THE JOURNAL OF COMPARATIVE NEUROLOGY 269:392-413 (1988)

Topographical Organization of Cortical Afferents to Extrastriate Visual Area PO in the Macaque: A Dual Tracer Study

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ABSTRACT

We have examined the origin and topography of cortical projections to area PO, an extrastriate visual area located in the parieto-occipital sulcus of the macaque. Distinguishable retrograde fluorescent tracers were injected into area PO at separate retinotopic loci identified by single-neuron recording.

The results indicate that area PO receives retinotopically organized inputs from visual areas V1, V2, V3, V4, and MT. In each of these areas the projection to PO arises from the representation of the periphery of the visual field. This finding is consistent with neurophysiological data indicating that the representation of the periphery is emphasized in PO. Additional projections arise from area MST, the frontal eye fields, and several divisions of parietal cortex, including four zones within the intraparietal sulcus and a region on the medial dorsal surface of the hemisphere (MDP).

On the basis of the laminar distribution of labeled cells we conclude that area PO receives an ascending input from V1, V2, and V3 and receives descending or lateral inputs from all other areas. Thus, area PO is at approximately the same level in the hierarchy of visual areas as areas V4 and MT.

Area PO is connected both directly and indirectly, via MT and MST, to parietal cortex. Within parietal cortex, area PO is linked to particular regions of the intraparietal sulcus including VIP and LIP and two newly recognized zones termed here MIP and PIP. The wealth of connections with parietal cortex suggests that area PO provides a relatively direct route over which information concerning the visual field periphery can be transmitted from striate and prestriate cortex to parietal cortex. In contrast, area PO has few links with areas projecting to inferior temporal cortex. The pattern of connections revealed in this study is consistent with the view that area PO is primarily involved in visuospatial functioning.

Key words: extrastriate cortex, prestriate cortex, visual system, parietal lobe, retinotopy

Analysis of the connections of extrastriate visual cortex has yielded two major insights into its organization. First, extrastriate areas can be arranged in a hierarchy determined by the laminar pattern of connections between areas (Rockland and Pandya, '79; Van Essen and Maunsell, '83). Second, this hierarchy can be subdivided into two interconnected "streams," one leading into the parietal cortex (dorsal stream) and one leading into the temporal cortex (ventral stream) (Ungerleider and Mishkin, '82). These streams are physiologically distinct and participate in different visual functions (Van Essen and Maunsell, '83; Desimone et al.,

Accepted October 6, 1987.

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Abbreviations

ag	annectent gyrus
ar	arcuate sulcus
ca	calcarine sulcus
ce	central sulcus
ci	cingulate sulcus
io	inferior occipital sulcus
ip	intraparietal sulcus
la	lateral sulcus
lu	lunate sulcus
ot	occipito-temporal sulcus
po	parieto-occipital sulcus
pom	parieto-occipital medialis sulcus
pr	principal sulcus
st	superior temporal sulcus

'85). A basic step in understanding each extrastriate visual area is to determine its place in the hierarchy of visual areas and its membership in the dorsal or ventral stream.

Area PO, first described by Covey et al. ('82), is a visual area located on the anterior bank of the parieto-occipital sulcus (Fig. 1). PO is unique among the currently known extrastriate areas in the macaque in that it does not have an expanded representation of central vision. Rather, the magnification factor remains nearly constant across eccentricity (Covey et al., '82; Gattass et al., '85). This emphasis on the visual field periphery is similar to that found in owl monkey area M (Allman and Kaas, '76), with which area PO may be homologous.

In the present study we examined the afferent connections of area PO by injecting distinguishable retrograde fluorescent tracers into portions of PO representing distinct retinal loci. This approach permitted us both to identify cortical areas projecting to PO and to analyze directly the retinotopic organization of afferent pathways.

Some of the results have been published in abstract form (Colby et al., '83).

MATERIALS AND METHODS

Animal preparation and maintenance

Three *Macaca fascicularis* monkeys (two females and one male) weighing between 3.2 and 3.8 kg were used. The preparation of the animals and their maintenance during recording have been described in detail previously (Gattass and Gross, '81). A week before the recording/injection session, a headbolt for holding the animal in the stereotaxic apparatus was implanted by use of aseptic procedures and under general anesthesia. For the recording session, the monkey was first given atropine (0.1 mg/kg) and sedated with diazepam (1 mg/kg). It was then restrained with ketamine hydrochloride (30 mg/kg), anesthetized with a mixture of halothane (2.5%), nitrous oxide (70%), and oxygen (30%), and intubated. The animal was secured in the stereotaxic head holder, immobilized with pancuronium bromide, and maintained under 70% nitrous oxide/30% oxygen. Temperature, EKG, and end-tidal CO_2 were monitored throughout.

Recording and visual stimulation

The fovea and the optic disc of the contralateral eye were projected onto a translucent Plexiglas hemisphere 1.2 m in diameter. The hemisphere was positioned so that the contralateral eye was at its center. The cornea was covered by a contact lens selected by retinoscopy to focus the eye at .6 m. The ipsilateral eye was occluded.

Single and multiunit recordings were made with tungsten microelectrodes. Receptive fields were plotted with projected stimuli including slits, spots, and edges (Gattass et al., '81). Several vertical penetrations were made to locate the upper and lower visual field representations within area PO in each animal.

Injection procedure

After the recording was completed, the nonexperimental hemisphere was gently retracted to expose the medial surface of the hemisphere that had been used for recording, and the dura overlying PO was opened. In one animal, the parieto-occipital sulcus was also opened to expose the anterior bank of the sulcus. In each case we used stereotaxic coordinates to identify points on the cortical surface corresponding to the recording sites. The injection micropipette was then inserted into cortex at an angle nearly normal to the cortical surface. This direct approach was used in order to avoid the problem of leakage of tracer along the electrode track. After the injection was completed, infusion of the paralyzing agent was terminated and, when normal breathing resumed, the animal was returned to its cage.

Tracers

The two fluorescent tracers used were bisbenzimide (Hoechst 33258) and nuclear yellow (Hoechst S 769121). These particular tracers were chosen because they have similar transport times, fluoresce at the same incident wavelength, and are readily distinguishable by hue (Kuypers et al., '79; Bentivoglio et al., '80a,b). Injections of 0.1 μl of a 10% suspension of each tracer were made by pressure and produced an injection site of approximately 3 mm^3. Bisbenzimide was used for three injections (1-L, 2-U, 3-L) and nuclear yellow for two (1-U, 2-L).

Histology

After a 48-hour survival period, animals were deeply anesthetized with an overdose of pentobarbital and perfused with 2 liters of normal saline followed by 4 liters of fixative (10% formalin in 0.1 M phosphate buffer with increasing concentrations of sucrose, ranging from 3% for the first liter to 20% for the last). Brains were removed and stored overnight in cold phosphate-buffered 30% sucrose formalin and were cut the next morning. Sections cut at 40 μm were mounted immediately from 0.45% saline onto gelatin-coated slides and dried quickly on a slide warmer at 50°C. When dry, slides were dehydrated through two changes of absolute alcohol (15 seconds each), cleared in xylene, and coverslipped with Eukitt. One brain was cut coronally (case 1) and the other two (cases 2 and 3) were cut parasagittally. Every tenth section was mounted and coverslipped without counterstaining for examination under the fluorescence microscope. Adjoining series of sections were stained with cresyl violet and for myelin (Gallyas, '69).

Histological identification of area PO

Covey et al. ('82) observed that area PO, as defined by electrophysiological mapping, can be distinguished from adjacent areas in sections stained for myelin by using the Heidenhain-Woelke method. Area PO can also be identified in sections stained for myelin by the Gallyas ('69) method, as shown in Figure 2. Area PO is relatively densely myelin-

