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Cortical Connections of Visual Area MT in the Macaque

LESLIE G. UNGERLEIDER AND ROBERT DESIMONE
Laboratory of Neuropsychology, National Institute of Mental Health, Bethesda, Maryland 20892

ABSTRACT

We have identified the cortical connections of area MT and determined their topographic organization and relationship to myeloarchitectural fields. Efferents of MT were examined in seven macaques that had received injections of tritiated amino acids, and afferents were examined in one macaque that had received injections of two fluorescent dyes. The injection sites formed an orderly sequence from the representation of central to that of peripheral vision in the upper and lower visual fields.

In addition to connections with the striate cortex (V1), connections were found between MT and a variety of extrastriate areas, including V2, V3, V3A, V4, V4t, VIP, MST, FST, possibly PO, and, finally, the frontal eye field. The connections of MT with V1, V2, and the dorsal and ventral portions of V3 were topographically organized and consistent with the visuotopic arrangement reported previously in these areas. V2 could be distinguished from V3 by the distinctive myeloarchitectural appearance of the former.

Connections with areas V4 and V4t also displayed at least a coarse visuotopic organization, in that the central representation of MT projected laterally in these areas and the peripheral representation projected medially. The lower visual field representation of V4 was located dorsally, on the prelunate convexity, while the upper field representation was located primarily on the ventral aspect of the hemisphere. V4t had a distinctively light myeloarchitecture and received projections from only the lower field representation of MT.

The remaining connections of MT were with areas located entirely in the dorsal half of the hemisphere. There were widespread connections with areas MST and FST in the superior temporal sulcus, with some evidence for a crude visuotopic organization in MST. Connections were also found with area VIP in the intraparietal sulcus, with area V3A on the annectent gyrus, possibly with area PO in the dorsomedial prestriate cortex, and, finally, with the frontal eye field on the anterior bank of the lower limb of the arcuate sulcus. Area FST and parts of both MST and VIP had a distinctive myeloarchitecture.

The pattern of laminar connections with V1, V2, and V3 indicated that MT projects "back" to these areas and they project "forward" to MT. That is, the projections to these areas from MT terminated in both the supragranular and infragranular layers and the projections to MT from these areas originated predominantly from cells located above granular layer IV (above layer IVC in V1). The pattern of laminar connections with V3A, V4, V4t, and PO was of the "intermediate" type in that the projections from MT to these areas were spread almost evenly across the layers, including layer IV, and the projections to MT originated (in the case of area V4) from cells in both the infragranular and supragranular layers. Finally, the pattern of laminar connections with MST, FST, and VIP indicated that MT projects "forward" to these areas and they project "back" to MT. That is, the projec-

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tions from MT terminated heavily in layer IV in these areas and the projections from these areas to MT originated primarily from cells in the infragranular layers. The connections of MT indicate that this area plays a major role in the relay of visual information from the striate cortex into the parietal lobe.

Key words: extrastriate cortex, prestriate cortex, visual system, parietal lobe, visuospatial function

Area MT is a visuotopically organized area within the extrastriate cortex of primates that appears to be specialized for the analysis of visual motion. Physiological studies have shown that MT contains a high proportion of cells selective for the speed and direction of stimulus motion (Zeki, '74, '78a,b; Baker et al., '81; Maunsell and Van Essen, '83a; Albright, '84; Felleman and Kaas, '84). Furthermore, MT contains a columnar organization for the axis of stimulus motion that is similar in many respects to the columnar organization for stimulus orientation found in striate cortex (Albright et al., '84). Since MT appears to be the only striate projection zone so highly specialized for the analysis of direction of motion (Zeki, '78a,b), it may play a special role in providing this information to other visual areas.

In two companion papers, we have traced the pathway from the central and peripheral representations of striate cortex (V1) and V2 to MT in the macaque (Ungerleider and Desimone, '86) and have mapped physiologically both MT and the areas surrounding it in the superior temporal sulcus (Desimone and Ungerleider, '86). In the present study, we report on the cortical afferents and efferents of MT in seven cases with injections of tritiated amino acids and one case with injections of two fluorescent dyes. We found "backward" projections to V1, V2, and V3, and "forward" or "intermediate" type projections to at least seven areas in prestriate, parietal, and prefrontal cortex. Our results are consistent with those recently reported by Maunsell and Van Essen ('83b), though we found connections in addition to the ones they described and interpret others somewhat differently than they do. We also report on the the topographic organization and myeloarchitecture of MT's projection fields. The results indicate that MT plays a major role in the relay of visual information from V1 into the parietal lobe.

METHODS

Eight *Macaca fascicularis* weighing 3.5–4.5 kg were used. Six of these monkeys (cases 1–6) received unilateral injections of tritiated amino acids in MT, and a seventh received injections of two fluorescent dyes, fast blue (case 7FB) and diamidino yellow (case 7DY), into different loci in MT. In all seven cases, the results were analyzed in detail and plotted on two-dimensional reconstructions of the cortex. One additional monkey (case 8) received an injection of tritiated amino acids into the upper bank of the superior temporal sulcus (STS) that included, but was not confined to, the far peripheral representation of the V1 projection zone in the STS. The results in this case were examined solely for the laminar distribution of label within V1.

Injections of MT

Most of the physiological, anatomical, and histological procedures have been described in detail previously (Desimone and Gross, '79; Ungerleider et al., '84) or in our two companion papers (Desimone and Ungerleider, '86; Ungerleider and Desimone, '86); only methods specific to this study will be described here.

The injections in cases 1–7 were made following electrophysiological determination of the receptive field at the injection site. In cases 1–5, receptive fields were recorded with an electrode attached to the 27-gauge syringe needle used to make the injection. In cases 6 and 7, which are the same as cases 1 and 3, respectively, of the preceding paper (Desimone and Ungerleider, '86), receptive fields were recorded with a separate electrode. In these two cases, the electrode was advanced through a 21-gauge guide tube that was lowered into the upper bank of the STS. After the desired receptive field was found, the electrode was withdrawn, and the injection needle was inserted through the guide tube to the same depth as the electrode. Receptive fields were not recorded in case 8, which had been prepared for a separate study.

In cases 1–6 and 8, we injected an equal-parts mixture of tritiated proline (New England Nuclear L-[2,3,4,5-^{3}H], specific activity 100–140 Ci/mmol) and tritiated leucine (New England Nuclear L-[3,4,5-^{3}H(N)], specific activity 100–140 Ci/mmol). The labeled amino acids, which had been evaporated and then reconstituted in 0.9% saline to give a final concentration of 50 μCi/μl, were injected at a rate of 0.02 μl /2 minutes. In each case, a single, unilateral injection of 0.15 μl was made. In case 7, 0.25 μl of a 2% solution of fast blue (FB) in 0.9 % saline was injected at one location in MT, and 0.5 μl of a 4% solution of diamidino yellow (DY) in 0.9% saline was injected at another; injections of both fluorescent dyes were made in the same hemisphere at a rate of 0.02 μl/minute. The properties of these dyes have been described previously by Keizer et al. ('83). In all cases, the needle was left in the brain for an additional 20 minutes following the injection.

Histological processing

In cases 1–6, after a 6-day survival period, the brains were fixed by perfusion with 0.9% saline followed by 10% formol-saline. They were then blocked stereotaxically, removed from the skull, photographed, and stored in 30% sucrose in 10% formol-saline until they sank. Frozen sections, 30 or 33 μm in thickness, were cut in a plane 20° from the frontal plane, so that the sections intersected the STS almost perpendicularly. Every fifth section was processed for autoradiography according to the procedures of Cowan et al ('72). The sections were mounted, dipped in

Kodak NTB2 emulsion, and exposed at 4°C for 12 weeks. Subsequently, the autoradiographs were developed in Kodak D19, fixed, and counterstained with thionin. Case 8 was processed in the same way but was cut in the frontal plane. In case 7, the survival period was increased to 7 days, and, following fixation with 10% formalin in 0.1 M phosphate buffer, the brain was perfused with 10% sucrose in phosphate buffer, followed by 20%, and finally by 30%. Sections to be analyzed for the presence of the fluorescent dyes were mounted directly from phosphate buffer as the brain was cut. These sections were left uncoverslipped, and they were stored at 4°C in light-tight boxes. Other procedures used in case 7 were similar to those in cases 1–6 and 8. In all cases, except case 8, a series of sections taken every 0.9 mm or 1.0 mm was stained for myelin by the method of Gallyas ('79). For purposes of analysis, the locations of concentrations of silver grains or fluorescently labeled cells were charted onto enlarged photographs of the myelin-stained sections, or, in case 8, of thionin-stained sections.

A two-dimensional reconstruction of the posterior half of the brain was made for each of cases 1–7. The reconstructions were made from moderately stiff wires (22-gauge tinned copper bus wire) bent around layer IV of photographically enlarged (6×) sections taken at 1–2 mm intervals. Marks were made on the wires at myeloarchitectural borders and other landmarks. The wires were then spaced at appropriate intervals on a flat surface and unfolded according to the principles described by Van Essen and Maunsell ('80). Connectional data were transferred onto these reconstructions from sections enlarged to the same magnification.

RESULTS

Injection sites

The injection sites of amino acids in cases 1–6 formed an orderly sequence from the central to the peripheral parts of the visual field representation in the upper and lower quadrants. The centers of the receptive fields of cells recorded at the injection sites were located at 2° eccentricity in the lower visual field (case 1), and at positions ranging from approximately 7° eccentricity (cases 2 and 3) to 20–35° eccentricity (cases 4–6) in both the upper and lower visual fields. The injections of the fluorescent dyes FB and DY in case 7 were located at 9° eccentricity in the upper field representation and 16° in the lower field representation, respectively.

In general, the amino-acid injection sites were oval in shape with approximate dimensions of 2.5–5.8 mm in length by 1.5–1.8 mm in width. The fluorescent dye injections, by comparison, were more circular in shape and smaller, with dimensions of 1.1–1.25 mm in length by 1.1–1.6 mm in width. In all cases, the injection site included all cortical layers. Surrounding each of the amino-acid injection sites, there was a halo of diffuse, light label. It was difficult to distinguish this halo of label from intrinsic connections of MT, since both occupied all cortical layers. Often, the halo of label appeared to extend beyond the borders of MT, but the possibility cannot be ruled out that this label beyond MT actually reflected a projection rather than spread from the injection site.

There was no evidence of leakage of label into the upper bank of the STS in either cases 1–6 or case 7DY, but there was clear leakage into the superficial layers of the upper bank in case 7FB. In case 7FB as well as other animals with injections within the upper bank of the STS (e.g., case 8 of the present study and case 2 of Desimone and Ungerleider, '86), there was label in portions of the inferior parietal lobule, intraparietal sulcus, and parahippocampal gyrus that were free of label in cases with injections confined to MT.

Based on an examination of the myelin-stained sections, the injection sites in cases 2, 3, 5, and 7DY were located well within MT, which we define as the heavily myelinated portion of the V1 projection zone in the STS (Desimone and Ungerleider, '86; Ungerleider and Desimone, '86). In case 1, the injection site appeared to be confined to MT but was close to MT's lateral border, raising at least the possibility of spread into V4t; however, since there were no additional projections in this case compared to the others, contamination of V4t is unlikely. In case 4, the injection site also appeared to be confined to MT but was located close to MT's medial border, raising the possibility of spread into MTp. The only additional projection found in this case compared to the others was a projection to PO, an area that receives projections from the peripheral representations of other visual areas (Colby et al., '83). The implications of the PO projection in this case, with an injection site representing 20° eccentricity, are considered later in the Results. In case 6, the injection site clearly included cortex outside of MT. The injection site was located at the MT/V4t border, involving the lower peripheral field representations of both areas and possibly of V4 as well. Since all but one or two of the projections in this case were similar to those in cases 1–5, we have included a description of this case in the Results.

Connections of MT

In addition to connections with V1, we found connections between MT and a variety of extrastriate visual areas, including V2, V3, V3A, V4, V4t, VIP, MST, FST, possibly PO, and, finally, the frontal eye field. Assignment of a cortical projection to a particular extrastriate visual area in the macaque is difficult, as the areas cannot be easily distinguished on the basis of cytoarchitecture. In a few studies, the pattern of callosal connections has been used to identify particular visual areas. This technique has proven most useful in locating the V1/V2 border, the anterior border of ventral V3, and a substantial portion of the anterior border of dorsal V3 (Zeki and Sandeman '76; Van Essen and Zeki, '78; Zeki, '78c; Newsome et al., '80; Van Essen et al., '82). It has not yet proven very useful, however, in identifying areas located anterior to V3. In the present study, we have assigned the connections of MT to a specific extrastriate area on the basis of distinctive myelination of the area and the visuotopic and laminar organization of the connection. Figure 1 shows a two-dimensional reconstruction of the cortex with the location of all the extrastriate areas we have found to be connected with MT. In the next section, we briefly describe each area that is connected with MT and summarize the myeloarchitectural, visuotopic, or laminar evidence for assigning the connection to that area. In a subsequent section, we describe the results in each individual case.

Connections with V1. In all cases, there was a single labeled zone in V1 whose visuotopic locus was consistent with the visuotopic locus of the injection site in MT (Gattass et al., '81; Daniel and Whitteridge, '61; Van Essen et al., '84). In cases 1–3 and 5, anterograde label was confined to layer IVB and the bottom of layer VI, while in cases 4 and 6, it included layer I as well (Fig. 2A). The injections in cases 4 and 6 were centered at eccentricities of 20° in the

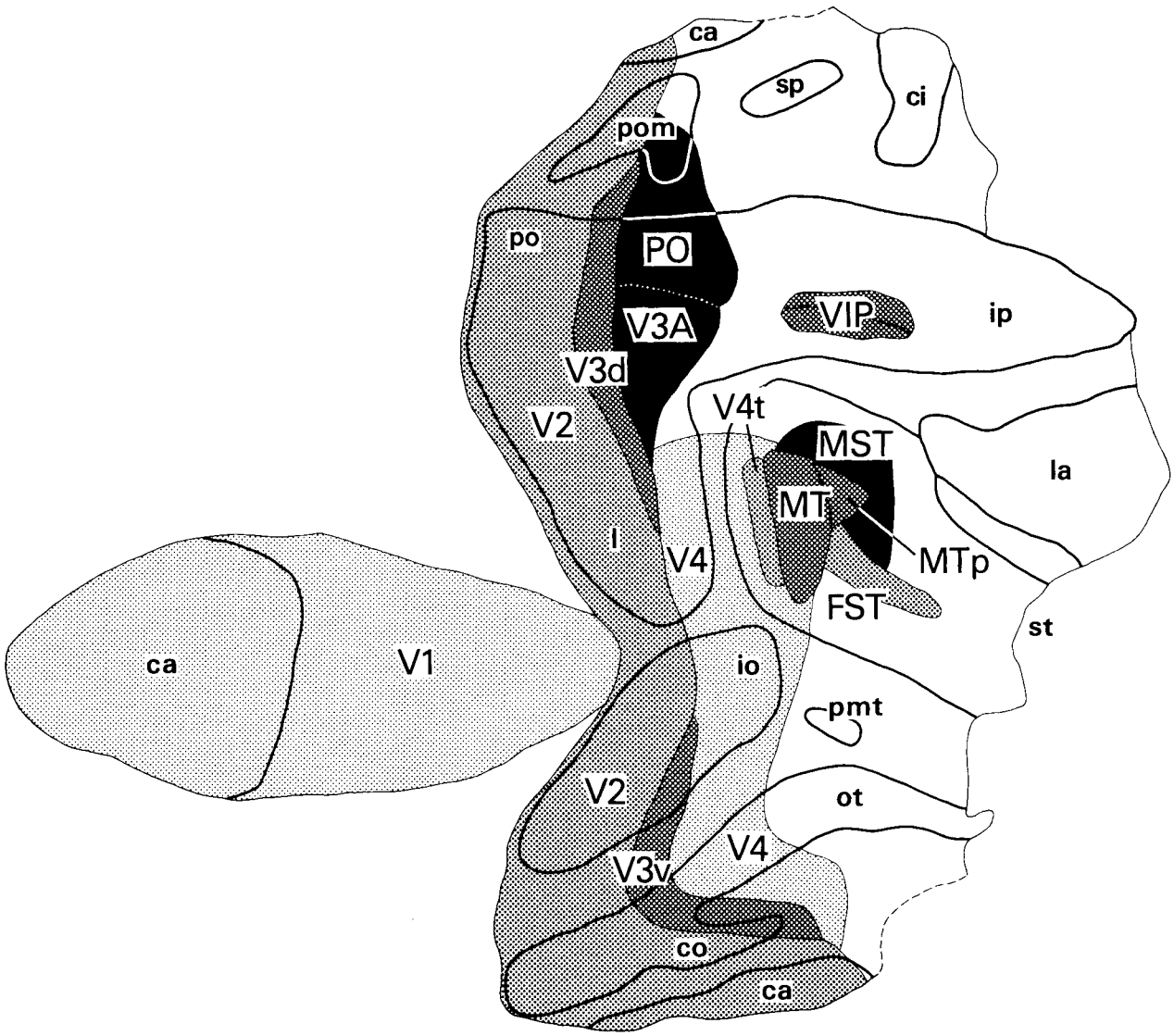


Fig. 1. Two-dimensional reconstruction of the macaque cortex, showing the location of all the extrastriate visual areas, excluding the frontal eye field, that we have found to be connected with area MT. Heavy lines indicate the boundaries of sulci, and dashed lines indicate the boundaries between neocortex and allocortex. Dotted line separating V3A and PO indicates that the border between these areas is uncertain. Abbreviations: ca, calcarine fissure; ce, central sulcus; ci, cingulate sulcus; co, collateral sulcus, ec, external calcarine sulcus; ip, intraparietal sulcus; io, inferior occipital sulcus; l, lunate sulcus; la, lateral sulcus; ot, occipitotemporal sulcus; pmt, posterior middle temporal sulcus; po, parieto-occipital sulcus; pom, medial parieto-occipital sulcus; sp, subparietal sulcus; st, superior temporal sulcus.

upper field representation and 34° in the lower field representation, respectively, whereas the injections in cases 1–3 were placed in more central visual field representations, suggesting that only peripheral visual field representations in MT project back to layer I in V1. Support for this conclusion was obtained from case 8, which had an injection that apparently included, but was not confined to, the far peripheral representation of the V1 projection zone located in the upper bank of the STS (Fig. 3). In this case, which had been prepared for an unrelated study, receptive fields were not recorded at the injection site; also, myelin-stained sections were not available and so it could not be determined whether the injection spread to MT or MTp or both. From the location of the projection, which terminated in the most anterior portion of the calcarine fissure, we judge the injection site in MT or MTp to have extended from at least 60° eccentricity to the outer limits of the visual field (for comparison, see Ungerleider and Desimone, '86: Fig. 6). In addition to label in layers IVB and VI of striate cortex in this case, there was exceptionally heavy label in layer I (Fig. 2A). The conclusion that only the peripheral representation of MT projects back to layer I of V1 must be regarded as tentative, however, as there was one exception, case 5, with an injection in the peripheral representation of MT (23°) but no label in layer I.

In cases 7FB and 7DY, labeled cells were found exclusively in layer IVB of V1. Since it has been reported that, following HRP injections into MT, a small proportion of cells in layer VI of V1 are labeled as well (Lund et al., '75; Maunsell and Van Essen, '83b), the failure to find such cells with two fluorescent dyes indicates that these dyes may fail to label some connections.

