

Cortical Projections of Area V2 in the Macaque

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To determine the locus, extent and topographic organization of cortical projections of area V2, we injected tritiated amino acids under electrophysiological control into 15 V2 sites in 14 macaques. The injection sites included the foveal representation and representations ranging from central to far peripheral eccentricities in both the upper and lower visual fields. The results indicated that all V2 sites project topographically back to V1 and forward to V3, V4 and MT. There is also a topographically organized projection from V2 to V4t, but this projection is limited to the lower visual field representation. V2 thus appears to project to virtually all the visual cortex within the occipital lobe. In addition to these projections to occipital visual areas, V2 sites representing eccentricities of ~30° and greater project to three visual areas in parietal cortex – the medial superior temporal (MST), parieto-occipital (PO) and ventral intraparietal (VIP) areas. This peripheral field representation of V2 also projects to area VTF, a visual area located in area TF on the posterior parahippocampal gyrus. Projections from the peripheral field representation of V2 to parietal areas could provide a direct route for rapid activation of circuits serving spatial vision and spatial attention.

In macaques, the major cortical projection target of area V1 is area V2 (Kuypers *et al.*, 1965; Cragg and Ainsworth, 1969; Zeki, 1969, 1971, 1976; Jones and Powell, 1970; Zeki and Sandeman, 1976; Rockland and Pandya, 1979, 1981; Lund *et al.*, 1981; Weller and Kaas, 1983; Van Essen *et al.*, 1986; Shiwa, 1987). Although a number of studies have described projections from V2 back to V1 and forward to several visuotopically organized extrastriate areas, including V3, V4, MT and PO, these reports were based almost entirely on injections of retrograde tracers outside of V2 (Rockland and Pandya, 1981; Felleman and Van Essen, 1983, 1984; Maunsell and Van Essen, 1983; Fenstemaker *et al.*, 1984; DeYoe and Van Essen, 1985; Kennedy and Bullier, 1985; Shipp and Zeki, 1985, 1989; Burkhalter *et al.*, 1986; Ungerleider and Desimone, 1986b; Colby *et al.*, 1988; Zeki and Shipp, 1989; Boussaoud *et al.*, 1991; Nakamura *et al.*, 1993). The only exception is a report by Zeki (1971) describing anterograde degeneration in V3, V4 and MT after small lesions in V2, and in that study the only part of V2 examined was the representation of the lower half of the central visual field. We therefore undertook to study the cortical efferents from all parts of V2, with the aim of defining the locus, extent and topographic organization of the entire V2 cortical projection system.

We report here on the cortical projections of area V2 in 15 cases with tritiated amino acid injections placed under physiological control into different retinotopic locations. Because we were interested in delineating the complete set of target areas to which V2 projects, our injections were large enough to include all cytochrome oxidase subregions within V2 at a given eccentricity. Our results indicated that V2 sends topographically organized projections back to V1 and forward to V3, V4 and MT, confirming prior reports (Zeki, 1971; Rockland

and Pandya, 1981; Maunsell and Van Essen, 1983; Fenstemaker *et al.*, 1984; Kennedy and Bullier, 1985; Burkhalter *et al.*, 1986; Ungerleider and Desimone, 1986b; Shipp and Zeki, 1989; Boussaoud *et al.*, 1991; Nakamura *et al.*, 1993). In addition, we found that the peripheral, but not central, field representation of V2 projects to a number of other visual areas located in the occipitoparietal cortex, including PO, MST and VIP, as well as to a portion of area TF (area VTF; Boussaoud *et al.*, 1991) located on the posterior parahippocampal gyrus. A brief report of some of these results has appeared previously (Ungerleider *et al.*, 1983).

Materials and Methods

Autoradiographic material from 14 adult *Macaca mulatta*, weighing between 3.2 and 4.5 kg, were used. In all animals except one, injections of tritiated amino acids were placed into retinotopically specified sites in V2, which were determined by electrophysiological recordings. The injection sites spanned eccentricities from central to peripheral vision in both the upper and lower visual fields (Van Essen and Zeki, 1978; Gattass *et al.*, 1981; see Fig. 2). In the one case without physiological recordings (case 1), the injection was placed into the foveal representation of V2 under direct visualization.

Receptive Field Recording

The experimental procedures for multiunit recordings have been described in detail elsewhere (Desimone and Gross, 1979; Gattass and Gross, 1981; Gattass *et al.*, 1981). Briefly, prior to the first recording session, under ketamine and sodium pentobarbital anesthesia, the animal was implanted with a bolt for holding the head in the stereotaxic apparatus and a stainless steel recording chamber. In each recording session, the animal was anesthetized with 2% halothane, followed by a 70:30% mixture of N₂O₂. Muscular paralysis was induced by pancuronium bromide and artificial ventilation was maintained by a respiratory pump connected to an endotracheal cannula. The level of expired CO₂, heart rate and rectal temperature were continuously monitored and kept within the normal physiological range. The right eye was fitted with a contact lens, which focused the eye to the surface of a 30 cm radius translucent hemisphere placed in front of the animal. The locations of the fovea and the center of the optic disk were projected onto the hemisphere. The horizontal meridian was taken to be a line through both these points and the vertical meridian an orthogonal line passing through the fovea.

Varnish-coated tungsten microelectrodes were used to record from small clusters of neurons. Visual receptive fields were plotted by moving three-dimensional white or colored bars onto the surface of the translucent hemisphere, under light-adapted conditions. Recordings continued until the desired visual field representation within V2 was located. In four cases, we also mapped receptive fields in the portions of V3 and V4 in which we anticipated finding projections from V2.

Injections of V2

In case 1, the injection was placed into the foveal representation of V2 under direct visualization of the cortex. In case 5, the injection was made with a 1 µl Hamilton syringe attached to a tungsten microelectrode. In the remaining cases, after the desired injection site was located electrophysiologically, a guide tube was advanced through the dura and

placed ~300 μm above the intended injection site. The microelectrode was then advanced through the guide tube and the visuotopic location of the injection site was confirmed. The electrode was then withdrawn from the guide tube and replaced by a 1 μl Hamilton syringe. We injected 0.15–0.3 μl of an equal-parts mixture of tritiated proline (New England Nuclear (Wilmington, DE, $1\text{-}[2,3,4,5\text{-}^3\text{H}]$, sp. act. 100–140 Ci/mmol) and tritiated leucine (New England Nuclear $1\text{-}[3,4,5\text{-}^3\text{H(N)}$], sp. act. 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 $\mu\text{Ci}/\mu\text{l}$, were injected at the rate of 0.02 $\mu\text{l}/2$ min. To minimize leakage of the tracer up the electrode track, the syringe was left in place for 30 min after the injection and then withdrawn into the guide tube, which was then removed from the brain. In the first 13 animals, we made unilateral V2 injections. Because no contralateral projections were observed in these cases, we injected V2 bilaterally in the remaining animal (cases 4 and 14), confident that no ambiguity would be introduced provided we avoided the representation of the vertical meridian.

Histological Processing

After survival times of 6–8 days, the animals received a lethal dose of sodium pentobarbital and were then perfused transcardially with 0.9% saline followed by 10% formol-saline. Their brains were blocked stereotaxically, removed from the skull, photographed and stored in 30% sucrose in 10% formol-saline until they sank. Frozen sections, 33 μm in thickness, were cut in the frontal plane. Every fifth section was mounted onto gelatinized slides, dehydrated, defatted and processed for autoradiography according to the procedures of Cowan *et al.* (1972). The sections were dipped in Kodak NTB2 emulsion and exposed at 4°C for at least 12 weeks. Subsequently, the autoradiographs were developed in Kodak D19, fixed and counterstained with thionin. Alternate sections were stained for myelin with the Gallyas (1979) procedure, or, in one case, by the Spielmeier method (Lillie, 1965). For purposes of analysis, the locations of concentrations of silver grains were charted onto enlarged photographs of the myelin-stained sections.

Assignment of Label to Specific Visual Areas

For each case, a two-dimensional map of the cortex was generated (Ungerleider and Desimone, 1986b; Gattass *et al.*, 1987). The locations of silver grains, myeloarchitectonic borders and recording sites were transferred onto the flattened maps.

We used myeloarchitectural differences to distinguish areas V2, V3v, V3d, PO, V4, V4t, MT and the densely myelinated zone (DMZ) of MST. The criteria we used to identify visual cortical areas have been described in detail and illustrated elsewhere (V2: Gattass *et al.*, 1981, 1987; Ungerleider and Desimone, 1986a; Rosa *et al.*, 1988; V3d and V3v: Burkhalter *et al.*, 1986; Gattass *et al.*, 1986, 1988; Newsome *et al.*, 1986; Ungerleider and Desimone, 1986b; Van Essen *et al.*, 1986; V4: Ungerleider and Desimone, 1986b; Gattass *et al.*, 1988; Boussaoud *et al.*, 1991; V4t: Schein *et al.*, 1982; Ungerleider and Desimone, 1986b; Gattass *et al.*, 1988; MT: Allman and Kaas, 1971; Ungerleider and Mishkin, 1979; Gattass and Gross, 1981; Van Essen *et al.*, 1981; Desimone and Ungerleider, 1986; Fiorani *et al.*, 1989; MST: Desimone and Ungerleider, 1986; Ungerleider and Desimone, 1986b; Fiorani *et al.*, 1989; Boussaoud *et al.*, 1990; PO: Gattass *et al.*, 1986; Colby *et al.*, 1988; Neunenschwander, 1989; Neunenschwander *et al.*, 1994).

We were also able to identify a heavily myelinated zone on the ventral portion of the lateral bank of the intraparietal sulcus, a zone we previously labeled VIP* and included as part of VIP on the basis of its connections with area MT (Ungerleider and Desimone, 1986b; Boussaoud *et al.*, 1991). However, Colby and Duhamel (1991) have shown that the neurons in the heavily myelinated zone have physiological properties more closely resembling those in LIP (Andersen *et al.*, 1987, 1990) than those in the remainder of VIP. Consequently, and in keeping with Blatt *et al.* (1990), we have termed this heavily myelinated zone 'LIPv' and have termed the remainder of LIP 'LIPd', which acknowledges the similarity in neuronal properties in the two portions of LIP as well as the differences in their myeloarchitectural appearance and connections with MT. Thus, in this report, the term VIP refers to the cortex only at the fundus of the intraparietal sulcus.