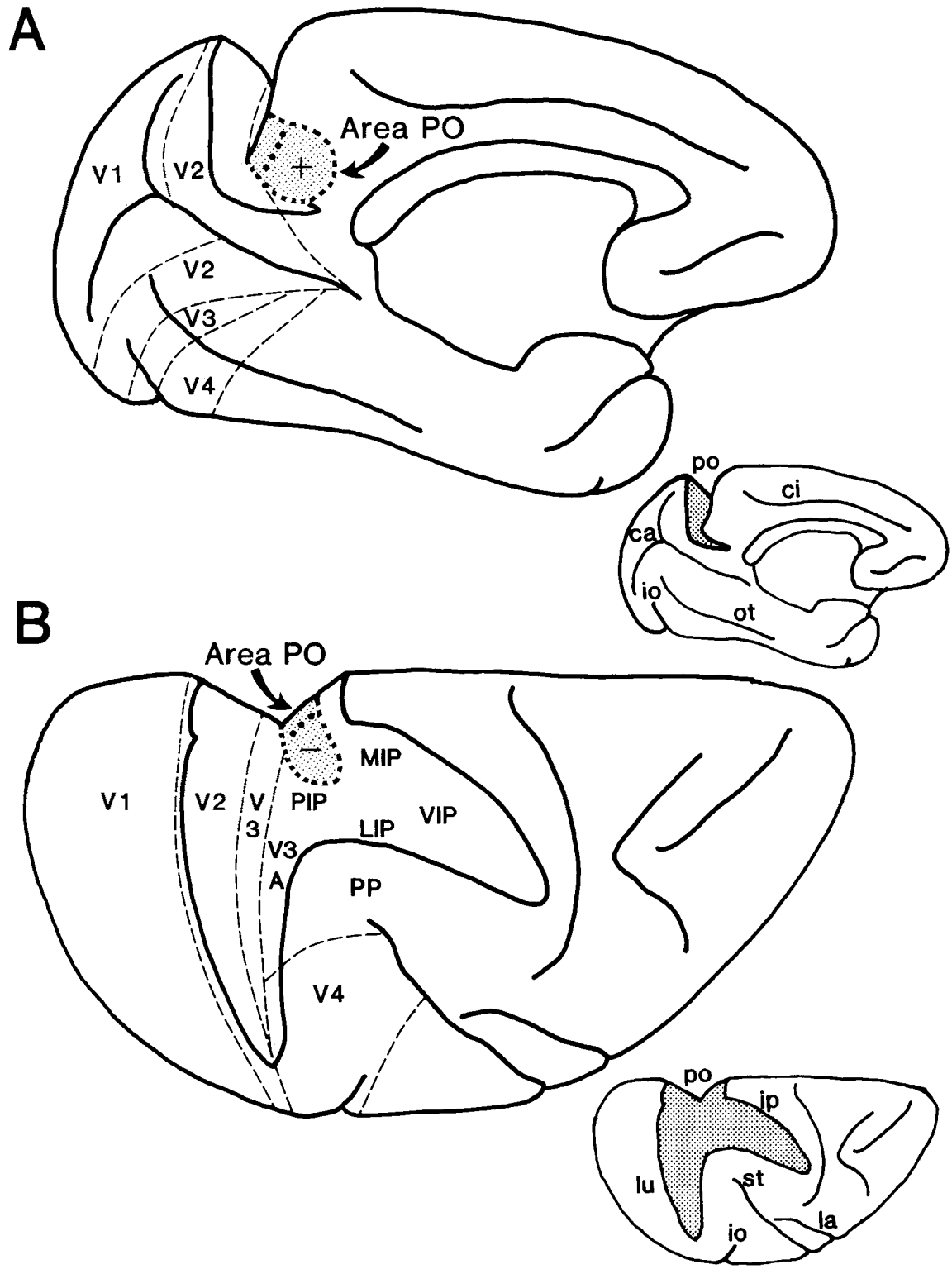

Fig. 1. A: Medial view of macaque cerebral cortex with parieto-occipital sulcus opened to show the location of visual area PO (shaded). Inset shows the extent of buried cortex (shaded) within the parieto-occipital sulcus (po) revealed in main figure. The dotted line across area PO indicates the representation of the horizontal meridian. The superior visual field (+) is represented medially in area PO, on the anterior bank of parieto-occipital sulcus and extending onto the precuneate gyrus on the medial surface of the hemisphere. B: Dorsal view of cortex with the lunate (lu), intraparietal (ip), and parieto-occipital (po) sulci opened to reveal visual areas within sulcal cortex, including area PO (shaded). Within area PO, the inferior visual field (−) is represented laterally, on the anterior bank of the parieto-occipital sulcus and extending into the intraparietal sulcus.

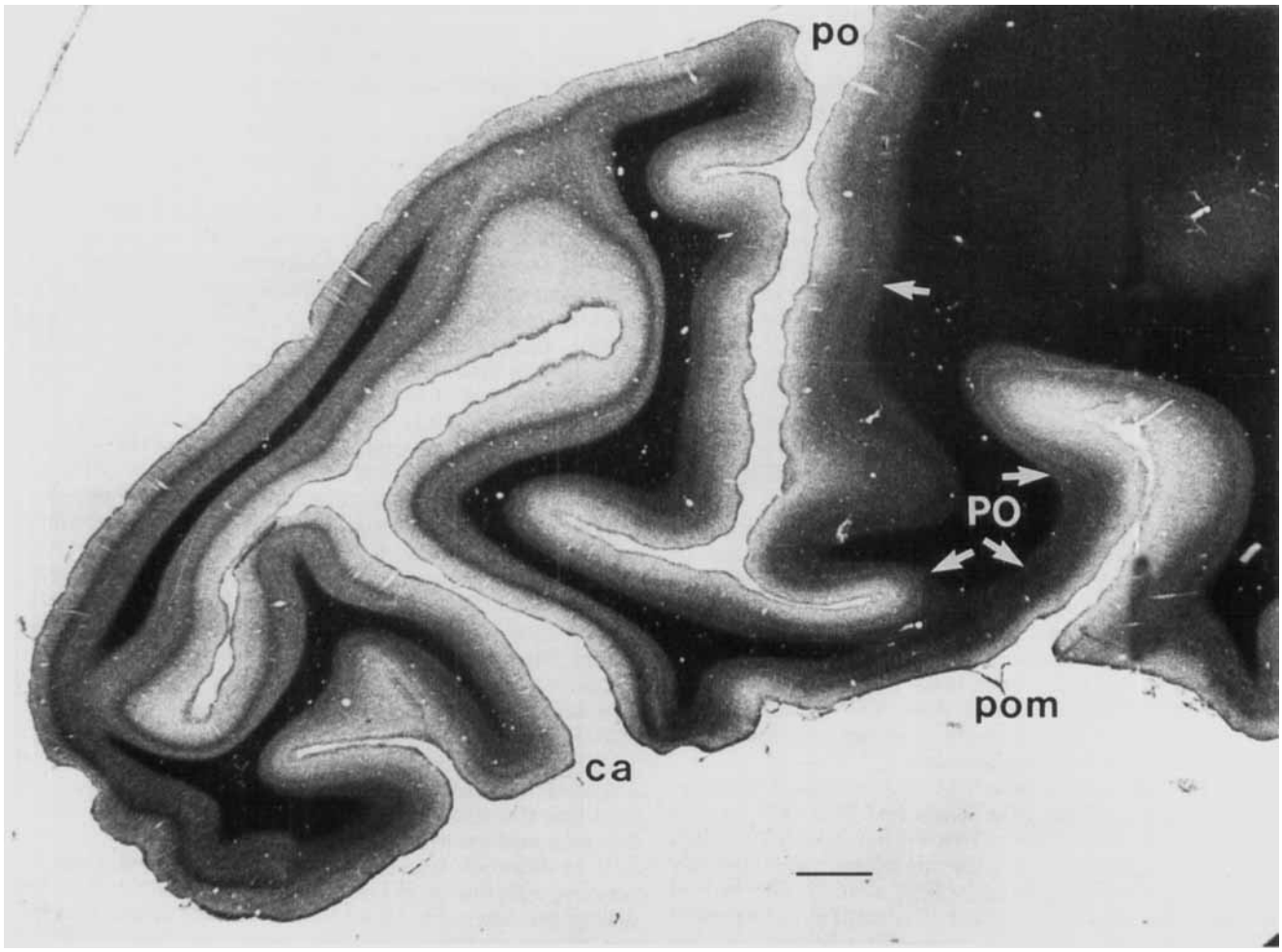

Fig. 2. Myeloarchitecture of area PO. Parasagittal section stained for myelin by the Gallyas method. The arrows indicate the borders of area PO within the parieto-occipital and parieto-occipital medialis sulci. Note lighter myelination in cortical regions dorsal to area PO. Scale bar = 2 mm.

ated with clear inner and outer bands of Baillarger separated from each other by a paler zone. Although the density of staining in PO is frequently comparable to that in ventrally adjacent areas V2 and V3, PO can be distinguished from these areas by the presence of numerous thick fibers in the lower layers which run parallel to the cortical surface. Area PO can also be distinguished from areas dorsal to it, which are more lightly myelinated and do not contain many tangential fibers. At each border, the myeloarchitectonic transition occurs over a distance of approximately 1 mm.

Two-dimensional reconstructions of cortex

The maps in Figures 5, 7, and 9 were drawn from flattened wire models of the cortex (Gattass and Gross, '81). A three-dimensional model was first constructed from wires bent to conform to layer IV in successive closely spaced (1.6 mm) sections. The wires were attached with scaled crosspieces, and the completed model was flattened by making cuts at selected locations. To facilitate flattening, area V1 was separated from extrastriate cortex along the V1/V2 border. This method produces flattened maps comparable to those produced by other methods (Van Essen and Zeki, '78; Van Essen and Maunsell, '80). Sulcal landmarks, myeloarchitectonic borders, and the locations of labeled cells were marked on drawings made from the flattened models.

Assignment of labeled cells to specific visual areas

We assigned the cells labeled after injections of area PO to specific visual areas by using distinctive myelination patterns and by referring to the results of previous mapping studies.

The borders of several prestriate areas can be identified in sections stained for myelin by using either the Heidenhain-Woelke or Gallyas method. The criteria for distinguishing the borders of V2, V3, V4, MT, and PO in sections stained by the Heidenhain-Woelke method have been described previously (Gattass and Gross, '81; Gattass et al., '81, '85, '88). Using the Gallyas method, we were usually able to distinguish several extrastriate areas, as described below. Because the quality of staining varies from section to section it was not always possible to discern each border in each section. Borders could be estimated from adjacent sections, however, and could usually be determined to within 1 mm. The uncertainty in determining myelin borders was sometimes greater when the plane of section was oblique to the cortical surface. For example, a myeloarchitectonically distinct zone in the medial bank of intraparie-

tal sulcus (MIP) was visible in the coronally cut case (#1) but could not be unambiguously identified in the two parasagittally cut cases.

The following sections describe the criteria used for identifying extrastriate visual areas in sections stained by the Gallyas method.

V2. Area V2 adjoins V1 at its posterior border. The anterior border of V2 was estimated on the basis of previous recording studies (Gattass et al., '81) and myeloarchitecture. Two myeloarchitectonic patterns are present: some regions within V2 show a homogeneous band of fibers from layer 6 to layer 4, while other regions show a heavy, broad inner band of Baillarger sharply separated by a much paler region from a thin outer band. The inner dark band is separated from the white matter by a paler region. The heavily myelinated portions of V2 correspond to regions of high cytochrome oxidase activity (Tootell et al., '83). In both the striated and the more homogeneous portions of V2, the area is characterized by prominent radial fibers which appear to span the cortex from layer 6 to layer 2.