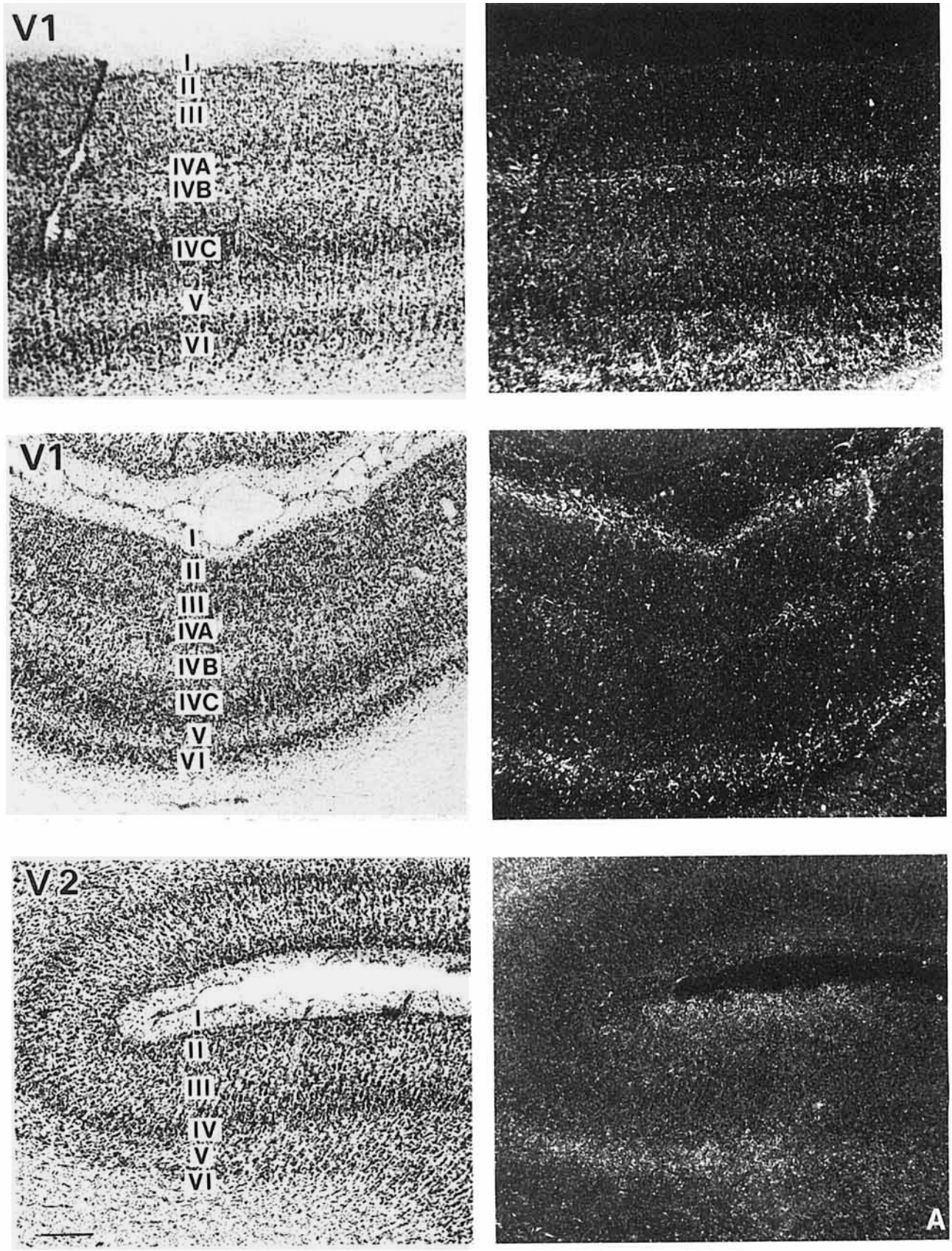
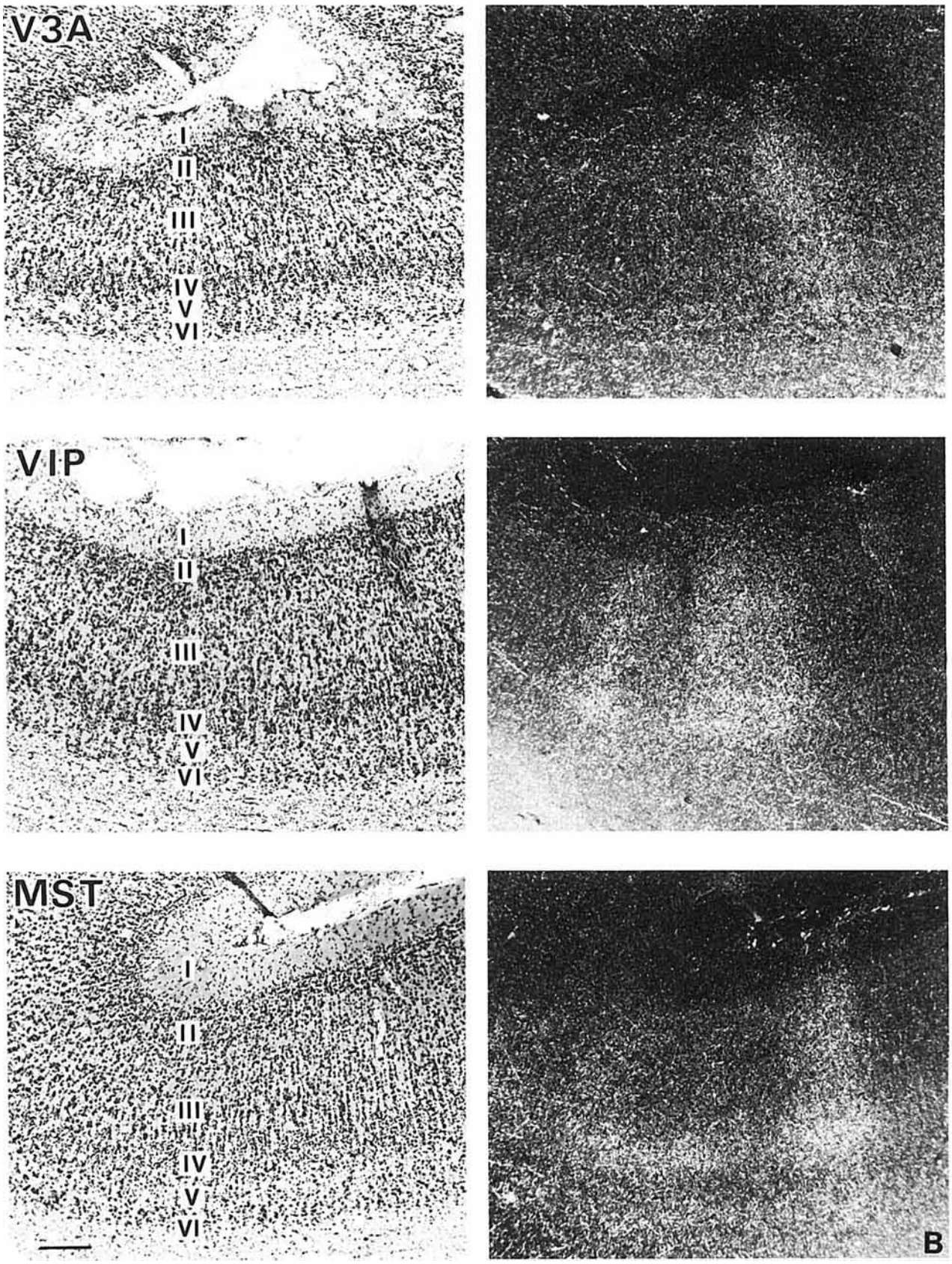


Fig. 2. Laminar patterns of projections. Brightfield (left) and darkfield (right) photomicrographs are of autoradiographic sections stained with thionin. A. Two patterns were observed in V1. In one (top), label was located both within layer IVB and extended from the white matter into the bottom of layer VI. In the other (middle), additional label was found in layer I; this second pattern was observed only in cases with injections that involved the peripheral field representation of MT. Laminar pattern shown for V2 (bottom) was also found in V3. B. Pattern shown for V3A (top) was also found in PO, and pattern shown for MST (bottom) was also found in FST. In the darkfield photomicrograph of VIP, the bright zone in the bottom left corner is due to densely labeled fibers. Scale marker indicates 250 μm.


V3A
I
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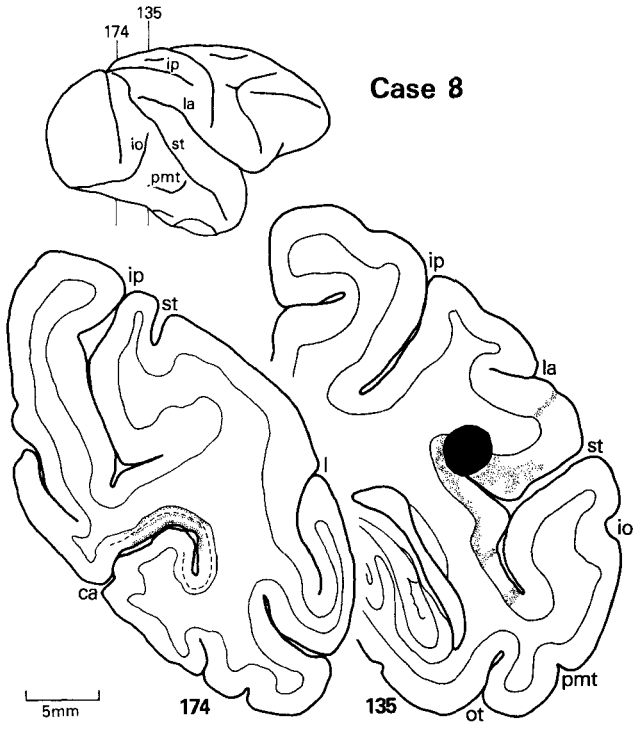


Fig. 3. Case 8: Injection of labeled amino acids (shown in black) was placed on the upper bank of STS (section 135) and included, but was not confined to, the far peripheral representation of the V1 projection zone. Note that label in V1 (section 174) was located in the anterior part of the calcarine fissure, which contains the representation of the far peripheral visual field. Sections shown are 7 mm apart. The laminar pattern of labeling in this case is shown in Figure 2A (middle). For abbreviations, see Figure 1.

Connections with V2. There were several patches of label in V2 in each of the cases. V2 was identifiable in myelin-stained sections except, in cases 2 and 3, at the representation of the fovea where the anterior boundary of V2 was unclear. The correspondence between V2 and a distinctive myeloarchitectural zone was first established in the macaque by Gattass et al. ('81) on the basis of electrophysiological mapping. In hematoxylin-stained sections, Gattass et al. described V2 as having a uniform pattern of myelination in the lower cortical layers. In sections stained with silver by the Gallyas ('79) method, we have seen additional myeloarchitectural detail in V2, and, in particular, have noted that it contains dark inner and outer bands of Baillarger separated by a thin light band (Fig. 4A,B). In some radial sections V2 also appears to have alternating zones of heavier and lighter myelination in the inner and outer bands of Baillarger. The more heavily myelinated zones probably correspond to the heavily myelinated horizontal strips in V2 found by Tootell et al. ('83) in tangential sections.

The visuotopic locus of the label in V2, like that of the label in V1, corresponded closely to the visuotopic locus of the injection site in MT (Gattass et al., '81). In all cases, anterograde label was heaviest in layers I and VI (Fig. 2A); in some but not all sections, it appeared to extend lightly throughout the supragranular and infragranular layers. Labeled cells in V2 were found almost exclusively in layer III, with only a few scattered cells in layers V and VI.

Connections with V3. In all cases, there were one or more patches of label just beyond the anterior border of V2, which we interpreted to be in V3. V3 has been shown in a number of studies to be a narrow area (2–5 mm wide) that borders V2 out to an eccentricity of at least 30° in the representations of the upper and lower visual field (Zeki, '69; Van Essen and Zeki, '78; Newsome et al., '80; Gattass et al., '85). The posterior border of V3 is the representation of the horizontal meridian, shared with V2, and the anterior border is the representation of the vertical meridian, shared with V3A, V4, and PO. Since the upper and lower visual field representations of V3 have somewhat different connections, properties, and possibly myeloarchitecture (Burkhalter and Van Essen, '83; Felleman and Van Essen, '84; Van Essen et al., '86; Ungerleider, unpublished data), it is useful to distinguish between them. Newsome et al. ('80) and more recently Van Essen et al. ('86) have suggested the term VP for the portion of V3 on the ventral surface of the hemisphere because of similarities with area VP in the owl monkey. We prefer the terms V3d and V3v for the dorsal and ventral portions of V3, respectively, because a homology between V3v and VP has not yet been shown. We will address this issue again in the Discussion.

In some sections, we could find a myeloarchitecturally distinct zone adjacent to V2 that appeared to correspond to V3d or V3v (e.g., see Fig. 4A,B), but we could not consistently distinguish the anterior border of this zone. Furthermore, in most cases the myeloarchitecture of this zone was heterogeneous, having both heavily and lightly myelinated subregions. Van Essen et al. ('86) have proposed that V3d corresponds to a heavily myelinated region anterior to dorsal V2, while V3v (their VP) usually appears lightly myelinated but cannot easily be identified on the basis of myeloarchitecture. However, Van Essen et al. note that not all of the cortex within the expected location of V3d is heavily myelinated and we concur with this observation. Moreover, we have found regions in the expected locations of V3d and V3v that have similar myeloarchitecture (see Fig. 4). Thus, we consider the issue of myeloarchitectural correlates of V3d and V3v an open one. Figure 11 shows our best estimate of the myeloarchitectonic borders of V3d and V3v in case 7, a brain that stained especially well. Label within V3d and V3v could be distinguished from that within V2 on the basis of V2's distinctive myeloarchitecture (see above).

Label within V3d and V3v could be distinguished from that in areas V3A, V4, and PO not only on the basis of its visual topography but also on the basis of its laminar distribution. Anterograde label in V3d and V3v was concentrated in layers I and VI, while that in V3A, V4, and PO had a more even distribution across all layers. Retrogradely labeled cells in V3d and V3v were located almost exclusively in layer III, while those in both V4 and the entire dorsomedial prestriate cortex, including V3A and PO, were more equally distributed between the infragranular and supragranular layers.

Like the connections of MT with V1 and V2, connections of MT with V3 appeared to be topographically organized. In cases 1, 5, and 7DY, with injections in MT sites representing the lower visual field, label was located in V3d, near the lower field representation of V2, whereas in cases 2 and 4, with injections in sites representing the upper visual field, label was located in V3v, near the upper field representation of V2. In case 3, with an injection on the representation of the horizontal meridian of MT, and in case 7FB, with an injection that apparently spread to this

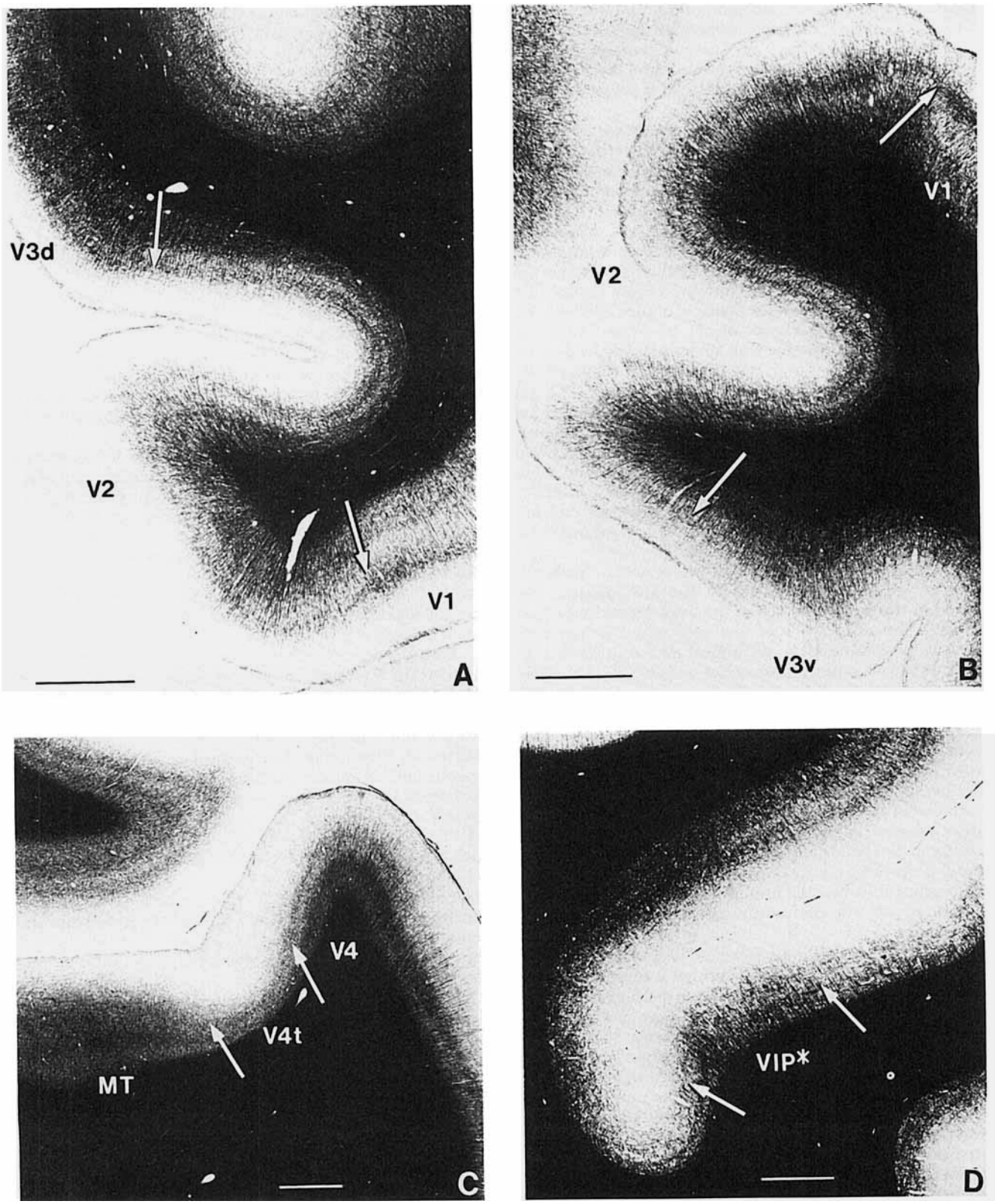


Fig. 4. Myeloarchitecture of the projection fields of MT. A. Areas V2 and V3d on the dorsomedial aspect of the hemisphere. B. Areas V2 and V3v on the ventromedial aspect of the hemisphere. Note the similarity in myeloarchitecture between V3d and V3v, although this did not hold in all locations in all animals. C. Areas MT, V4t, and V4 within STS. D. VIP* within the intraparietal sulcus. The VIP projection field extended beyond VIP* to include more medial cortex at the fundus of the sulcus. For myeloarchitecture of FST and MST, see Ungerleider and Desimone ('86). Scale marker indicates 1 mm.

representation, label was located in both V3d and V3v and in both the upper and lower field representations of V2. Furthermore, as injections were placed in more peripheral field representations of MT, label was found more medially in V3d and V3v, near more peripheral representations of V2.

Connections with the dorsomedial prestriate cortex, including V3A and PO. The organization of the dorsomedial prestriate cortex immediately anterior to dorsal V2 and V3d is somewhat unclear at present. At its lateral end lies V3A (Zeki, '78c), and at its medial end lies PO (Covey et al., '82), but the borders of V3A and PO are not well defined and the cortex between them, in the anterior annectent gyrus, may belong to either area or neither. A large portion of the dorsomedial prestriate cortex receives inputs from the peripheral field representations of V1 or V2 (Zeki, '80; Colby et al., '83; Ungerleider et al., '83; Ungerleider, unpublished data), suggesting that the region emphasizes the visual periphery. Unlike dorsal V2 and V3d, which receive inputs representing the lower visual field only, V3A and PO each receives inputs representing both the upper and lower visual fields. The upper visual field representation of PO lies on the medial aspect of the hemisphere, adjacent to the lower visual field representations of V2 and V3d, while the lower field representation of PO lies more laterally, mainly in the parieto-occipital sulcus adjacent to V3A and area 5 (Covey et al., '82). The visuotopic organization of V3A is not yet completely understood.

