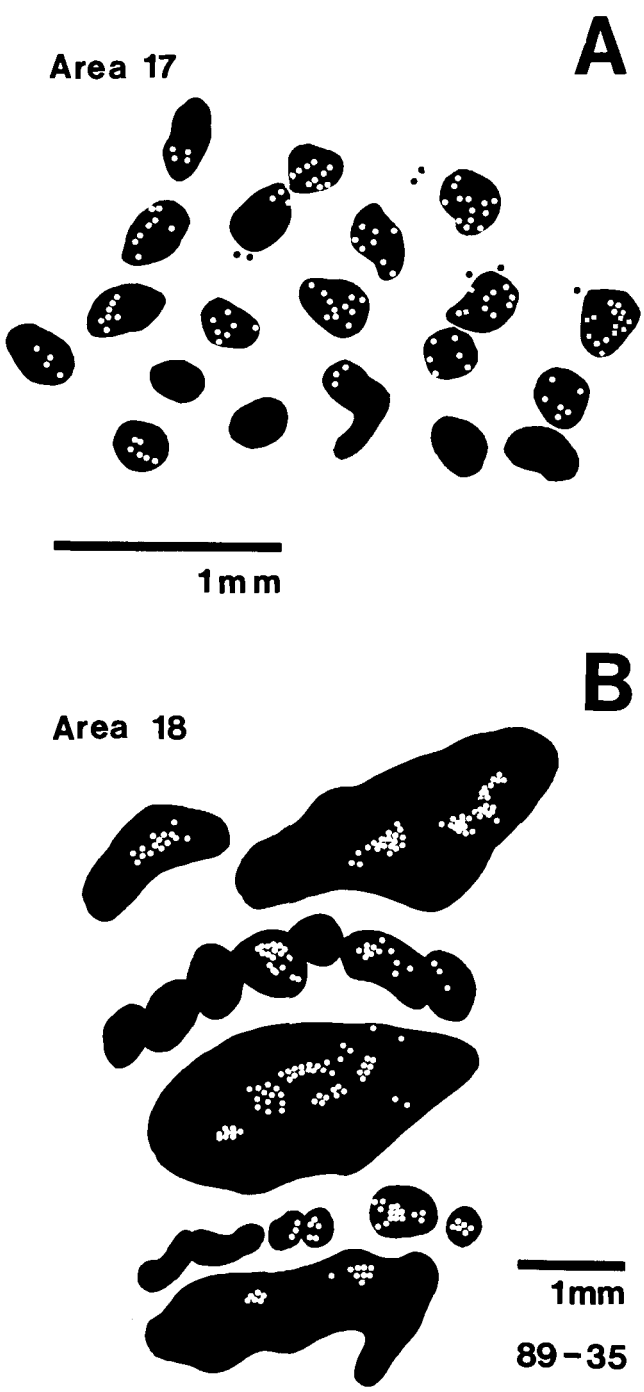

Fig. 8. Graphic reconstructions of labelled cell bodies in areas 17 (**A**) and 18 (**B**) resulting from an injection of WGA-HRP in DM in owl monkey 89-35. Solid black indicates CO-dense regions. White dots denote labelled cell bodies. With little exception, cells in area 17 are in CO-dense blobs, while cells in area 18 are in every CO-dense band. Bands of labelled cells in area 18 are both thick and thin. The total extent of transported tracer in area 17 is not shown (see Fig. 3 for the total extent of label in area 17).

Fig. 7. Darkfield photomicrographs of transported tracer in area 17 in case 89-35 (**A**) and 88-32 (**C**), and in area 18 in case 89-35 (**D**). Sections processed for cytochrome oxidase (**B**) and (**E**) were taken at the same magnifications as A and D. The arrows point to the same blood vessels in each section. Blood vessels were used to align the different sections so that labelled cell bodies and axon terminals could be related to cortical architecture. Labelled cells in area 17 (A) are in small puffs that are coextensive with the cytochrome oxidase blobs (B). In area 18, thick and thin bands of labelled cells and axon terminals (D) are coextensive with every cytochrome oxidase rich band (E). Sections are from supragranular layers of flattened cortex. Scale bar = 1 mm for A–E.

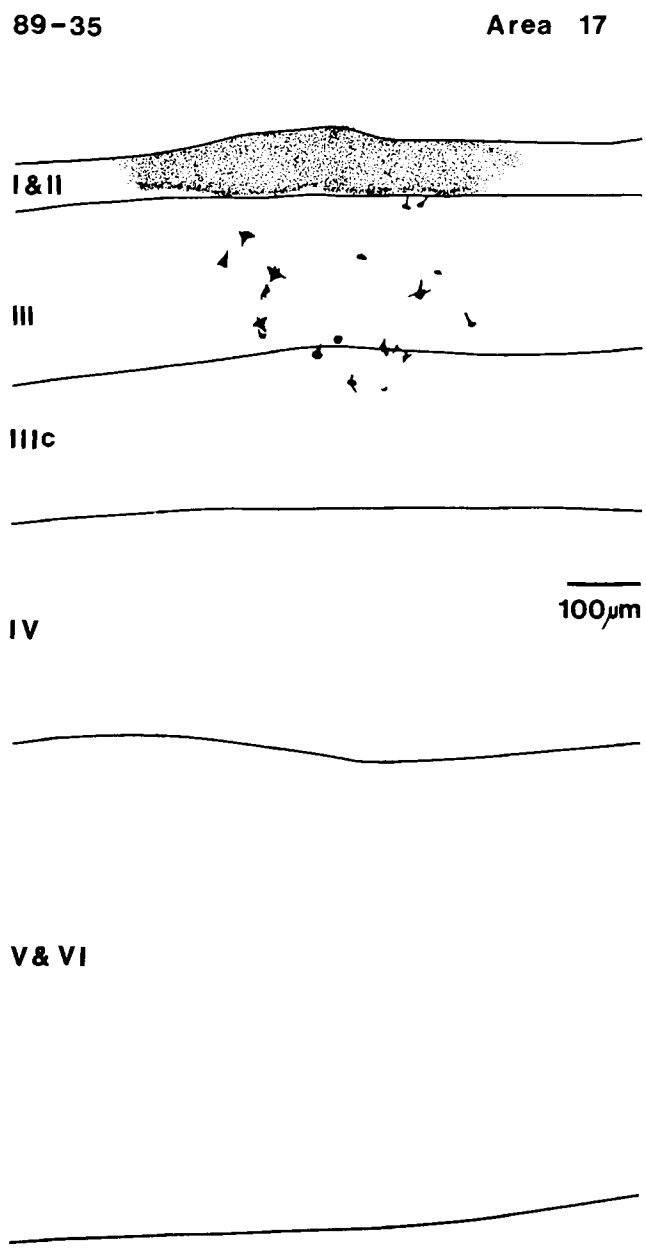

Fig. 9. A reconstruction of laminar patterns of labelled neurons and axon terminals in area 17 resulting from a DM injection in owl monkey 89-35. In this case, the laminar distribution of labelled cells and terminals could easily be discerned by matching adjacent myelin stained and cytochrome oxidase sections with sections containing labelled cell bodies and axon terminals. Retrogradely labelled cell bodies were predominantly in superficial layer III and a few labelled cells were in the superficial portion of layer IIIc. Anterogradely labelled axon terminals (fine dots) were in layers I and II and were more broadly distributed. Layers after Hassler ('67).

area 18 corresponding to the horizontal meridian. Patchy concentrations of labelled cell bodies and axon terminals were also observed with the caudal half of MT representing central and paracentral vision. Another focus of labelled cell bodies and axon terminals was in cortex we defined by location and dense myelination as DM. In marmosets, DM appears to be more wedge-shaped in myelin-stained sections (Fig. 13). The location of the label suggests that central and paracentral vision are represented more laterally in DM in marmosets than in owl monkeys.

Squirrel monkey. In one squirrel monkey, a large injection (Fig. 16) of WGA-HRP was placed in caudolateral area 17 representing central vision of the upper visual quadrant (Cowey, '64). The injection also involved cortex of the upper bank of the calcarine fissure, but this second region in area 17 produced no transported tracer in visuotopically matched parts of area 18 or MT. The injection produced some intrinsically transported tracer within 2 mm of the injection site. Dense patches of labelled neurons and terminals were in ventromedial area 18 and in MT, and a clear focus of labelled neurons and terminations was in DM. Because of the involvement of the injection in the central visual representation in area 17, sparsely labelled neurons were also in DLc. Similar results were obtained in a second squirrel monkey (not shown) with a smaller injection into dorsal area 17, except there was less transported tracer in all targets.

Galago. A previous report described extremely sparse amounts of transported tracer in the region of DM in some, but not all cases of area 17 injections in galagos (Cusick and Kaas, '88a), suggesting that a pathway to DM exists, but is minor in prosimians. To further test this hypothesis, we placed multiple injections of WGA-HRP in dorsolateral area 17 in two galagos. Results were similar in both cases. As shown in Figure 17, intrinsic connections around the injection site were patchy and similar to those described previously by Cusick and Kaas ('88a). Patches of dense anterograde and retrograde label were found in central parts of area 18, representing central and paracentral vision, and in caudal MT, also representing central and paracentral vision. A moderately dense focus of labelled neurons and terminations were also observed in central DL, as previously reported for injections close to or involving central vision in area 17 (Cusick and Kaas, '88a). Finally, sparse patches of labelled neurons and terminals were found in central DM as defined by myeloarchitecture and position. As in marmosets, DM in galagos appears to be wedge-shaped rather than rectangular.

Talapoin monkey. Injections of WGA-HRP were placed into parts of dorsal area 17 representing central and paracentral vision of the lower quadrant in two Old World talapoin monkeys. In one case (Fig. 18), an injection just medial to the approximate location of the representation of the horizontal meridian produced only a few local foci of intrinsic connections in area 17. A single, dense zone of labelled neurons and terminations was in medial area 18 in the portion representing paracentral vision of the lower quadrant, and also in a location in caudomedial MT, devoted to paracentral vision of the lower quadrant. A large, dense focus of labelled cell bodies and axon terminals was found in a myelin-dense wedge in the expected location of DM. This location presumably represents parafoveal vision near the horizontal meridian of the lower visual quadrant.