V3. Adjacent to V2 is a thin strip of cortex which contains the dorsal (V3d) and ventral (V3v) portions of area V3 (Gattass et al., '85, '88; Burkhalter et al., '86; Newsome et al., '86). Area V3d frequently stands out as being more densely myelinated then adjacent areas (see Burkhalter et al., '86, Fig. 3). Also, the outer band of Baillarger is thinner than that in V2 and the thick inner band is not well separated from the white matter. Area V3v is less easy to distinguish but, as in V3d, there is no separation between the inner band and the white matter.

V3A. The location of area V3A was estimated from previous recording studies (Van Essen and Zeki, '78; Gattass et al., '85, '88). Area V3A is less densely myelinated than V3d, and both the inner and the outer bands are relatively thin. Unlike the inner band in V3d, that in V3A is well separated from the white matter. V3A could thus be readily distinguished from V3d. The remaining borders of V3A were not clearly defined in myelin-stained sections.

V4. Area V4 is distinguished by background staining lighter than that in V3 or V3A, so that the bands of Baillarger, which are both thin in V4, are quite crisp and distinct. The outer band is darker than that in V2 or V3, and the inner band is well separated from the white matter. While the posterior border of V4 is reasonably clear in myelin-stained sections, the anterior border, especially in the ventral portion of V4, is not distinct. The location of V4 has also been determined physiologically (Maguire and Baizer, '84; Gattass et al., '85, '88).

V4T. Area V4T is a small, myeloarchitectonically distinct zone in the ventral bank of superior temporal sulcus (STS) between areas V4 and MT (Schein et al., '82; Maguire and Baizer, '84; Ungerleider and Desimone, '86b; Gattass et al., '88). In V4T, the background is pale in myelin-stained sections and the bands of Baillarger are quite thin compared to those in V4 (see Ungerleider and Desimone, '86b: Fig. 4C). There is clear separation between the two bands as well as between the inner band and the white matter.

MT. Area MT is a heavily myelinated zone in the ventral bank of STS which in some cases extends into the fundus (see Ungerleider and Mishkin, '79: Fig. 6; Van Essen et al., '81: Fig. 1; Gattass and Gross, '81). Area MT contains a homogeneous dark band of fibers, extending from layer 6 to the bottom of layer 3, which largely obscures the bands of Baillarger.

MST. Area MST is a myeloarchitectonically heterogeneous area in the dorsal bank of STS (Newsome and Wurtz, '82) and is distinct from area FST in the fundus of STS (Desimone and Ungerleider, '86). MST contains both a medial, lightly myelinated zone (near the fundus) and a lateral, densely myelinated zone (toward the lip of the sulcus). The lateral border of the area MST coincides with the lateral border of the densely myelinated zone (see Ungerleider and Desimone, '86a: Fig. 4A).

PP. The region referred to as PP includes cortex within the lightly myelinated lateral portion of the dorsal bank of STS and the cortex of the posterior inferior parietal lobule (Desimone and Ungerleider, '86). It is approximately equivalent to area 7a.

PIP. The posterior intraparietal area (PIP) is a distinct region in the fundus of the intraparietal sulcus. PIP lies at the posterior end of the sulcus where it joins the parieto-occipital sulcus. While the anterior and lateral extent of this area remain uncertain, it can be differentiated from adjacent areas PO and V3d in sections stained by myelin, in which it stands out as a more lightly staining zone.

MIP. The medial intraparietal area (MIP) is located dorsal and anterior to area PO in the medial bank of the intraparietal sulcus. It is characterized by a thin, dense inner band of Baillarger, well separated from the white matter. This band appears along the middle third of the medial bank and extends from the posterior end of the sulcus to about the midpoint. MIP falls within the visual zone defined by Macko et al. ('82) and Macko and Mishkin ('85) on the basis of 2-DG studies.

LIP/VIP. The lateral bank of the intraparietal sulcus is a myeloarchitectonically heterogeneous zone. It is not yet clear how the myelin divisions correspond to connectionally defined zones and we have not attempted to assign labeled cells to different areas. We have, however, distinguished between cells falling in the lightly myelinated, lateral portion of the lateral bank and those falling in the heavily myelinated portion. These divisions were first noted by Seltzer and Pandya ('80), using the Heidenhain technique, and were called POae and POai. These regions run the length of the sulcus on the lateral bank: POai is closer to the fundus while POae is nearer to the lateral lip of the sulcus.

Two similar divisions are visible in material stained by the Gallyas method. The first is a heavily myelinated region near the fundus, similar in staining density to area MT. This region contains a portion of the ventral intraparietal area (VIP), defined by Maunsell and Van Essen ('83) as the MT projection zone near the fundus of the sulcus. This MT projection zone consists of both a densely myelinated portion on the lateral bank of the sulcus and an adjacent, lightly myelinated portion in the fundus (see Ungerleider and Desimone, '86b: Fig. 4). The second myeloarchitectonically distinct region is lateral to the heavily myelinated portion of VIP on the lateral bank of the intraparietal sulcus. This region is lightly myelinated and extends from the lateral border of VIP to the lip of the sulcus. It corresponds, in part, to the lateral intraparietal area (LIP), described by Andersen et al. ('85) as the zone in the lateral bank of intraparietal sulcus which projects to frontal cortex.

There remains considerable ambiquity concerning the borders of LIP. In particular, LIP contains both a lightly myelinated zone and a heavily myelinated zone (Andersen, personal communication). The heavily myelinated zone appears to overlap that in VIP. Since each of these areas has

been defined on connectional rather than on cyto- or myeloarchitectonic grounds, a dual-injection experiment would be required to determine whether these areas are entirely distinct. For present purposes, we have not attempted to distinguish between them and have assigned all labeled cells in the heavily myelinated portion of the lateral bank (shown by the dotted line in the flattened maps) to a conjoint area LIP/VIP.

Retinotopic location of labeled cells

To determine the visuotopic organization of each projection we relied on published and unpublished data from studies of the retinotopic organization of V2 (Gattass et al., '81), MT (Gattass and Gross, '81), and V3 and V4 (Gattass et al., '88) carried out in this laboratory. In these studies, a series of 20–40 electrode penetrations was made in each hemisphere in a grid pattern with a spacing of 1–2 mm. On each penetration, receptive fields were determined for multiunit recordings separated by at least 500 μm. Each electrode penetration was reconstructed on drawings of cresyl-stained sections and the receptive field progression for each section was plotted (see, for example, Fig. 8 and 9 in Gattass et al., '81). Where two comparable sections from different hemispheres were available, there was good agreement in the receptive field locations recorded at equivalent positions. Maps of the visuotopic organization of prestriate areas V2, V3, and V4, and MT were constructed from these series of sections.

In the present study, we used the complete series of available sections to estimate the retinotopic position of labeling in V1, V2, V3, V4, and MT. For each patch of label we determined the receptive field locations of cells at corresponding sites in the best-matching section from the above series. We then plotted the estimated receptive field position of each patch of label on hemispheric maps, as shown in Figure 4. We emphasize that these are only approximations since there may be considerable variation in topography from case to case.

Physiological identification and retinotopic mapping of PO

We recorded in area PO in each animal to establish the location of the upper and lower visual field representations in that animal. Area PO was identified both by the size of the receptive fields and by the degree of responsivity to visual stimulation. Dorsal to area PO, cells were visual but were very difficult to drive and receptive fields were larger than those in PO. This dorsal zone was previously included in area PO (Gattass et al., '85) because it is visually responsive. A reexamination of the data from the cases in which PO was mapped (Covey et al., '82) indicates that cells in this dorsal zone gave consistently weaker visual responses and that the transition point corresponds to the dorsal myelin border of PO as shown in Figure 2. The present results further indicate that this dorsal zone has a set of connections different from that found for area PO (see below).

Ventral to area PO, in area V2, cells gave much crisper responses to visual stimuli and receptive fields were an order of magnitude smaller than in PO. The location of the upper and lower visual field representations in area PO was in accord with previous mapping studies of the area (Covey et al., '82).

Examples of receptive field location progressions in two penetrations through area PO are illustrated in Figure 3. Figure 3A shows an electrode penetration close to the midline in which we recorded from area PO on the medial surface of the hemisphere. As the electrode traversed the upper field representation of PO, large peripheral receptive fields near the horizontal meridian (field #1) gave way to relatively more central, but still large, fields closer to the superior vertical meridian (field #3). Figure 3B shows a more lateral pass through the lower visual field representation. Here, the electrode passed down the posterolateral wall of the precuneate gyrus through a visual zone dorsal to area PO, crossed the white matter, and then entered PO near its lateral border, encountering cells with receptive fields near the lower vertical meridian (fields 1–4). The electrode then passed out of the cortex, crossed the floor of the parieto-occipital sulcus, and reentered cortex in area V2 (fields 5 and 6). On entering V2, the receptive field position moved suddenly away from the vertical meridian, receptive field size decreased markedly, and responses became much brisker.

Injection sites

In cases 1 and 2, we placed separate deposits of distinguishable tracers at sites representing the upper (1-U, 2-U) and lower (1-L, 2-L) contralateral visual field quadrants. In case 1, the "upper" field injection included the horizontal meridian and part of the lower field periphery. In case 3, we injected a single tracer into a lower visual field site (3-L) in PO. The second injection in this case was placed immediately dorsal to PO, as judged from myelin-stained sections. This deposit, unlike the others, produced substantial labeling of cells in the cingulate sulcus and on the crown of prelunate gyrus and did not yield labeled cells in V1. Results obtained from this injection will not be considered here.