Finally, because we were unable to identify unequivocally the borders

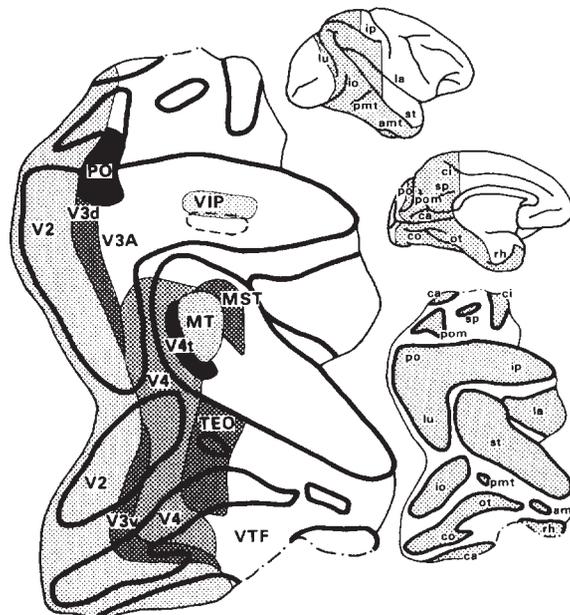


Figure 1. Two-dimensional reconstruction of the macaque cortex, showing the location of the extrastriate visual areas found to be connected with V2. Heavy lines indicate the boundaries of the sulci and the dotted-dashed lines indicate the boundaries between the neocortex and allocortex. The gray area on the lateral and medial surface views of the hemisphere (upper right) indicates the region represented in the two-dimensional reconstruction, whereas the gray area on the small two-dimensional reconstruction indicates cortex within sulci.

of areas VIP, TEO and VTF, their locations were inferred from previous anatomical and physiological studies (Maunsell and Van Essen, 1983; Ungerleider and Desimone, 1986b; Boussaoud *et al.*, 1991). The location and the extent of the visual cortical areas just described are illustrated in a two-dimensional reconstruction of the macaque extrastriate cortex in Figure 1.

The Correspondence of Receptive Fields to Injection Sites

In addition to the receptive field recorded at the injection site, for each case we calculated a back-transformed receptive field, using a method similar to the one described by Maunsell and Van Essen (1983). Briefly, back-transformed receptive fields were determined, first, by mapping the projection to V1 on a flattened map of V1; and then by overlaying this map onto the visuotopic maps of V1 published previously (Daniel and Whitteridge, 1961; Van Essen *et al.*, 1986). Finally, the coordinates overlaid by the V1 projection were used to draw the back-transformed receptive field.

Results

The results are based on data from 15 injections of tritiated amino acids. We will first describe the locations of the injection sites and the projections from V2 back to V1. We will then summarize the projections from central field representations in V2 to extrastriate visual areas and compare them with those from peripheral field representations. We will then describe the laminar distribution of V2's projections; finally, we will present data from individual cases.

V2 Injection Sites

Figure 2 shows a flattened map of V2 with the locations of the injection sites as well as the visual field representation described by Gattass *et al.* (1981). As shown in the figure, one injection (case 1) was placed in the foveal representation, five injections (cases 2–6) were placed at eccentricities of $<30^\circ$ and four (cases 7–10) were placed at eccentricities of 30° or greater. Five

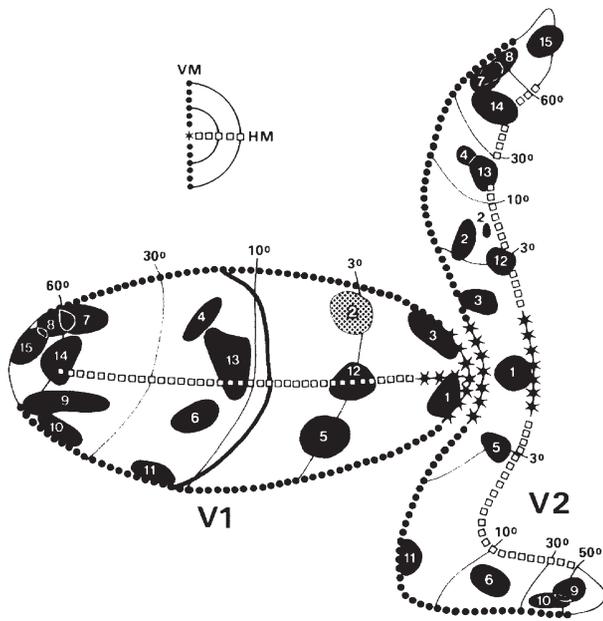


Figure 2. Location of the injection sites in V2 (at right) and of the feedback projections to V1 (at left), shown on two-dimensional reconstructions of the cortex. Injection sites are shown without the surrounding halo. The representation of the vertical meridian (VM) is illustrated with circles, the horizontal meridian (HM) with squares, the foveal representation with asterisks and the isoeccentricity lines with thin lines. In case 2, the feedback projection to V1 could not be determined because of a lesion in V1 (cross-hatching) at the presumed location of this projection.

additional injections were placed at the representation of either the vertical (case 11) or the horizontal meridian (cases 12-15) of V2, and therefore necessarily spread to adjacent areas. The injection at the vertical meridian (case 11) involved V1, while those at the horizontal meridian involved either V3d (cases 12 and 13), PO (case 14) or cortex in an as yet undefined visual area medial to PO (case 15).

Projections from V2 to V1

Figure 2 also summarizes the projections from V2 back to V1 on a flattened map as well as the visual field representation in V1, as described previously (Daniel and Whitteridge, 1961; Van Essen *et al.*, 1986; Gattass *et al.*, 1987). In all cases except case 2, there was a single labeled zone in V1 whose visuotopic locus was highly consistent with the visuotopic locus of the injection site in V2 (Gattass *et al.*, 1981). In case 2, the projection to V1 was absent due to an infarct in the part that should have been labeled. A comparison of the receptive fields recorded at the V2 injection sites with the visual field representations of the projections in V1 indicates, on the whole, a good agreement between the two. However, the label in V1 always covered more of the visual field representation than that covered by the receptive field recorded in V2. In only one case (case 3) was the visual field representation of the projection in V1 non-overlapping with the receptive field recorded in V2.

Projections from Central and Peripheral Field Representations in V2

The projections to extrastriate cortex from the portions of V2 representing the central 30° of the visual field are summarized

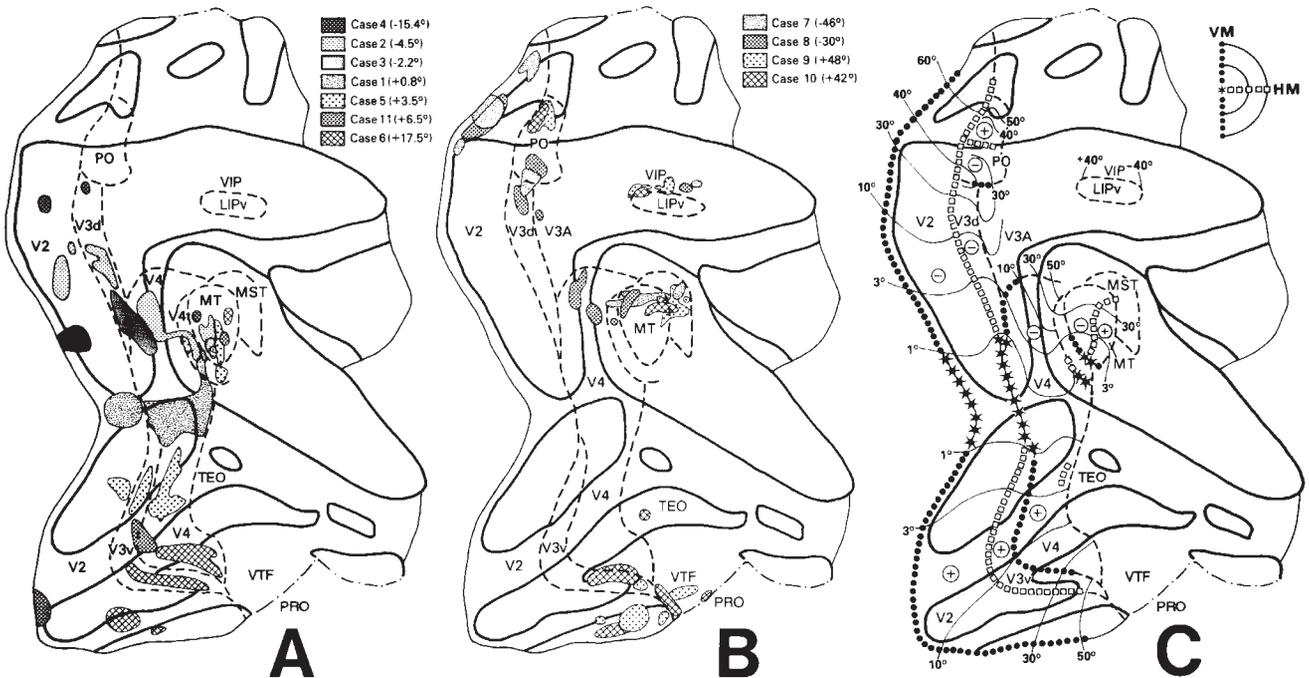


Figure 3. Summary figure illustrating the distribution of labeled terminals in extrastriate cortex following injections of tritiated amino acids into V2 sites representing the central 30° of the visual field (A) and eccentricities beyond 30° (B). The data are shown on a two-dimensional reconstruction of the cortex. Myeloarchitectonic borders of visual areas are indicated with dashed lines. The projections from the individual cases were plotted on this map to best retain their locations relative to sulcal and myeloarchitectonic borders. Visual topography of the extrastriate visual areas receiving projections from V2, shown on a two-dimensional map of the cortex (C). In the map and in the inset at the upper right, the representation of the vertical meridian (VM) is illustrated with filled circles, the horizontal meridian (HM) with unfilled squares, the fovea with asterisks, the isoeccentricity lines with thin lines, the upper visual field with a plus sign and the lower visual field with a minus sign. For other conventions, see Figure 1.

on a flattened map in Figure 3A. Projections from V2 were found in V3d, V3v, V4, V4t and MT. In all these areas, the projections were in topographic register with the portion of the visual field represented at the V2 injection site. However, in areas V4t and MT, the projection zones showed a great deal of overlap, reflecting the coarse retinotopy of these areas relative to that of V2 (Gattass and Gross, 1981; Gattass *et al.*, 1981; Van Essen *et al.*, 1981; Desimone and Ungerleider, 1986; Fiorani *et al.*, 1988). The corresponding data from peripheral field (30° or greater) injections in V2 are summarized in Figure 3B. As shown in the figure, the periphery of V2 projects topographically to V3d, V3v, V4, V4t and MT, as was found with central field injections. However, in addition, the periphery of V2 projects to areas PO, MST and VIP and to the most posterior part of area TF (which we term VTF, after Boussaoud *et al.*, 1991). Among these areas receiving projections from the periphery, both PO and VIP showed a segregation of projections from the upper and lower visual field representations of V2. Finally, isolated cases also showed projections from peripheral V2 to V3A, TEO and area prostriata (Sanides, 1972), and from central V2 to prefrontal area 8.