Label was found in the dorsomedial prestriate cortex in all cases except case 1, in which the MT injection was located in the representation of the most central portion of the field. The absence of a projection in case 1 is consistent with the predominance of peripheral over central field inputs into the dorsomedial prestriate cortex (Zeki, '80; Colby et al., '83; Ungerleider et al., '83; Ungerleider, unpublished data). In all of the other cases with amino-acid injections (cases 2–6), label in the dorsomedial prestriate cortex could be assigned to either V3A or PO or both. In the case with two fluorescent dye injections (case 7), labeled cells were distributed extensively throughout the dorsomedial prestriate cortex in both the supragranular and infragranular layers. In most instances, however, we were unable to assign them unequivocally to either V3A or PO; the most lateral part of the cortex containing labeled cells appeared to be within V3A and the most medial part within PO, but we cannot rule out the possibility of a separate area between them.

In cases 2–6, anterograde label in V3A was distributed almost evenly across all layers, without a concentration in layer IV (Fig. 2B). This laminar pattern distinguished label in V3A from that in V3d posteriorly, where it was concentrated in layers I and VI, as well as from that in VIP anteriorly, where it was concentrated in layer IV. A further difference between the projections to V3A and V3d is that those to V3A arose from both the upper and lower field representations of MT whereas those to V3d came only from the lower field representation.

In cases 4 and 6, there was additional anterograde label within the parieto-occipital sulcus and medial parieto-occipital sulcus that clearly fell within area PO (Covey et al., '82). The injections in these two cases were in sites representing more peripheral visual field locations than those in all but one other case (case 5), consistent with the finding that inputs to PO from V2 arise only from visual field representations beyond 20° eccentricity (Ungerleider et al., '83). However, since in one of the two present cases (case 6) the injection site spread into V4t and possibly V4, the projection from MT to PO must be regarded as tentative. In each of the two cases with projections to PO, label was contained in all cortical layers, without a heavy concentration in layer IV. Although both cases also contained projections to V3A with a similar laminar pattern, the two projections are clearly separate, since the one to V3A was least 10 mm distant from the one to PO.

Connections with V4 and V4t. Label in areas V4, V4t, or both was found in the six cases with injections restricted to MT (cases 1–5 and 7DY), in addition to the one case (case 6) in which the injection contaminated V4 and V4t. Zeki ('73, '77, '78b) originally described the "V4 complex" as the cortex on the prelunate convexity that lies between V3, V3A, and MT. On the basis of connections with V2 and results of electrophysiological mapping, Ungerleider et al. ('83) and Gattass et al. ('85) proposed that the portion of V4 studied by Zeki contained the lower visual field representation in V4 while the upper field representation was located ventrally, adjacent to the upper field representation in V3. In our companion study (Desimone and Ungerleider, '86), we distinguished within Zeki's original V4 complex a separate area, V4t, which is a narrow area bordering MT.

Although in myelin-stained sections V4 exhibits prominent inner and outer bands of Baillarger, we cannot yet confidently distinguish V4 from some of the surrounding areas by using myeloarchitectural criteria alone. V4t, by contrast, has only light myelination, which distinguishes it from both MT, medially, and V4, laterally. The characteristic myeloarchitectural appearance of V4, V4t, and MT is shown in Figure 4C.

In both the dorsal and ventral halves of the hemisphere, label within V4 could be distinguished from that in V3d and V3v on the basis of its laminar distribution. While anterograde label in V3d and V3v was concentrated in layers I and VI, that in V4 was generally more evenly distributed throughout the cortical layers. In addition, whereas labeled cells in V3d and V3v were located almost exclusively in layer III, those in V4 were often located in layers V and VI as well. One curious feature of the laminar distribution of label in V4 was its variability from one patch of label to another. Anterograde label in some patches included layer IV, while in others it did not. Likewise, retrogradely labeled cells in some patches were located predominantly in layers V and VI, in other patches predominantly in layer III, and in still other patches the cells were more evenly distributed between the infragranular and supragranular layers.

Of all cortical areas with anterograde label following the MT injections, the lightest was V4, and in case 3 there may have been no label in V4 at all. The density of label in V4t, by contrast, approached that found in other areas. Anterograde label in V4t was distributed throughout all layers, although in some sections it appeared concentrated in layer IV. In many sections, however, it was difficult to distinguish the label in this cortex from the halo surrounding the injection site. Like the labeled cells in V4, those in V4t were found in both the supragranular and infragranular layers.

The topography of connections between MT and both V4 and V4t was consistent with the proposed visuotopic organization of these areas (Ungerleider et al., '83; Gattass et al., '85; Desimone and Ungerleider, '86). Label from the central field injection cases (cases 1–3) was located laterally

in V4 and V4t, whereas label from the peripheral field cases (cases 4–6 and 7DY) was located further medially. Furthermore, label from the upper field injection cases (cases 2 and 4) was located ventrally in V4, whereas label from the lower field injection cases (cases 1, 5, and 7DY) was located dorsally in V4 and in V4t. Of the two cases with injections involving the representation of the horizontal meridian of MT, label in one (case 7FB) was located both ventrally in V4 and dorsally in V4 and V4t, but label in the other (case 3) appeared to be confined to V4t.

Connections with VIP. In all cases, there was label in the ventral part of the posterior bank of the intraparietal sulcus. As Maunsell and Van Essen ('83b) have previously termed this MT projection zone VIP, we have followed their terminology. VIP may also overlap with area POa of Seltzer and Pandya ('80), which was defined on the basis of architecture and was found to be connected with both the middle portion of the preoccipital gyrus and the rostral portion of the inferior parietal lobule.

Most of VIP is characterized by heavy myelination that is nearly as prominent as that in MT (Fig. 4D). The size of the heavily myelinated region of VIP is on the average about 10 mm from caudal to rostral and about 3 mm from medial to lateral. In two of the six cases with injections confined to MT (cases 1 and 3), label was confined to this heavily myelinated region, while in the other four cases (cases 2, 4, 5, and 7DY) there were at least two patches of label, one within the heavily myelinated region and one medial to it. Since the first two cases had injections within the central visual field representation of MT, the heavily myelinated region of VIP may be more concerned with the central visual field and the less heavily myelinated region with the periphery. It remains a possibility, however, that the two myeloarchitectural regions actually correspond to two separate areas. Therefore, to distinguish the heavily myelinated portion of VIP from the remainder, we will refer to the former as VIP*.

Anterograde label in VIP was heaviest in layer IV (Fig. 2B) and thus was easily distinguished from the projection to V3A, several millimeters posterior, in which the label was distributed equally across all the layers (Fig. 2B). Labeled cells in VIP were concentrated in layers V and VI but were also found in layer III.

Connections with MST. In all cases there was label within the cortex of the STS medial to MT. A small portion of the cortex medial to MT is occupied by MTp, which is the lightly myelinated portion of the V1 projection zone in the STS (Ungerleider and Desimone, '86). We regard MT and MTp as two distinctive parts of a single visual area. The remainder of the medial cortex is occupied by MST, which partially surrounds both MT and MTp (Desimone and Ungerleider, '86). In the preceding study, we found that MT has connections predominantly with MST, although there may also be connections with MTp. Since we cannot distinguish between the two areas architecturally, for simplicity we have designated all projections into the cortex medial to MT as being in MST, even though some may actually fall within MTp.

The architecture of MST is heterogeneous. Much of MST is occupied by a densely myelinated zone (DMZ) in the upper bank of the sulcus that is nearly as prominent as MT, whereas the remainder of MST is less heavily myelinated and less distinctive. MT projects extensively within both the densely and lightly myelinated portions of MST.

In the preceding study, we found that MST contains at least a crude topographic representation of the entire visual field, such that the central visual field is emphasized posteriorly and the peripheral visual field anteriorly. Consistent with this organization in MST, the projection in the central field case, case 1, was confined to the posterior part of the cortex medial to MT, whereas the projections in the other, more peripheral field, cases extended far anteriorly (Fig. 12). In several cases there were two or more separate projections in MST.

Anterograde label in MST was heaviest within layer IV (Fig. 2B), while labeled cells were densest in the infragranular layers.

Connections with FST. In all cases, there was label in area FST, which is located in the fundus of the STS anterior to MT (Desimone and Ungerleider, '86; Ungerleider and Desimone, '86). Although Maunsell and Van Essen ('83b) appear to have included FST within MST, there are several reasons for distinguishing between the two areas. First, FST has a distinctive myeloarchitecture characterized by radially oriented fiber bundles and clear inner and outer bands of Baillarger (see Ungerleider and Desimone, '86: Fig. 4C). Second, MST contains a higher proportion of directionally selective cells than does FST (Desimone and Ungerleider, '86). And third, MST and FST receive separate projections from MT.

There was little evidence for topography in the connections of MT with FST (Fig. 12). Instead, there appeared to be a convergence of inputs to FST from all parts of MT, which is consistent with the very large receptive fields we recorded in FST (Desimone and Ungerleider, '86). Anterograde label in FST was concentrated in layer IV, while labeled cells were located predominantly in the infragranular layers.

Connections with the frontal eye field. In three of the six cases with injections confined to MT (cases 1, 2, and 4) there was a very small, sparse projection to the frontal eye field (Fig. 13), which is located on the anterior bank of the arcuate sulcus and on the prearcuate gyrus posterior to the principal sulcus (Bruce and Goldberg, '85). We failed to find any retrograde label in the frontal eye field, however, in our uncontaminated fluorescent dye case (case 7DY).

Contralateral connections. In only one of the five cases with amino-acid injections confined to MT (case 4) did we observe anterograde label in the contralateral hemisphere; in several other cases, there were labeled fibers crossing in the splenium of the corpus callosum, but we were unable to follow these fibers to their termination. In case 4, the heaviest label in the contralateral hemisphere was in MT itself, where it was distributed across all cortical layers. Other areas labeled contralaterally were V3A, VIP, and MST. The label in these areas had the same laminar distribution as that in the homotypic areas of the ipsilateral hemisphere, although the label was considerably sparser contralaterally. In the case with a fluorescent dye injection confined to MT (case 7DY), labeled cells were found contralaterally only in MT (Fig. 11B), and all but one of these cells were in layer III. In the other fluorescent dye case (case 7FB), labeled cells were also found contralaterally in MST and FST (Fig. 11C), but since the injection in this case contaminated the upper bank of the STS, contralateral projections from these areas to MT must be interpreted cautiously.

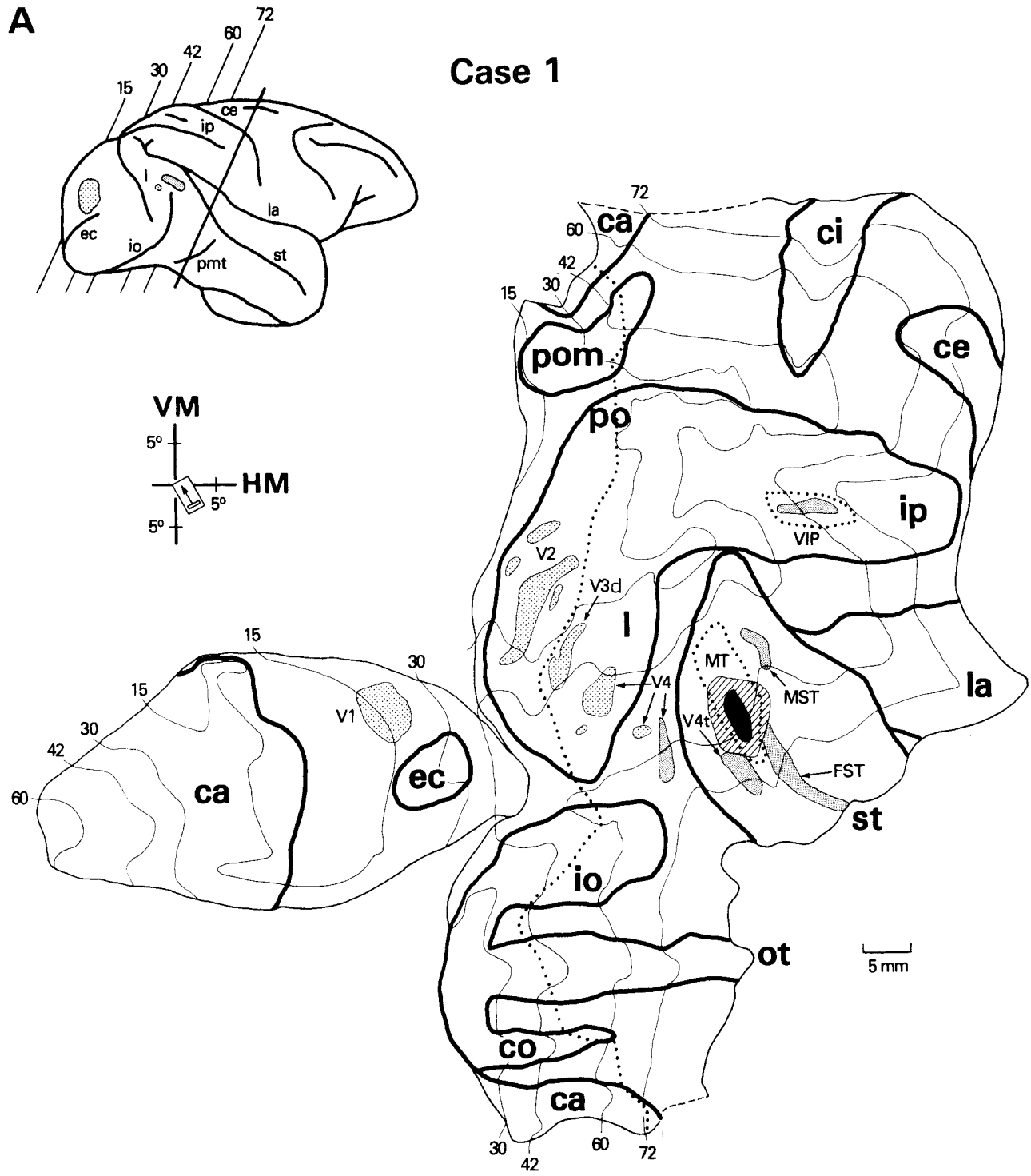


Fig. 5. Case 1: Distribution of labeled terminals. A. Projections are shown on a two-dimensional reconstructions of the cortex. Projections that included granular layer IV are shown in dark shading, projections that excluded granular layer IV are shown in light shading, and the injection site is shown in black. The striped area surrounding the injection site indicates cortex nonspecifically labeled by the injection halo or intrinsic connections of MT. The visual areas containing each of the projections are indicated on the map. The dotted lines indicate the boundaries of V2, MT, and VIP* derived from myeloarchitecture, the heavy lines indicate the boundaries of sulci, and the dashed lines indicate the boundary between neocortex and allocortex. The thin lines running through the map indicate layer IV contour lines from selected cross sections whose locations are shown on a lateral view of the hemisphere at top left. The heavy line through the lateral view of the hemisphere indicates the location of the most anterior section unfolded in the map (i.e., the limit of the reconstruction). The receptive field and directional preference of the cells recorded at the injection site are shown at left, below the lateral view of the hemisphere. B. Projections and injection site are shown on the cross sections whose locations are indicated in A. V1 is indicated by the dashed line through the middle of the cortex, and the myeloarchitectural boundaries of V2, MT, and VIP* are indicated by the arrows. In this figure and in Figures 6–9, distance between sections numbered consecutively is 300 μm. For abbreviations, see Figure 1.

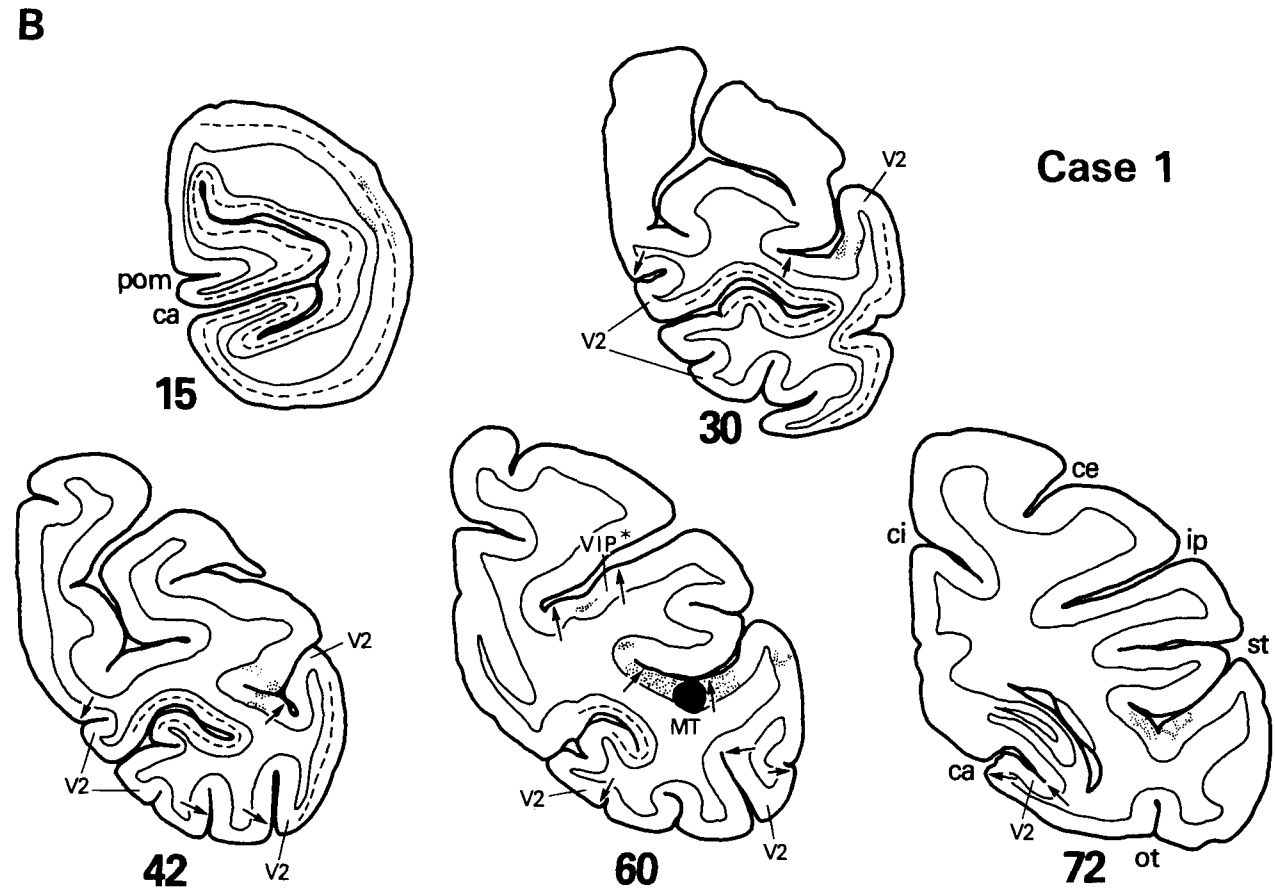


Figure 5 (cont'd)

Individual cases

The anatomical results in each case are illustrated on two-dimensional reconstructions and selected cross sections in Figures 5–11. On the reconstructions, the injection site is indicated in black, the injection halo and intrinsic connections of MT in stripes, anterograde label that included granular layer IV in dark shading, anterograde label that excluded granular layer IV in light shading, and retrogradely labeled cells in dots. The myeloarchitecturally defined borders of V2, VIP*, and MT are also shown in the figures. The relationships among the anatomical connections and the myeloarchitectural zones within the STS are summarized separately in Figure 12.