All five injections were centered near layer IV and were restricted to area PO, as determined by recording and myeloarchitecture. For four of the injections in this series, the extent of the receptive fields of cells recorded near the injection site is shown in column 1 of Figure 4. The fifth injection (1-U) was more anterior than any of the recording sites in this case. On the basis of previous mapping experiments in PO (Covey et al., '82) and our own recordings in other brains, we estimate that this injection was centered in a portion of PO representing the upper visual field.

RESULTS

Overview of connections and topography

Retrogradely labeled neurons from each tracer deposit were found in 12 cortical areas. Labeling was strong in area V2 and in the lateral bank and fundus of the intraparietal sulcus (LIP/VIP). Moderate retrograde labeling was consistently present in V1, in area MT, and in two distinct regions within the intraparietal sulcus, termed here the medial intraparietal area (MIP) and the posterior intraparietal area (PIP). Sparse to moderate labeling was observed in areas V3d/v, V3A, V4T, MST, and PP.

Several additional areas contained labeled neurons after some but not all injections. These included a medial division of parietal cortex, termed here the medial dorsal parietal area (MDP), area V4, the frontal eye fields, and the dorsal prelunate area (DPL).

In V1 and V2, for which the retinotopic organization has been described in detail, there was good correspondence between the retinotopic location of the injection sites as determined by recording and the retinotopic locus of neu-

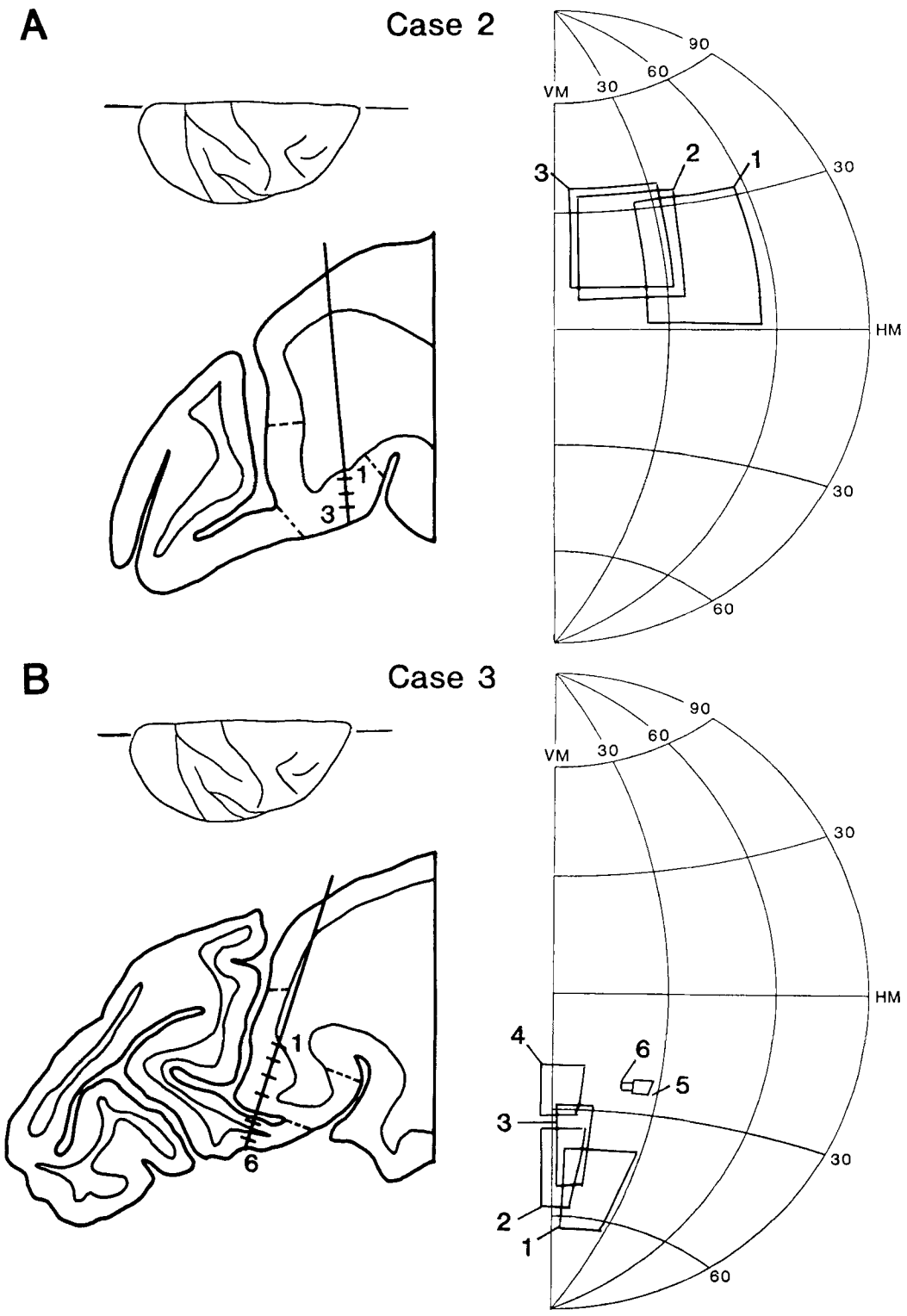

Fig. 3. A: Reconstruction of an electrode penetration through the medial portion of area PO in case 2. The level of the parasagittal section is indicated on the small dorsal view of the brain. The receptive field positions of cells or cell clusters encountered in area PO are indicated on the hemisphere map at right. The borders of area PO, as determined by myeloarchitecture, are indicated by dashed lines. B: Electrode penetration through the lateral portion of area PO in case 3. Recording sites 1–4 are within area PO; sites 5 and 6 are in area V2.

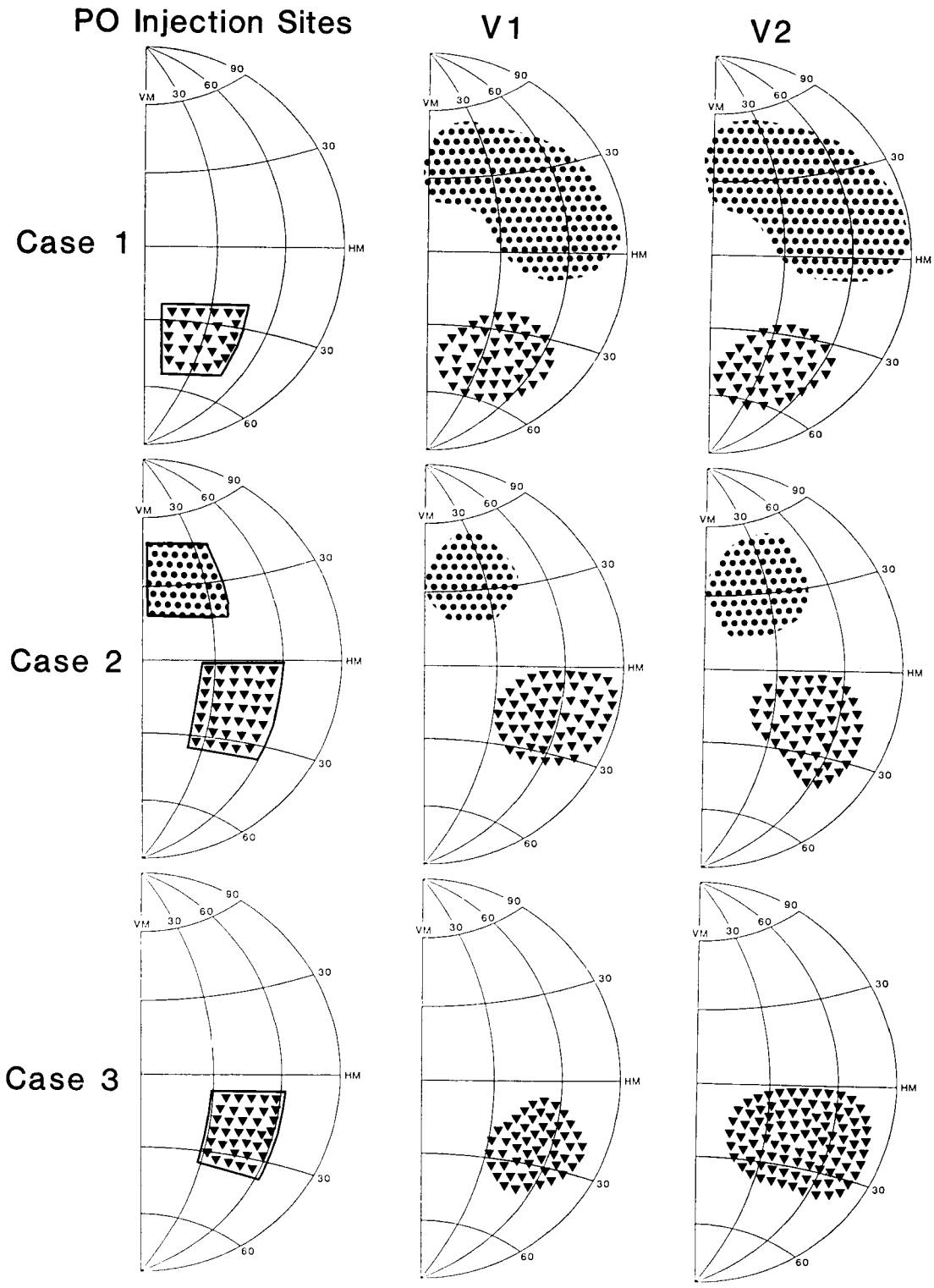

Fig. 4. Column 1: Receptive fields recorded at injection sites in area PO for cases 1, 2, and 3. The receptive field was not recorded at the upper field injection site in case 1. Columns 2 and 3: Extent of the visual field representation labeled in areas V1 and V2 after injections in area PO. In this and all subsequent figures, dots are used to indicate cells labeled from upper field injections while triangles indicate cells labeled from lower field injections.