Figure 3C summarizes the visual topography of V2's projection fields within extrastriate cortex based on the results of the present study in conjunction with the known locations of the representations of the vertical and horizontal meridians determined in prior electrophysiological mapping studies (Zeki, 1969, 1971, 1977, 1978; Van Essen and Zeki, 1978; Gattass and Gross, 1981; Gattass *et al.*, 1981, 1987, 1988; Van Essen *et al.*, 1981; Albright *et al.*, 1984; Maguire and Baizer, 1984; Desimone and Ungerleider, 1986; Newsome *et al.*, 1986; Maunsell and Newsome, 1987; Rosa *et al.*, 1988; Neuenschwander *et al.*, 1994).

Laminar Distribution of Projections

There was a halo of diffuse, light label in all cortical layers surrounding each of the amino acid injection sites. Adjacent to this halo, eight out of 15 cases also showed intrinsic projections within V2, typically extending 6–13 mm from the center of the injection site. Intrinsic projections usually appeared as columns spanning all layers (Fig. 4), with the labeling in layer IV either equal to or weaker in strength than that within the other layers. Within area V1, heavy anterograde label was found in layers I, IVB and VI in most cases, but in some cases only layers I and VI were heavily labeled. Weak, diffuse label in area V1 was also occasionally found in layer II and to a lesser extent in layer V. Anterograde label in the remainder of the areas was always heaviest in layer IV. Within areas V3d, V3v, V4 and MT, the label usually appeared in vertical columns which included all cortical layers, with the heaviest labeling in layers IV and III and extremely sparse labeling in layer VI (see Fig. 4). Within areas V4t and PO, the label was more restricted; it was heaviest in layer IV and included layer III but rarely included the deeper and more superficial layers. Within areas MST, VIP and VTF, the label was still more restricted, in that it was confined to layer IV; this was also true for the single cases with label in areas V3A and TEO. Within prefrontal area 8, the projection appeared as a column, with the heaviest labeling in layer IV. Within area prostriata, the label was located within the middle of the cortex.

Individual Cases

Foveal V2: Case 1

In this case, the injection was placed at the foveal representation

of V2. The resulting distribution of labeled terminals is illustrated on cross sections, and on a lateral view and a flattened map of the cortex in Figure 5. This was the only case in which the injection was placed under direct visualization of the cortex rather than under physiological control. However, the location of the projection within V1 indicated that the injection site did indeed involve the fovea, as intended, mainly involving the upper field representation. Anterior to the injection site, there was a large, continuous patch of label, extending into the foveal representations of V3, V4 and V4t (Desimone and Ungerleider, 1986; Gattass *et al.*, 1988; Fiorani *et al.*, 1989). A small separate patch of label was also observed in the foveal representation of MT (Gattass and Gross, 1981; Van Essen *et al.*, 1981; Desimone and Ungerleider, 1986). In addition, there was a patch of intrinsic label dorsal to the injection site within V2. Finally, in this case, there was a small projection to area 8 in prefrontal cortex, just anterior to the ventral limb of the arcuate sulcus.

Central Lower Field: Cases 2 and 3

In case 2, the injection of tritiated amino acids was placed at 4.5° eccentricity in the lower field representation of V2. Figure 6 shows the resulting distribution of labeled terminals. The injection of the tracer resulted in two injection sites centered at about the same eccentricity: one large injection site on the posterior bank of the lunate sulcus and another, smaller site on

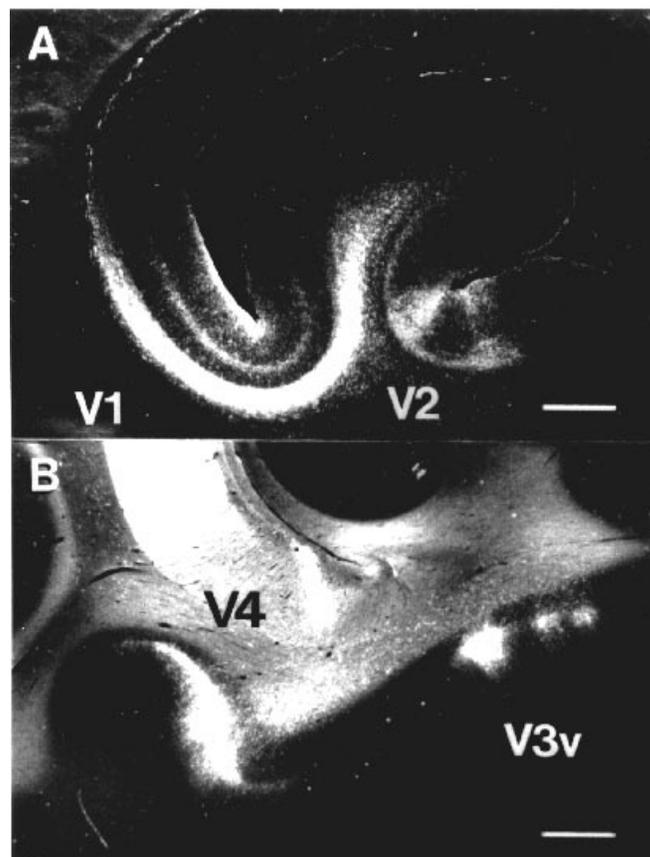


Figure 4. Laminar patterns of projections from V2. Dark field photomicrographs of autoradiographic sections stained with thionin. In V1 (A) labeled terminals are located in layers I, IVB and VI, and intrinsic connections within V2 occupy all layers (A), while in V3 and V4 (B) labeled terminals are heaviest in layer IV and often appear as vertical columns extending into adjacent layers. Scale bar = 1 mm.

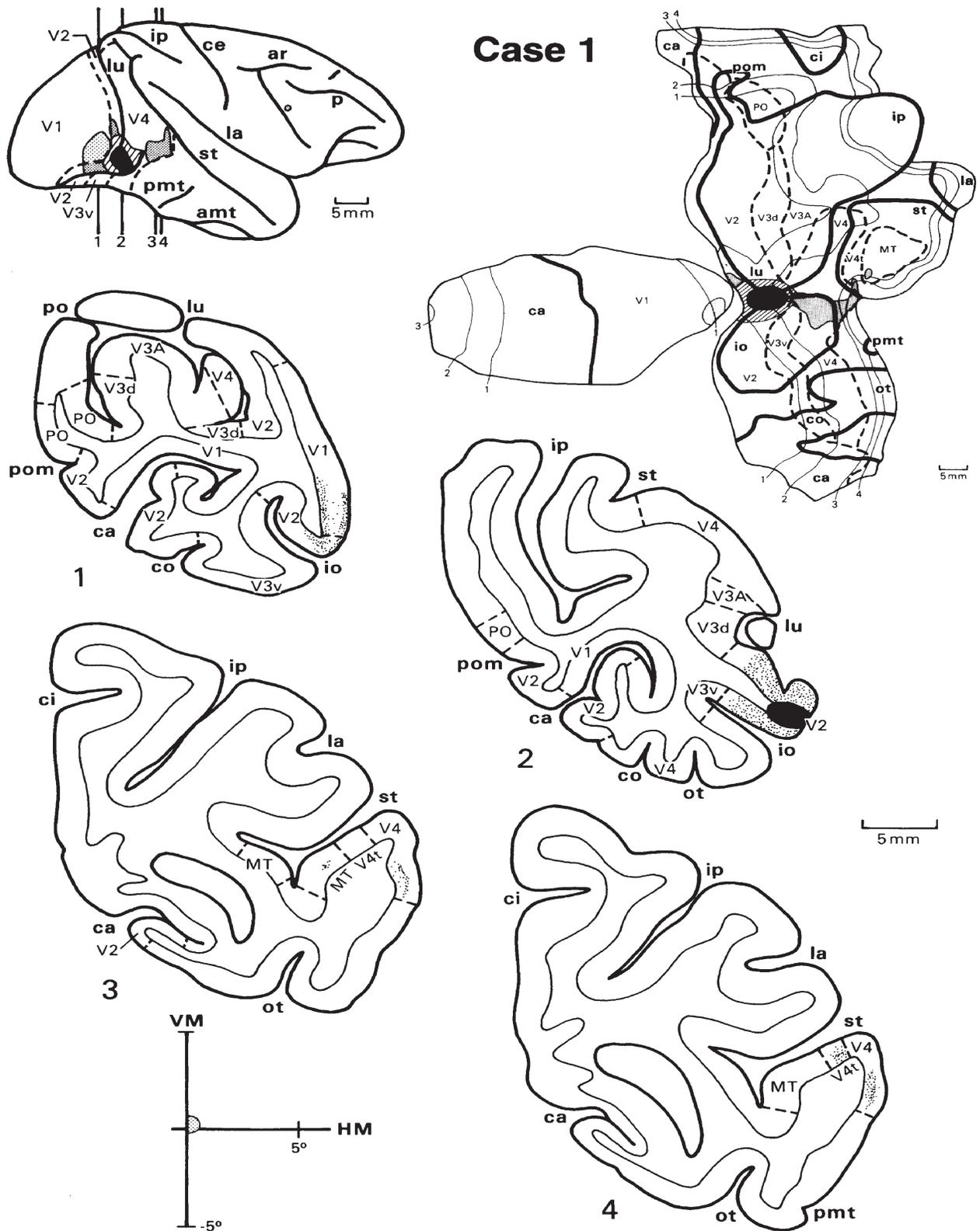


Figure 5. Case 1: distribution of labeled terminals following an injection into the foveal representation of V2, shown on coronal sections at the levels indicated on the lateral view of the hemisphere (upper left) and on a two-dimensional map (upper right). The two-dimensional map has been cut at the V1/V2 border, with V1 shown on the left and V2 on the right. The thin lines running through the map indicate layer IV contour lines from the selected cross-sections (1–4). On the coronal sections, the injection site is shown in black, the dots indicate the relative density and laminar distribution of labeled terminals, and the dashed lines indicate the myeloarchitectonic borders of visual areas. On the lateral view of the hemisphere, the injection site is shown in black, the halo surrounding the injection site with stripes, projections including layer IV in dark gray and projections excluding layer IV in light gray. Note the small projection in area 8 anterior to the arcuate sulcus. The portion of the visual field corresponding to the back-transformation of the projection to V1 is shown in gray at the lower left. For other conventions, see Figures 1 and 3.