In a second talapoin monkey, (not shown) one small injection of WGA-HRP was placed mediocaudally and another smaller injection of WGA-HRP was located rostrolaterally in parts of area 17 representing foveal (the rostralward bulge) and parafoveal vision of the lower quadrant, respectively. A focus of labelled neurons and terminals was immediately rostrolateral to the bulge in part of area 18 related to foveal vision, and another smaller focus of transported tracer was more medial in area 18 representing the lower quadrant. Two locations also contained labelled neurons and axon terminals in caudal MT. Finally, antero-

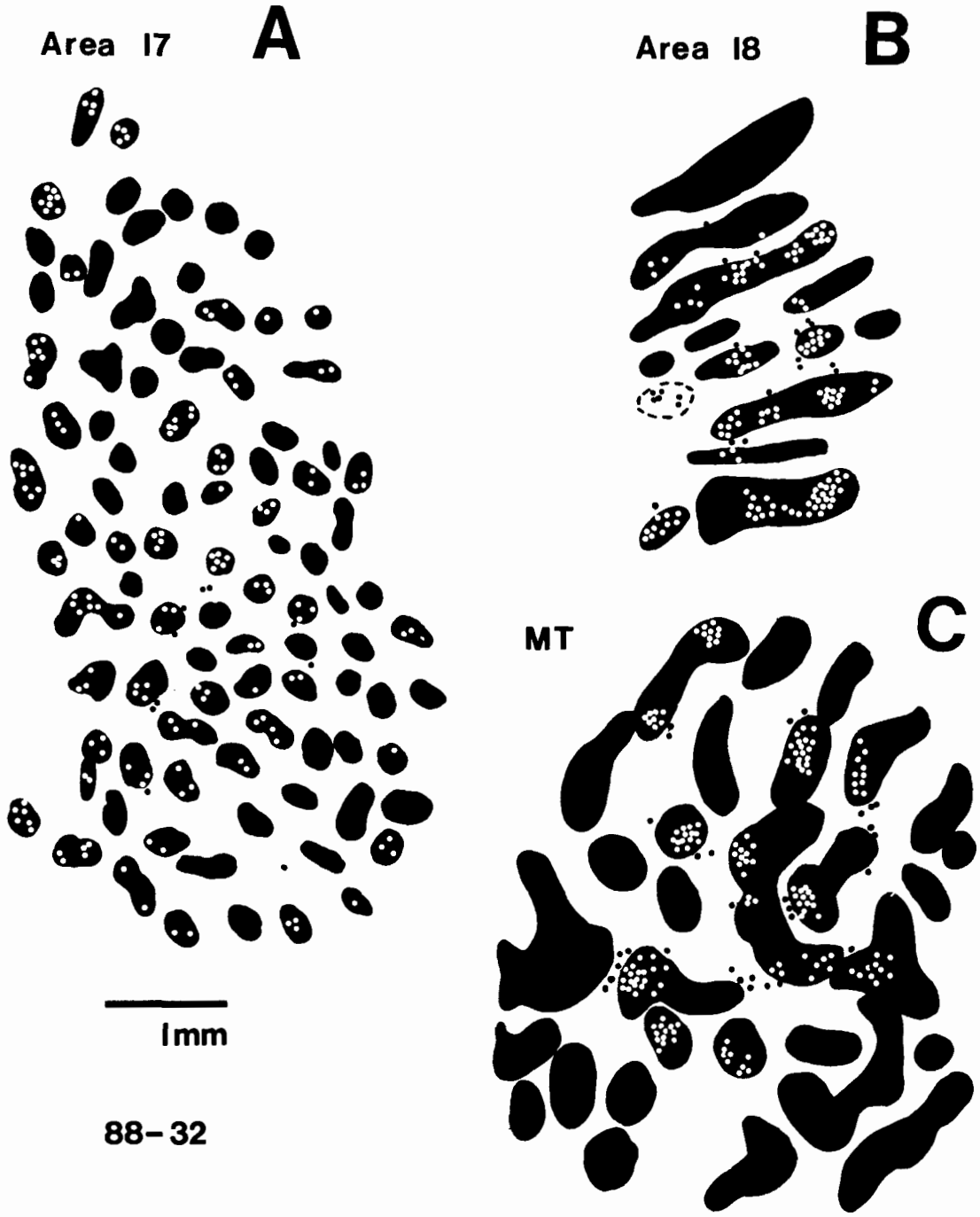

Fig. 10. Graphic reconstructions of retrogradely labelled cells in area 17 (**A**), 18 (**B**), and MT (**C**), relative to cytochrome oxidase-dense regions (black) for case 88-32. Labelled cells in area 17 are in CO-dense blobs, and labelled cells in area 18 are in every CO-dense band. Bands were not obviously distinguishable as thick or thin in this case. Labelled cells in MT were also in patches and were coextensive with a CO-dense mottled pattern. The total extent of labelled neurons and terminals in areas 17 and 18 is not shown. The dotted line in B represents an approximated boundary. Modified from Krubitzer and Kaas ('90a).

grade and retrograde label in DM was in an elongated zone in the caudolateral portion of the field, suggesting a convergence of connections from area 17 to DM.

Patas monkey. In one Old World patas monkey, a series of seven closely spaced injections of WGA-HRP were placed in a dorsolateral portion of area 17 near the border of area 18 (Fig. 19). In macaque monkeys (see Weller and Kaas, '83), and presumably in patas monkeys, this cortex represents central vision of the upper visual quadrant. The injections produced labelled cell bodies and axon terminals in scattered foci in area 17, dense patches of neurons and terminals in adjoining ventral area 18, several small patches in MT, a location in DL (V4), and three distinct patches in the DM region.

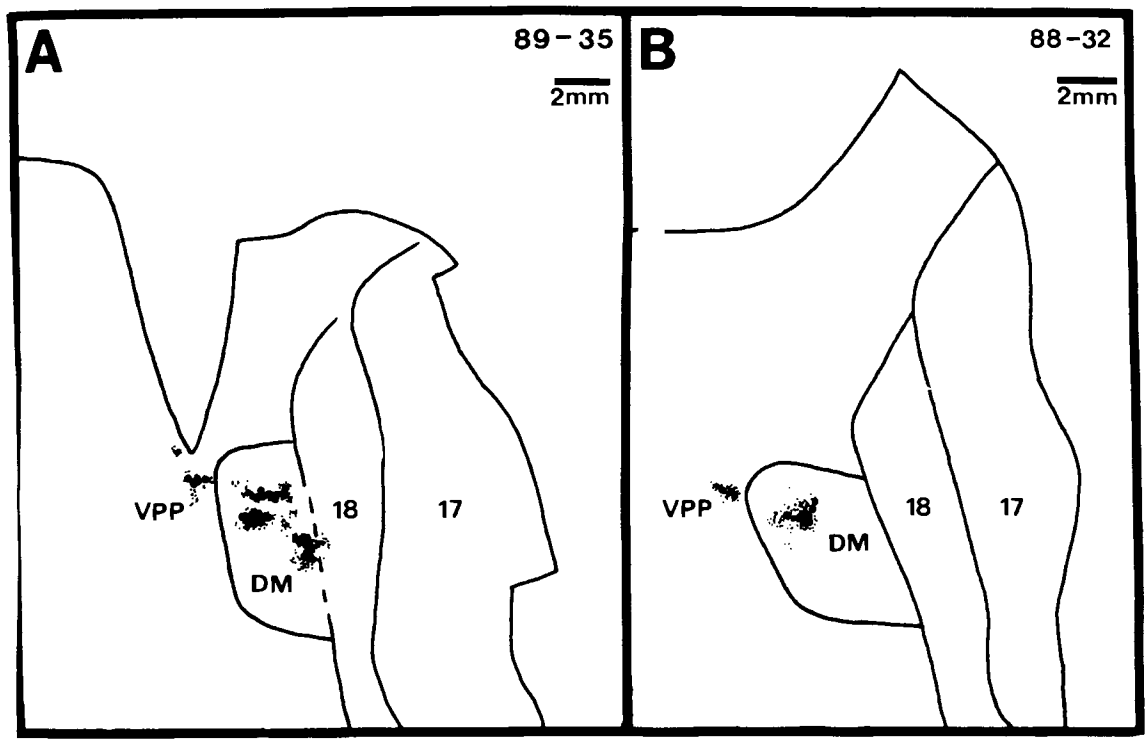

Fig. 11. Callosally transported tracer from DM injections for case 89-35 (**A**), and 88-32 (**B**). In each case, transported tracer is most dense in a mirror symmetric location to that injected in the contralateral hemisphere. Additional anterograde and retrograde label is also in VPP.

Macaque monkeys. Injections of WGA-HRP were placed in area 17 of two macaque monkeys. In one case, a large injection was placed in dorsolateral area 17 near the representation of the horizontal meridian. Resulting bidirectionally transported tracer was in area 18 (V-II), DL (V4), MT and the DM region. Such a pattern has been demonstrated in a number of previous studies (see Discussion). In the second macaque, a row of 9 injections was made in dorsolateral area 17 in the representation of central vision of the upper quadrant (Fig. 20). Labelled neurons and terminations were in ventral area 18, near the representation of central vision in the upper quadrant, and in MT in a similar representation. A very small patch of labelled cell bodies and terminals was in DL/V4, and several small clusters of labelled cell bodies and axon terminals were clearly identified in a darkly myelinated wedge of cortex just rostral to the medial border of area 18, in the DM region. The results indicate that inputs from the upper visual quadrant representation in area 17 reach the DM region in macaque monkeys.

DISCUSSION

The general principle that the neocortex of mammals is subdivided into a patchwork of areas, each having a different and at least partially unique functional role, is widely accepted. However, specific schemes of how cortex is subdivided in primates continue to differ (e.g., Boussaoud et al., '90; Sereno and Allman, '91; Felleman and Van Essen, '91; Kaas and Krubitzer, '91; Sousa et al., '91). Nevertheless, some cortical areas have been identified with assurance in several primate taxa. Most notably, areas 17 (V-I), 18 (V-II), and MT are visual areas that are clearly defined and widely recognised in a range of primate species although, until a few years ago, descriptions of V-II as area 18 varied greatly, and no field approximating MT was recognised in classical architectonic descriptions. We have suggested (e.g., Krubitzer and Kaas, '90b; Kaas and Krubitzer, '91) that the number of visual areas common to all or most primates is likely to be greater than three, and have provided architectonic and connectional evidence for considering as many as seven visual areas as part of a basic primate plan. The present report examines the validity of one of these proposed subdivisions in owl monkeys, DM, and provides evidence that this dorsomedial visual area is a common subdivision of the primate visual system (Fig. 21). Toward this effort, we have examined the architecture, retinotopic organisation, and connections of DM in owl monkeys, and then examined other primates for identifying features of DM, such as relative position, input from area 17, and dense myeloarchitecture. We conclude that DM is a valid subdivision of visual cortex in owl monkeys, and that DM exists in

Fig. 12. The myeloarchitecture of neocortex in the DM region in a galago (**A**), an owl monkey (**B**), and an Old World talapoin monkey (**C**). The densely myelinated DM and VPP regions are outlined in thin black lines. In all species, cortex has been flattened, cut parallel to the cortical surface, and stained for myelin. DM stains darkly for myelin relative to area 18 caudally, DI, laterally, and M, medially. A darkly myelinated oval of cortex just rostral to DM is termed VPP. These sections are taken from the middle cortical layers. Xs mark the darkly staining white matter. Rostral is to the right and medial is to the top. Other conventions as in previous figures.