rons labeled by retrograde transport. We conclude that projections from V1 and V2 to area PO are retinotopically organized. In V3d, V3v, V3A, V4, and MT, labeled neurons also occupied locations in retinotopic register with the injection sites, indicating that projections from these areas are also organized retinotopically. In higher-order areas, including LIP/VIP, MIP, PIP, MST, and MDP, neurons labeled with tracers deposited at separate sites in area PO were fully or partially segregated. We infer that some degree of retinotopic organization may be present in these latter

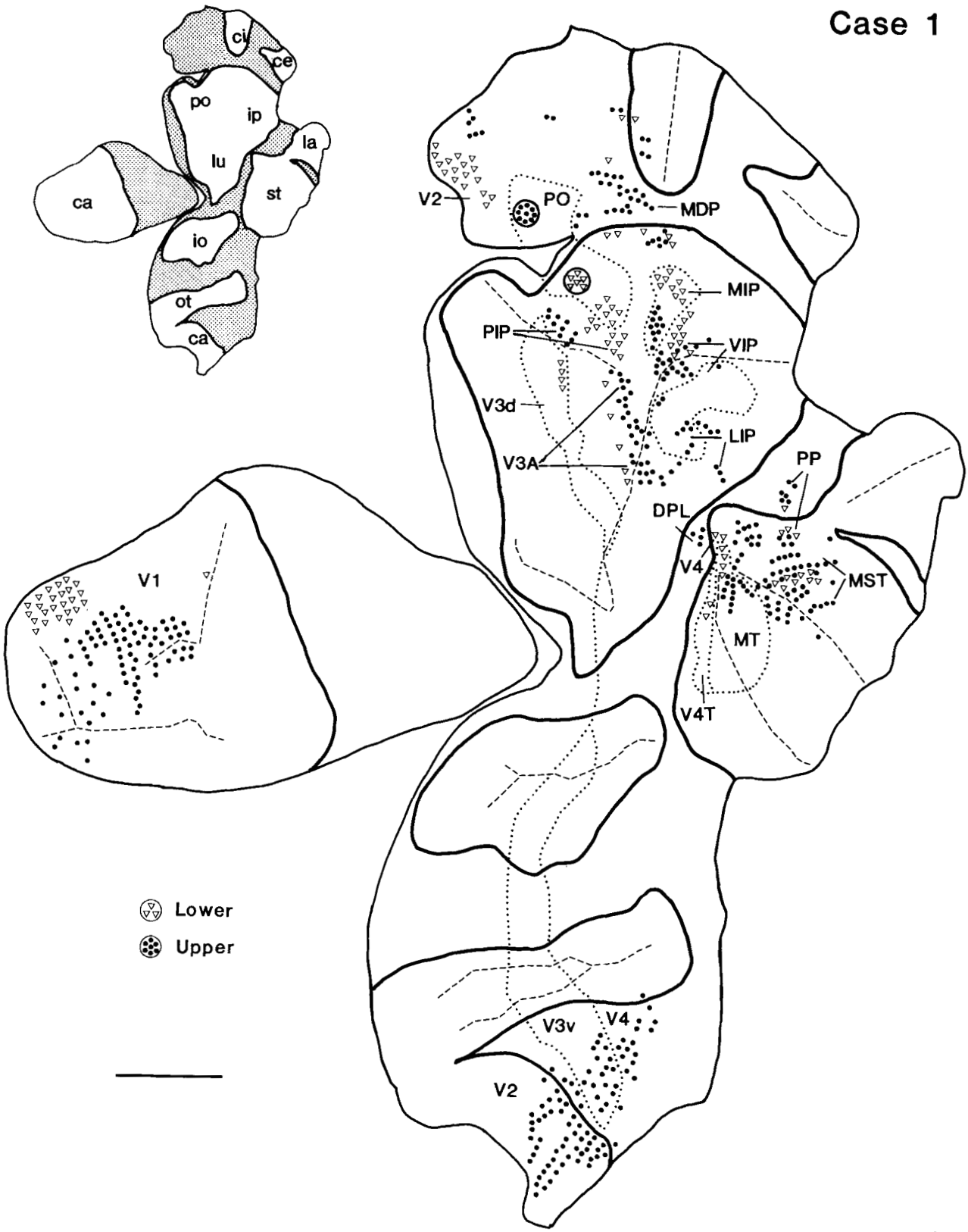

Fig. 5. Flattened map of posterior cortex in case 1. Inset shows gyral cortex as shaded; clear zones represent cortex within sulci. To permit flattening, a cut was placed between area V1 and the remainder of posterior cortex. The main figure shows the distribution of labeled cells after upper field (dots) and lower field (triangles) injections in area PO. Symbol-filled rings in PO indicate location of injection sites in PO. Heavy lines indicate sulcal borders, dashed lines show fundi, and dotted lines indicate borders discernible in sections stained for myelin. Sulci are identified by lowercase letters: ca, calcarine; ci, cingulate; io, inferior occipital; ip, intraparietal; la, lateral; lu, lunate; ot, occipitotemporal; po, parieto-occipital; st, superior temporal. Labeled areas are indicated by upper case letters: V1; V2; V3d; V3v; V3A; V4; V4T; MT; MST; LIP, lateral intraparietal area; MDP, medial dorsal parietal area; MIP; medial intraparietal area; PIP, posterior intraparietal area; VIP, ventral intraparietal area. Scale bar = 10 mm.

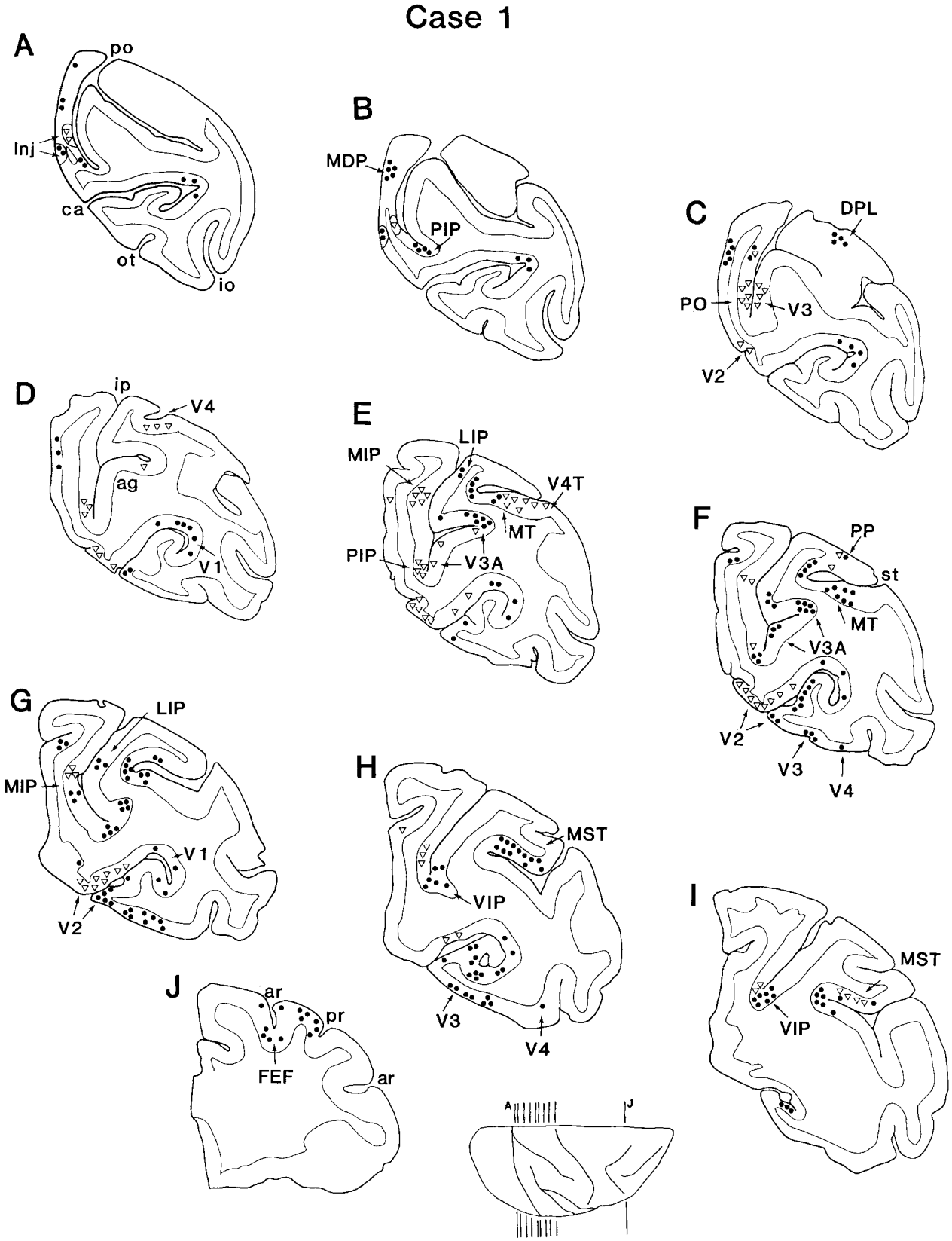

Fig. 6. Coronal section showing the distribution of labeled cells in cortex in Case 1. Injection sites (Inj) are shown in sections A (the most posterior section) and B. Dots indicate cells labeled from the lower field injection, triangles indicate neurons labeled from the lower field injection. FEF, frontal eye fields; ag, annectent gyrus; ar, arcuate sulcus; pr, principal sulcus; other abbreviations as in Figure 5. Section levels are indicated on the small dorsal view of the brain.