Case 1. The injection site in case 1 was placed in MT at an eccentricity of 2° in the lower visual field representation, and projections were found to V1, V2, V3d, V4, V4t, VIP, MST, FST, and the frontal eye field (Figs. 5, 12, 13). The projection to V1 was to a single continuous zone centered at approximately the same visuotopic locus in V1 (Daniel and Whitteridge, '61; Gattass et al., '81; Van Essen et al., '84) as that of the injection site in MT. The labeled zone was somewhat smaller than we would expect from the size of the receptive field measured at the injection site, since a corner of the receptive field included the center of gaze but the labeled zone in V1 did not.

There were several patches of label within the myeloarchitectural boundary of dorsal V2 and an additional patch within V3d. The patches in V2 were located on the posterior bank of the lunate sulcus, across the V1/V2 border from the V1 projection, and they seemed to form strips running anteromedially toward the V2/V3 border. The projection to V3d was located in the fundus of the lunate sulcus, just anterior to the strips in V2.

Anterior to the V3d projection, there were several patches of label on the anterior bank of the lunate sulcus, on the prelunate gyrus, and on the lower bank of the STS immediately lateral to MT. All of these patches, except possibly the most anterior part of the one in the STS, were located eiher within cortex that has been described as V4 (Zeki, '73, '77, '78b; Gattass et al., '85) or within V4t (Desimone and Ungerleider, '86). The label in V4 was very light but covered the largest surface extent of any of the cases. Label in both V4 and V4t was distributed through most layers, although layer IV was included in some of the V4 patches but not in others. As expected from the lower field representation of the injection site in this case, there was no label ventrally in either V2, V3v, or V4. In addition, there was no label in either V3A or PO, consistent with the central visual field representation of the injection site.

There were strong projections to areas VIP, MST, and FST and a weak projection to the frontal eye field. The projection to VIP was limited to a narrow strip, centered within the heavily myelinated portion of VIP (VIP*). The projection to MST was located posteriorly in the STS, where we have found a representation of the central visual field physiologically (Desimone and Ungerleider, '86). This pro-

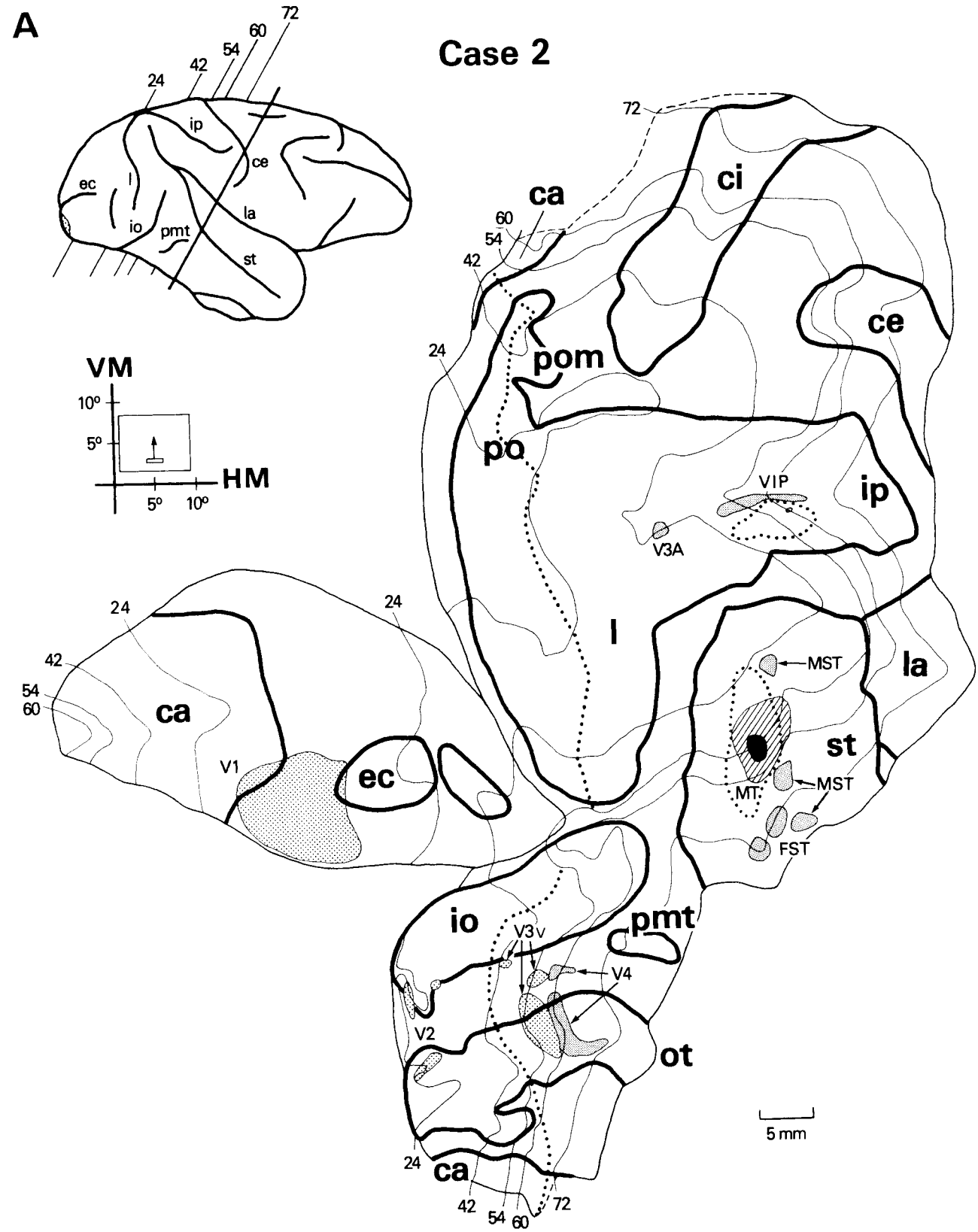


Fig. 6. Case 2: Distribution of labeled terminals. For conventions and abbreviations, see Figures 1 and 5.

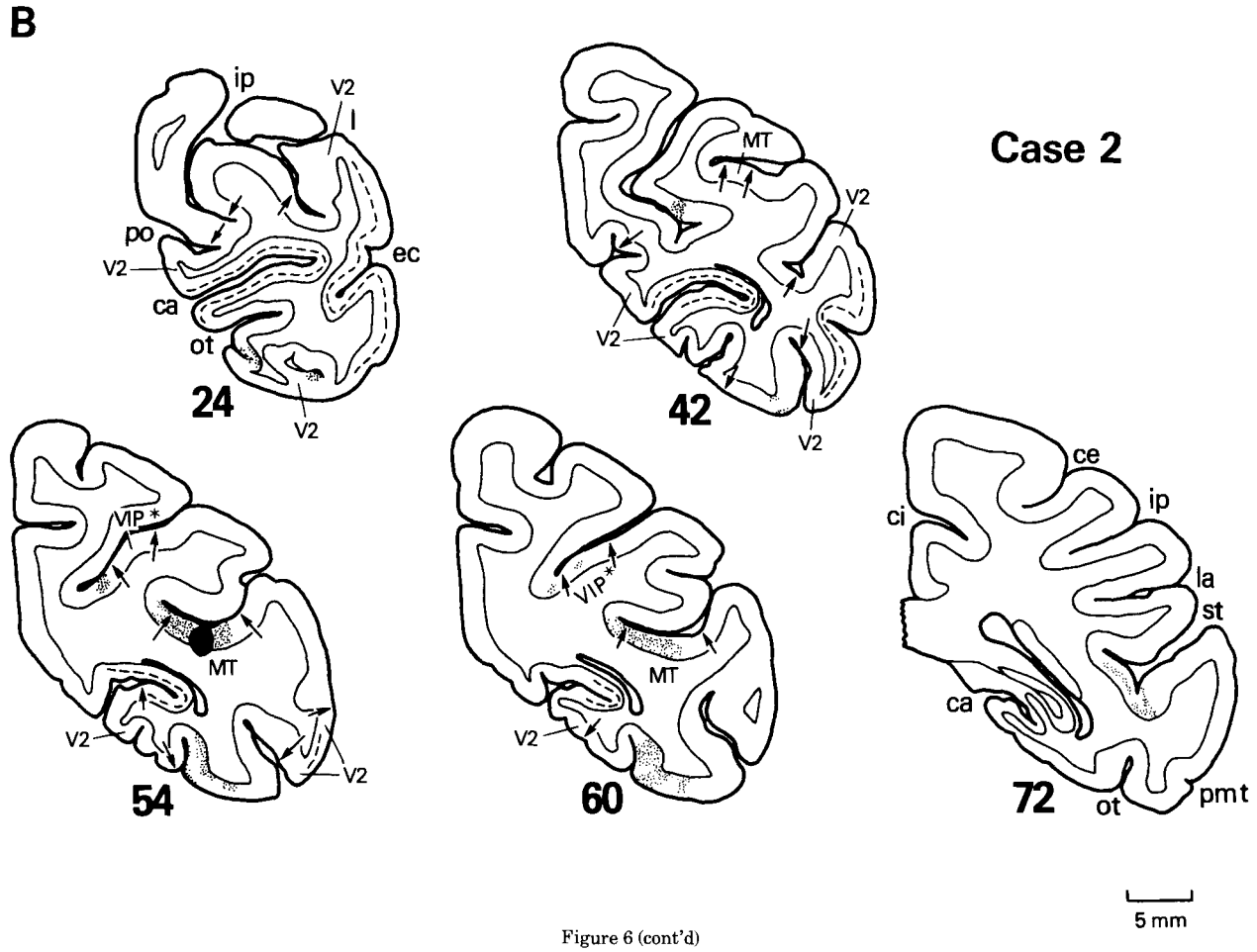


Figure 6 (cont'd)

jection was not confined to a single myeloarchitectural zone, but fell partially within the densely myelinated zone (DMZ) on the upper bank of the STS (Fig. 12). By contrast, the projection anterior to MT in FST appeared to be completely confined within the borders of this myeloarchitecturally distinct area (Fig. 12). The projection to the frontal eye field consisted of one small patch of label on the anterior bank of the inferior limb of the arcuate sulcus (Fig. 13).

Case 2. The injection site in case 2 was placed in MT at an eccentricity of 7° in the upper visual field representation, and projections were found to the same areas as in case 1, with the addition of a projection to V3A (Figs. 6, 12, 13). Furthermore, as a consequence of the injection involving the upper visual field in this case, the resulting projections to areas V1, V2, V3, and V4 were shifted to the ventral aspect of the hemisphere. The projections to V1 and V2 were located near the representation of the vertical meridian at the V1/V2 border and appeared to be at approximately the same eccentricity as that of the receptive field measured at the MT injection site (Gattass et al., '81). The projection to V2 was located at the posterior tips of the inferior occipital and occipitotemporal sulci, and the projection to V3v was located anterior to the one to V2. Further anteriorly, the distribution of label shifted from layers I and VI to include all layers, including layer IV, and we interpret this shift in label to mean that the projection crossed the anterior border of V3v into V4. Consistent with the location of label near the representation of the vertical meridian at the V1/V2 border, the label in V3v and V4 was located at their common border, which also represents the vertical meridian (Newsome et al., '80). The fact that the patches in V3v and V4 were located just across from those in V2 suggests that the visual field representations in all three of these areas are roughly congruent, at least with respect to eccentricity in the upper visual field.

In addition to the projections ventrally to V1, V2, V3v, and V4, there was a clear projection dorsally to area V3A. The projection was located at the anterior end of the annectent gyrus, where V3A has been reported to lie (Zeki, '78c; Gattass et al., '85; Ungerleider et al., in preparation). Unlike the representations of the upper and lower fields in V1 through V4, those in V3A are both located dorsally in the hemisphere. Thus, the projection from the upper field of MT to V3A is consistent with V3A's visuotopic organization. Furthermore, the absence of a V3A projection in case 1, a central-field case, and its presence in case 2, a more peripheral-field case, are consistent with the emphasis of the peripheral visual field in V3A.

There was a strong projection to VIP in this case, which, except for one tiny patch of label, was located entirely medial to the heavily myelinated part of VIP (VIP*). There were also projections to MST and FST, which were particularly complex (Fig. 12). There were three patches of label in MST; all avoided the densely myelinated zone in the upper bank of the STS, and one extended into FST. There were two additional patches of label in FST, but only one patch

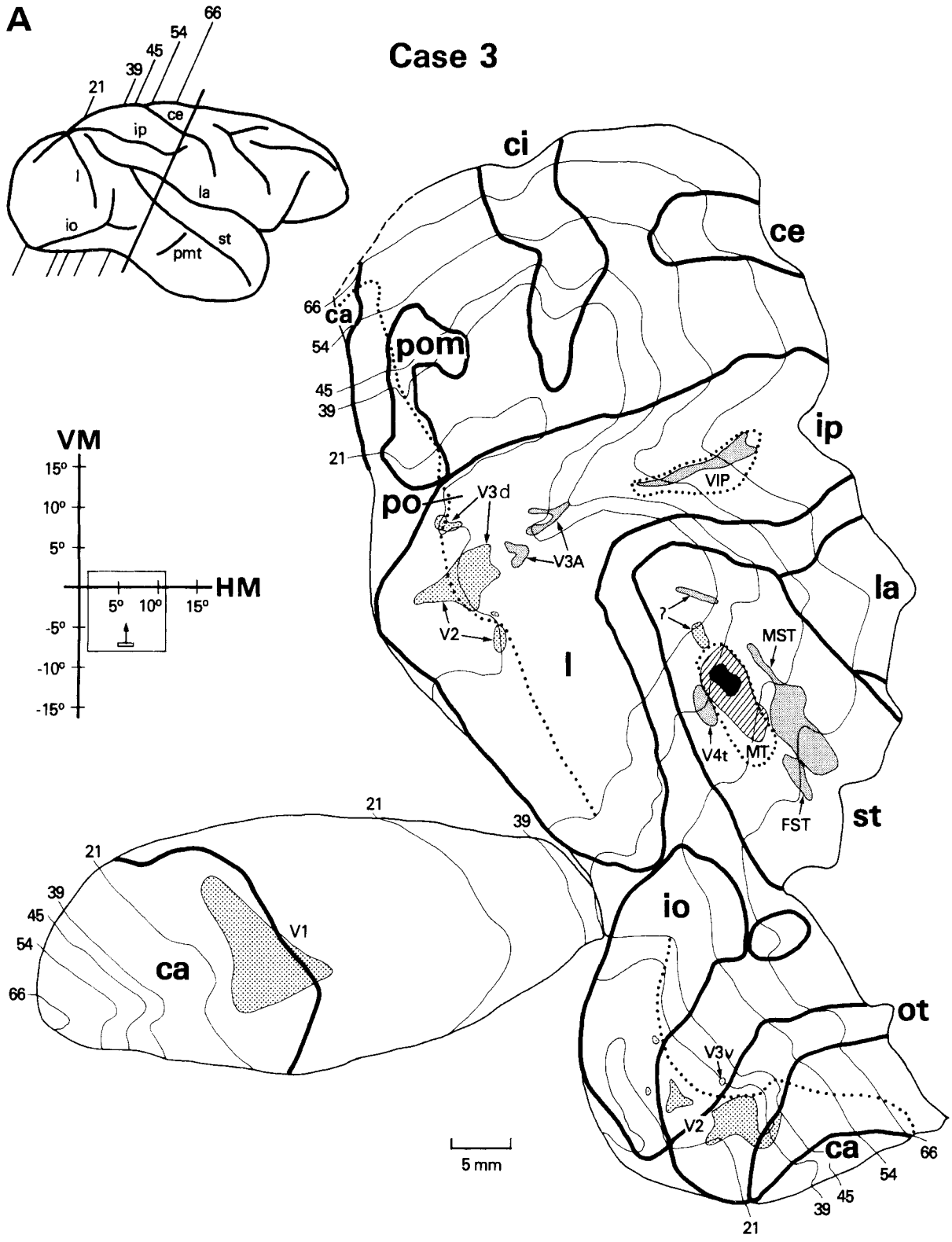


Fig. 7. Case 3: Distribution of labeled terminals. For conventions and abbreviations, see Figures 1 and 5.

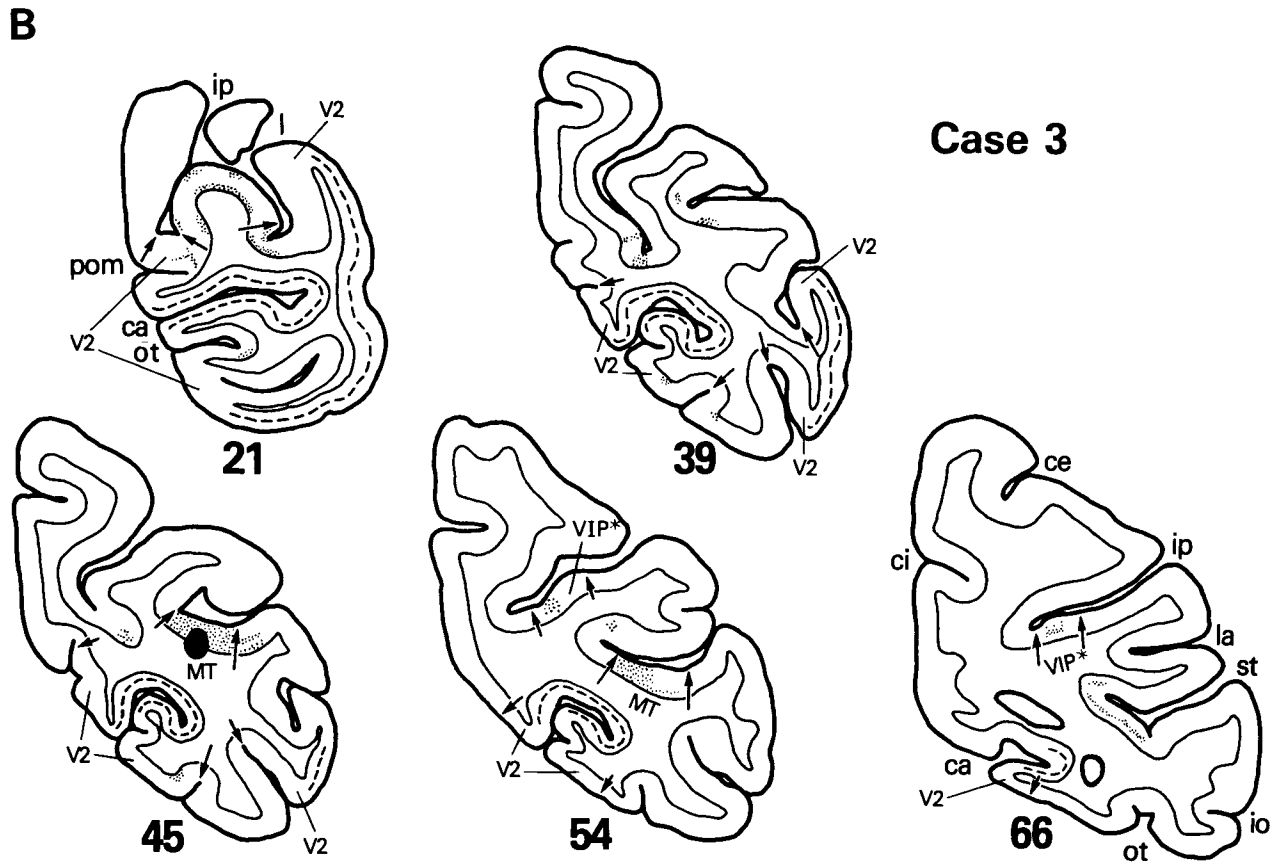


Figure 7 (cont'd)

was clearly confined to it. Finally, there was a projection to the frontal eye field, which consisted of two small patches of label (Fig. 13). One patch was located on the anterior bank of the inferior limb of the arcuate sulcus, as in case 1; the other, less than 1 mm away, was located on the cortical surface.