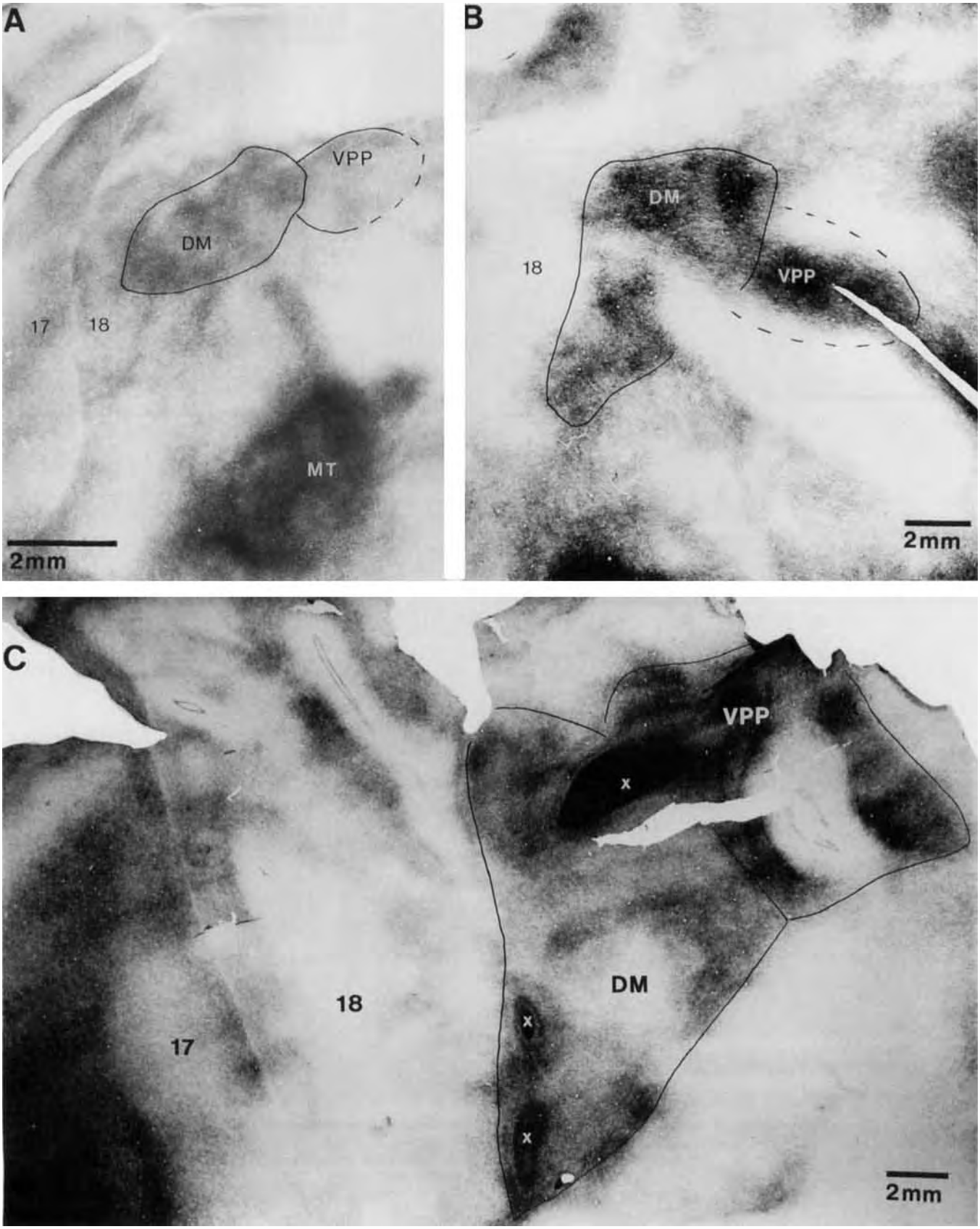

Figure 12

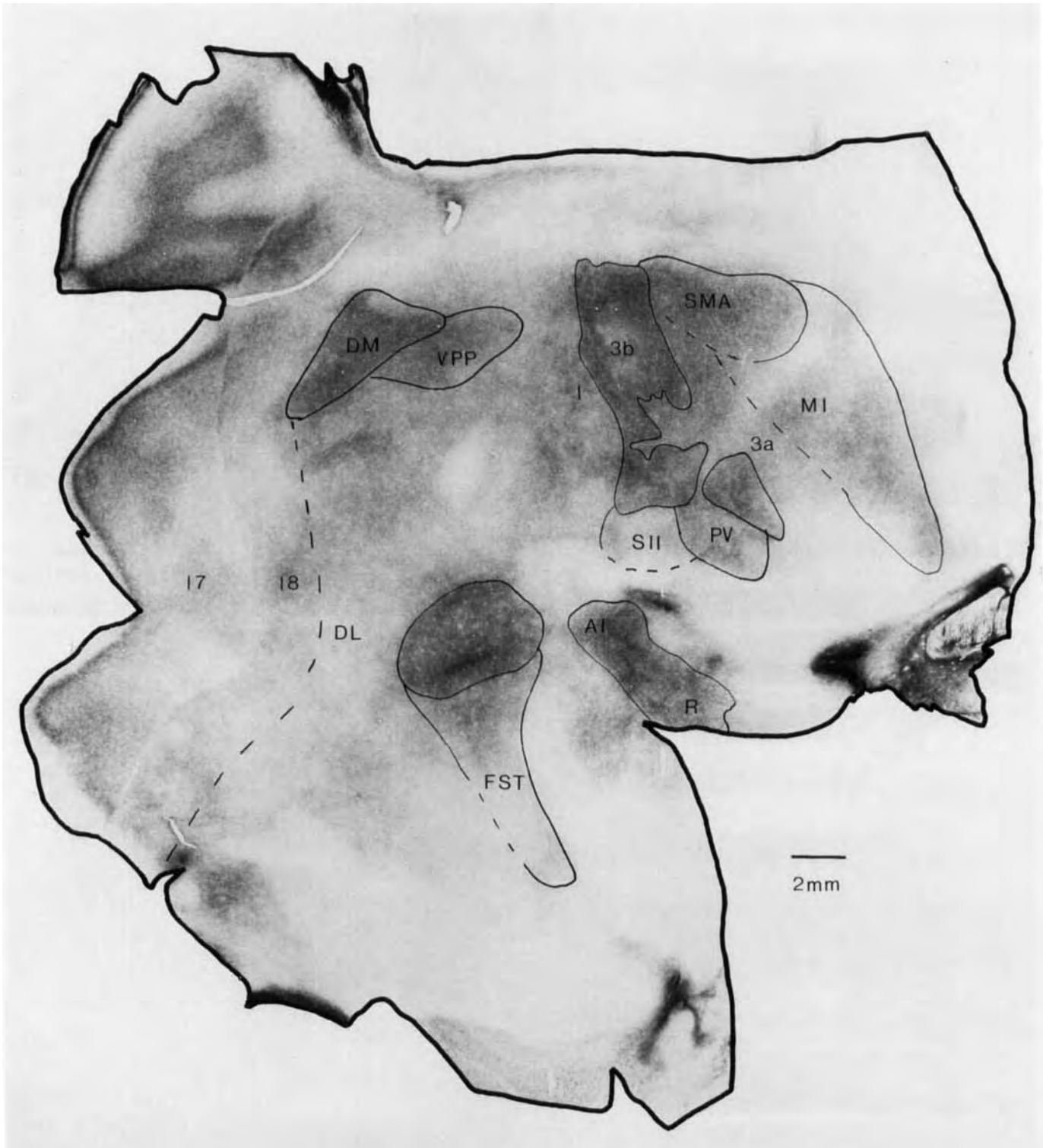

Fig. 13. The myeloarchitecture of neocortex in a marmoset. Note similarities in myelin staining and relative position of DM and surrounding cortical fields with Figure 12. Also apparent in this figure are cortical fields 17, MT, FST, VPP, auditory fields A1 and R, and somatosensory area 3b. Other fields were defined when the entire series of sections was analysed. Because this preparation gives the position of fields in the entire neocortex, the relative position of fields to each other is an important criterion.