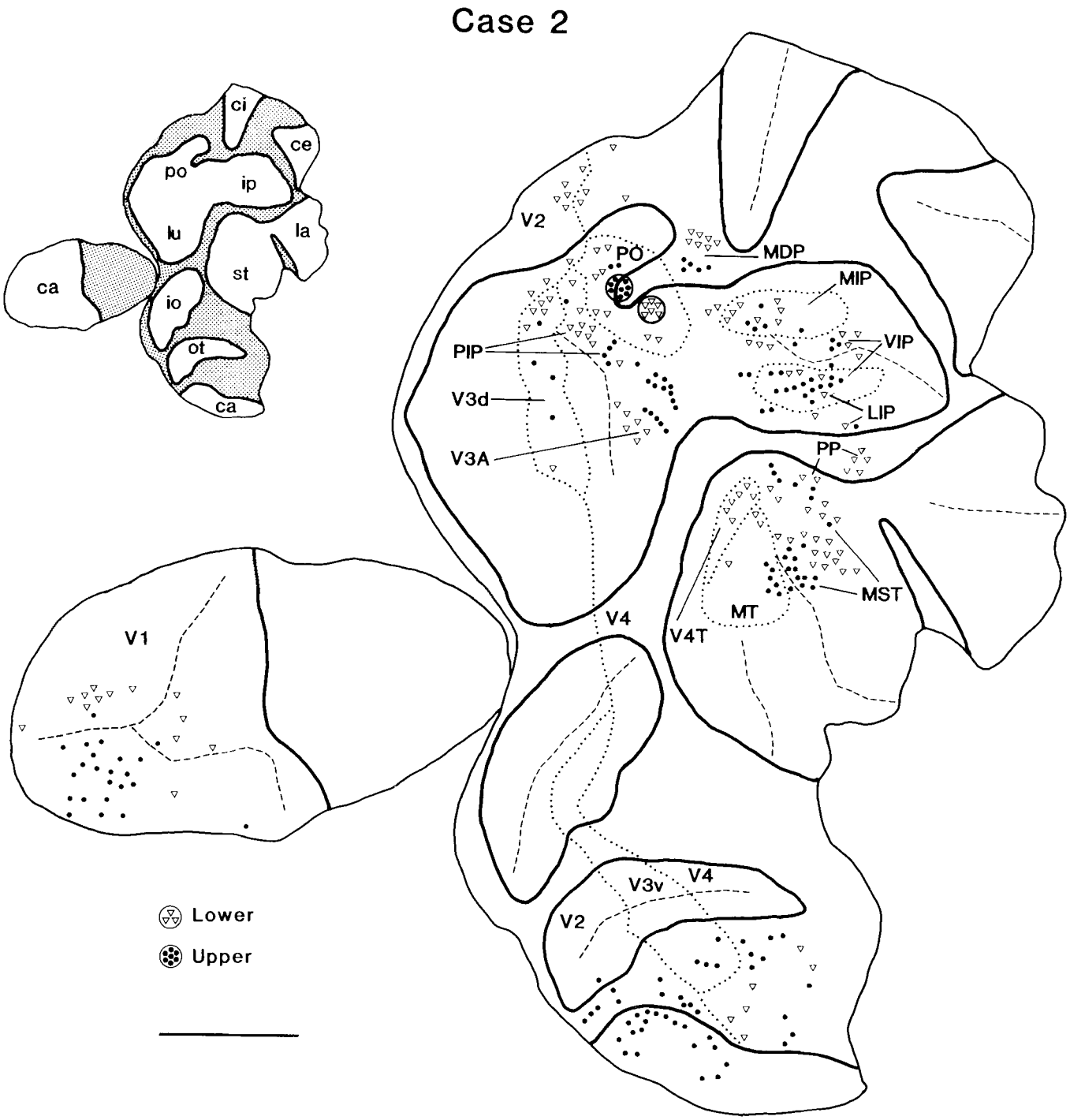

Fig. 7. Flattened map of posterior cortex in Case 2. Conventions as in Figure 5.

areas, though they probably do not contain orderly retinotopic maps consistent from case to case.

The results for each case are displayed both on flattened maps of posterior cortex (Figs. 5, 7, 9) and on drawings of individual sections (Figs. 6, 8, 10).

Connections of area PO

Area V1. After all five PO injections, moderate labeling was seen in V1. Within V1, label was confined to the calcarine sulcus and usually to the more anterior portion of the sulcus, containing the representation of the most peripheral part of the visual field (Daniel and Whitteridge, '61). Injections into the upper field representation in PO labeled cells primarily in the ventral bank and fundus of the calcarine sulcus while injections into the lower field representation produced labeling of neurons in the dorsal bank (Figs. 6G, 8H, 10F).

In each case there was good agreement between the location of receptive fields recorded near the PO injection site and the part of the retinal map in V1 that was found to

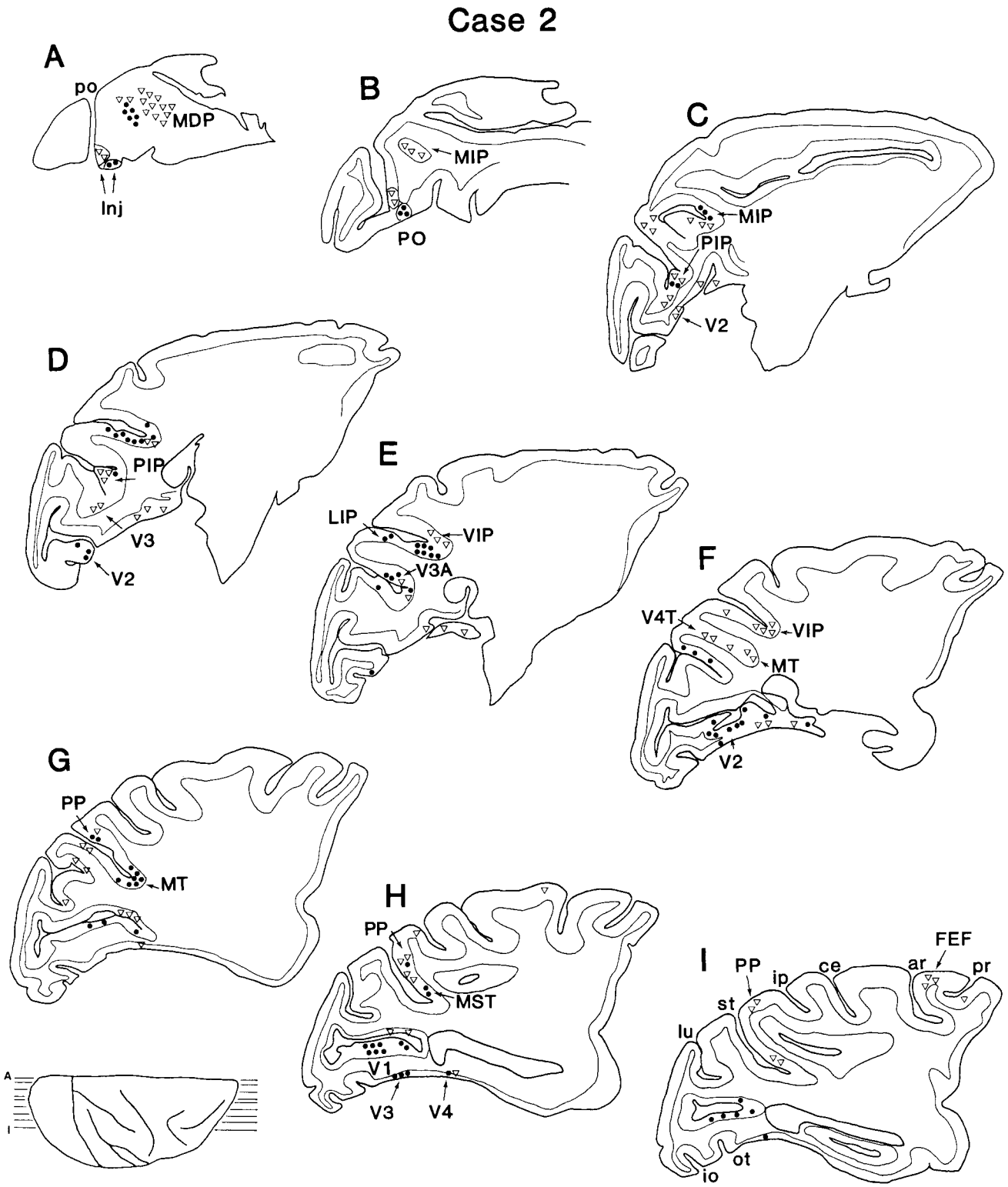

Fig. 8. Parasagittal sections showing the location of labeled cell bodies in cortex in case 2. Injection sites are shown in sections A (the most medial section) and B. Section levels are indicated on the small dorsal view of the brain.

contain labeled cells, as shown in Figure 4. The extent of the labeled region in V1 was similar to that of the multiunit receptive field recorded near the injection site.

Area V2. The heaviest cortical labeling from each PO injection was seen in area V2. Labeled neurons were identified as being in V2 on the basis of myeloarchitecture and proximity to the V1/V2 border.