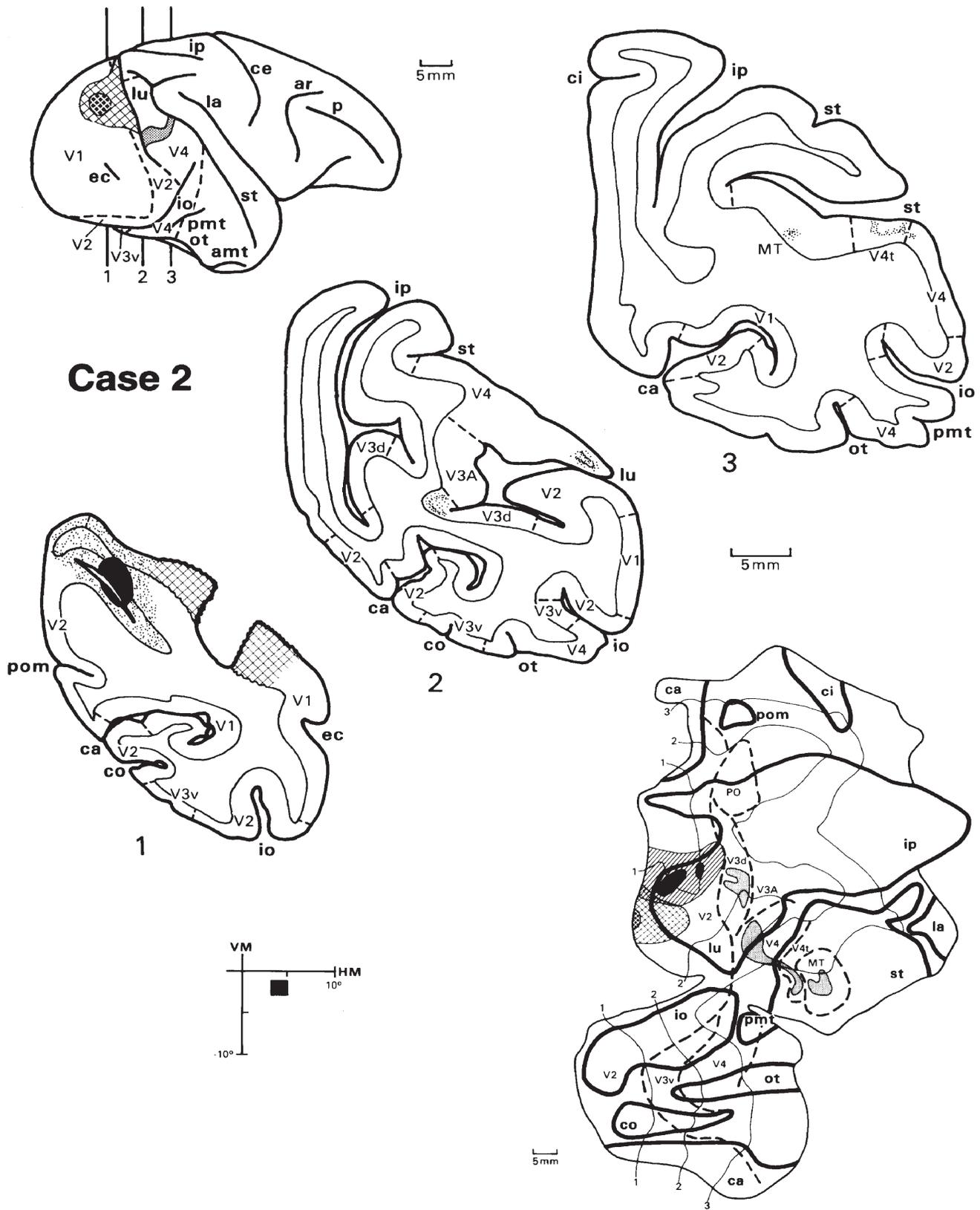


Figure 6. Case 2: distribution of labeled terminals following an injection into the central lower field representation of V2, shown on coronal sections at the level indicated on the lateral view of the hemisphere and on a two-dimensional map. In this case, the use of a tungsten microelectrode attached to the microsyringe produced a large cortical lesion in the central lower field representation of V1 (see section 1), which is indicated by the dark cross-hatching on the lateral view of the hemisphere. Surrounding this lesion, there was a zone of necrotic tissue, which is indicated by the lighter cross-hatching both on the lateral view and on section 1. The receptive field recorded at the injection site is shown in black at the lower left. For other conventions, see Figure 5.

the annectent gyrus that was confined to the upper two cortical layers. This animal apparently suffered an infarct during the course of the experiment and, as a consequence, there was a lesion in the central lower field representation of V1 (Fig. 6, section 1). The location of this lesion in V1 covered the expected locations of the projections from both injection sites in V2. Consequently, we could not determine with certainty whether or not the injection site on the annectent gyrus had been effective. However, the pattern of labeling in extrastriate cortex suggested that it was. Although V3d, V4, V4t and MT each contained a single projection zone within their central lower field representations, these projection zones extended from

close to the representation of the vertical meridian to close to that of the horizontal meridian (Gattass and Gross, 1981; Van Essen *et al.*, 1981; Desimone and Ungerleider, 1986; Gattass *et al.*, 1988; Fiorani *et al.*, 1989). Likewise, the injection on the posterior bank of the lunate sulcus was close to the vertical meridian representation of V2, while the one on the annectent gyrus was closer to the horizontal meridian representation. In case 3, the injection was also placed in the lower field representation of V2, but at a somewhat more central eccentricity. The resulting label in V3d, V4, V4t and MT closely resembled that found in case 2, except that more central visual field representations were labeled in case 3 (see Fig. 7).

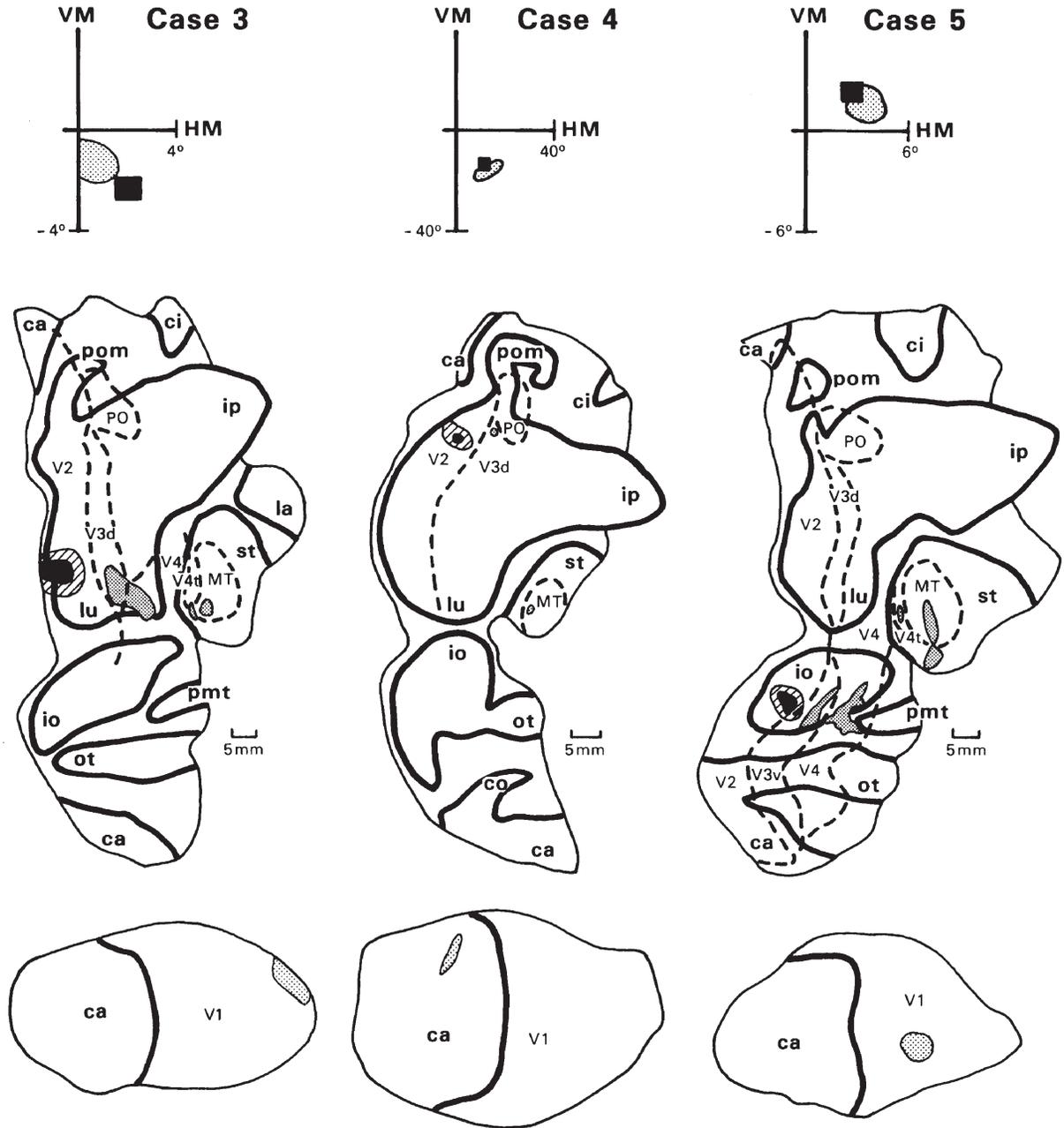


Figure 7. Cases 3, 4 and 5: distribution of labeled terminals following injections into the central lower (cases 3 and 4) and upper (case 5) field representation of V2, shown on two-dimensional maps of the cortex. The two-dimensional maps of V1, the same orientation as in Figure 2, are shown below the maps of extrastriate cortex. For conventions, see Figures 5 and 6.

Intermediate Lower Field: Case 4

Figure 7 shows the results from an injection of tritiated amino acids into the lower field representation of V2 at an eccentricity of $\sim 15^\circ$. In this case, the injection was very small and, in addition to the label in V1, only two other patches of labeled terminals were found: one in V3d and another in MT. Although the location of the label in both V1 and MT coincided topographically with the location of the receptive field recorded at the injection site, the label in V3d seemed to be at the most peripheral portion of the area, suggesting that V3d in this animal did not extend beyond $\sim 20^\circ$ eccentricity. The absence of a projection to either V4 or V4t may be related to the small size of the injection site. Alternatively, it is possible (though improbable) that the effective injection was confined to a thick cytochrome oxidase-rich stripe of V2, i.e. the subregion of V2 that projects to MT and V3d but not to V4 (DeYoe and Van Essen, 1985; Shipp and Zeki 1985; Hubel and Livingstone, 1987; Nakamura *et al.*, 1993).

Central Upper Field: Case 5

In this case, the injection was placed at 3.5° eccentricity in the upper field representation of V2, as shown in Figure 7. Although the receptive field recorded at the injection site did not extend to the horizontal meridian, the location of the injection site at the anterior border of V2 and the location of the projection zone in V1 both indicated that the horizontal meridian representation may have been included in the injected region. Five separate patches of labeled terminals in extrastriate visual cortex resulted from this injection. Areas V3v, V4 and MT each contained a single labeled zone which was located in their central upper field representations and extended to (or included) their horizontal meridian representations. Another patch of label was located just anterior to the myeloarchitectonic border of V4t, in a region that could be V4t's central upper field representation (see Discussion). Finally, an extremely small patch of label was found within the myeloarchitectonic borders of V4t, in what should be its central lower field representation (Desimone and Ungerleider, 1986; Fiorani *et al.*, 1989).