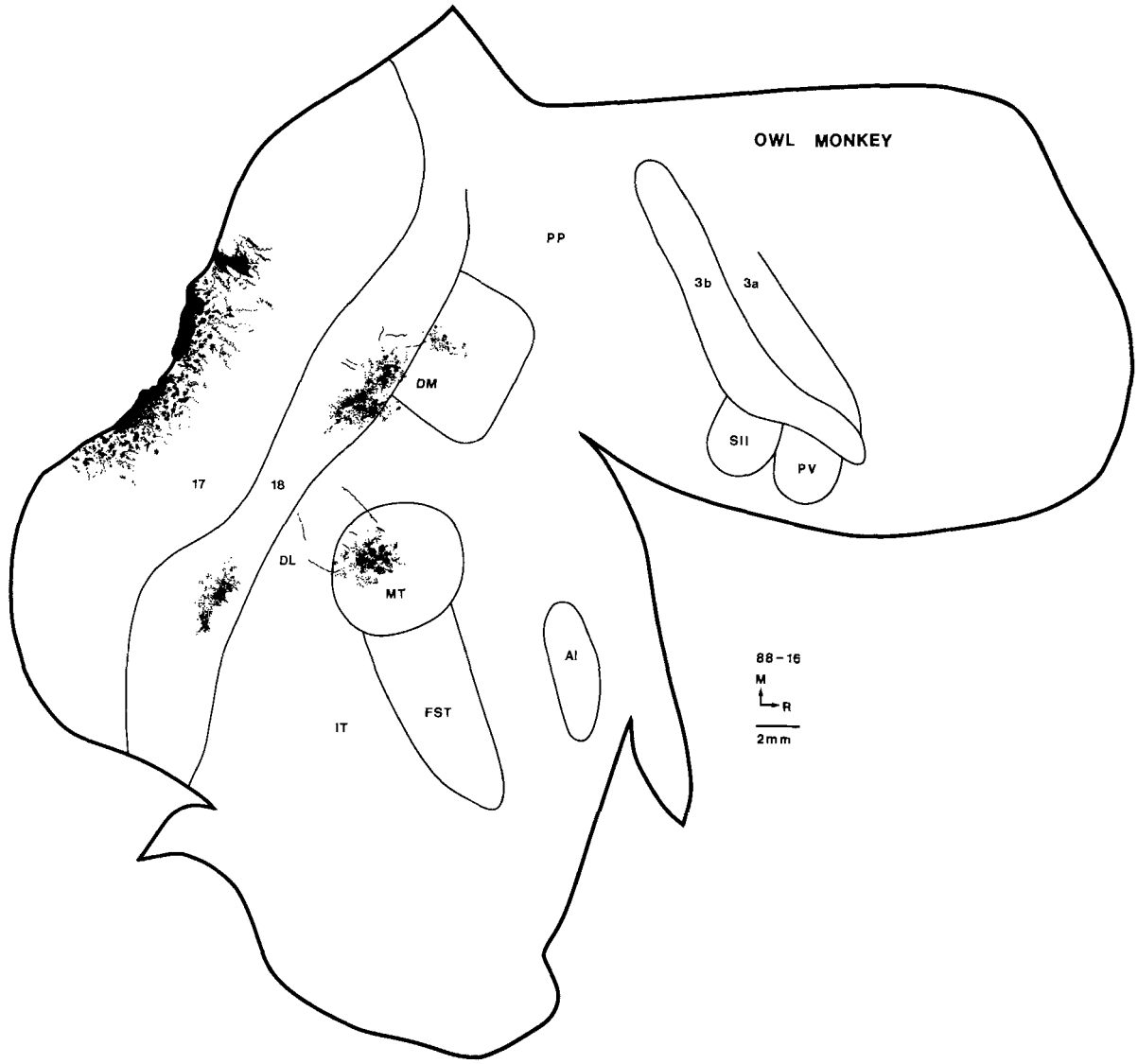

Fig. 14. Connections of area 17 in owl monkey 88-16. An injection of WGA-HRP was placed in a part of area 17 representing paracentral vision along the zero horizontal meridian. Labelled cell bodies and axon terminals have been reconstructed and related to myeloarchitecture in sections cut parallel to the surface of the flattened cortex. Because of cuts in calcarine cortex and the flattening of cortex, the injection site (black) appears split. Local transported tracer in area 17 was patchy and located as far as 3 mm from the injection site. Patchy connections are also apparent in medial and lateral portions of area 18, and in central MT. Sparse connections were in caudal DM. Conventions as in previous figures.

a range of primate species. Thus, schemes of visual cortex organisation in other primates should include a DM. In addition, we provide further information on the connections of DM that indicate that the field is predominantly part of the dorsal stream of visual processing (Ungerleider and Mishkin, '82), while having access to inputs typically associated with both the ventral and dorsal streams (see DeYoe and Van Essen, '88).

DM is a valid visual area in owl monkeys

As Brodmann's ('09) "organs of the brain," cortical areas should have structural and physiological distinctions reflecting their unique and specialised functional roles. There is a general consensus that cortical areas can be identified by architectonic and histochemical features, patterns of connections with other structures, and, for sensory fields, the presence of a systematic representation or map of a receptor surface (e.g., Campbell and Hodos, '70; Kaas, '82, '90; Rosenquist, '85; Van Essen, '85; Sereno and Allman, '91). Other types of evidence, such as the presence of a population of neurons with distinctive reponse properties and the specific deactivation effects on behaviour, can provide useful experimental support for proposed subdivisions. However, cortex is subdivided with the greatest accuracy when several types of evidence are used in combination. Common errors in subdividing cortex include placing all or parts of several areas in a single area, or subdividing parts of individual areas into separate fields. For example, the traditional area 18 of macaque monkeys (and humans) clearly contains several visual areas including V-II (the

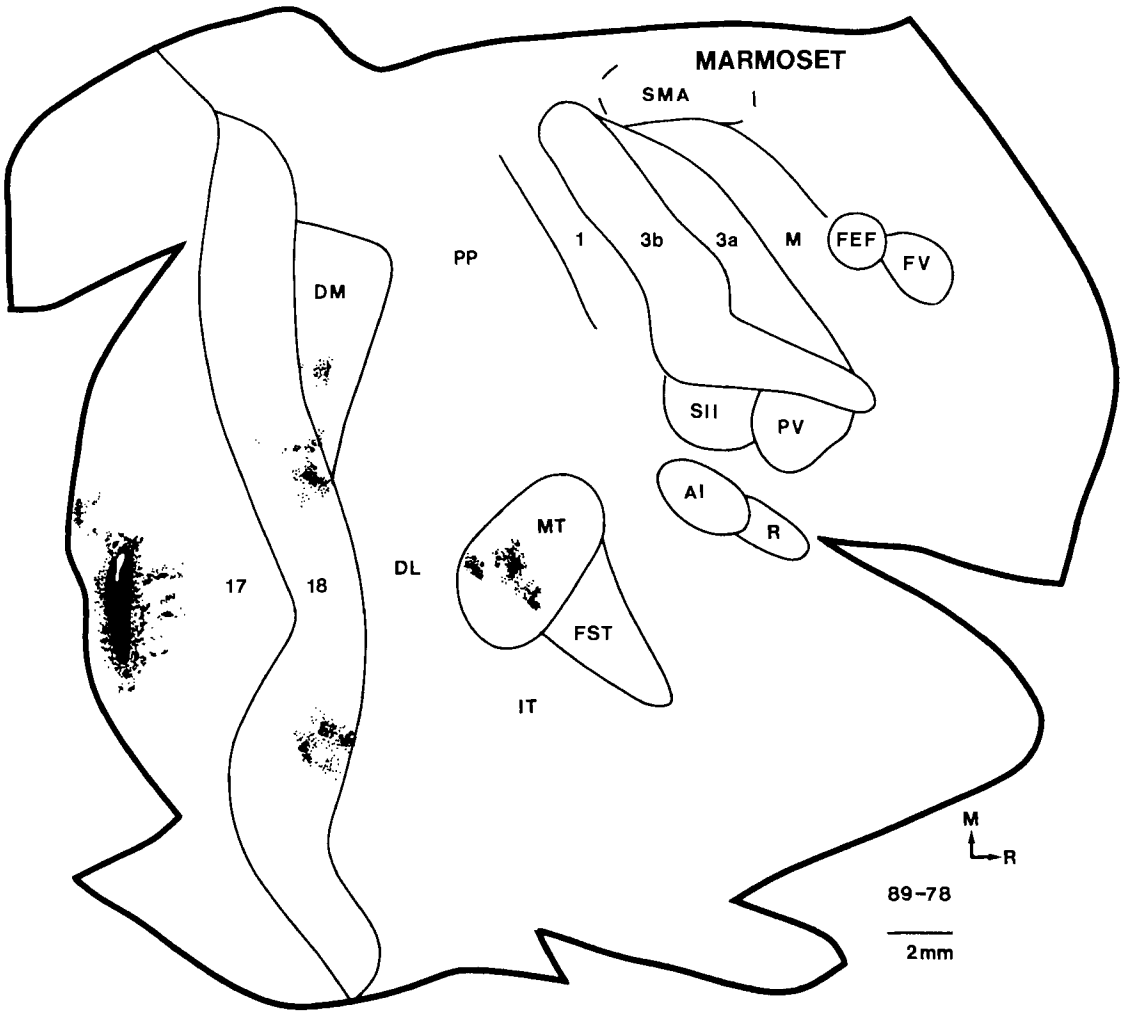

Fig. 15. Connections of area 17 in marmoset 89-78. As in the owl monkey in case 88-16 (Fig. 14), the injection of WGA-HRP was in part of area 17 representing paracentral vision along the zero horizontal meridian. Patchy anterograde and retrograde label was located in central MT, medial and lateral parts of area 18, and in DM. Conventions as in previous figures.

contemporary "area 18") and the extrastriate areas bordering area 18. Also, Brodmann ('09) appears to have considered the distinct, monocular portion of area 17 in squirrels as a medial portion of area 18.

In owl monkeys, DM seems to have the important identifying features of a visual area. First, DM contains a small, *second order* (split) representation of the contralateral hemifield in a rectangle of cortex along the rostral border of dorsomedial V-II (Allman and Kaas, '75; present results). Second, response properties of single neurons in DM are consistant throughout the DM representation (Petersen et al., '80, '88; Baker et al., '81). Thus, DM appears to be a single visual area rather than a composite of parts of two or more fields. Third, DM has been outlined by myeloarchitectonic criteria in a number of studies (Allman and Kaas, '75; Wagor et al., '75; Krubitzer and Kaas, '90b). The area is also distinguished in brain sections processed for cytochrome oxidase (Tootell et al., '85). In the present investigation we demonstrated that the complete outer border of DM can be seen in single brain sections cut parallel to the surface of flattened cortex and stained for myelin, and that the representation of the visual hemifield corresponds to this distinct myeloarchitectonic field. Thus, architectonic distinctiveness is a reliable feature of DM. Fourth, it is apparent from this study and the earlier report of Wagor et al. ('75) that DM has a distinctive pattern of connections with other visual areas, and that different locations in DM have similar patterns of connections with other visual areas. Finally, DM is bordered by several distinguishable visual areas. The complete caudal border of DM is formed by part of area 18, which can be reliably identified by retinotopic features and architectonic characteristics (Allman and Kaas, '74a; Tootell et al., '85; Krubitzer and Kaas, '90b; present report). The medial edge of DM borders the medial area, M, which contains another systematic representation of the visual hemifield (Allman and Kaas, '76), is less densely myelinated than DM (e.g., present report), and has a different pattern of connections with other visual areas (Graham et al., '79). VPP and other portions of posterior parietal cortex border DM rostrally, and this cortex is less responsive to visual stimuli in anaesthetised monkeys, has different architectonic fea-