Labeled cells were concentrated in the medial portions of V2, where the peripheral visual field is represented (Gattass et al., '81). The upper field injections labeled cells in

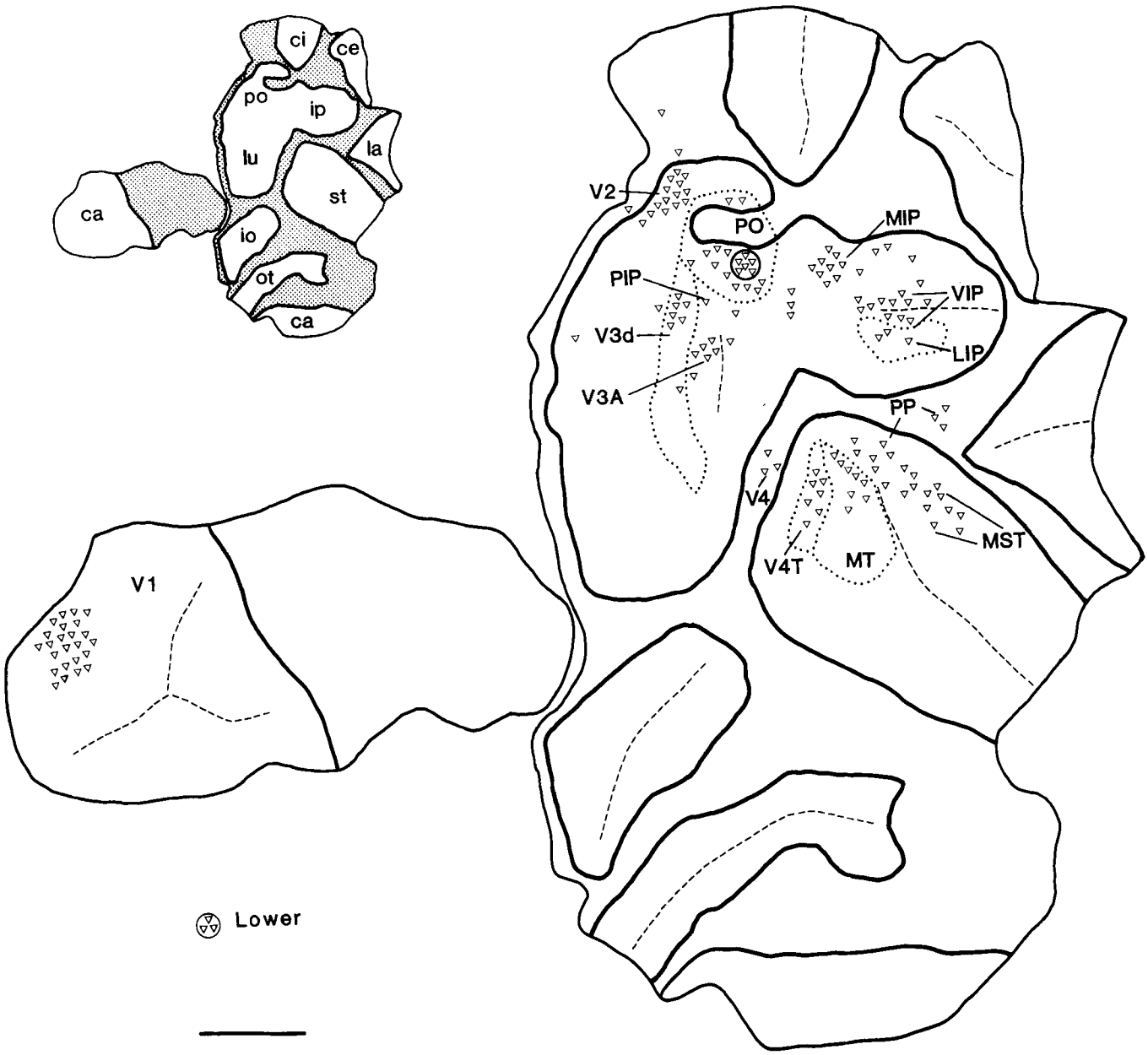

Fig. 9. Flattened map of posterior cortex in case 3. A single lower field injection was made in area PO. Conventions as in Figure 5.

the lower bank of the calcarine sulcus and on the adjacent ventromedial surface of the hemisphere (Figs. 6F, 8F). The lower field injections produced neuronal labeling on the medial surface of the hemisphere just dorsal to the calcarine sulcus (Figs. 6F, 8C, 10B) and on the posterior bank of the lunate sulcus (Fig. 10A). The peripheral location of the labeled cells in V2 is best appreciated on the flattened maps. These show that labeled cells were found at the extreme ends of V2, on the dorsomedial and ventromedial surface of the hemisphere, avoiding the lateral portions of V2 entirely (Figs. 5, 7, 9).

The retinotopic location of the labeled cells was estimated from the electrophysiologically derived maps of Gattass et al. ('81). Virtually no cells were labeled within the representation of the central 15°. As shown in Figure 4, there was good correspondence between the retinotopic location of each injection site in PO and the retinotopic location in V2 of neurons labeled retrogradely from that site.

The projection from V2 to area PO has also been demonstrated by anterograde tracing techniques (Ungerleider et al., '83). As in the present study, the projection was found to be retinotopically organized such that cells in the lower

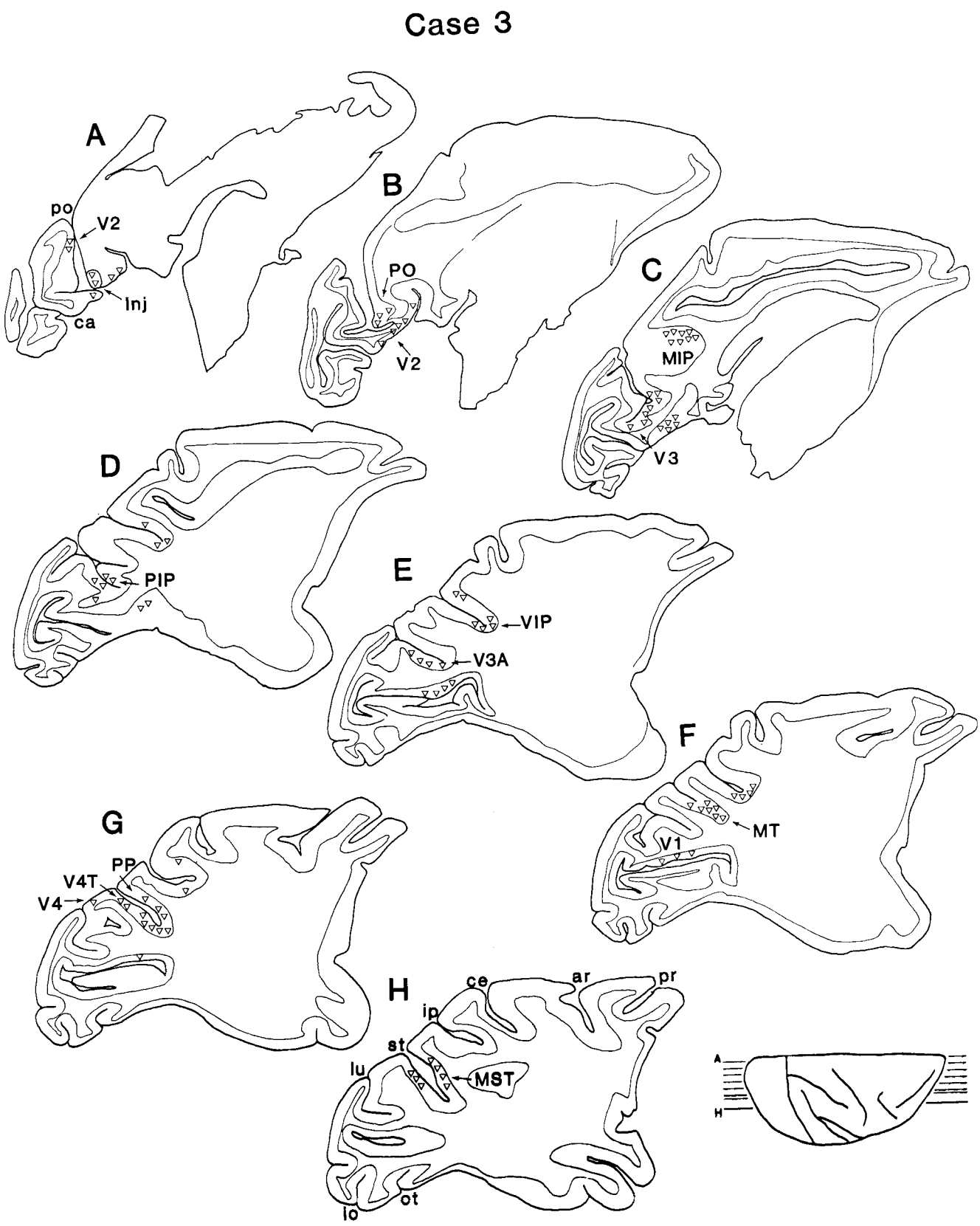

Fig. 10. Parasagittal sections showing the location of labeled cells in case 3. Injection site is shown in section A, the most medial section. Section levels are indicated on the small dorsal view of the brain.