Intermediate Upper Field: Case 6

Figure 8 shows the distribution of labeled terminals following an injection of tritiated amino acids into the upper field representation of V2 at an eccentricity of 17.5° . The locations of the labeled terminals in V1, V3v, V4 and MT closely matched the visual field topography of the injection site. As expected, no label was found in V4t, an area which contains only a representation of the lower visual field (Desimone and Ungerleider, 1986; Fiorani *et al.*, 1989). Also, unlike case 5, no label was found outside of MT in the superior temporal sulcus. As shown in Figure 8, case 6 had a patch of intrinsic label in V2 within the calcarine sulcus, which was centered ~ 6 mm from the center of the injection site. Finally, like case 1, case 6 showed a small projection (not illustrated) to area 8 in the prefrontal cortex, at the anterior lip of the ventral limb of the arcuate sulcus.

Peripheral Lower Field: Cases 7 and 8

Figure 9 shows the distribution of labeled terminals after an injection into the peripheral lower field of V2 at an eccentricity of 46° (case 7). Although the receptive field recorded at the injection site did not include the vertical meridian, both the location of the injected region and the projection back to V1 indicated that the vertical meridian had been involved. Like the previous cases, this case showed topographically organized

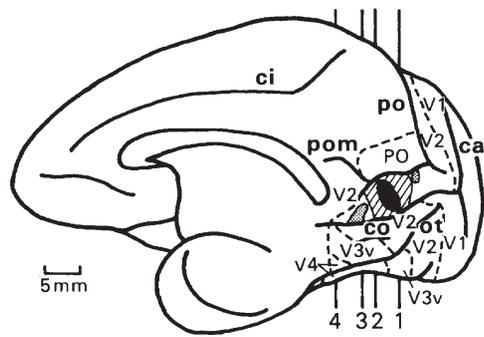
projections to V3d, V4 and MT. The projection to V4 was continuous with the one to MT and extended medially beyond the myeloarchitectonic border of MT into MTp, i.e. MT's far peripheral field representation (Ungerleider and Desimone, 1986a). Unlike the other cases, this case also showed projections to PO, MST and VIP. The projection to PO was continuous with the one to V3d and included the representation of the vertical meridian, which is located at the border between the two areas (Neuenschwander *et al.*, 1994). The projection to MST was adjacent to the one to MTp; this projection was confined to the densely myelinated zone (DMZ) on the upper bank of the superior temporal sulcus. The projection to VIP was restricted to a small zone at the fundus of the intraparietal sulcus, anteromedial to the ventral border of LIPv. This case also showed two separate patches of intrinsic connections in V2, one more central and another more peripheral than the injection site.

As in case 7, the injection in case 8 was placed in the representation of the peripheral lower field of V2, but at a lesser eccentricity (30°). The injection site in case 8 crossed the V1/V2 border and undoubtedly also included a small portion of the peripheral lower field representation of V1 (Fig. 10). Like case 7, case 8 showed topographically organized projections back to V1 and forward to V3d, V4 and MT, as well as additional projections to PO and VIP. Unlike case 7, this case showed a small projection to V4t but none to MST, the same finding obtained in the central and intermediate lower field cases. Thus, the difference between cases 7 and 8 in the projections to V4t and MST is probably related to the less eccentric visual field representation of the injection site in case 8. Case 8 also showed a small projection to V3A, close to its border with V3d. This projection may be related to involvement of the peripheral field representation of V1, which has been shown to project to V3A (Zeki, 1980). Alternatively, the projection to V3A may arise from the peripheral field representation of V2. If so, then the periphery of V2 must have a weak or inconsistent connection with V3A, since peripheral field cases 7 and 10 (see below) did not show this projection.

Peripheral Upper Field: Cases 9 and 10

Figure 11 shows the distribution of label after an injection into the peripheral upper field of V2 at an eccentricity of 48° (case 9). Similar to case 7, projections were found back to V1 and forward to V3v, PO, MTp, MST and VIP. The label in VIP extended into the heavily myelinated portion of LIP, i.e. LIPv (Fig. 11, section 4). In addition, there was a projection to an undefined region located between V3A and LIPv (Fig. 11, section 1). Unlike most previous cases, there was no projection to V4, which is in agreement with the electrophysiological finding that the upper visual field representation of V4 does not extend beyond $35\text{--}40^\circ$ (Gattass *et al.*, 1988). However, this case did show a projection anterior to the far peripheral upper field representation of V2 in the region we have termed VTF (Boussaoud *et al.*, 1991). Finally, two separate patches of intrinsic label were found in V2.

As in case 9, the injection in case 10 was placed in the peripheral upper field of V2 (42°). In this case, as in case 9, areas V3v, PO, MTp, VIP and VTF all contained labeled terminals (Fig. 10). In addition, as for the more central and intermediate upper field cases, case 10 also showed labeled terminals in V4 and MT; in both areas the label was in their peripheral upper field representations. Finally, this was the only case to show projections to TEO and area prostriata.



Case 7

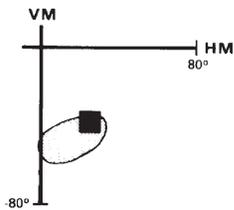
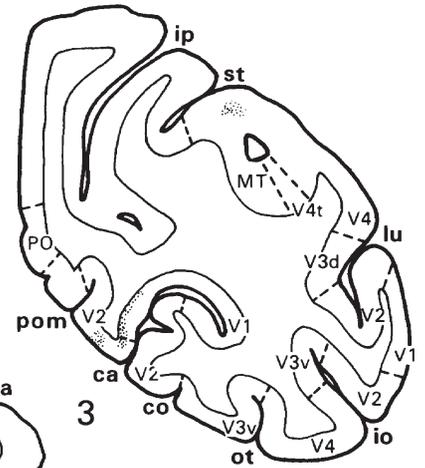
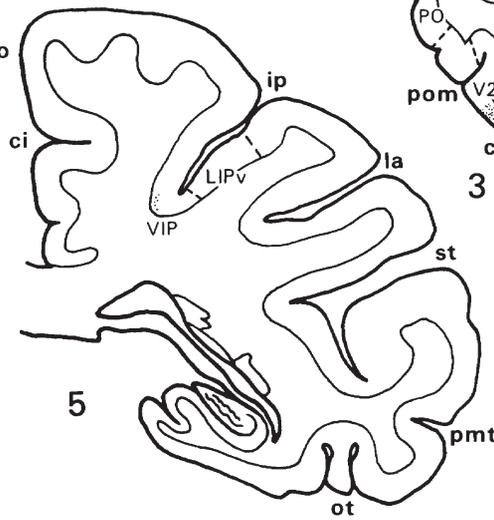
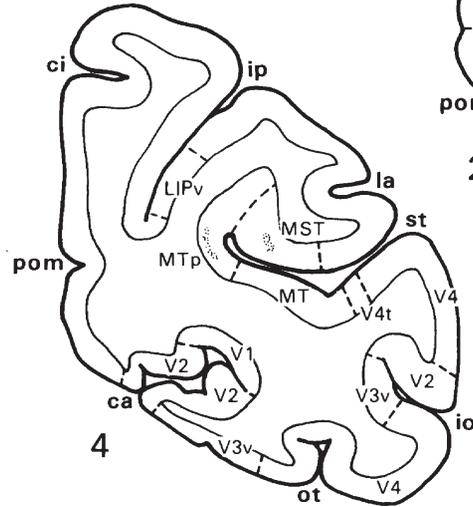
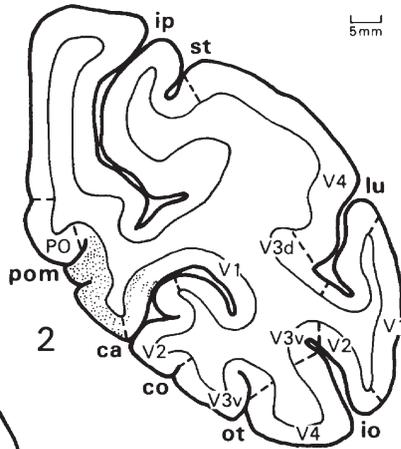
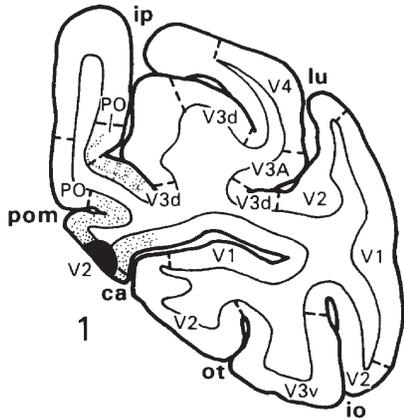
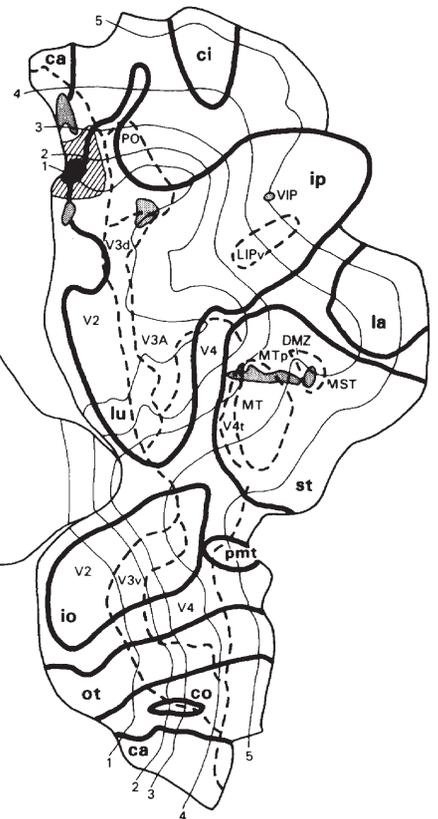


Figure 9. Case 7: distribution of labeled terminals following an injection into the peripheral lower field representation of V2, shown on coronal sections at the levels indicated on the medial view of the hemisphere and on a two-dimensional map. For conventions, see Figures 5 and 6.