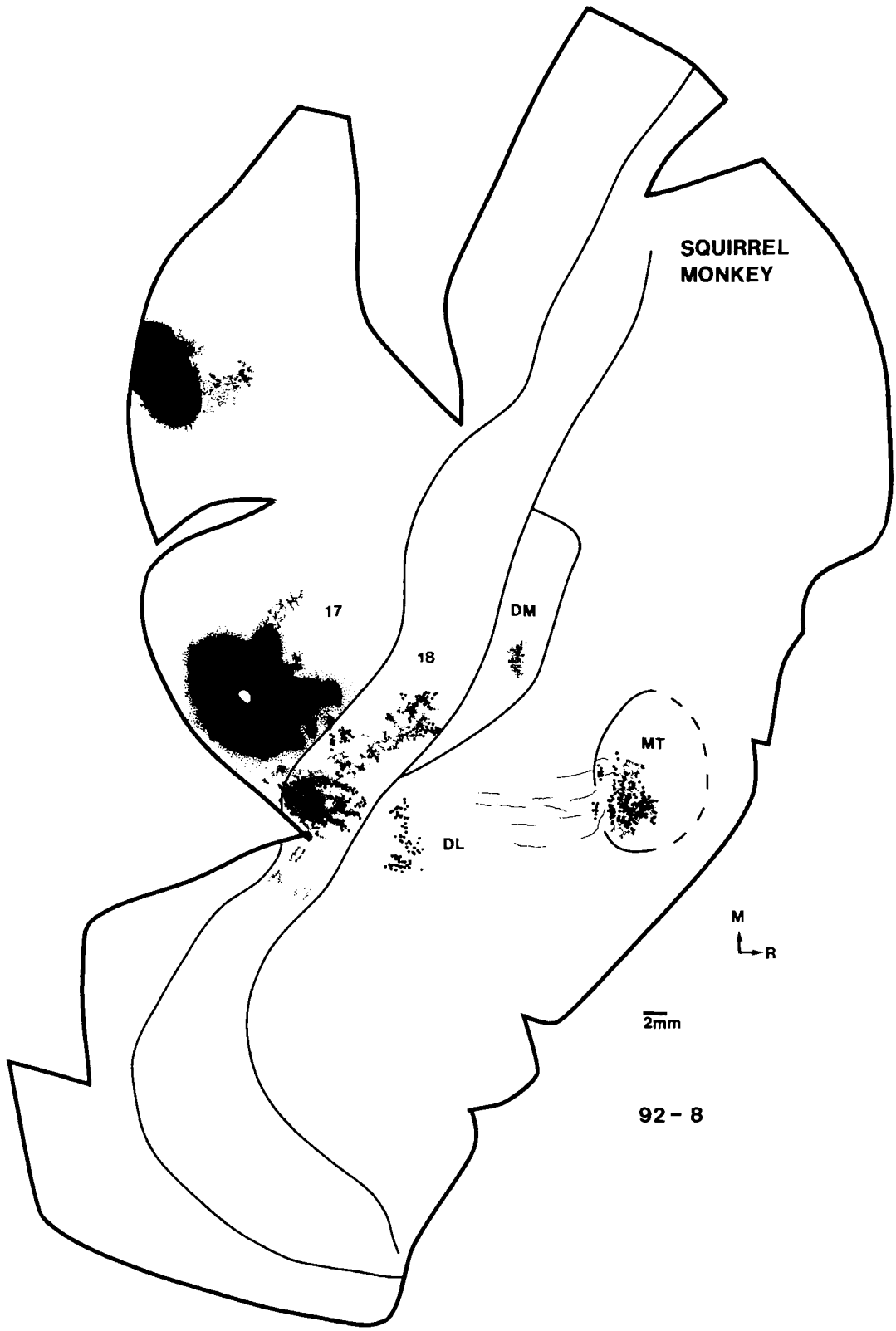

Fig. 16. Connections of area 17 in squirrel monkey 92-8. In this case, an injection of WGA-HRP was placed in the upper visual quadrant representation in area 17, just lateral to the representation of central vision. The injection spread slightly into the representation of the peripheral horizontal meridian in the calcarine cortex, but little, if any, transported tracer appears to have resulted from this spread. As in the previous cases, bidirectionally transported tracer is dense in area 18, in the representation of the upper visual quadrant just off central vision, in area MT in the expected location of the upper central quadrant representation, and in the DM region. A few labelled cell bodies were apparent in the dorsolateral visual area, due to the location of the injection near the representation of central vision. Conventions as in previous figures.

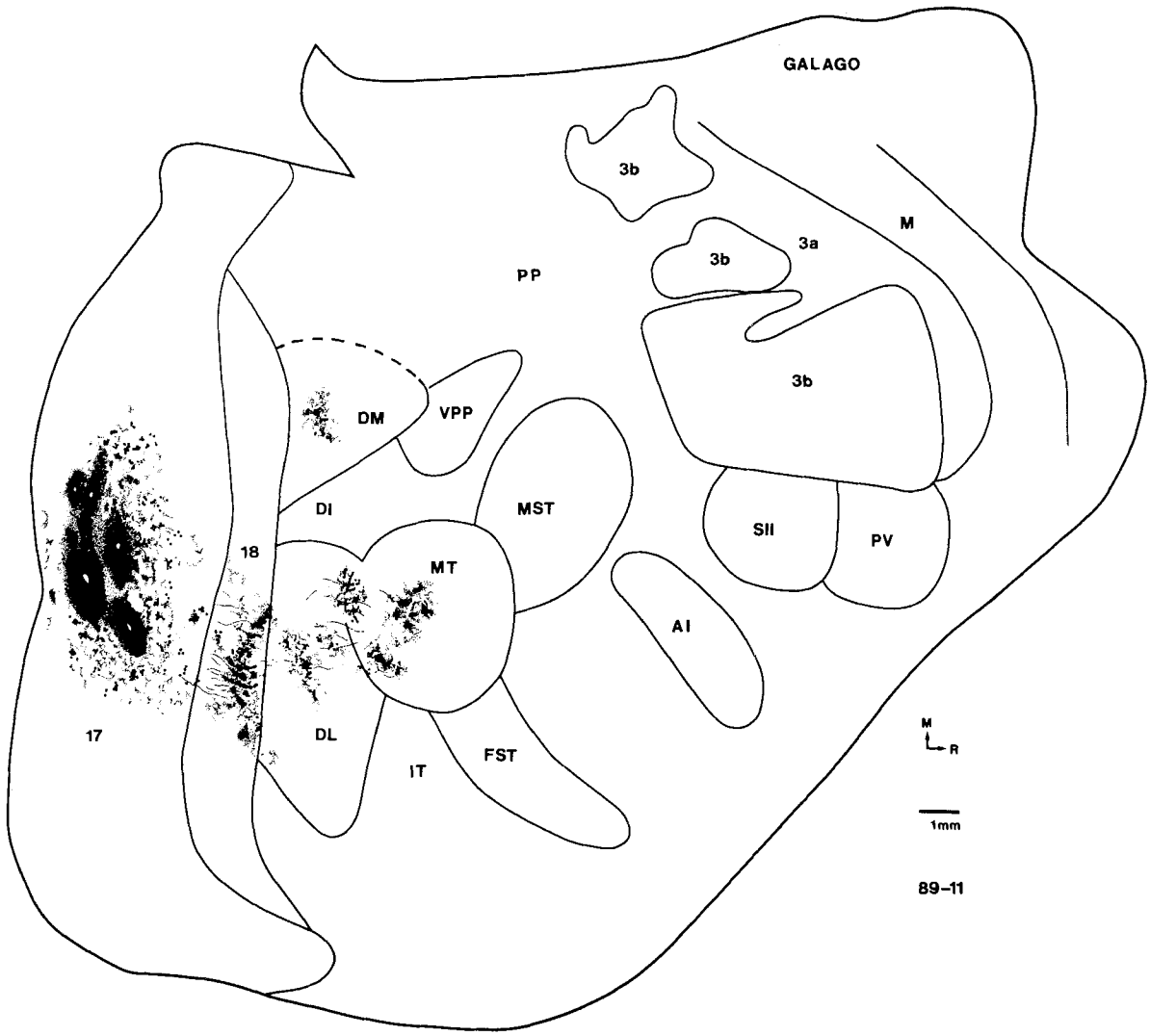

Fig. 17. Connections of area 17 in galago 89-11. In this case, five small injections of WGA-HRP were placed in area 17 in the representation of the upper quadrant and included portions of the horizontal meridian and central vision representation. As in the previous cases, bidirectionally transported tracer was observed locally in area 17, in area 18, in MT, and in DM. As in the squirrel monkey where portions of the central field representation were involved in the injection site, transported tracer in this case was also observed in DL.

tures, and different connections with other areas of cortex (e.g., Allman and Kaas, '75; Kaas et al., '77; present report). Taken together, features of retinotopic organisation, physiological uniformity of neurons, architecture, connections, and relative position all support the proposal that DM is a valid subdivision of visual cortex in owl monkeys.

The connections of DM, and the role of DM in visual processing

This is the first full report on the cortical connections of DM in owl monkeys. Although some of the connections of DM have been previously reported (Wagor et al., '75; Lin et al., '82), modular connections of DM with areas 17, 18, and MT, and connections of DM with the frontal lobe have not been described.

DM receives feedforward inputs from areas 17 and 18. An early degeneration and autoradiographic study of DM projections failed to reveal connections with these areas (Wagor et al., '75), perhaps because the distributed and superficial terminations of the feedback connections were difficult to observe with these less sensitive methods. Subsequently, Lin et al. ('82) noticed sparse, but obvious terminations concentrated in layer IV of DM after injections of ^{3}H proline in area 17, and found that an injection of HRP that included DM and adjacent posterior parietal cortex labelled a scattering of neurons in area 17, largely in layer III. An earlier report on area 18 (VII) projections (Kaas and Lin, '77) also revealed inputs to DM from both medial and lateral portions of area 18. Thus, there is evidence from the present results and two previous studies that widespread portions of areas 17 and 18, including the representations of both upper and lower visual quadrants, provide feedforward inputs to DM. What was not apparent from the earlier studies is that specific modular components of areas 17 (the blobs) and 18 (the CO-dense bands) are the major sources of input to DM.