Case 3. The receptive field measured at the injection site in case 3 was centered in MT at an eccentricity of 8° in the lower visual field, but it crossed the horizontal meridian into the upper visual field as well (Fig. 7). Projections were found to the same areas as in case 2, except for the absence of a projection to the frontal eye field (Figs. 7, 12). Consistent with the involvement of the representation of the horizontal meridian of MT at the injection site, there was a single projection to V1 but split projections to the dorsal and ventral portions of V2 and V3. Like the projection to V1, the projections to V2 and V3 included the representation of the horizontal meridian, which forms the boundary between the two areas (Zeki, '69, '78c; Gattass et al., '81). The projection to V3v was a small one, which may relate to the fact that the injection site involved mainly the lower field representation of MT.

Whereas the projection to V4 in the other cases was weak, in case 3 it may have been absent altogether. The only possible candidates for a V4 projection were two small patches of label posterior to MT in the STS, but it is not clear whether this labeled cortex lies within V4. The only other label in the "V4 complex" was in V4t. It is interesting to note that the injection in case 3 involved the representation of the horizontal meridian, and, similar to case 3, we have seen projections to V4t in cases with injections involving the representation of the horizontal meridian at the V2/V3 border (Ungerleider and Desimone, '86: Fig. 7).

As in case 2, there were projections to both VIP and V3A. The projection to VIP was confined to a narrow strip within its heavily myelinated part (VIP*). The projection to MST in this case was extensive and included both the densely myelinated zone on the upper bank of the STS and cortex lateral to it. The projection to FST, by contrast, was completely contained within the myeloarchitectural borders of the area.

Case 4. The injection site in case 4 was located in the upper visual field representation of MT, as in case 2, but was placed farther peripherally, at an eccentricity of 20° (Fig. 8). As expected, the projections were similar to those in case 2, but the projections to V1 through V4 were shifted further medially in case 4, reflecting the more peripheral representation of the injection site (Figs. 8, 12). In addition, there was a new projection to area PO.

In areas V1 though V4, the label was located ventrally in

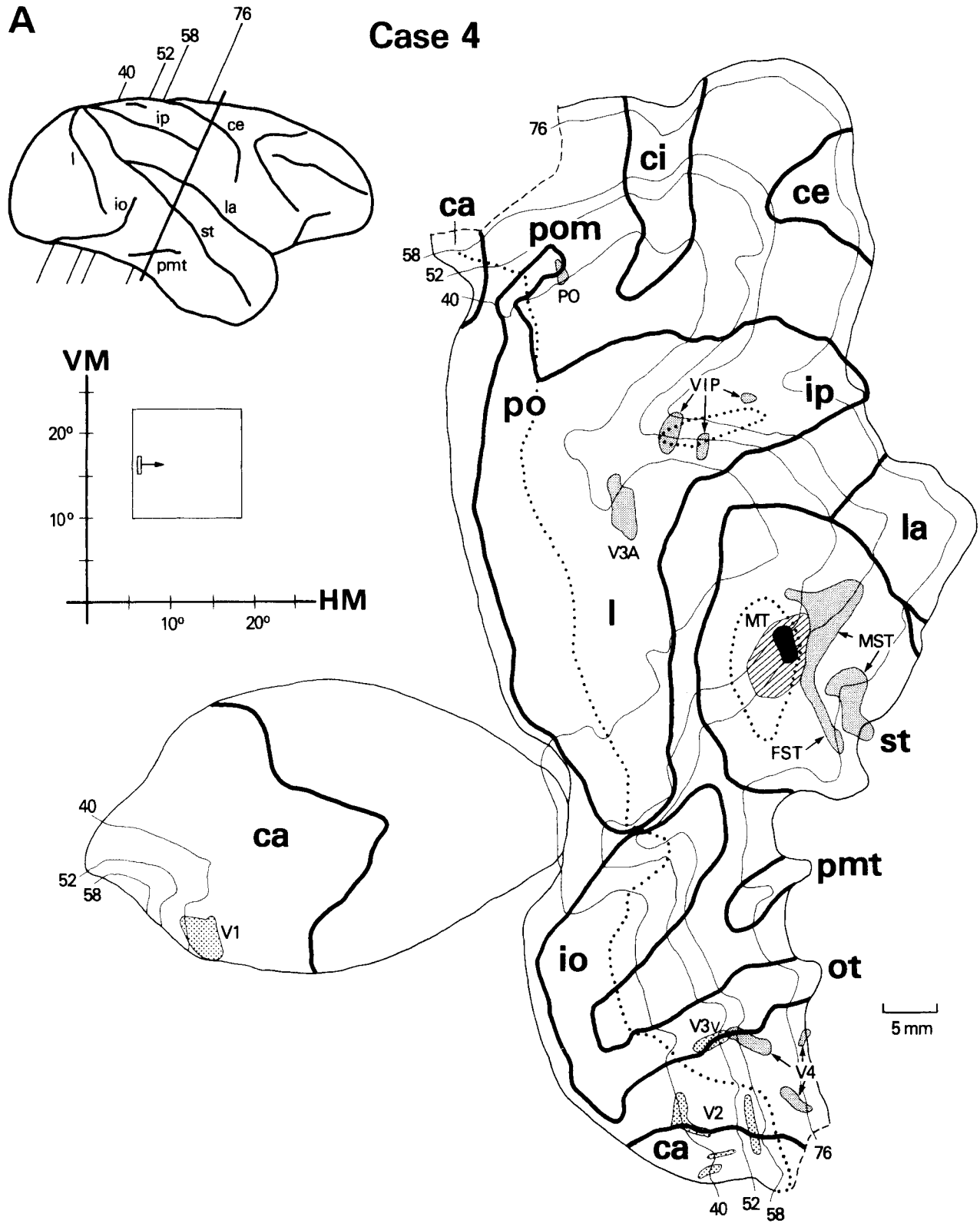


Fig. 8. Case 4: Distribution of labeled terminals. For conventions and abbreviations, see Figures 1 and 5.

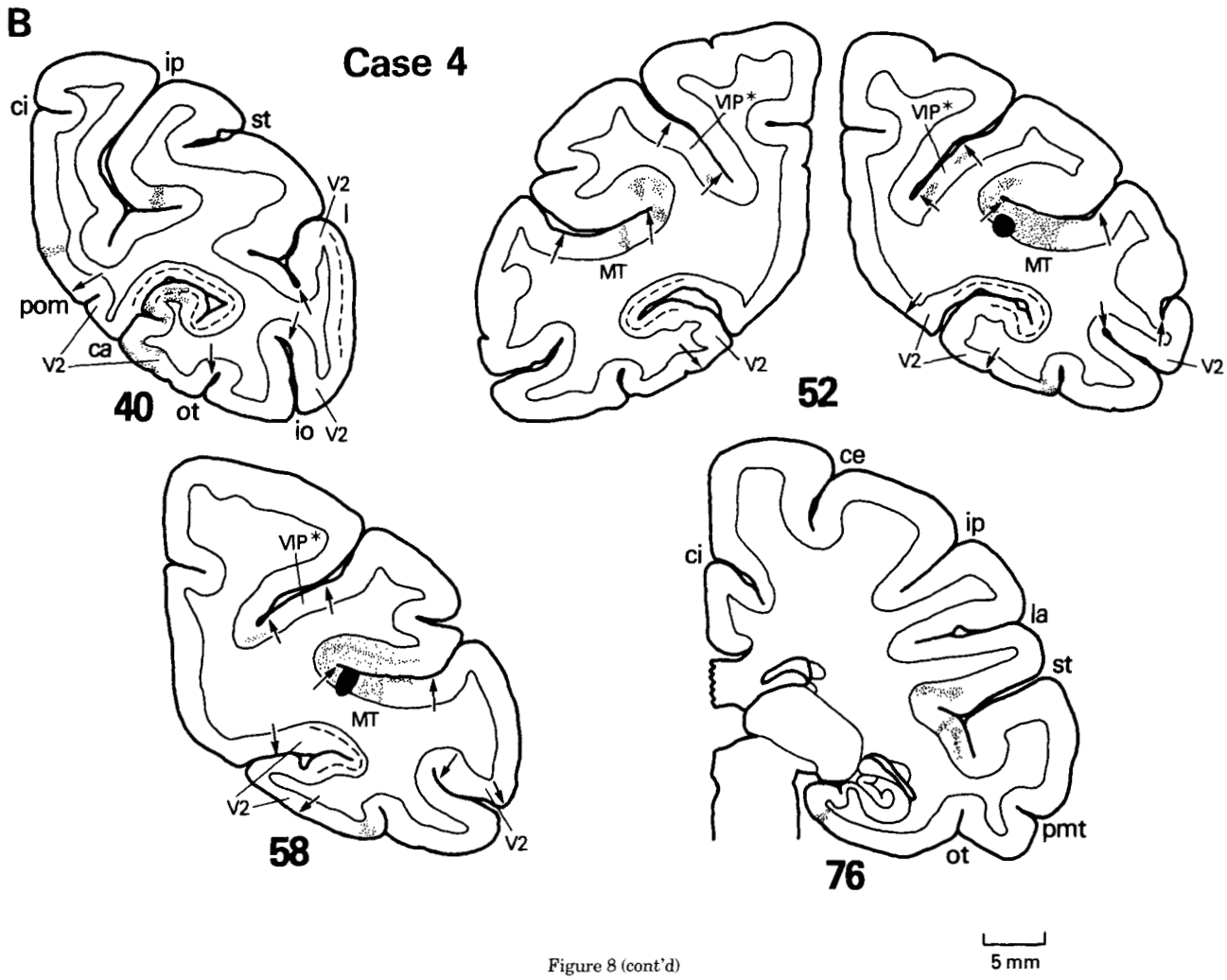


Figure 8 (cont'd)

the hemisphere, close to the representation of the vertical meridian in these areas, which lies at the V1/V2 border and the V3v/V4 border. As in most other cases, the label in V2 was patchy, was somewhat more extensive than the label in V1, and seemed to involve a greater portion of V2's than V1's visual field representation. The label in V4 was also patchy but was much lighter than the label in either V2 or V3v.

Interestingly, the projection to area V3A was in approximately the same location in the annectent gyrus as the projection in case 2 but was several times larger. Since the injection site in case 4 was located farther out in the peripheral field representation than the injection site in case 2, the larger projection may be related to the emphasis of the peripheral visual field in V3A. The more peripheral representation in case 4 may also explain the presence of a projection to PO. PO receives inputs from peripheral field representations of V2 beyond about 20° eccentricity but not from more central field representations (Colby et al., '83; Ungerleider et al., '83). The presence of an MT projection to PO in case 4, with an injection centered at 20° eccentricity, but not in case 2, with an injection centered at 7° eccentricity, is thus consistent with the pattern of V2 projections to PO.

The projection to VIP was particularly complex in that there were three separate patches of label that bore no clear relationship to the heavily myelinated portion of VIP (VIP*). The projection to MST was extensive; there were two large patches of label, one of which was continuous with the label in FST (Fig. 12). The projection to the frontal eye field was virtually identical to that found in case 2 (Fig. 13).

In contrast to all of the other cases with amino acid injections, in case 4 label was also found in the contralateral hemisphere, where it was heaviest in MT itself but present in V3A, VIP, and MST as well (Fig. 8B).

Case 5. The injection site in case 5 was centered within the lower visual field representation of MT, as in case 3, but was placed farther peripherally at an eccentricity of 23° (Fig. 9). As in case 3, the injection apparently spread to the representation of the horizontal meridian of MT, for there was label along the representation of the horizontal meridian of V2 in its upper visual field (Fig. 9). The involvement of the upper field representation was probably minor, however, for the label ventrally, in the upper field representation of V2, was both lighter and less extensive than dorsally, in the lower field representation; also the label in V1 did not appear to extend beyond the representation of

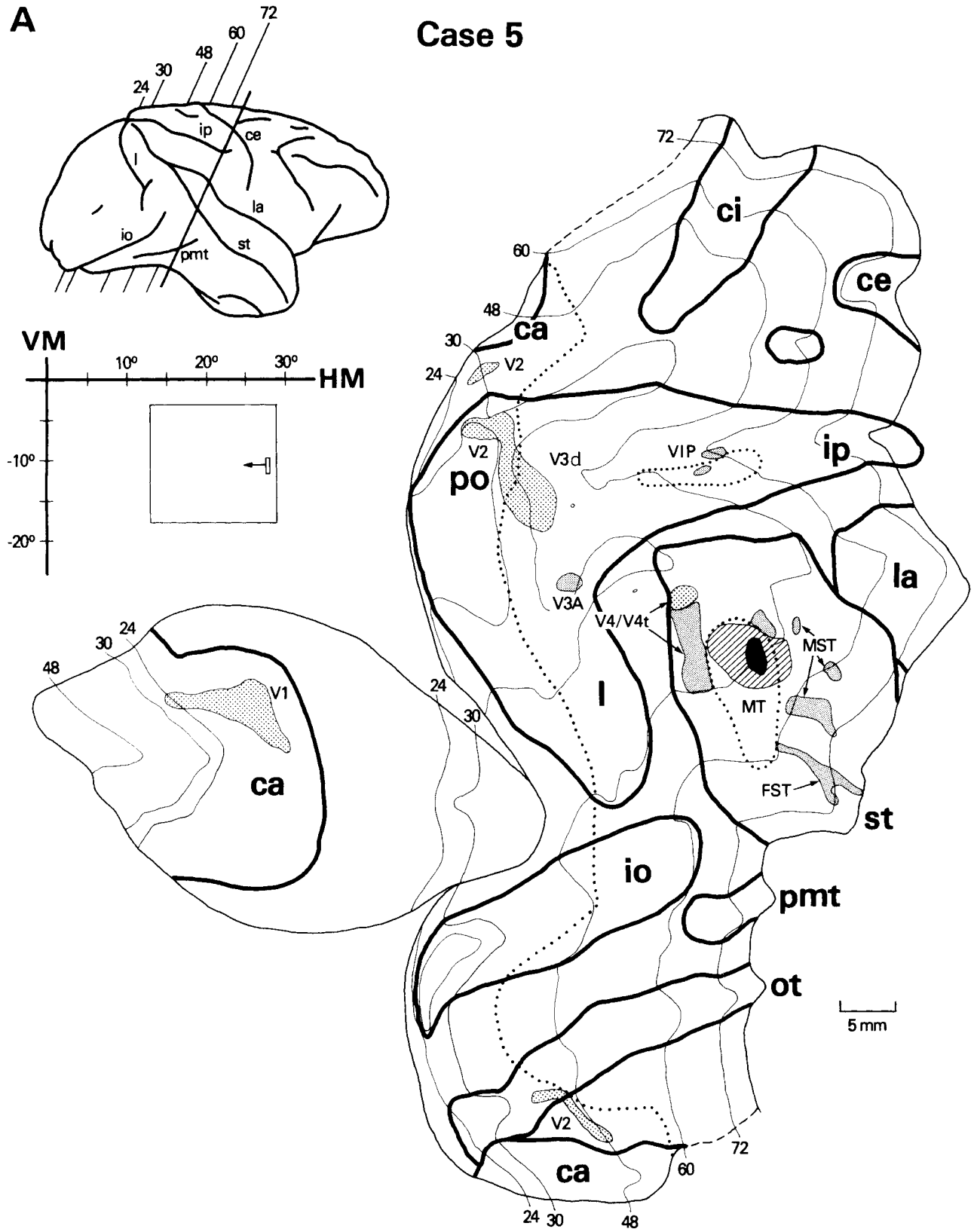


Fig. 9. Case 5: Distribution of labeled terminals. For conventions and abbreviations, see Figures 1 and 5.

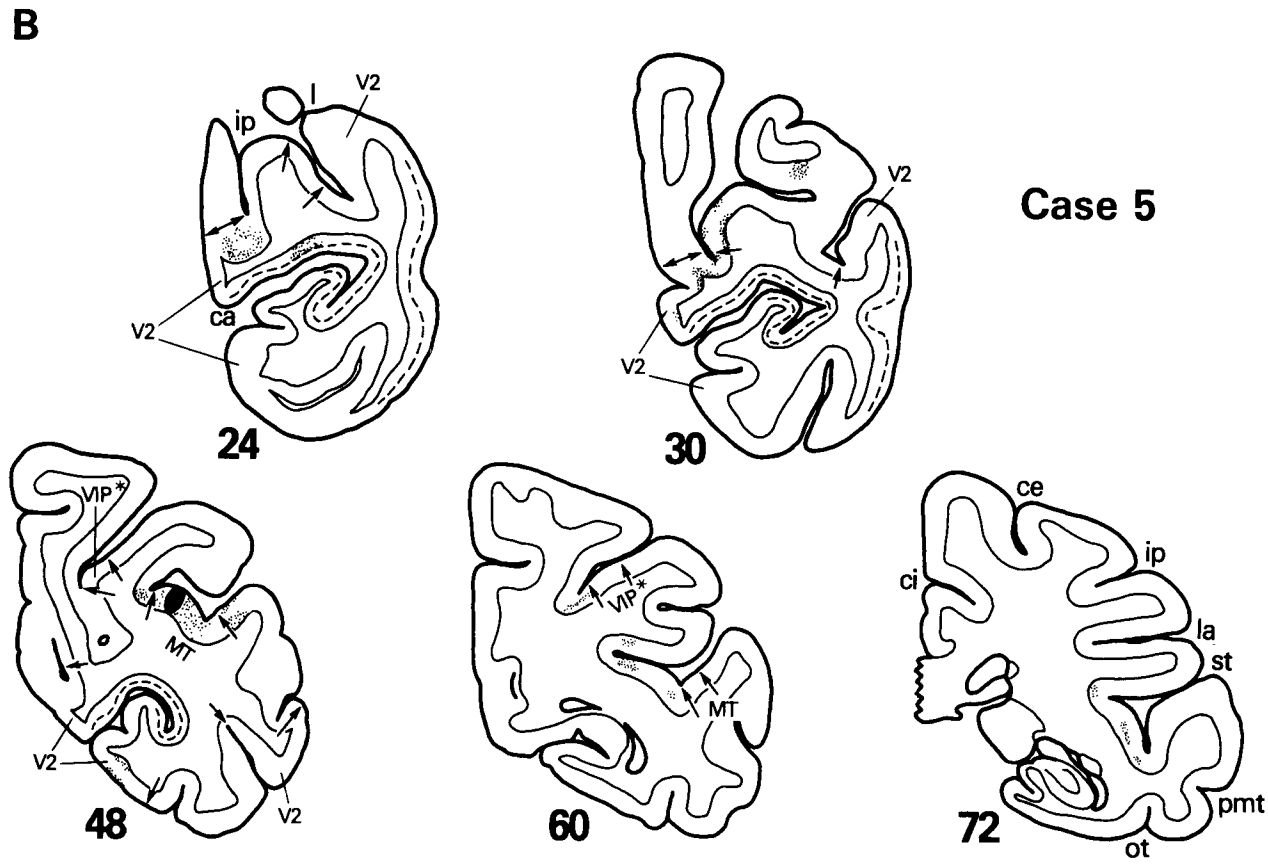


Figure 9 (cont'd)

the horizontal meridian into the upper visual field. Dorsally, the label in V2 was located in the parieto-occipital sulcus and extended across the representation of the horizontal meridian into V3d on the annectent gyrus. Ventrally, the label was confined to V2, probably because there was not enough involvement of the upper field representation at the injection site to reveal a projection ventrally to either V3v or V4.