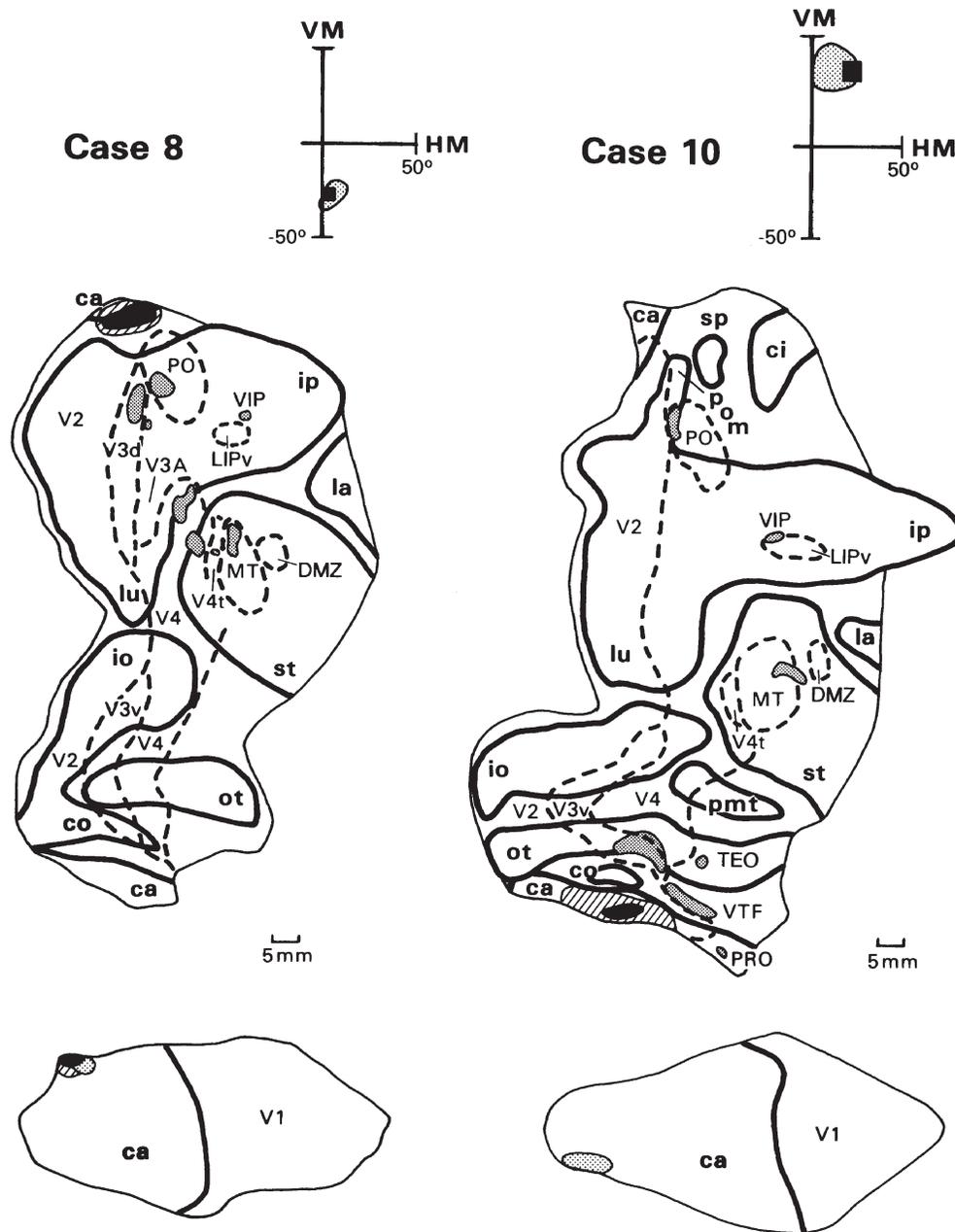


Figure 10. Cases 8 and 10: distribution of labeled terminals following injections into peripheral lower (case 8) and upper (case 10) field representations of V2, shown on two-dimensional maps of the cortex. For conventions, see Figures 5 and 6.

The Vertical Meridian: Case 11

In case 11 we injected the representation of the vertical meridian in the upper field of V2 (i.e. the V1/V2 border) at 6.5° eccentricity after making a series of parasagittal penetrations in which we mapped receptive fields across areas V2, V3v, V4, TEO and VTF (Fig. 12). Following this injection, we found two separate patches of labeled terminals. One patch was located on the lateral bank of the occipitotemporal sulcus and extended laterally onto the convexity. The receptive fields recorded in this cortical region either included or were close to the vertical meridian and had approximately the same eccentricity as the field recorded at the injection site (Fig. 12, see fields 10–13). Thus, the representation of the vertical meridian of V2 projects to the one located at the V3v/V4 border. The second patch of

labeled terminals was within the central field representation of MT (Gattass and Gross, 1981; Van Essen *et al.*, 1981; Desimone and Ungerleider, 1986). An examination of the receptive fields recorded on the row of penetrations illustrated in Figure 12 indicates that the borders of areas as determined by myeloarchitecture closely match reversals in receptive field progressions. In addition, the receptive fields at these borders are close to, but not necessarily centered on, the meridians, consistent with the findings of Gattass *et al.* (1988). Thus, the vertical meridian is represented at the V1/V2 and V3v/V4 borders, while the horizontal meridian is represented at the V2/V3v and V4/TEO borders. The TEO/VTF border coincides with the representation of the visual field periphery and therefore of neither meridian.

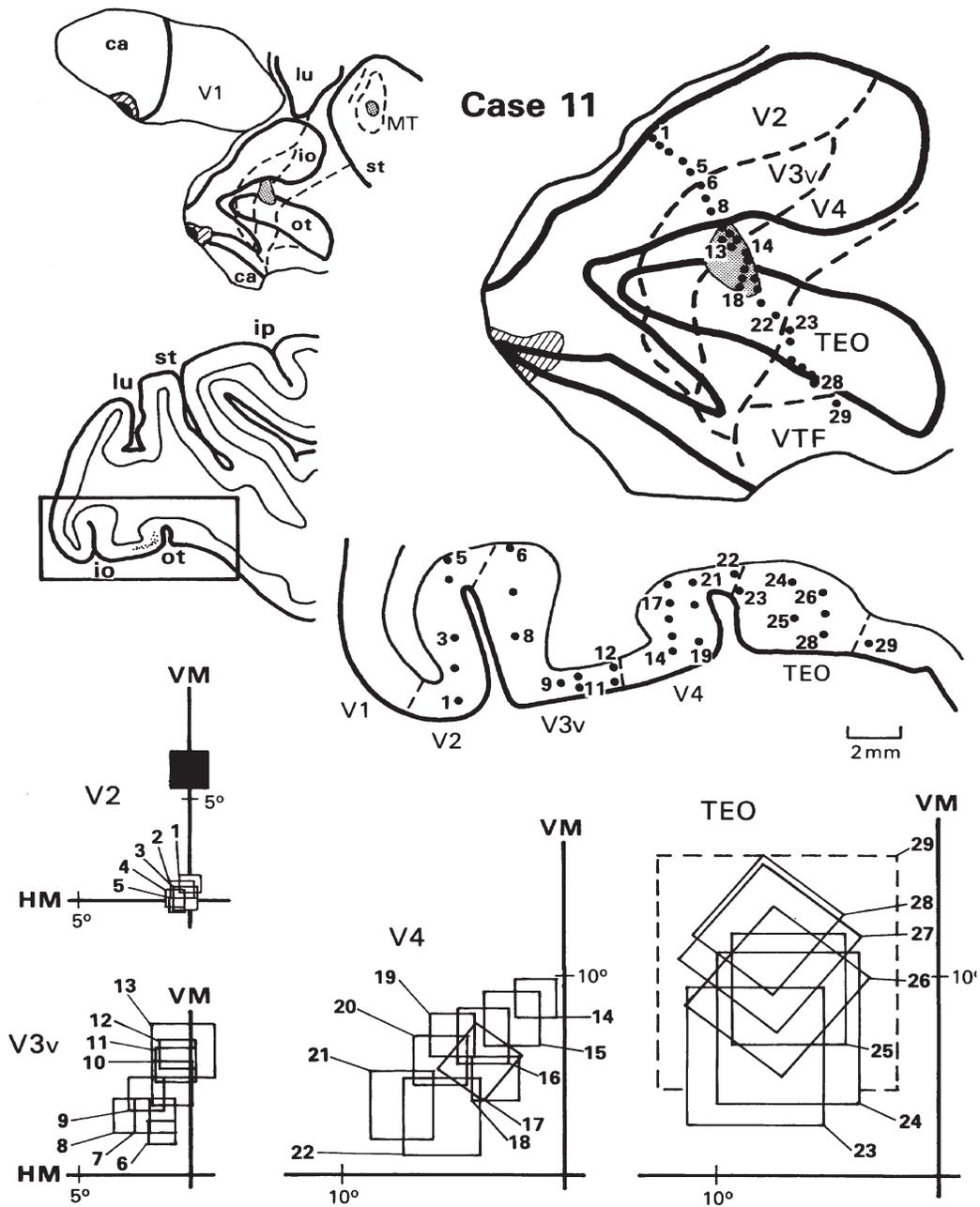


Figure 12. Case 11: relationship between the location of the receptive field recorded at the injection site in V2 and those recorded in the projection zones of V3v and V4. The receptive field recorded at the injection site is shown in black, while those recorded within areas V3v, V4 and TEO are shown as unfilled squares below; the receptive field indicated by the dashed square at the bottom right was recorded anteriorly to TEO. The locations where these receptive fields were recorded are shown both on the parasagittal section at the middle right and on the two-dimensional map at the top. The injection site is shown in black on the two-dimensional maps at the top and the projections are shown in gray on the maps and in dots on the parasagittal section at the middle left. For other conventions, see Figures 5 and 6.

The Horizontal Meridian at the V2/V3d Border: Cases 12 and 13

Figure 13 shows the distribution of labeled terminals after an injection at the anterior border of V2 at an eccentricity of 2.6° in the lower visual field (case 12). An examination of the injection site as well as the location of the projection back to V1 indicates that the representation of the horizontal meridian at the V2/V3d border was probably involved in the injection, as was a small portion of V3d itself. Dorsally in the hemisphere, a large patch of terminal label was found spanning V3d and V3A; a second, smaller patch of label was also found in V3A. Another patch of

label was found spanning the central lower field representation of V4 and V4t. Near this patch, a separate projection was found in the central visual field representation of MT. All of these projections could reflect the involvement of either V2 or V3d, or both. Ventrally in the hemisphere, two separate patches of labeled terminals were found. One was located within V2 and included its anterior border, i.e. the representation of the horizontal meridian, while the other was located within V4 close to its anterior border, i.e. where the horizontal meridian is presumably re-represented (see Discussion).