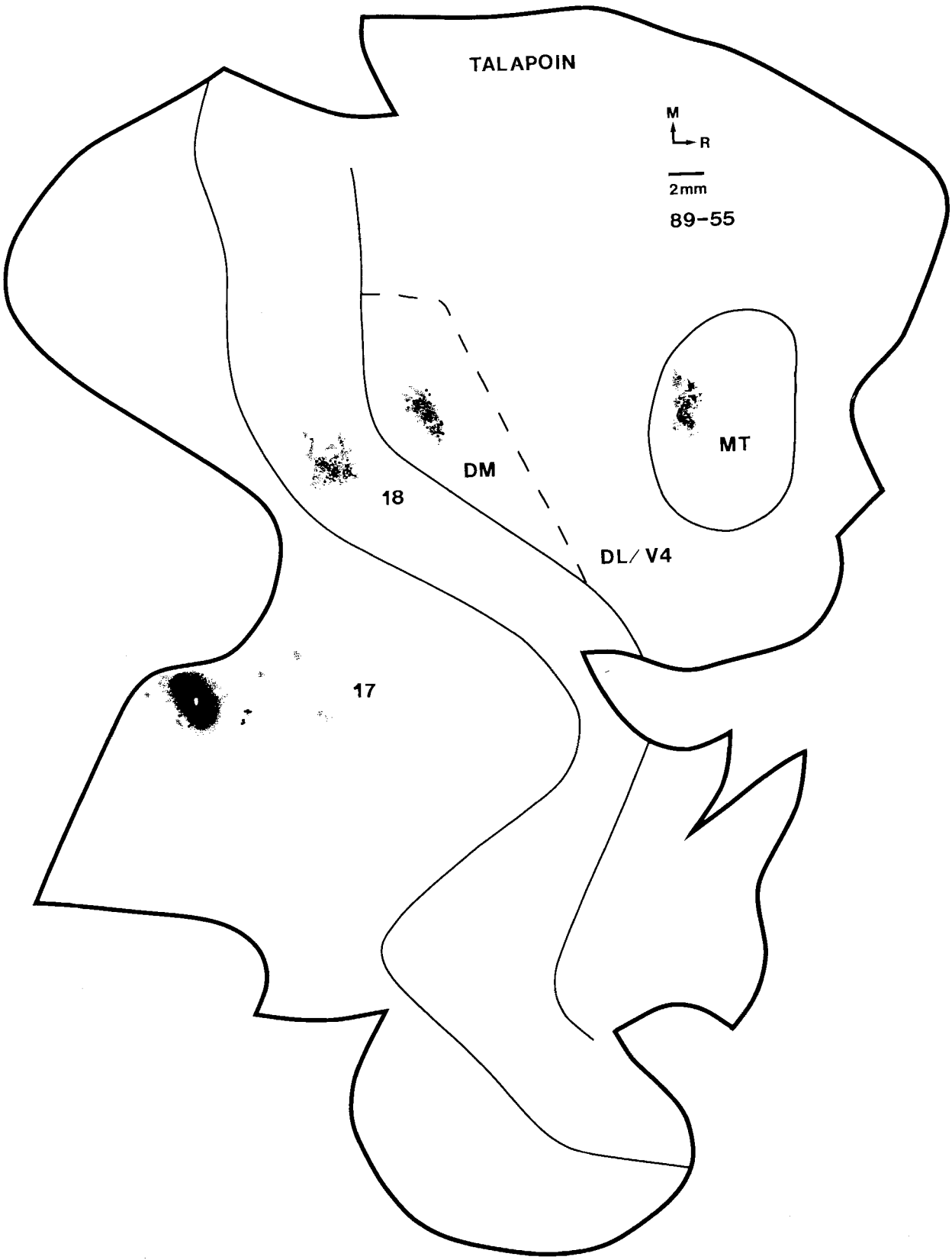

Fig. 18. Anterograde and retrograde label in area 18, MT, and DM after an injection of WGA-HRP in part of area 17 representing the lower visual quadrant in talapoin 89-55. Areas 17, 18, DM, and MT were defined by myeloarchitecture in cortex that had been flattened and cut parallel to the cortical surface. DL/V4 is used to mark the location of the fields DL and V4 as defined in New World and Old World monkeys, respectively. Conventions as in previous figures.

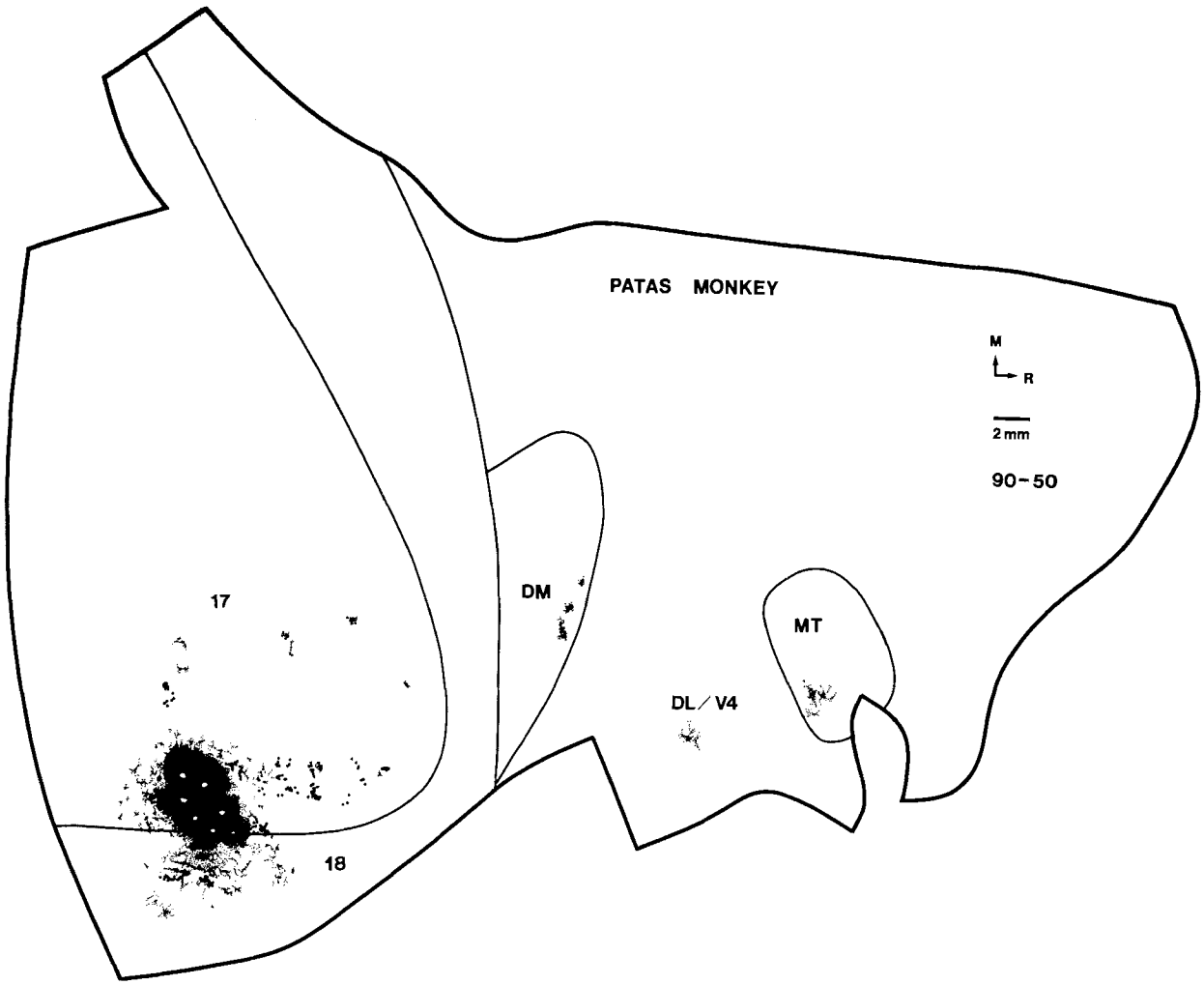

Fig. 19. Connections of area 17 in patas monkey 90-50. A cluster of seven injections of WGA-HRP was placed near the dorsolateral border of area 17 in the expected location of the representation of central vision of the upper quadrant. Bidirectionally transported tracer was found in areas 18, MT, DL/V4, and rostral DM. Portions of calcarine, frontal and temporal cortex have been removed from this case. Conventions as in previous figures.

Other major connections of DM were with areas of the dorsal stream of visual processing (Ungerleider and Mishkin, '82), namely VPP, MT, and MST (Fig. 21A). These feedforward connections of DM were previously revealed by degeneration methods (Wagor et al., '75). Studies on the connections of posterior parietal cortex (Kaas et al., '77), MT (Weller et al., '84; Krubitzer and Kaas, '90b), and MST (Weller et al., '84) indicate that the projections to DM are of the feedback type. The present results demonstrate that the interconnections of DM with MT are associated with the CO-dense subdivisions of MT (Fig. 10C), and suggest that MT has some type of modular organisation. The distribution of connections within MT from other visual areas is also extremely patchy (e.g., Krubitzer and Kaas, '90b; Kaas and Morel, '92; present investigation), and studies of evoked metabolic activity in MT reveal distributed subregions devoted to either global or local motion processing (Tootell and Born, '91; Born and Tootell, '92).

DM also had connections with DLr, M, and VP (possibly including VA; Fig. 21A). Wagor et al., ('75) noted feedforward inputs to the DLr region and M in some cases, but did not detect inputs to VP. Projections of DM to the visuomotor areas, FEF and FV, have not been previously reported. However, injections in FEF of owl monkeys produced small amounts of label in the DM region (Huerta et al., '87). The major callosal connection of DM with DM and VPP in the opposite hemisphere have also been previously described (Wagor et al., '75).

The evidence indicates that DM receives potentially activating inputs from specific modules in areas 17 and 18, and distributes information to an array of visual areas that are associated largely with the dorsal stream of visual processing, thought to be important in spatial aspects of vision, visual attention, and motion perception (Ungerleider and Mishkin, '82). The modules providing the inputs to DM are parts of three processing channels that have been distinguished in primates (see Livingstone and Hubel, '88; De Yoe and Van Essen, '88 for review). Using the terms of De Yoe and Van Essen ('88), two major processing channels, the magnocellular or M channel and the parvocellular or P channel originate from separate classes of ganglion cells in the retina, remain segregated in the lateral genicu-