There was label within V4t, as in case 3, plus additional label in the most anterior part of V4 just lateral to V4t and posterior to MT in the STS. Near the injection site, the label was located in all layers, but it excluded layer IV near the posterior end of the sulcus. Like other cases involving the peripheral visual field, there was label in V3A; however, unlike case 4, there was no label within the expected portion of PO. There were two patches of label in VIP, one within its heavily myelinated part (VIP*) and one immediately medial to it. There were several separate patches of heavy label within MST and a single large patch within FST (Fig. 12). No label was found within the frontal eye field.

Case 6. Although the injection site in case 6 clearly involved cortex outside as well as inside MT most of the projections resembled those of the other cases, and we have therefore included a reconstruction of the case for comparison (Figs. 10, 12). The receptive field measured at the injection site was centered at an eccentricity of 34° in the lower visual field representation. Even though the receptive field was directionally selective, we could not determine histologically if it was recorded from neurons on the border of MT or from neurons just beyond MT in V4t or V4, because the recording electrode track was obscured by damage from the injection needle. Electrophysiological recordings from this animal indicate that receptive fields measured near the injection site in all three areas (i.e., MT, V4t, and V4) were located in the representation of the lower peripheral visual field (Desimone and Ungerleider, '86).

The projections in case 6 included all of the areas found in the other cases plus a new zone on the ventromedial aspect of the temporal lobe. The label in V1 was centered in the lower field representation but appeared to extend close to the representation of the horizontal meridian. Additional evidence that the injection site may have involved the representation of the horizontal meridian in either MT or at the V4/V4t border was that there were split projections to both V3d and V3v and a projection to ventral V4. The projection to dorsal V4 could not be distinguished from the spread of label into this area from the injection site. The label in both V3d and V3v was located near the representation of the horizontal meridian at the border with V2, and the label in ventral V4 appeared to be located at the anterior border of V4, which also represents the horizontal meridian (Gattass et al., '85). One puzzle is why there were projections to V3v and ventral V4 but not to ventral V2, an arrangement exactly opposite to the one in case 5.

The projection to the ventral temporal cortex found in case 6 but not in cases 1–5 was located in the occipitotemporal sulcus anterior to the label in V4. We have previously

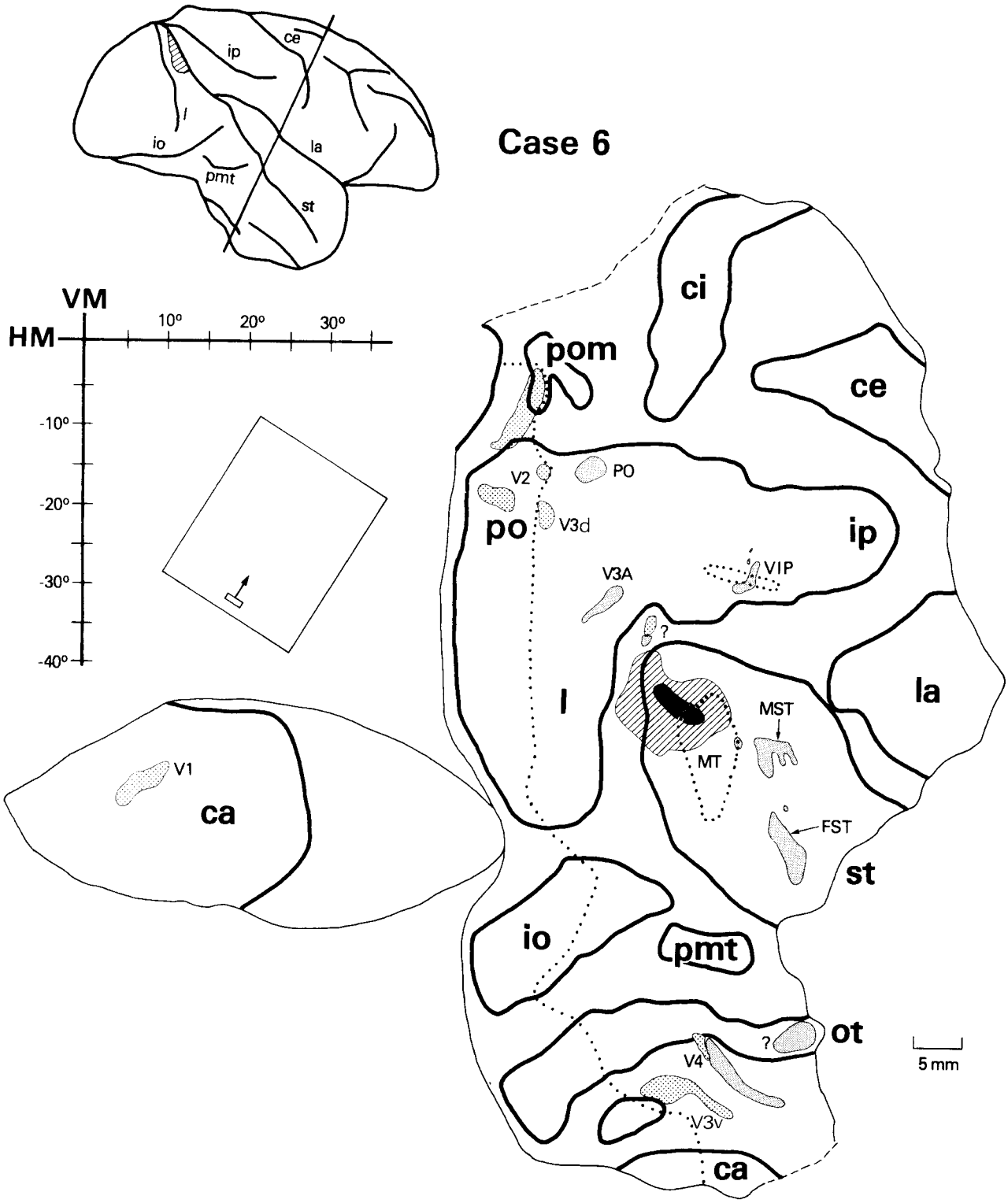


Fig. 10. Case 6: Distribution of labeled terminals. Distance between sections numbered consecutively is 330 μm. All other conventions are the same as in Figure 5. For abbreviations, see Figure 1.

seen projections to this region from injections within the peripheral field representation of V4 (unpublished data). The projections to V3A, MST, and FST were generally similar to those found in the other cases. As in case 4, an upper peripheral field case, there was also a projection to PO. In case 6, however, this projection was located in the parieto-occipital sulcus, where PO's lower peripheral field representation is reported to lie (Covey et al., '82). The VIP projection in case 6 extended closer to the posterior lip of the intraparietal sulcus than in the other cases, possibly due to the involvement of V4 at the injection site. We have seen projections into the cortex near the lip of the intraparietal sulcus in other cases with injections of V4 (unpublished data).

Case 7. The injections of diamidino yellow (DY) and fast blue (FB) in case 7 were centered in MT at eccentricities of 16° in the lower and 9° in the upper visual field representations, respectively. Because of the contamination of the upper bank of the STS with the FB dye, consideration of the results from this injection are limited to only those visual areas that also contained cells labeled with the DY dye. With the exception of the frontal eye field and possibly PO, all of the areas that contained anterogradely labeled terminals in cases 1–5 also contained cells retrogradely labeled with DY and FB (Figs. 11, 12).

In V1, the patches of DY- and FB-labeled cells were well separated, near the representation of the vertical meridian in the lower and upper visual fields, respectively. In V2, DY-labeled cells were confined to the representation of the lower field and FB-labeled cells were concentrated in the representation of the upper field. A small patch of FB-labeled cells in the lower field representation of V2, near the V2/V3d border, suggests that there may have been some minor involvement of the horizontal meridian in MT by the FB injection. Both the DY- and FB-labeled cells in V2 were organized into a striking pattern of strips running between the representations of the vertical and horizontal meridians. A tendency for such a pattern was noted in some of the cases with injections of amino acids, but the pattern was much clearer in this instance.

In V3, as in V2, the DY-labeled cells were confined to the lower field representation (V3d) and the FB-labeled cells were located predominantly in the upper field representation (V3v). In this case we were able to estimate the borders of V3 from the myeloarchitecture, as shown in Figure 11. Both DY- and FB-labeled zones in V3 were located just across the V2/V3 border from zones of the same label in V2. There were a few FB-labeled cells in V3d, which, like the FB-labeled cells in dorsal V2, again suggests some involvement of the representation of the horizontal meridian by the FB injection.

The topographic distribution of label in V4 was similar to that in V3 in that DY-labeled cells were confined to V4's lower field representation and FB-labeled cells were located mainly, but not exclusively, in V4's upper field representation. The DY-labeled cells in V4's lower field representation tended to congregate in narrow strips running along the prelunate gyrus, whereas the FB-labeled cells in V4's upper field representation were concentrated in the occipitotemporal sulcus. There were virtually no labeled cells in V4t, possibly because V4t was so limited in extent in this animal (see Fig. 12).

Several patches of labeled cells were distributed throughout the part of the dorsomedial prestriate cortex that lies buried within the junction of the lunate, parieto-occipital, and intraparietal sulci. One patch of FB-labeled cells was centered within the region that has been described as V3A. Two patches composed primarily of DY-labeled cells (intermixed with a few FB-labeled cells) could also be interpreted to be within V3A but appeared to be medial to the V3A projections seen in the other cases. One of the patches was medial enough to fall within area PO or, alternatively, it could lie within a separate visual area located between V3A and PO. DY-labeled cells in the more medial of the two patches were contained predominantly in layer III, whereas those in the more lateral patch were more evenly distributed between the infragranular and supragranular layers. Thus, although the results indicate that MT receives projections from the dorsomedial prestriate cortex, it is not yet possible to assign the connections to particular visual areas.

Large numbers of DY- and FB-labeled cells were found in the infragranular layers of areas MST, FST, and VIP, both within and medial to the latter area's heavily myelinated part. In addition, there were two cortical regions that contained FB-labeled cells but did not receive anterograde projections in any of the cases with injections confined to MT. One of these regions was in the parietal cortex, both in the lunate-intraparietal cleft (see "?" above V3A in Fig. 11) and on the inferior parietal lobule. The other region was in the temporal cortex, anterior to area V4. The labeled cells in both regions presumably reflect connections with the cortex contaminated by the FB injection on the upper bank of the STS.

Finally, there were both DY- and FB-labeled cells in the contralateral hemisphere (Fig. 11B,C). The DY-labeled cells were exclusively in MT, in the same part of the area as the part injected in the opposite hemisphere. The same was true of the FB-labeled cells, except that a few of these cells were found in the contralateral MST and FST as well.

DISCUSSION

We have found that, in addition to connections with V1, area MT in the macaque has reciprocal connections with a number of areas in prestriate, parietal, and prefrontal cortex. In the following discussion, we first consider how the connections of MT help define the topography and organization of visual areas in extrastriate cortex. We then consider the laminar organization of MT's connections and the pathway from striate cortex through MT into the parietal lobe. Figure 14 illustrates the location of all the areas to which MT projects in the macaque. Similarities between the connections of MT in the macaque and the connections of MT in a variety of other primates have been comprehensively reviewed by Weller et al. ('84) and will not be reviewed here.

Organization of extrastriate visual areas

V2 and V3. Physiological and anatomical studies have shown that V2 and V3 form belts surrounding V1, with alternating representations of the vertical and horizontal meridians at the borders (Cragg and Ainsworth, '69; Zeki, '69, '78c; Gattass et al., '81, '85; see Figs. 1, 14). The topography of MT's connections with V2 and V3 confirms this organization and suggests that the visual field maps in V2 and V3 are roughly congruent. However, the map in V3 may be compressed relative to that in V2, since V3 is both narrower and shorter than V2; in several of the MT injection cases, the resulting label in V3 did not extend as far medially as did the label in V2 (see cases 1, 4–6, and 7DY).

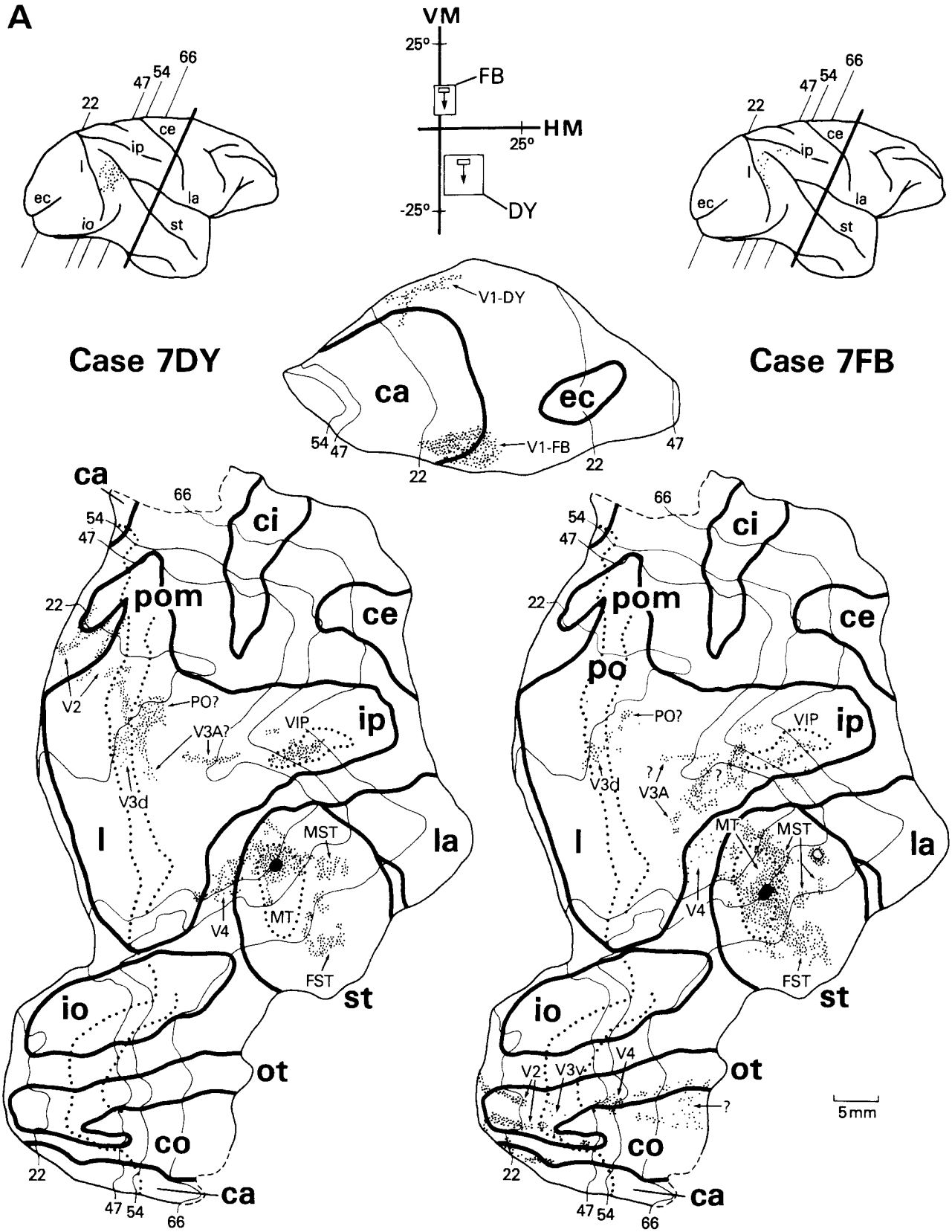
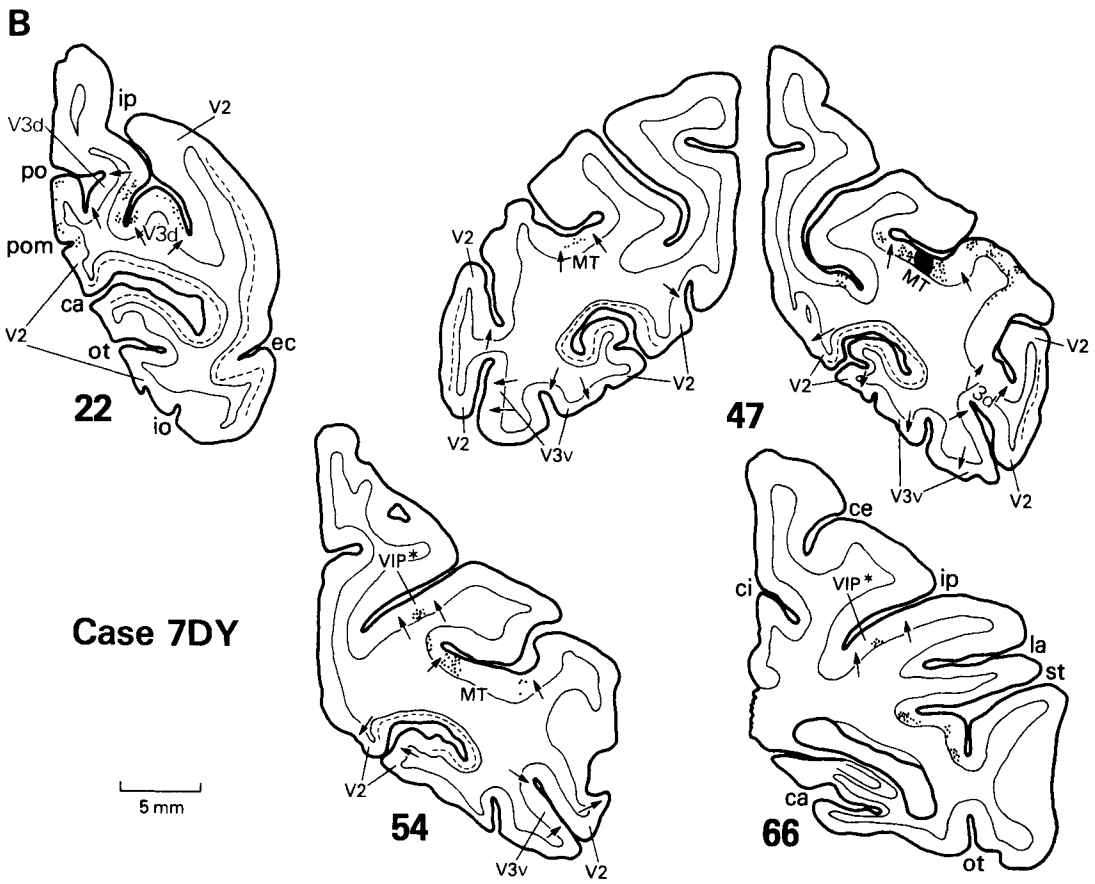