In case 13 we also injected the anterior border of dorsal V2,

but at a more peripheral field representation (Fig. 14). Although the receptive field recorded at the injection was centered at an eccentricity of 15.4° , the projection back to V1 indicated that eccentricities as peripheral as 25° were probably involved. As in case 12, the injection in case 13 included the representation of the horizontal meridian, and the resulting pattern of projections in the two cases was similar. Case 13 showed projections to V3d, V3A, V4, V4t and MT. Consistent with the more peripheral field representation of the injection site in case 13, the projections were located in more peripheral portions of these areas. In

addition, a small patch of labeled terminals was found in area PO. Area PO was also labeled in cases 7–10, which all had injections involving the peripheral field representation of V2, i.e. eccentricities of 30° or greater. Finally, we saw two separate patches of labeled terminals within V2 itself, one close to the injection site and another, farther away, close to the lip of the lunate sulcus. Because the second patch excluded layer IV, it was probably a projection back from V3d rather than an intrinsic connection of V2. Although the injection in this case, as in case 12, involved the representation of the horizontal meridian, we

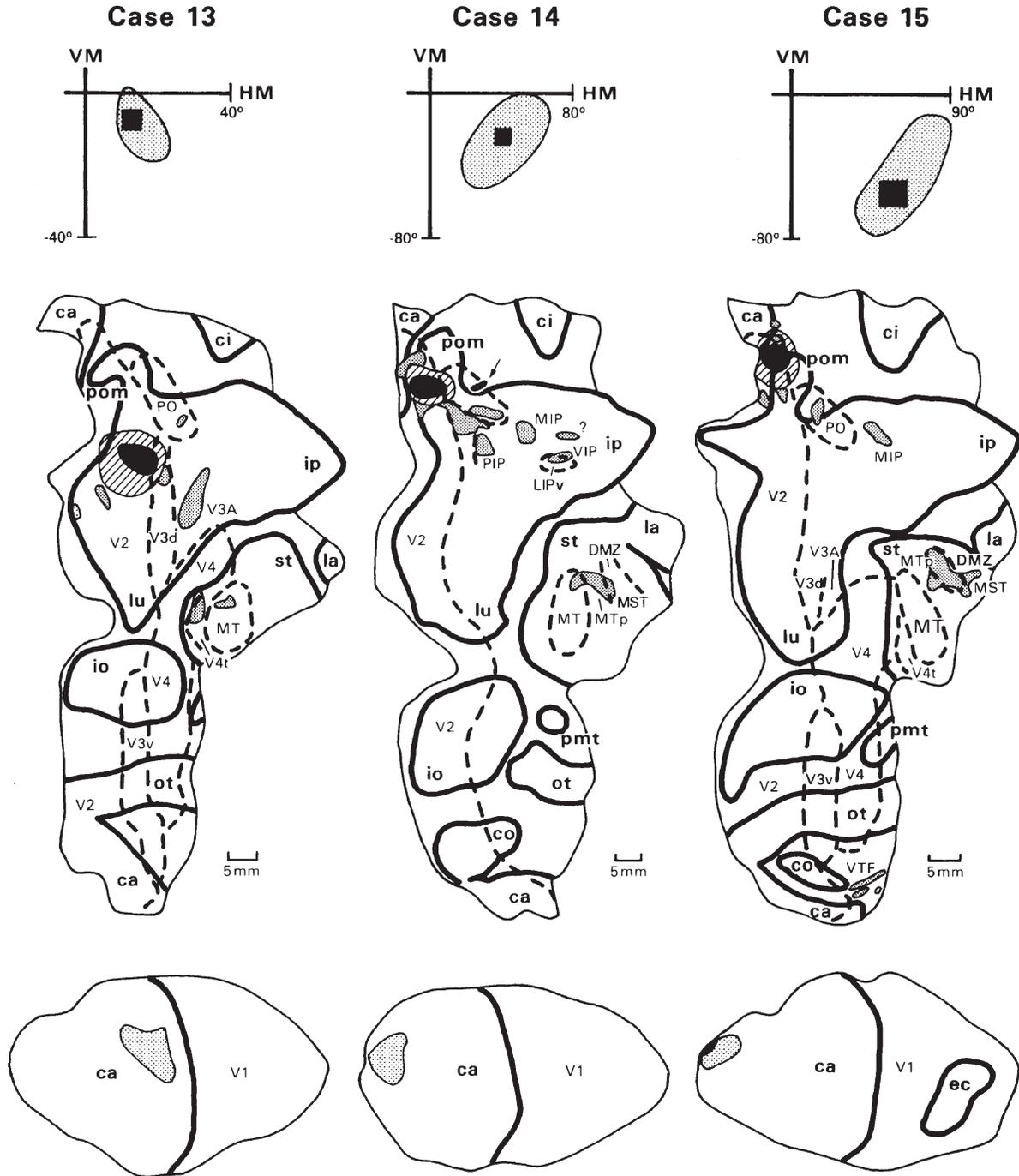


Figure 14. Cases 13, 14 and 15: distribution of labeled terminals following injections into the peripheral lower field representation of V2, shown on two-dimensional maps of the cortex. For conventions, see Figures 5 and 6.

did not find a projection ventrally at the anterior border of V2, where the horizontal meridian is re-represented.

The Horizontal Meridian at the Anterior Border of Far Peripheral V2: Cases 14 and 15

In case 14 we injected the peripheral field representation of V2 at an eccentricity of 48° in the lower visual field (Fig. 14). The injected region was located on the posterior bank of the parieto-occipital sulcus and included the sulcal floor, spreading into the ventral portion of area PO. To reach the intended injection site, the syringe needle entered the anterior bank of the parieto-occipital sulcus and, as a consequence, a small amount of tracer was also deposited in the dorsal portion of area PO (Fig. 14, case 14, see arrow). Like several of the other peripheral field cases, this case showed projections to the peripheral field representations of V1, V3d and MT (including MTp), as well as projections to MST, PO and VIP. This case showed additional projections to areas PIP and MIP (Colby *et al.*, 1988), and to another zone medial to VIP which has not as yet been defined. Labeled terminals within PIP and MIP probably derived from involvement of area PO in the injected region. This case, like case 13, did not show a projection to the anterior border of V2 ventrally in the hemisphere.

The injection site in case 15 resembled that in case 14, except that the injected region spread into an area medial to PO rather than into PO itself. This case, like the peripheral field cases with injections confined to V2 (cases 7–10), showed projections back to V1 and forward to PO, MTp, MST and VTF. This case also showed a projection to MIP, which may have resulted from spread of the tracer beyond the V2 border. Finally, like cases 13 and 14, this case did not show a projection to the anterior border of V2 ventrally in the hemisphere.

Discussion

The results of this study demonstrate that V2 projects topographically back to V1 and forward to V3, V4 and MT. In addition, peripheral, but not central, field representations of V2 project to a number of other extrastriate visual areas, including PO, MST, VIP and the portion of area TF on the parahippocampal gyrus which we previously termed VTF (Boussaoud *et al.*, 1991). In isolated cases, we also saw projections from V2 to TEO, V3A, prefrontal area 8 and area prostriata. In the following sections, we first discuss the topographic organization of the projection fields of V2, then compare the projections of V2 in macaques with those that have been described in other primate species and finally discuss the relevance of central versus peripheral field projections.

Visual Topography of Extrastriate Cortex

Area V3

There are currently two different views regarding the organization of V3 in macaques. Based on electrophysiological mapping studies, Gattass and his colleagues (Gattass *et al.*, 1988) have argued that the entire region bordering V2 anteriorly is a single visual area which contains a representation out to 30–40° eccentricity in both the upper (V3v) and lower (V3d) visual fields. By contrast, Van Essen and his colleagues have argued that V3d and V3v are different visual areas based on differences in projections from V1, myeloarchitecture and neural response properties (Burkhalter *et al.*, 1986; Newsome *et al.*, 1986; Van Essen *et al.*, 1986). These investigators have termed the upper and lower visual field representations anterior to V2, areas V3

and VP respectively. The data presented here demonstrate that although V1 may project asymmetrically to V3, V2 does not. Whereas the upper field representation of V2 projects to V3v, the lower field representation of V2 projects to V3d. Further, central field representations of V2 project laterally within both V3v and V3d, while more peripheral field representations project more medially (Fig. 3). Our results also show that the visual field representation within V3 may extend beyond 40° eccentricity (see cases 7 and 9) but does not extend to 80° (case 15). Thus, there is a reduction in the extent of the visual field represented as one moves from V2 to V3, consistent with the findings from electrophysiology (Gattass *et al.*, 1981, 1988). Finally, our results show that V3d shares the representation of the vertical meridian with areas V4 (case 3) and PO (case 7), which is again consistent with findings from electrophysiology (Gattass *et al.*, 1988).

Area V4

Although V4 was originally described as being located on the prelunate gyrus (Zeki, 1973; Van Essen and Zeki, 1978), it is now clear from more extensive mapping studies that the area extends ventrally into the occipitotemporal cortex. The area contains a representation of the visual field out to ~40° eccentricity, with the lower visual field represented dorsally in the hemisphere and the upper visual field represented ventrally (Gattass *et al.*, 1988). Consistent with these electrophysiological findings, we found projections to both upper and lower visual field representations of V4 from V2 sites representing eccentricities up to but not greater than 46° eccentricity. In addition, the vertical meridian representation of V2 projects to the V3/V4 border (cases 3 and 11), where the vertical meridian is again represented (Gattass *et al.*, 1988). Dorsally in the hemisphere, the representation of the horizontal meridian of V2 projects anteriorly to the V4/V4t border (cases 12 and 13), which also contains a horizontal meridian representation (Desimone and Ungerleider, 1986). Ventrally, however, the horizontal meridian of V2 does not appear to project to the V4/TEO border, but rather projects to a region within V4 itself (case 12). This anatomical finding agrees with the observation of Gattass *et al.* (1988) that the horizontal meridian representation of ventral V4 is usually located caudal to the area's anterior border.

Area V4t

Area V4t has been defined as the region lying between V4 and MT on the lateral bank of the superior temporal sulcus; physiological evidence indicates that the area contains a representation of the lower visual field only (Schein *et al.*, 1982; Desimone and Ungerleider, 1986; Ungerleider and Desimone, 1986b; Gattass *et al.*, 1988). We saw projections to V4t from the lower field representations of V2 up to 46° eccentricity (case 7), with some evidence for a crude central to peripheral field organization as one progresses from lateral to medial within the area. Frequently, the projection to V4t from lower field V2 was continuous with the projection to V4. In only one upper field case, case 5, with an injection placed at 3.5° eccentricity, did we see a projection to V4t in its presumed lower field representation. This case also showed a separate projection anterior to the foveal representation of MT. The projection to V4t may have resulted from involvement of the representation of the horizontal meridian of V2 at the injection site, while the projection anterior to MT may indicate that V4t, at least in this animal, had a small upper field representation.

Area MT

Dubner and Zeki (1971) first described the existence in macaques of a visual area located in the superior temporal sulcus with directionally selective neurons. This area has come to be called MT (Gattass and Gross, 1981; Van Essen *et al.*, 1981; Desimone and Ungerleider, 1986) to acknowledge its homology with a visual area located in the middle temporal lobe of New World monkeys (Allman and Kaas, 1971). In all V2 cases, there was a projection to MT. Central field injections (those centered at eccentricities of $<30^\circ$) produced labeled terminals in the heavily myelinated part of MT, whereas peripheral field injections (those centered at eccentricities $\geq 30^\circ$) produced labeled terminals medial to the heavily myelinated part of MT, i.e. within MTp (Desimone and Ungerleider, 1986). A crude central to peripheral field trend and an upper versus lower field segregation was observed in the projections (Fig. 3), which is in keeping with the visuotopic map reported for this area (Ungerleider and Mishkin, 1979; Gattass and Gross, 1981; Van Essen *et al.*, 1981; Desimone and Ungerleider, 1986). Although it has been reported that the vertical meridian is represented at the lateral border of MT (Gattass and Gross, 1981; Van Essen *et al.*, 1981), one V2 case with an injection at the representation of the vertical meridian (case 7) showed labeled terminals at the border of MT, but the other (case 11) did not. We have no explanation for this anomaly.