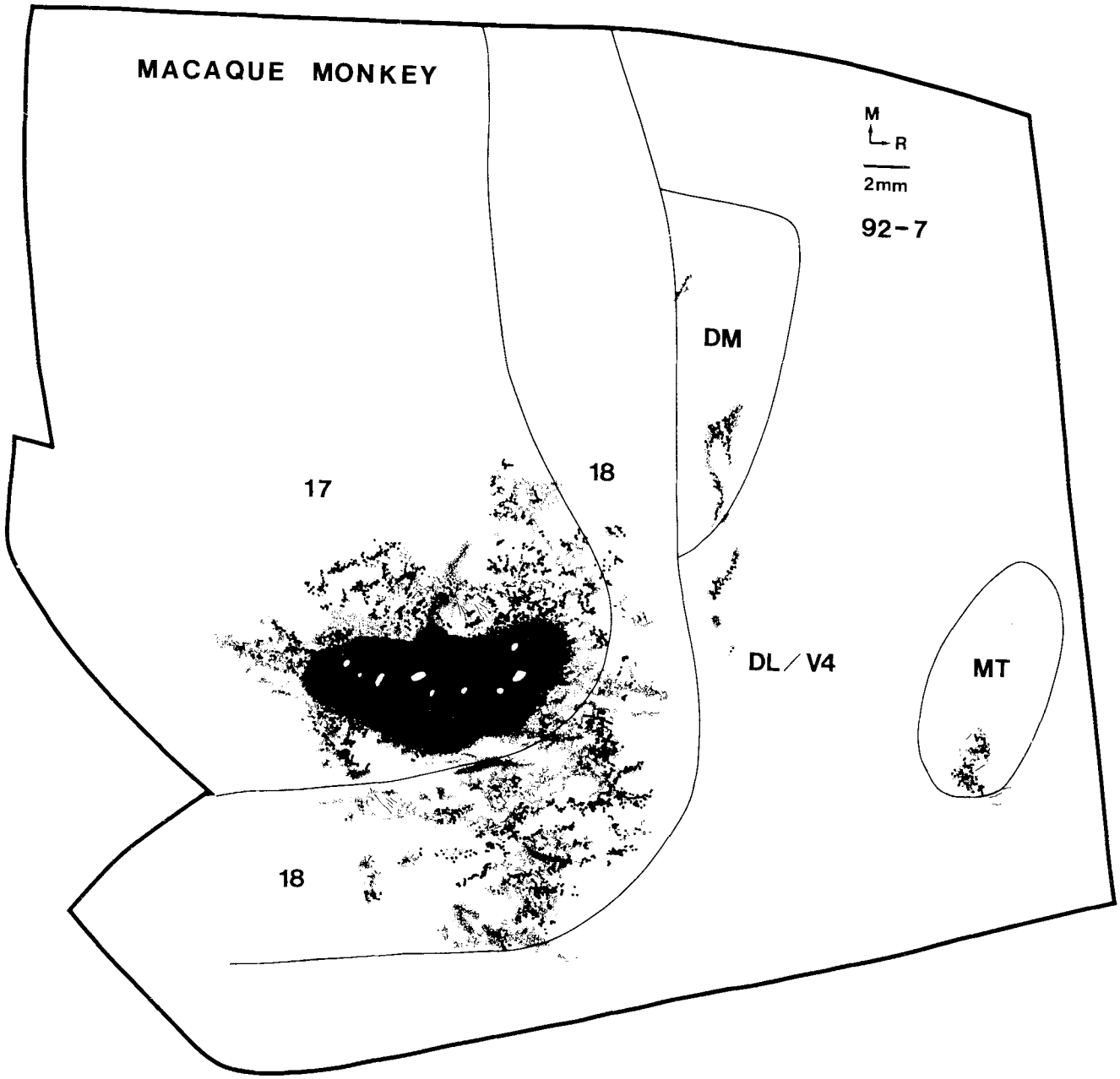

Fig. 20. Connections of area 17 in macaque monkey 92-7. The pattern of connections from area 17 in the macaque is identical to those illustrated in the previous figures for the other primates. Nine injections were placed in a row in area 17 near the representation of central vision of the upper visual quadrant. Bidirectionally transported tracer from the injection sites was in areas 18, MT and in the heavily myelinated wedge of cortex that is in the location of DM. Also, because the representation of central vision was involved in the injection, a small patch of labelled cells and terminations were in DL/V4. Conventions as in previous figures.

late nucleus, and terminate in separate layers of area 17. There, the P channel splits to activate blob or interblob regions and creates the parvocellular blob or P-B channel, and the parvocellular interblob or P-I channel, respectively. The M channel is thought to be important in the detection of motion, and projects to alternate CO-dense bands in area 18, and ultimately provides the major inputs to the dorsal stream of Ungerleider and Mishkin ('82). The P-B channel is thought to relate largely to colour vision and projects to alternate CO-dense bands in area 18, while the P-I channel relates to several aspects of form vision, and projects to the interstripes or CO-sparse regions of area 18. Both the P-B and P-I channels are thought to provide most of the activation of the ventral stream of visual processing for object vision and recognition.

The present results add complications to this oversimplification of the modular aspects of early visual processing. The outputs of DM to posterior parietal cortex clearly identify DM with the dorsal stream of processing, which is thought to be dominated by the M channel. Yet, both P-B

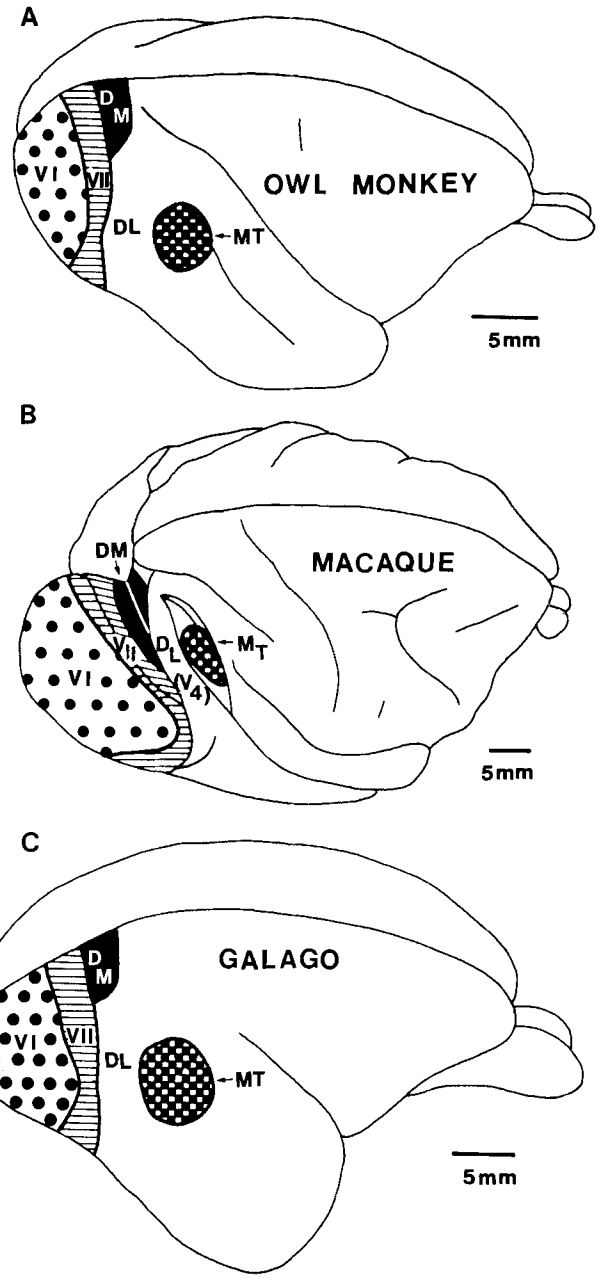

Fig. 21. A summary figure of the proposed organisation of visual cortex in New World (**A**), Old World (**B**), and prosimian (**C**) primates. Our results suggest that at least four visual cortical areas, V-I, V-II, MT, and DM are common to all primates, including humans. Patterns of connections from area 17, relative position, and dense myeloarchitecture area are all useful criteria for defining DM in primates. Conventions as in previous figures.

output from area 17 and P-B and M outputs from area 18 reach DM. Thus, posterior parietal cortex has the potential to receive significant amounts of P-B information via DM. While colour could be important in the dorsal stream, this may not be the sole contribution of the P-B channel to DM. First, we now know that both P-B and P-I regions of area 17 have M as well as P types of input (Maunsell et al., '90; Lachica et al., '92, '93). Thus, the P-B outputs may be relaying some M channel information. Second, the observations that the blobs are well developed in both nocturnal and diurnal primates (see Preuss et al., '93 for review) has led some investigators (e.g., Allman and Zuker, '90; Lachica et al., '93) to suggest that the blobs serve functions other than colour vision, which would be most useful for daytime vision. However, to the extent that the P-B and M channels are dominated by P or M inputs, respectively, the projections from both P-B and M bands in area 18 allow for an integration of two types of information in DM.

While the response properties of neurons in DM have been quantitatively studied, the known properties are not distinct enough from those in other areas to generate a hypothesis about the specific functions of DM (Baker et al., '81). However, neurons in DM have both an early transient response and a large sustained discharge (Petersen et al., '88), and many neurons in DM are directionally selective (Baker et al., '81; present results) suggesting that DM plays a role in motion analysis. These response characteristics are consistent with the present results on the modular connections of DM, that indicate that both M and P streams activate DM.

The most dense output of DM is to VPP, a subdivision of posterior parietal cortex that may correspond to the ventral intraparietal area, VIP, of macaque monkeys (Maunsell and Van Essen, '83), although VIP has recently been divided into VIP and a lateral intraparietal area (LIP) by some investigators (see Desimone and Ungerleider, '86; Andersen et al., '90; Felleman and Van Essen, '91). DM also projects to MT, MST, and FSTd; all of these areas are interconnected and feedforward to subdivisions of posterior parietal cortex (Weller et al., '84; Krubitzer and Kaas, '90b; Kaas and Morel, '93). Other connections of DM are with DLr, VP, and M. DLr in squirrel monkeys is strongly associated with the dorsal stream through cortical connections (Cusick and Kaas, '88b; Steele et al., '91). While little is known about VP connections or the role of VP in visual processing (see Newsome et al., '86; Burkhalter et al., '86), VP is associated with the dorsal stream by connections with FSTd and MT (Weller et al., '84; Krubitzer and Kaas, '90b; Kaas and Morel, '93). Little is known about M, but projections to posterior parietal cortex, DI and MT, have been reported (Graham et al., '79). Thus, M also appears to be related to the dorsal stream. In macaque monkeys, the apparent homologue of M is termed the parietal occipital area (PO) (Colby et al., '88).

The connection pattern of DM reflects several general characteristics of visual cortical connections that have been widely reported. First, most areas appear to be predominantly interconnected with either dorsal "attention" channels or ventral "recognition" channels (see Morel and Bullier, '90; Baizer et al., '91). Second, connections are distributed in a patchy fashion across parts of other fields. This suggests that all cortical fields are likely to be modularly organised. Correlations of connections with architectonic specialisations within fields have only been made for some fields, but undoubtedly more structural specialisations within cortical fields will be revealed. Third, the two major processing streams (dorsal and ventral) of visual cortex clearly interact. This is most compelling when one examines modular connections (e.g., Krubitzer and Kaas, '89b, '90a,b). Fourth, interactions with the eye movement fields of motor cortex occur at a number of levels in processing networks. Connections with motor and eye movement fields at several stages of sensory processing

have been demonstrated for somatosensory (Krubitzer and Kaas, '90c; Krubitzer et al., '93), auditory (Morel and Kaas, '92), and visual (e.g., Huerta et al., '87; Weller and Kaas, '87; Krubitzer and Kaas, '90b; Kaas and Morel, '93) systems. The most logical conclusion from these findings is that behaviour can be elicited from each level of cortical processing, so that, in a sense, every field can be considered a cortical end state, or the final stage at which sensory information may be processed. Thus, entire processing networks are not necessarily activated during stimulus detection, perception, and ultimately motor (behavioural) output. Finally, callosal connections generally occur with the same field and one or two adjacent fields (see Cusick and Kaas, '86). These additional fields with callosal connections are adjacent to the field injected in the opposite hemisphere, and also have the most dense ipsilateral connections with the field injected. This suggests that small clusters of fields interact closely within and between hemispheres.

Does DM exist in other primates?