Fig. 11. Case 7: Distribution of cells retrogradely labeled with fluorescent dyes of fast blue (FB) or diamidino yellow (DY). A. The distribution of DY-labeled cells is shown on the map at left, and the distribution of FB-labeled cells is shown on the map at right. The injection sites are indicated in black, and the small light-gray zone on the map at right indicates where FB label spread into the superficial layers of the cortex on the upper bank of STS. The density of dots on the maps indicates the relative density of labeled cells. The distributions of DY- and FB-labeled cells in V1 are indicated on the map at top. The approximate myeloarchitectural boundaries of V3v and V3d could be visualized in this case and are shown with dotted lines. Distance between sections numbered consecutively is 330 μm. All other conventions are the same as in Figure 5. B, C. Distributions of DY- and FB-labeled cells, respectively, shown on the cross sections whose locations are indicated in A. The dots indicate the relative density of labeled cells. Examples of labeled cells in the contralateral MT are shown for case 7DY in section 47 of B and for case 7FB in section 54 of C. For abbreviations, see Figure 1.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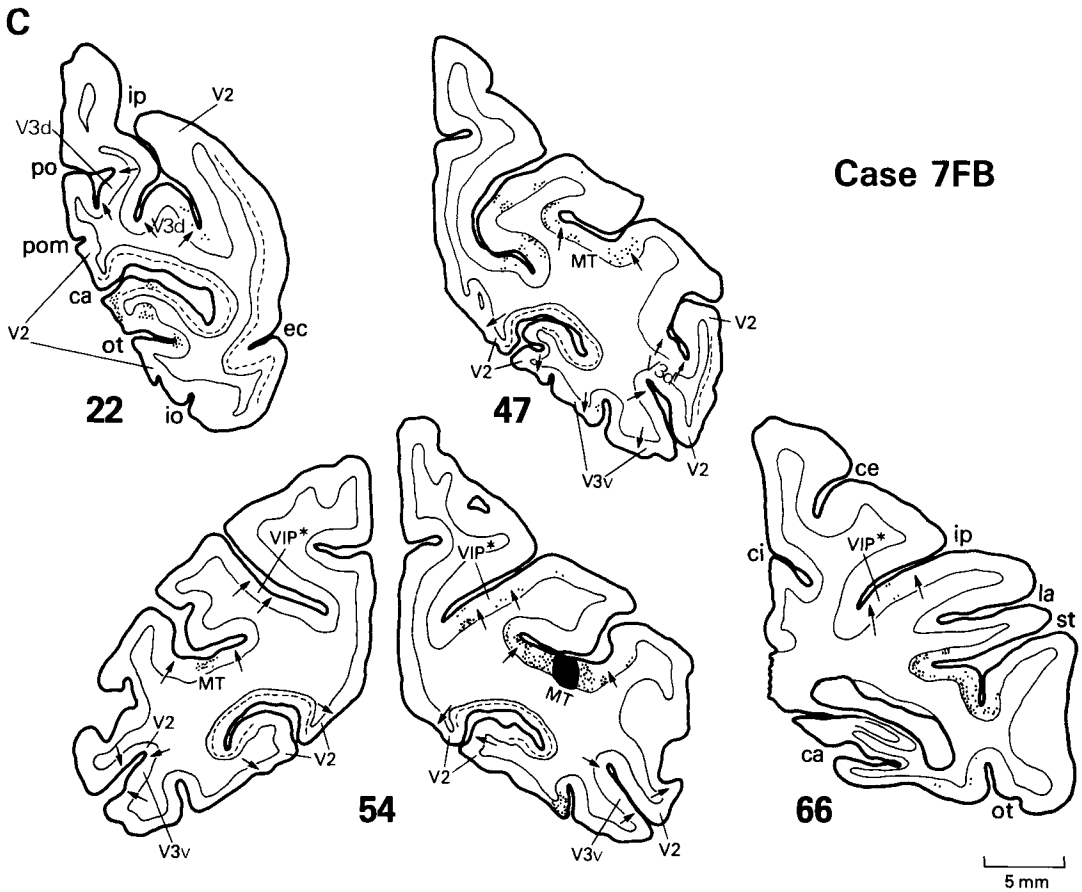
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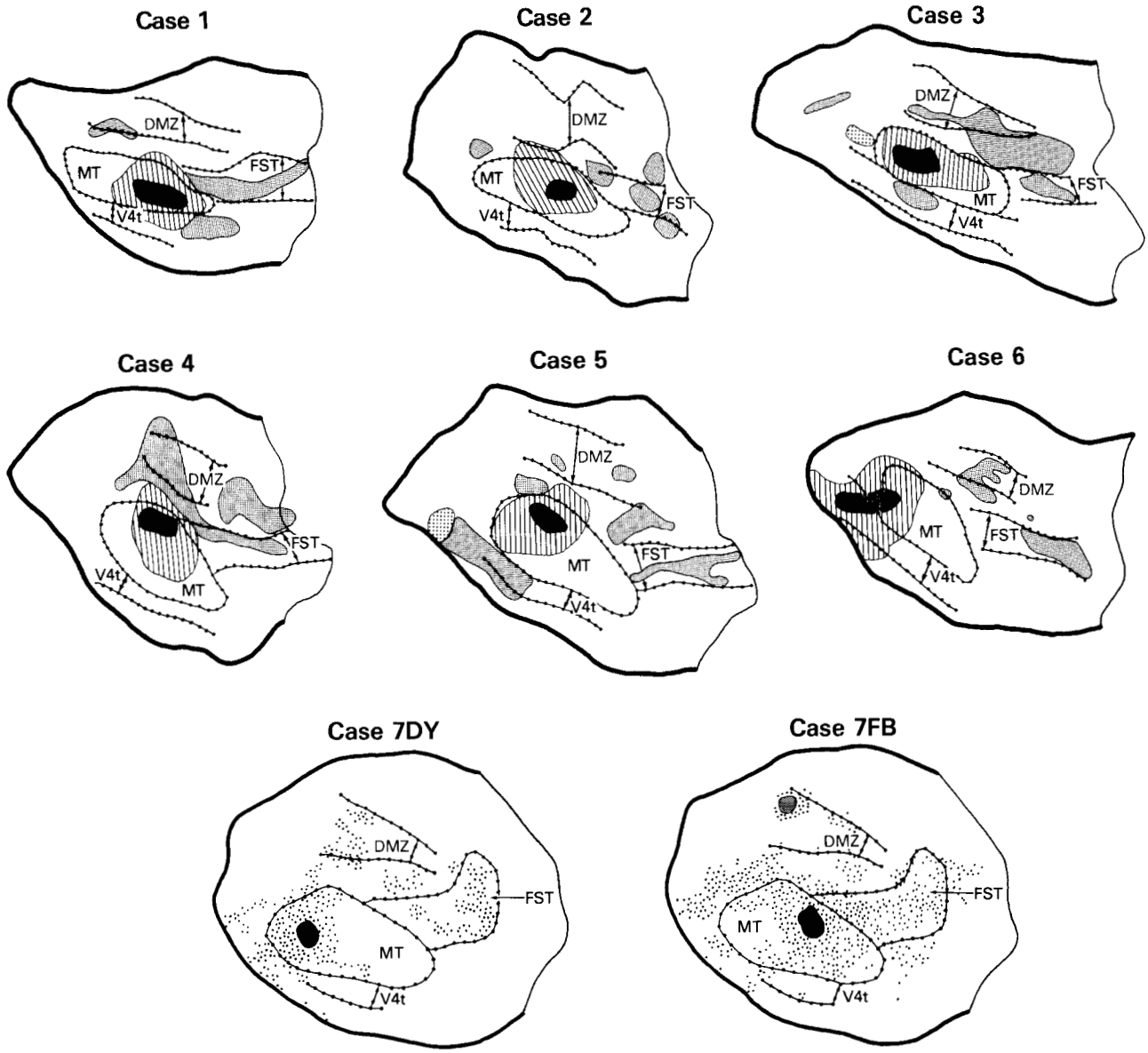

Fig. 12. Distribution of label in STS and its relation to myeloarchitectural zones in each case (see Figs. 5–11). The dotted lines indicate the myeloarchitectural boundaries of MT, V4t, FST, and the densely myelinated zone (DMZ) of the upper bank of STS. Conventions as in Figure 5.

In all cases the connections with V2 were patchy, and in many cases these patches seemed to form strips running from the representation of the vertical toward the representation of the horizontal meridian (see especially case 7). Recently, DeYoe and Van Essen ('85) and Shipp and Zeki ('85) have reported that cells projecting from V2 to areas MT and V4 are organized into alternating strips and that the strips with cells projecting to MT have a high proportion of units selective for directionality or disparity. Thus, just like directionally selective cells in V1 (Movshon and Newsome, '84), those in V2 project preferentially to MT. However, unlike the cells in V1 that project to MT, those in V2 appear to be organized not only horizontally by lamina (layers IVB and VI in area V1 and layer III in area V2), but vertically, in strips, as well.

MT's connections with the dorsal half (lower field representation) of V3 were indistinguishable from its connections with the ventral half of V3 (upper field representation) in both topography and laminar organization. In addition, myeloarchitecture in the dorsal and ventral halves of V3 was, in some locations, similar (see Fig. 4A,B). Because dorsal V3 is reciprocally connected with V1 while ventral V3 is not (Burkhalter and Van Essen, '83; Felleman and Van Essen, '84; Van Essen et al., '86; Ungerleider, unpublished data), we use the terms V3d and V3v to distinguish between the two. It has been suggested that the ventral half of V3 is a separate visual area from the dorsal half, and the name "VP" has been proposed for the ventral half (Newsome et al., '80; Van Essen et al., '86). To us, it is not yet clear that the differences between V3d and V3v are

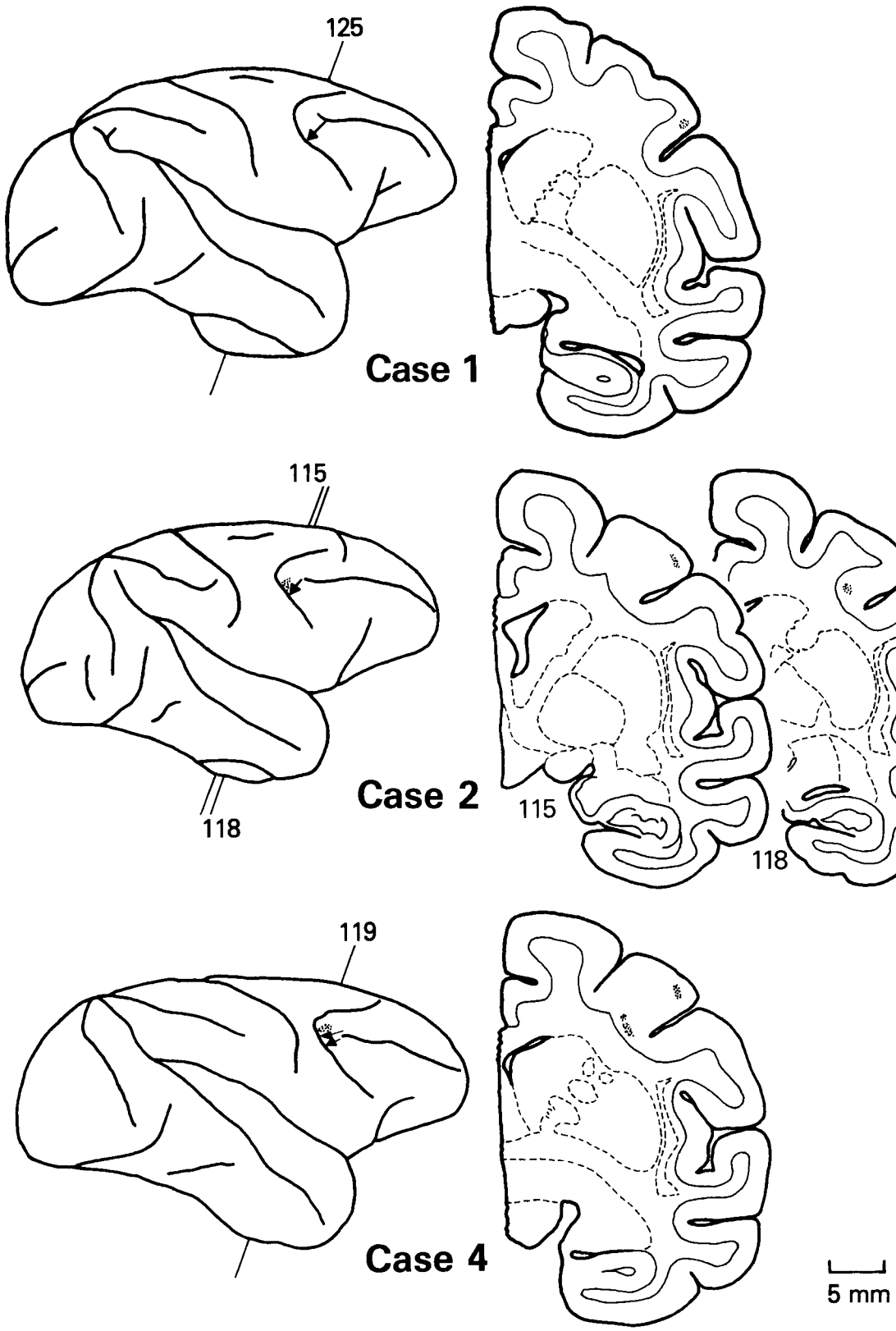

Fig. 13. Projections to the frontal eye field in cases 1, 2, and 4. Arrows on the lateral views of the hemisphere indicate the location of label within the anterior bank of the arcuate sulcus.

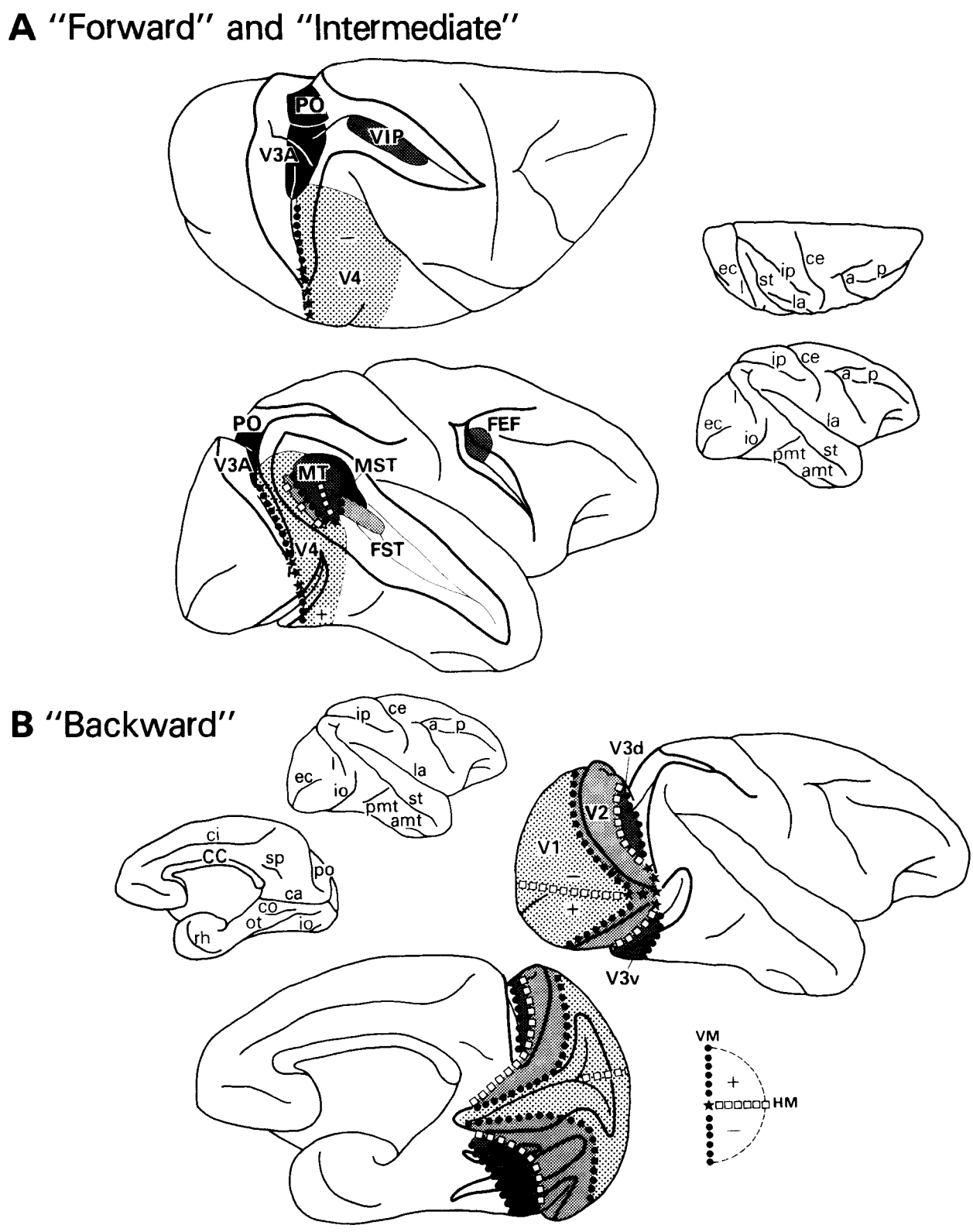

Fig. 14. The location and extent of the areas to which MT projects, illustrated on views of the hemisphere with the sulci partially opened. A. Areas that receive "forward" or "intermediate" projections of MT, shown on dorsal and lateral views of the hemisphere. B. Areas that receive "backward" projections of MT, shown on lateral and medial views of the hemisphere. The representation of the vertical meridian is indicated by dots, the horizontal meridian, by squares, the center of gaze, by stars, and the upper and lower visual fields, by plus and minus signs, respectively. The region labeled MT includes MTp, and the region labeled V4 includes V4t. For abbreviations, see Figure 1.

sufficiently great that they should be considered as separate areas. By comparison, different portions of the visual field maps in V1 and V2 also have somewhat different connections (Zeki, '80; Ungerleider et al., '83; Ungerleider, unpublished data) and properties (Poggio et al., '75; Zeki, '83; Livingston and Hubel, '84), yet V1 and V2 are each regarded as a single area. In cases such as V3, the use of related (but different) names for two parts of a single visual field map may help in distinguishing between the two parts while maintaining their relationship to the complete map. We do not, however, favor the term VP for the ventral part of V3, as it implies a homology with area VP in the owl monkey. Little is known about the topography, connections, neural properties, or architecture of area VP in the owl monkey, and it therefore seems premature to propose a homology with the ventral part of V3 in the macaque.

The difference in anatomical inputs to V3v and V3d does suggest some difference in the way visual information from the upper and lower visual fields is processed. In the lower visual field representation of striate cortex, the output of cells in layer IVB is directed to areas V2, MT, and V3d, whereas in the upper field representation, layer IVB's output is apparently directed only to V2 and MT (Lund et al., '75; Maunsell and Van Essen, '83b; Ungerleider, unpublished data). Since layer IVB cells are thought to provide information derived indirectly from the magnocellular layers of the lateral geniculate nucleus (Lund et al., '75), this specialized information may be utilized more fully in the lower than in the upper visual field. Alternatively, any special contribution of V3d to the processing of IVB output may shift, for the upper visual field, to either V2 or MT. Thus, there could be a difference in the relative contributions of magnocellular and parvicellular inputs to the upper and lower visual field representations of all three areas, V2, V3, and MT.

V4 and V4t. The projections of MT support the notion that V4 is a beltlike area beyond V2 and V3 (Ungerleider et al., '83; Gattass et al., '85; Ungerleider, '85). Like the projections to V2 and V3, projections to V4 from the lower field representation of MT were located dorsally, those from the upper field representation of MT were located ventrally, and those from the horizontal meridian of MT were located both dorsally and ventrally. Within both the upper and lower field representations, central field sites in MT projected laterally in V4 and peripheral field sites projected medially.

Although the projections of MT indicate a gross visuotopic organization in V4, at least with regard to the representations of central versus peripheral and upper versus lower visual fields, they do not reveal any of the details. Locally, the topography of V4 may be highly complex. On the prelunate convexity, Van Essen and Zeki ('78) have described several representations of the vertical meridian, and Maguire and Baizer ('84) have described two representations of the lower visual field separated by a representation of the vertical meridian. By contrast, Gattass, Sousa, and Gross (personal communication) have suggested that V4 contains one coarse representation of the visual field with single points in the field represented along "lines" in V4. Our results are consistent with all of these proposed organizations, since single injections within MT sometimes resulted in several separate patches of label within V4. The clearest tendency in our results was for projections from the horizontal meridian of MT to be concentrated anteriorly in V4t and the adjacent part of V4. Several previous studies have also suggested a representation of the horizontal meridian at or near the V4/V4t border (Maguire and Baizer, '84; Desimone and Ungerleider, '86; Gattass et al., '85). Unlike projections to V4, however, those to V4t arose only from MT sites representing the lower visual field, consistent with our physiological findings that only the lower visual field is represented in V4t (Desimone and Ungerleider, '86).