Area MST

In the absence of an independent anatomical marker, it is not possible to localize precisely area MST, an area medial to MT in the superior temporal sulcus. However, the medial portion of the area is characterized by a densely myelinated zone (DMZ; Desimone and Ungerleider, 1986). We saw projections within DMZ after peripheral field injections with eccentricities $>45^\circ$ (cases 7, 9, 14 and 15). In one of these cases (case 7), the projection within DMZ was separate from the one located medial to MT, i.e. within MTp. Thus, the far peripheral field representation of V2 projects directly to MST and this projection appears to be additional to the one that the far peripheral representation sends to MTp.

Area PO

Area PO has been defined as a myeloarchitecturally distinct area, containing a complex visuotopic map with a de-emphasis of the central field representation (Covey *et al.*, 1982; Gattass *et al.*, 1986; Neuenchwander, 1989; Neuenchwander *et al.*, 1994). Peripheral field injections in V2 at eccentricities of 30° and greater (cases 7–10) showed projections to PO which had an upper versus lower field segregation. While upper field cases (cases 9 and 10) showed projections medially in PO, lower field cases (cases 7 and 8) showed projections laterally, which is consistent with the visuotopic organization described for PO (Covey *et al.*, 1982; Gattass *et al.*, 1986; Colby *et al.*, 1988; Neuenchwander, 1989; Neuenchwander *et al.*, 1994). The absence of projections to PO after injections in more central field portions of V2 may be related to the difference in cortical magnification in these two visual areas (Gattass *et al.*, 1986); it is unlikely to be related to some technical factor, as Colby *et al.* (1988) also found projections to PO from peripheral but not central field V2 using retrograde tracers. Finally, an injection involving the vertical meridian in peripheral field V2 (case 7) produced label that included the V3d/PO border, consistent with the representation of the vertical meridian at this location (Gattass *et al.*, 1986; Neuenchwander *et al.*, 1994).

Area VIP

In the present study, and in keeping with the studies by Blatt *et al.* (1990), Colby and Duhamel (1991) and Colby *et al.* (1993), we have defined VIP as the area at the fundus of the intraparietal sulcus ventral to the heavily myelinated zone (LIPv) on the lateral bank. We saw projections to VIP after V2 injections involving eccentricities of 30° and greater; in some cases the projection extended laterally to include a small portion of LIPv. These results are consistent with those of Cavada and Goldman-Rakic (1989), who observed retrogradely labeled cells in peripheral field V2 following injections that included the ventral portion of the lateral bank of the intraparietal sulcus. Although no one has yet reported mapping VIP electrophysiologically, our results suggest an upper versus lower field segregation within the area of caudal versus rostral (see Fig. 3B).

Area VTF

In their mapping study of area TEO, Boussaoud *et al.* (1991) found evidence for another visual area on the parahippocampal gyrus anterior to V2 and V3v, and medial to V4 and TEO. They termed this area VTF because it was the portion of architectonic area TF (Bonin and Bailey, 1947) that was visually responsive. Although occupying a position close to that of the temporal ventral posterior area (area TVP) reported in *Cebus* (Sousa *et al.*, 1991), VTF appears to be located more medially in the hemisphere. We found projections to VTF in two cases (cases 9 and 10) with injections involving the far peripheral upper field representation of V2. Although it might be argued that this region represents the far periphery of ventral V4, VTF and ventral V4 have a markedly different appearance both cyto- and myeloarchitectonically. A third case (case 15) with an injection involving the far peripheral lower field representation of V2 also showed a projection to VTF. However, in this case the tracer spread beyond the V2 border and thus the projection cannot be defined with certainty as arising from V2.

Other Projection Fields

In one case (case 10), V2 projections were found in TEO and in area prostriata; in another (case 8), V2 projections were found in V3A; and in two others (cases 1 and 6), projections were found in area 8 of the prefrontal cortex. The projection to TEO, though unreliable in the present study, has been confirmed in our laboratory using retrograde tracers placed in TEO (Distler *et al.*, 1993; Nakamura *et al.*, 1993). Similarly, even though we saw a projection to area 8 in two cases only, this projection has been seen previously in a study using retrograde tracers placed in the prefrontal cortex (Barbas, 1988). The failure to find consistent projections to either TEO or area 8 in the present study may be attributed to the fact that anterograde tracing techniques are less sensitive than retrograde ones (but see Huerta *et al.*, 1987). Regarding the projection to V3A, this projection arose from a case with a peripheral field injection placed on the vertical meridian of V2. Thus, it is possible that the projection resulted from involvement of the periphery not of V2 but rather of V1, which is known to project to V3A (Zeki, 1980). The projection to area prostriata in our single case must await verification.

Comparison with Other Primate Species

V2 has been mapped in both the macaque and several other primate species (Covey, 1964; Allman and Kaas, 1974; Van Essen and Zeki, 1978; Gattass *et al.*, 1981; Rosa *et al.*, 1988), and a number of its connections have been described previously. The projection from V2 back to V1 has been found in the nocturnal

prosimian *Nicticebus* (Preuss *et al.*, 1993), and in the New World monkeys *Saimiri* and *Cebus* (Tigges *et al.*, 1973, 1974, 1981; Wong-Riley, 1978; Sousa *et al.*, 1991). As in the macaque, the projection from V2 to V1 in these other primate species appears to be topographically organized. The projection from V2 to DL, the presumed homologue of macaque V4 (Weller *et al.*, 1991), has also been described in New World monkeys, including *Saimiri* (Steele *et al.*, 1991) and *Aotus* (Weller and Kaas, 1985). Similarly, the projection from V2 to MT has been demonstrated in several New World monkeys, including *Callithrix*, *Saimiri* and *Aotus*, as well as in the prosimian *Galago* (Spatz and Tigges, 1972; Wall *et al.*, 1982; Weller *et al.*, 1984; Krubitzer and Kaas, 1990a). Finally, in *Saimiri* and *Aotus*, V2 has been reported to project to area DM (Krubitzer and Kaas, 1990b), an area that could be the homologue of macaque V3d or PO (Krubitzer and Kaas, 1990b; Neuenschwander *et al.*, 1994). On the other hand, Kaas and Morel (1993) found a projection from V2 to FST in *Aotus* that we failed to see in macaques. Also, we found V2 projections to areas MST, VIP and VTF which have not yet been described in other primate species.

Central versus Peripheral Visual Field Projections

There is accumulating evidence for differences in the cortical projections of central and peripheral visual field representations. Zeki (1969), for example, first noted that the foveal representation of V1, but not the remainder of the area, projects directly to V4, a finding recently replicated by Nakamura *et al.* (1993). In addition, Zeki (1980) reported that peripheral but not central V1 projects to V3A (see also Ungerleider and Mishkin, 1982). Moreover, Ungerleider and Desimone (1986b) found that V3A receives a projection from peripheral but not central MT. Finally, Colby *et al.* (1988) demonstrated direct input to PO from peripheral but not central field representations of V1 and V2. We, too, found that peripheral but not central field V2 projects directly to PO. Injections placed at eccentricities of 30° or greater produced label in PO, but those placed at lesser eccentricities did not. In addition, we found that peripheral but not central field V2 projects to areas MST, VIP and VTF. These projections also arose from the portions of V2 representing eccentricities of 30° or greater.

Differences between peripheral and central field inputs can be related, at least in part, to differences in the cortical magnification factor. For example, injections in the central field representation of one area with a high magnification factor and small receptive fields, such as V2, are less likely to label areas with a low magnification factor and large receptive fields, such as PO, which de-emphasize the central visual field. Differences between peripheral and central field inputs must also be related to the extent of the visual field represented within an area. For example, area V4 has a representation of the visual field only up to 40° eccentricity (Gattass *et al.*, 1988). It is therefore not surprising to find that terminal label in V4 is absent after injections in the far periphery of V2. The third difference between peripheral and central field inputs may be related to the visual processing requirements of an area. As originally pointed out by Ungerleider (1986; see also Desimone and Ungerleider, 1989; Baizer *et al.*, 1991), 'ventral stream' areas, i.e. those within the occipitotemporal cortex, receive preferential inputs from central field representations, which is consistent with the role of these areas in object vision (Ungerleider and Mishkin, 1982). By contrast, 'dorsal stream' areas, i.e. those within occipitoparietal cortex, receive preferential inputs from peripheral field representations, which is consistent with the role of these areas

in spatial vision (Gattass *et al.*, 1990). The presence of projections from peripheral field V2 to parietal areas PO, VIP and MST supports this notion. In this context, it is tempting to speculate that area VTF, another target of peripheral field V2, might also play a role in spatial vision. This speculation is consistent with the projection the area also receives from posterior parietal cortex (Suzuki and Amaral, 1994).

What is the significance of direct projections from the peripheral visual field of V2 to parietal areas, if, presumably, these areas receive indirect input from peripheral V2 via other routes, such as the one through MT? Earlier we proposed that, within the 'ventral stream', direct inputs from foveal V1 to V4, bypassing V2, and from V2 to TEO, bypassing V4, might provide a means for coarse-grained information to arrive rapidly in the temporal lobe (Nakamura *et al.*, 1993). This advance information about a stimulus might aid in constructing within area TE the initial representation of the overall shape and color of an object, with the fine-grained information arriving later to fill in the important details. If this analysis is correct, then, by extension, the projections from peripheral field V2 to parietal areas could provide a direct route for information about the periphery to quickly reach parietal cortex and thereby rapidly activate circuits for spatial vision and spatial attention.

Notes

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Note Added in Proof

After this paper had been accepted, another study of V2 connectivity was published [Stepniewska I, Kaas JH (1996) Topographic patterns of V2 cortical connections in macaque monkeys. *J Comp Neurol* 371:129-152].

Appendix: Abbreviations

Cortical Visual Areas

DMZ	densely myelinated zone of MST
LIP	lateral intraparietal area
LIPv	ventral portion of LIP
MIP	medial intraparietal area
MST	medial superior temporal area
MT	middle temporal area
MTp	peripheral portion of MT
PIP	posterior intraparietal area
PO	parieto-occipital area
PRO	area prostriata
TEO	posterior inferior temporal cortex
V1	primary visual cortex
V2	visual area 2
V3A	visual complex V3 part A
V3d	dorsal portion of visual area 3
V3v	ventral portion of visual area 3
V4	visual area 4
V4t	V4 transition zone
VIP	ventral intraparietal area
VTF	visual part of parahippocampal TF

Cortical Sulci

amt	anterior middle temporal sulcus
ar	arcuate sulcus
ca	calcarine fissure
ce	central sulcus
co	collateral sulcus
ec	external calcarine sulcus
io	inferior occipital sulcus
ip	intraparietal sulcus
la	lateral sulcus
lu	lunate sulcus
orb	orbital sulcus
ot	occipitotemporal sulcus
p	principal sulcus
pmt	posterior middle temporal sulcus
rh	rhinal sulcus
sp	subparietal sulcus
st	superior temporal sulcus

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