Without the history of other concepts of visual cortex organisation in primates, the present evidence for the ubiquity of DM in primates would seem rather compelling. In all primates examined, including three species of Old World monkeys, different New World monkeys, and prosimian galagos, cortex in the expected location of DM had two major identifying features of DM: direct input from area 17 and dense myelination. The evidence of input from area 17 would seem especially persuasive since only three regions of cortex consistently have been found to have inputs from all of area 17 across taxa: areas 18, MT, and the DM region (DL/V4 receives input only from the central representation of V-I). Areas 18 and MT are widely accepted as fields common to all primates. Yet, cortex in the region of DM, with input from area 17 in Old World monkeys, has long been considered to be part of a belt-like region, V3, bordering most of area 18 (Myers, '65; Zeki, '69; Cragg, '69). Subsequently, an additional target area of area 17, in cortex just rostral to V3, in V3A, has been observed (Zeki, '80). Another proposal is that dorsal V3 is a visual area that is separate from ventral V3, and that only dorsal V3 receives input from area 17 (Van Essen, '85; Burkhalter et al., '86; Van Essen et al., '86).

In New World monkeys, the organisation of the DM region has also been described differently by various investigators. In addition to owl monkeys, we have described a DM in marmosets and squirrel monkeys, using dense myelination, relative position, and connections with MT as identifying features (Krubitzer and Kaas, '90b). Although connections between DM and MT in marmosets and galagos appeared to be inconsistent, this may have been a consequence of underestimating the size of DM in these species. Also, Weller et al. ('91) have suggested that a densely myelinated dorsomedial region in squirrel monkeys is DM because its connections with areas 17 and 18, DLr, MT, MST, VPP, FST, and the VP region resemble those of DM of owl monkeys. In contrast, in cebus monkeys, Sousa et al. ('91) denote a region, which receives input from area 17, in the expected location of DM, as part of a larger V3 that is portrayed as bordering both dorsal and ventral parts of area 18, much like that proposed for Old World macaque monkeys (e.g., Boussaoud et al., '90).

We also describe projections from area 17 to a densely myelinated region we define as DM in prosimian galagos (Fig. 21C). Elsewhere, we identified the same region as DM in galagos on the basis of dense myelination, position, and connections with MT (Krubitzer and Kaas, '90b). Previously, Cusick and Kaas ('88a) detected labelled neurons and terminals in the DM region after injections of WGA-HRP in area 17 in some, but not all, galago cases, and speculated that region might be DM. However, electrophysiological recordings in the DM region of galagos resulted in a summary map for a dorsal area (D) that was more like M in retinotopic organisation than DM (Allman et al., '79). Possibly, the recordings were partly from DM and partly from other visual areas. Since there was no reported architectonic distinctiveness in this region of cortex, it is difficult to say with certainty that all of the recording sites were restricted to a single field. Nevertheless, an important observation was that neurons in this dorsomedial region just rostral to area 18, in the approximate location of DM, had receptive fields in the upper visual quadrant, a result that is incompatible with the concept of a dorsal V3 (V3d) occupying this region, since V3d only represents the lower visual quadrant.

It seems unlikely that all of the different proposals of organisation for the DM region are correct, with quite different areas occupying the same cortex in different species of primates, since a number of criteria used to distinguish a cortical field are similar for most primates in this DM region (i.e., myeloarchitecture, response properties, cortical connections). In addition, all primates evolved from a common ancestor, and all primate brains should be understandable in terms of modifications of a common plan along branching lines of descent (see Kaas, '92). Much of the evidence gathered on the organisation of parastriate cortex in the last twenty years has been in conflict with the early concept, stemming largely from Brodmann ('09), that area 17 is surrounded (or nearly so) by two ring-like fields, area 18 (V-II), and area 19 (V-III). Instead, the bulk of the evidence has supported the general proposal of Allman and Kaas (e.g., '75, '76) that a number of visual areas border area 18. The change in thinking is reflected in current proposals in macaque monkeys where V2 is shown to be bordered by V3, V4, and PO (Desimone and Ungerleider, '86) or V3, V4, VP, PO, and posterior intraparietal area (PIP) (Felleman and Van Essen, '91). The major difference between these two schemes is whether quite separate ventral and dorsal parts of "V3" are considered subdivisions of one area or comprise two distinct areas. There are problems with either view. We believe the majority of the data supports the hypothesis that V3d and V3v in macaque monkeys are separate fields, and that much of V3d, and at least part of V3A, are parts of a single field, DM, that exists in most or all other primates, including humans.

V3d and V3v are separate cortical fields in macaque monkeys. There are a number of reasons for concluding that dorsal V3 (V3d) and ventral V3 (V3v) in macaque monkeys are separate fields. First, Van Essen et al. ('86) and Burkhalter et al. ('86) present good evidence that V3d and V3v (termed VP by these investigators) are not parts of the same visual area since dorsal V3 receives area 17 projections while ventral V3 does not. This conclusion is consistent with our present observations. Thus, in macaque monkeys, connections of V3d and V3v with area 17 differ. In addition, Van Essen et al. ('86) note that dorsal V3 is densely myelinated, while ventral V3 is not. Finally, quantitative studies of the response properties of single neurons in V3d and V3v (VP) revealed marked differences between the two regions, with less colour selectivity and more

directional selectivity in V3d (Burkhalter et al., '86). Therefore, most of the criteria used to distinguish cortical areas (i.e., architecture, physiology, and connections) are present for distinguishing V3d from V3v in macaque monkeys. We add here the observation that V3d and V3v are portrayed by various investigators (e.g., Desimone and Ungerleider, '86; Felleman and Van Essen, '91) as separated by a large expanse of V4, making V3 the only postulated visual area (or sensory area) that is widely separated by an intervening cortical field. Taken together, the evidence strongly supports the contention that V3d and V3v in macaque monkeys are separate fields or parts of separate fields.

V3d and portions of V3A correspond to DM. We also feel that it is unlikely that V3d in macaque monkeys is a complete visual area by itself. Rather, V3d and the adjacent portion of the upper field representation in V3A form a single, complete field. Indeed, when one closely examines existing data, there seems to be no compelling reason for recognising V3d and V3A as separate areas. Instead, the two proposed areas seem quite similar. First, Gattass et al. ('88) found that V3d could not be distinguished from V3A in their myelin-stained material, and that V3d and V3A together form a densely myelinated region, like DM of owl monkeys. While Van Essen et al. ('86) used myeloarchitecture to denote a V3d that does not include V3A, their photomicrograph of the V3/V3A junction shows that both are located within a region of somewhat uneven, but dense myelination (See Fig. 8 of Van Essen et al., '86). Furthermore, the transition zones and areas of uncertainty along the rostral and caudal boundaries of V3, depicted in their study and a related study (Burkhalter et al., '86), are as wide (1–1.5 mm) as the V3 field itself. This suggests that the margin of error in defining the V3 region in standard planes of sections is great, and that the actual width of the field may approximate that of DM observed in the present investigation in macaque, patas, and talapoin monkeys. Others (Girard et al., '91) show V3A as thicker and somewhat more myelinated than V3. Since cortex in the V3/V3A region is located on the fundus of the lunate sulcus, it is easy to suppose that minor architectonic differences are largely the result of folding cortex (see Welker, '90). Second, there appears to be no electrophysiological basis for separating V3d and V3A. Receptive field sequences across the V3/V3A boundary where the lower visual quadrant representation in V3d joined the upper field quadrant representation in V3A appeared continuous (see Fig. 13 of Gattass et al., '88). Indeed, the investigators themselves (Gattass et al., '88, page 1836) express some uncertainty when defining the location of the V3/V3A boundary. Also, no differences in neural response properties or receptive field sizes for V3d and V3A were reported. Third, V3A was first distinguished from V3d by Van Essen and Zeki ('78) using callosal connections as a marker for V3 boundaries, but in a reconsideration of the callosal patterns in the V3 region, Van Essen et al. ('86, page 477) concluded that "callosal connections may be a less accurate marker of V3 boundaries than has been previously suggested." Thus, it is not obvious that callosal connection patterns identify V3 and V3A as separate areas. Fourth, both the V3d (see above) and V3A regions (Zeki, '80; Perkel et al., '86; present results) have connections with area 17. Although Zeki ('80) concluded that only parts of area 17 representing peripheral vision project to V3A, Perkel et al. ('86; also see present results) found labelled cells in this region after injections of fluorescent dyes in parts of area 17 representing central vision. Fifth, the conclusion of Van Essen et al. ('86) that V3d receives inputs from only the part of area 17 that represents the lower visual quadrant is not supported by present results in macaque monkeys and other Old World monkeys. Clearly, inputs also come from parts of area 17 that are devoted to the upper quadrant. Finally, if V3 alone were a distinct cortical field it would only represent the lower visual quadrant (e.g., Felleman and Van Essen, '91). While an emphasis on near vision (see Previc, '90) may lead to a relative enlargement of the representation of the lower visual field, such as in MT of macaques (Maunsell and Van Essen, '87), it seems improbable that any visual area would completely lack a representation of the upper visual quadrant. A lack of an upper quadrant representation in a particular cortical field implies that there are functions performed in the lower field that cannot be performed in the upper field. Of course, VP has been proposed as a field representing only the upper visual quadrant (e.g., Newsome et al., '86) and a V4t has been proposed as representing only the lower visual quadrant. However, evidence from connection studies suggest that V4t is part of a larger, complete representation, MTc (Kaas and Morel, '93), and VP may also be part of a larger representation (VP + VA) of a complete visual field. Studies of connections (e.g., Weller and Kaas, '85; Krubitzer and Kaas, '90b; Weller et al., '91; present investigation) and evoked metabolic activity (Tootell, personal communication) indicate that information from the lower visual quadrant reaches the VP/VA region. Taken together, it appears as if the present limits of V3d and V3A in macaque monkeys are incorrect since the evidence used to distinguish V3d from V3A is vague at best. Instead, we hypothesise that V3d and caudal portions of V3A form a single complete field, DM, in all primates.

We do not mean to imply that there are no fields rostral to "V3 + portions of V3A" (DM) in macaque monkeys, or that these fields do not fall within a well myelinated region. Indeed, there is convincing evidence for a field rostral to DM in Old World monkeys. Most notably, Girard et al. ('91) cooled dorsolateral V-I representing central vision in the lower quadrant and found responses to visual stimuli to be more completely suppressed in the V3 region than the V3A region. Since DM would not have two large, spatially separate representations of the lower quadrant, some of the recordings assigned to V3A may have been outside what we would define as DM. The proposed DM would include a lower field representation from V3d, and an upper field representation from portions of V3A.

In conclusion, the evidence for DM as a valid visual area in owl monkeys seems almost as extensive and compelling as that for V-I (area 17), V-II (area 18), and MT. More limited but still compelling evidence suggests that DM is a visual area not only in owl monkeys, but in other primates as well (Fig. 21). Finally, our proposal that DM exists in other primates, and thus V3d and V3A, as presently defined, are not valid visual areas, seems more parsimonious than proposals that different visual areas occupy this same region in different primates.

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