The density of label in V4 following MT injections indicated that the connections between the two areas may be relatively weak. Anterograde label in V4 was nearly always lighter than in other cortical areas, and the density of retrogradely labeled cells in V4 was less than in V2 or V3, suggesting that V4 provides a less important input to MT. In keeping with this suggestion, we have also found weak and variable retrograde and anterograde label in MT following injections of V4 (unpublished data).

The dorsomedial prestriate cortex, including V3A and PO. The visuotopic organization of the dorsomedial prestriate region that includes areas V3A and PO is perhaps even more complex than that of V4. On the basis of physiological recordings, Van Essen and Zeki ('78) have reported that V3A contains more than one representation of some parts of the visual field. We were unable to discern any visuotopic organization in the connections of MT with V3A, probably because of the difficulty in comparing results across animals in a relatively small area with a complex topography. Our anatomical results in PO were limited to two cases, and thus, little can be concluded with regard to topography. Nonetheless, in the case with an MT injection site representing the upper visual field (case 4), label was found in the portion of PO where the upper field representation has been described by Covey et al. ('82), and in the case with an injection site that included the lower field representations of MT, V4t, and possibly V4 (case 6), label was located in the portion of PO where a lower visual field representation has been described (Covey et al., '82). Moreover, both of these cases had injections into loci representing the peripheral visual field, consistent with the emphasis of the peripheral field in area PO. Finally, Colby et al. ('83) have observed retrogradely labeled cells in the peripheral field representation of MT following fluorescent dye injections of PO.

VIP. Projections from MT to VIP did not appear to be topographically organized. In each case, the projection consisted of one or more patches of label in the bottom half of the posterior bank of the intraparietal sulcus. Despite the absence of any clear topography, there was both anatomical and architectural evidence that the VIP projection field may contain two separate areas. The cortex in the lateral part of the projection field was heavily myelinated and was therefore clearly distinguishable from the cortex in the medial part of the projection field, at the bottom of the sulcus. In all but two injection cases, there were projections from MT into both zones, and in some of the cases (cases 2, 5, 7DY, and 7FB), there was a gap in the label at the border between the two zones. In the two cases that were the exceptions (cases 1 and 3), the injections were placed within the central visual field representation of MT and the resulting label was confined to the heavily myelinated zone. The difference between these two cases and the others may reflect either variability in the connections of MT or a reduced emphasis of the central visual field in the medial, more lightly myelinated, zone. The latter interpretation is supported by the fact that the peripheral representation of

V2 projects to this medial zone (Ungerleider, unpublished data). Although Maunsell and Van Essen ('83b) did not report on the myeloarchitecture of the VIP field, examination of their maps suggest that the projection from MT in their cases were directed primarily to the medial, more lightly myelinated portion of VIP. The lateral, heavily myelinated portion of VIP (VIP*) appears to fall within the internal division of area POa (POa-i) of Seltzer and Pandya ('80). POa-i runs the full length of the sulcus, however, and is therefore considerably larger than VIP*. It is not clear whether VIP* overlaps with area LIP of Andersen et al. ('85), which was identified as an area on the lateral bank of the intraparietal sulcus having strong connections with area 8.

MST and FST. The results from both the present study and our companion paper (Desimone and Ungerleider, '86) indicate a coarse visuotopic organization within MST, namely, an emphasis of the central visual field in the posterior part of MST and of the peripheral field in the anterior part. Thus, in case 1, with an injection in the parafoveal representation of MT, label was confined to the most posterior part of MST, whereas in more peripheral-field cases, label extended into the anterior part of MST. The results from case 7 suggest that there may also be a coarse separation between the representations of the upper and lower visual fields in MST, since there was almost no overlap of retrogradely labeled cells from the two dyes, one injected into the upper and the other into the lower field representations of MT. Whatever organization exists in MST is undoubtedly complex, as label in most cases was widespread and often patchy.

There was even less evidence for visuotopic organization in FST than in MST. Widespread label within FST was found in all cases, including both central and peripheral field injection cases. Consistent with these anatomical results, our physiological findings indicate that neurons in FST have very large receptive fields that often include large parts of both the central and peripheral visual field (Desimone and Ungerleider, '86: Figs. 13–15).

The frontal eye field. In three of our cases with injections confined to MT, there was a clear, though sparse, projection to the frontal eye field. The projection was limited to the same small zone on the anterior bank of the inferior limb of the arcuate sulcus and, in two cases, the immediately adjacent cortex on the prearcuate gyrus. Although Maunsell and Van Essen ('83b) failed to find such a projection, it has been confirmed in cases with injections of HRP or fluorescent dyes placed in the frontal eye field (Barbas and Mesulam, '81; Andersen et al., '85). Whether the projection from MT to the frontal eye field is reciprocated is unknown, for no one has yet reported such a projection, and we failed to label the frontal eye field in our uncontaminated fluorescent dye case. It may be that labeling of such long connections with the DY dye requires more than a 7-day survival period. In any event, MT probably does not provide the major source of visual inputs to the frontal eye field, since the projection from MT is weak compared to those from a number of other visual areas, such as V4, MST, and LIP (Andersen et al., '85; Barbas and Mesulam, '81; Ungerleider, unpublished data).

Laminar organization of connections

Kuypers et al. ('65) and Tigges et al. ('73, '74) first noted that projections from area 17 to area 18 have a different laminar pattern of termination from that of the reciprocal projections from area 18 to area 17. Whereas projections from area 17 to area 18 terminate predominantly in granular layer IV, those from area 18 to area 17 avoid granular layer IV and terminate instead in the supragranular and infragranular layers. This finding was extended in numerous studies of both Old World and New World primates that demonstrated that connections among areas 17–19 and MT are all characterized by one of two types of laminar organization (Spatz and Tigges, '72; Tigges et al., '74, '81; Spatz, '77; Wong-Riley, '78; Rockland and Pandya, '79; Wall et al., '82; Maunsell and Van Essen, '83b; Weller et al., '84; Kennedy and Bullier, '85; Weller and Kaas, '85). "Forward" connections, directed rostrally from these areas, arise predominantly from cells in the supragranular layers of a given area and terminate predominantly in layer IV of the more rostrally located area. "Backward" connections, directed caudally from these areas, arise mainly from cells in the infragranular layers of a given area and terminate in both the supragranular and infragranular layers but not in layer IV of the more caudally located area. Using these principles of laminar organization, Maunsell and Van Essen ('83b) have arranged the multiplicity of visual areas that have now been discovered in the macaque into a cortical hierarchy. Friedman ('83) has shown that the multiple areas in the somatosensory system can similarly be arranged into a cortical hierarchy, suggesting that these principles of laminar organization may apply to all sensory systems.

On the basis of the laminar pattern of connections, our results indicate that areas V1, V2, and V3 project forward to MT and that MT projects forward to VIP, MST, and FST. In all cases, these projections are reciprocal, such that VIP, MST, and FST project back to MT, and MT projects back to V1, V2, and V3. These results are similar to those reported by Maunsell and Van Essen ('83b). In addition, we found a sparse and variable projection forward from MT to the frontal eye field.

Maunsell and Van Essen ('83b) originally described an "intermediate" type of laminar pattern in the connections between MT and V4. We found that not only did the connection between MT and V4 exhibit this intermediate type of laminar pattern, but so did the connections of MT with areas V4t, V3A, and PO. In V4, both labeled cells and terminals tended to form patches whose laminar organization varied from patch to patch. As noted previously by Maunsell and Van Essen ('83b), labeled terminals were present in layer IV in some patches, but in other patches the labeled terminals seemed specifically to exclude layer IV. Likewise, labeled cells were concentrated in the supragranular layers in some patches, the infragranular layers in other patches, and were evenly divided between the supragranular and infragranular layers in still other patches. Since there are a small number of directionally selective cells in V4 (Desimone and Ungerleider, '86; Desimone and Schein, unpublished data), it is possible that the patchy connections with MT and the variable laminar pattern are related to the areal and laminar organization of these cells. Interestingly, Weller et al. ('84) noted in the owl monkey a similar patchy and variable laminar pattern of projections from MT to DL (the dorsolateral visual area), a possible homolog of V4.

Although the connections of MT with V4t, V3A, and PO were not as patchy as those with V4, the laminar pattern of labeling in these areas resembled that in V4 in that it did not consistently indicate either forward or backward

projections. Maunsell and Van Essen ('83b) have suggested that this intermediate type of laminar pattern reflects connections between areas that are at the same level in the cortical hierarchy. It is tempting to speculate that the intermediate type of laminar pattern reflects some functional relationship, such as mutual inhibition, among areas located at the same hierarchical level.

The pathway from striate cortex into the parietal lobe

It has been proposed that striate cortex is the source of two corticocortical pathways, each involving several different visual areas (Ungerleider and Mishkin, '82). One pathway is directed ventrally into the temporal lobe and is crucial for object recognition. The other is directed dorsally into the parietal lobe and is crucial for spatial perception and visuomotor performance. The primary evidence for this distinction comes from the contrasting behavioral effects of temporal and parietal lesions in monkeys (Pohl, '73; Iwai and Mishkin, '68; Brody and Pribram, '78; Mishkin and Ungerleider, '82; for reviews, see Mishkin, '72; Gross, '73; Dean, '76, '82; Ungerleider and Mishkin, '82; Mishkin et al., '83; Desimone et al., '85). Lesions of inferior temporal (IT) cortex cause severe deficits in performance on a wide variety of visual discrimination but not visuospatial tasks. Monkeys with IT lesions are impaired, for example, in learning pattern and object discriminations and in distinguishing between a familiar and a novel object. By contrast, posterior parietal lesions do not affect visual discrimination performance but instead cause severe deficits in visuospatial performance, such as visually guided reaching and judging which of two identical objects is located closer to a visual landmark. A similar dissociation between the effects of temporal lobe and parietal lobe damage has also been found in humans (e.g., Newcombe and Russell, '69; for review, see Ungerleider and Mishkin, '82). Physiological evidence lends further support for the distinction between the functions of the temporal and parietal lobes, as neurons in the IT (Gross et al., '72; Desimone et al., '84) but not parietal cortex (Robinson et al., '78) are highly sensitive to the shape, color, or texture of a stimulus, whereas neurons in parietal cortex are more sensitive to the direction of stimulus motion and tracking eye movements (Lynch et al., '77; Robinson et al., '78; Mountcastle et al., '81; Newsome and Wurtz, '82; Sakata et al., '83). Although pattern vision and visuospatial functions in nonprimates have been associated with the geniculostriate and tectofugal systems, respectively (e.g., Schneider, '67), it has been found in the monkey that both functions are largely dependent on striate cortex (Mishkin, '66; Mishkin and Ungerleider, '82). Thus, the IT cortex appears to be part of a system that originates in striate cortex and is necessary for recognizing objects, while the posterior parietal cortex is part of a system that also originates in striate cortex but is necessary for appreciating the spatial relationships among objects.

The results of the present study suggest that MT is much more closely associated with the occipitoparietal system than with the occipitotemporal system and may, in fact, provide a major link between striate cortex and the parietal lobe. As shown in Figure 15, MT projects to two areas, VIP and MST, that are located in area PG (Bonin and Bailey, '47) of parietal cortex, and these areas project, in turn, to additional areas in PG cortex (Mesulam et al., '77; Ungerleider, unpublished data). Moreover, area PO, which receives projections from V3A and probably from the far peripheral field representation of MT (Colby et al., '83), is also connected with VIP and MST, as well as with other parts of PG cortex (Mesulam et al., '77; Colby et al., '83). Finally, V3A itself receives projections predominantly from the peripheral field representation of MT. Thus, there are a number of routes by which information from MT can reach the parietal lobe.

A comparison of the physiological properties of MT with parietal neurons also indicates that MT plays an important role in parietal function. MT neurons are sensitive to the direction of stimulus motion (Zeki, '74; Maunsell and Van Essen, '83a; Albright, '84; Albright et al., '84). These neurons provide inputs to area MST, which not only has neurons selective for the direction of stimulus motion in the tangent plane, like neurons in MT, but also has neurons selective for the direction of motion in depth or the direction of tracking eye movements (Newsome and Wurtz, '82; Sakata et al., '83; Saito et al., '84; Desimone and Ungerleider, '86). Sensitivity to complex motion and tracking eye movements has also been reported for neurons in the inferior parietal lobule (Motter et al., '81; Sakata et al., '83), to which MST appears to project (Mesulam et al., '77; Ungerleider, unpublished data). Thus, information about direction of motion provided by MT cells may be the basis of a parietal system for visually guided behavior. Consistent with this idea, Newsome et al. ('85) have recently reported that chemical inactivation of MT causes a deficit in smooth pursuit eye movements.

As Figure 15 illustrates, MT provides a major but not the sole route from striate cortex into the parietal lobe. Area V4, for example, projects to PG cortex within the intraparietal sulcus (Seltzer and Pandya, '80; Ungerleider, unpublished data), although the identity of the recipient visual area is not yet established. In addition, it appears that there is a preferential projection into the parietal lobe from the peripheral field representations of several of the lower-order visual areas. The far peripheral field representation of V2 projects to the medial part of area VIP (Ungerleider, unpublished data), and the peripheral field representations of V1, V2, and V3 project to either V3A or PO or both (Zeki, '80; Colby et al., '83; Ungerleider et al., '83; Ungerleider, unpublished data). Thus, there are other potential pathways into the parietal lobe besides the one through MT, especially from inputs representing the peripheral visual field. This convergence of inputs to the parietal cortex from the peripheral visual field is not surprising given the importance of the peripheral field in spatial function (Mishkin and Ungerleider, '82).

By contrast to its pivotal position in the occipitoparietal pathway, MT probably occupies only an ancillary position in the occipitotemporal pathway, and indeed monkeys with MT lesions appear normal on visual pattern discrimination tasks (Ungerleider and Mishkin, unpublished data). The primary input to both areas TEO and TE of the IT cortex is provided by area V4 (Desimone et al., '80; Felleman and Van Essen, '83; Fenstemaker et al., '84), and V4, in turn, receives its major projections from V2 and V3 (Zeki, '71; Ungerleider et al., '83; Felleman and Van Essen, '84; Ungerleider, '85). Furthermore, unlike neurons in MT, those in V4 are sensitive to many stimulus features important for object recognition (Desimone et al., '85), and lesions involving primarily V4 have a devastating effect on the ability of monkeys to perform pattern discriminations (Iwai and Mishkin, '68; Cowey and Gross, '70; Mishkin, '72). Thus, V4 appears to play a far more important role than MT in the object recognition functions of the occipito-temporal pathway.

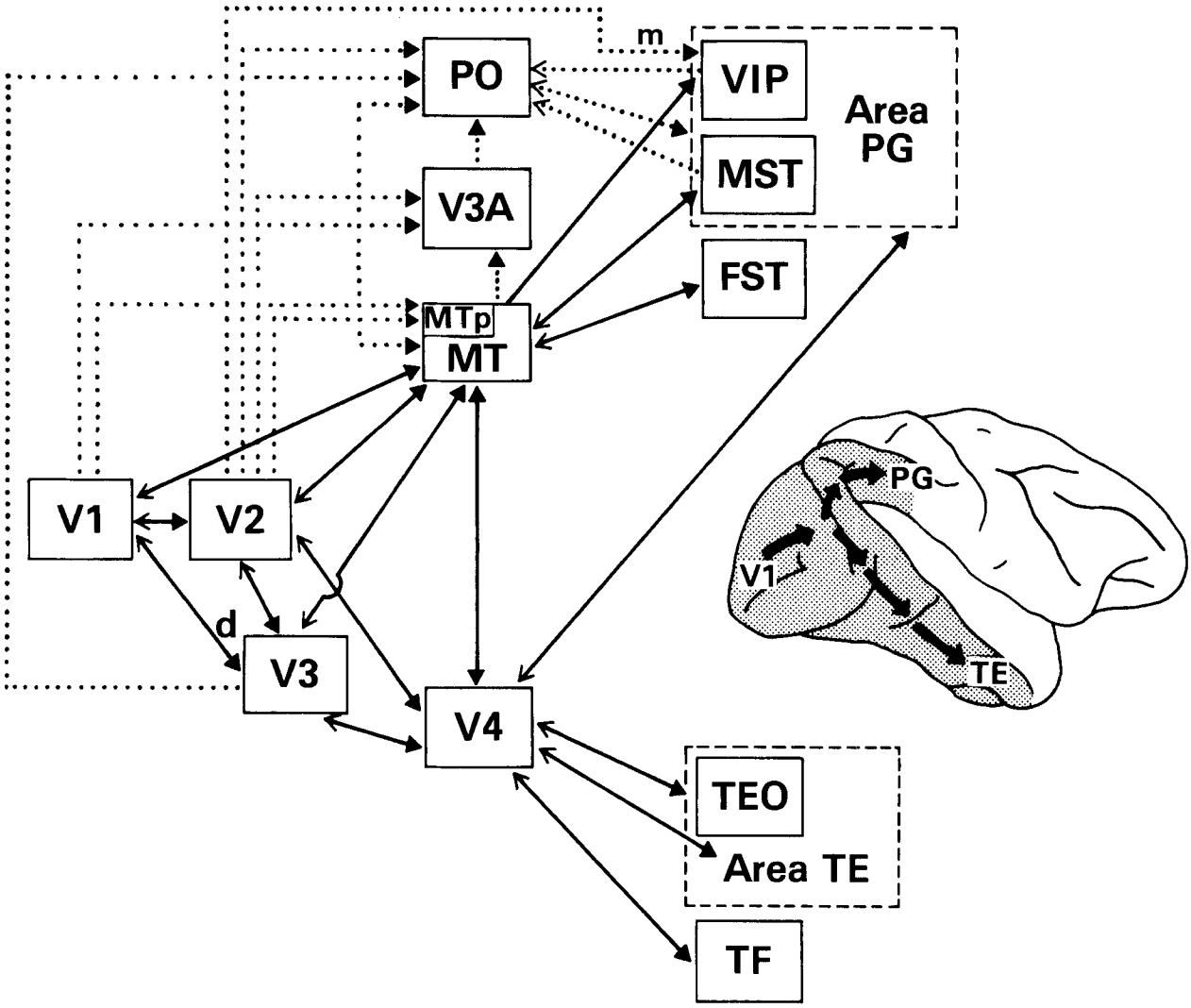

Fig. 15. Summary of visual cortical areas and their known connections. Heavy arrowheads indicate "forward" projections, which terminate predominantly in layer IV, and light arrowheads indicate "backward" projections, which avoid granular layer IV and terminate instead in the supragranular and infragranular layers. "Intermediate" projections are indicated by two, reciprocal, heavy arrowheads. The absence of a reciprocal arrowhead does not indicate the absence of a projection but only that it is still unknown. Solid lines indicate projections that arise from both central and peripheral field representations, whereas dotted lines indicate projections that arise exclusively from peripheral field representations. "d" indicates that the projection from V1 to V3 is limited to V3d. "m" indicates that the projection from V2 to VIP is limited to VIP's medial portion. The projections of Mtp and the connections of V4t are as yet unknown and are therefore not illustrated. The results suggest that MT provides a major route from striate cortex into the parietal lobe. Other potential visual pathways into the parietal lobe include those carrying inputs representing the peripheral visual field. The major route from striate cortex into the temporal lobe is via area V4.

Recently, our proposal of two parallel visual processing systems in the cortex of the macaque has been applied to the owl monkey by Weller et al. ('84). In their scheme also, MT occupies a critical position in the occipitoparietal system for spatial vision, whereas DL is assigned a position equivalent to that of V4 in the occipitotemporal system for object vision. Further comparisons among the visual systems of different animals, both lower and higher on the evolutionary scale, will be needed for a deep understanding of this interesting but puzzling separation of visual functions.

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