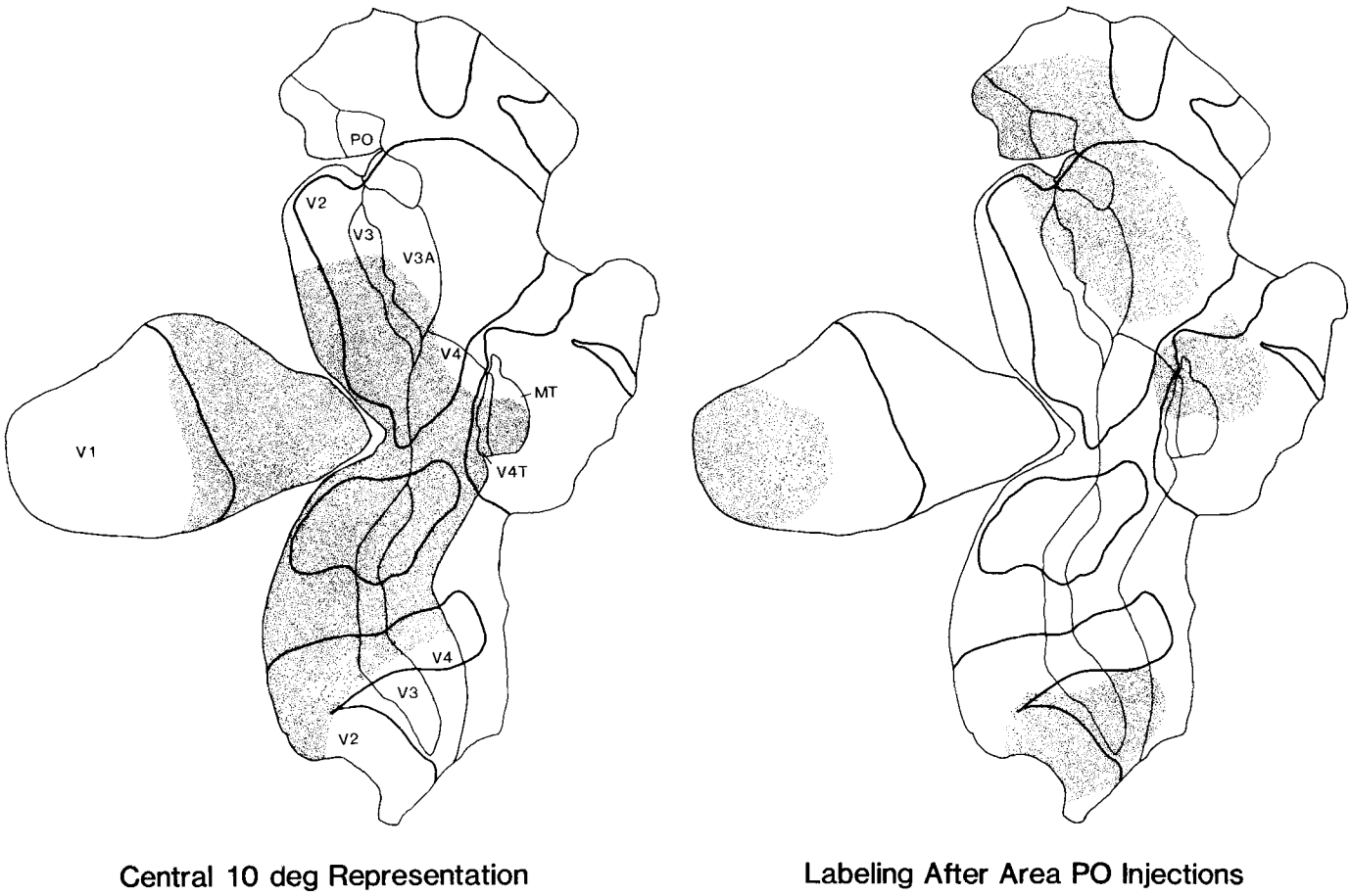

Fig. 11. Cortical regions labeled by tracers deposited in the peripheral field representation in area PO (right) lie outside the zone of striate and prestriate cortex representing the central 10° (left).

peripheral field representation of V2 project to lateral portions of area PO, while cells in the upper peripheral field representation project to area PO on the medial surface of the hemisphere.

Area V3. Sparse to moderate labeling was observed in area V3 after all five injections. Area V3 is a narrow strip of cortex adjacent to V2. The dorsal portion, V3d, represents the lower visual field (Gattass et al., '85, '88). The ventral portion, V3v, represents the upper visual field and is referred to as area VP by Van Essen and colleagues (Burkhalter et al., '86; Newsome et al., '86). Labeled cells were assigned to V3 on the basis of myeloarchitecture and proximity to V2.

In each case, labeled neurons in V3 were concentrated medially, where the peripheral portion of the visual field is represented (Newsome et al., '80, '86; Gattass et al., '85, '88). The distribution of labeled neurons within V3 varied with the location of the tracer deposits in area PO. Injections into the upper visual field representation yielded sparse label on the ventral surface, anterior to and separate from the corresponding patches of label in V2 (Figs. 6F–H, Fig. 8H). Lower field injections gave rise to labeling near the fundus of the lunate sulcus (Figs. 6C, 8D, 10C).

The retinotopy we have observed in the projections from V3 to area PO is in accord with mapping studies which indicate that V3 forms a partial belt around V2 and that the visual field representation in V3 is roughly congruent with that in V2 (Gattass et al., '85, '88; Newsome et al., '86). The visual field map in V3 is quite compressed compared to that in V2 and represents relatively less of the far periphery. The limited extent of the peripheral field representation in V3 may help to account for the fact that comparatively few cells were labeled.

Area V3A. After each PO injection, moderate labeling was observed in area V3A, which spans the annectent gyrus and the anterior bank of the lunate sulcus. Area V3A differs from areas V1, V2, and V3 in that it comprises a representation (or representations) of both the upper and lower visual fields within a single continuous zone on the dorsal surface (Van Essen and Zeki, '78; Gattass et al., '85). The presence of distinct but adjacent patches of label from upper and lower field injections supports the identification of this zone as area V3A.

In case 1, as shown on the flattened map, neurons labeled from the upper field injection formed a continuous band spanning the anterior aspect of the annectent gyrus and the anterior bank of the lunate sulcus; cells labeled from the lower field injection were fewer and were located more posteriorly on the anterior annectent gyrus (Figs. 5, 6E,F). In case 2, the labeled neuronal populations were confined to the anterior bank of lunate sulcus but their relative locations were the same (Figs. 7, 8E). The lower field deposit of case 3 gave rise to neuronal labeling on the anterior aspect of the annectent gyrus, in a position similar to that seen in case 1 (Figs. 9, 10E).

These results are consistent with previous mapping stud-

ies which show that V3A contains a lower field representation posteriorly, adjacent to V3, and an upper field representation anteriorly, adjacent to V4 (Van Essen and Zeki, '78). In both double-tracer cases, cells labeled from the lower field injection lay posterior to cells labeled from the upper field injection, although the location of the labeling in relation to gyral morphology was variable. The present results suggest that the projection from V3A to area PO is retinotopically ordered.

Area V4. Very few labeled cells were observed in area V4. Area V4 adjoins area V3v ventrally and areas V3d and V3A dorsally and was identified by myeloarchitecture and gyral morphology (Van Essen and Zeki, '78; Gattass et al., '85, '88). Sparse labeling occurred in V4 from all injections.

The location of the labeled cells varied systematically with the retinotopic locus of the tracer deposit site (Figs. 5, 7, 9). Tracers deposited at upper field sites were transported to neurons on the ventromedial surace of the hemisphere and in the medial bank of the occipital temporal sulcus (Figs. 6H, 8H). Tracers deposited at lower field sites were transported to the posterior tip of superior temporal sulcus (Fig. 6D) and the crown of prelunate gyrus (Fig. 10G).

The distribution of labeled cells following upper and lower field injections corresponds to the visual topography of V4 as described in mapping studies which show that upper fields are represented ventrally while lower fields are represented dorsally (Van Essen and Zeki, '78; Maguire and Baizer, '84; Gattass et al., '85, '88). Sparse labeling from the lower field injection was observed in ventral V4 in case 2 (Fig. 7). These findings are congruent with the observation that part of the lower field periphery is represented ventrally in V4 (Gattass et al., '88).

Dorsal prelunate area. After one of the two upper field injections (1-U) a small region on the dorsal prelunate gyrus contained labeled cells (Figs. 5, 6C). These may have been within the dorsal prelunate area (DPL), a small area representing the upper visual field exclusively (Van Essen, '85). The portion of area V4 adjacent to DPL represents only the lower visual field (Gattass et al., "85, '88), and in this case, the adjacent cortex (Fig. 6D) contains a small patch of label from the lower field injection. The relation between the two patches is indicated more clearly on the flattened map of this case (Fig. 5). The identification of this small zone as DPL remains tentative because the "upper" field injection site in this case included the horizontal meridian. Thus, the prelunate label here could be part of V4.

Area V4T. In area V4T, sparse to moderate neuronal labeling occurred after all three lower field injections (Figs. 6E, 8F, 10G). Labeled neurons were located medially and posteriorly in V4T, adjacent to the portion of MT in which the visual field periphery is represented.

Although no previous studies have focused specifically on the connections of V4T, Ungerleider and Desimone ('86b) have demonstrated a projection to the lower field representation of PO following an anterograde injection that included both V4T and MT. In the present study, labeled cells were found in V4T only after injections into the lower field representation of PO in accord with mapping studies which indicate that V4T contains a representation of only the lower visual field (Desimone and Ungerleider, '86; Gattass et al., '88).

Area MT. In area MT, neuronal labeling occurred after all tracer deposits and cells labeled from the upper and lower field injections were completely segregated. The pattern of labeling in superior temporal sulcus is best appreciated by examining the flattened maps of cortex (Figs. 5, 7, 9). Tracers deposited at cortical sites representing the upper visual field were transported to neurons in a relatively anterior part of MT (Figs. 6E, 8F) while lower field deposits gave rise to more posterior labeling (Figs. 6F, 8G, 10F).

The topographic pattern observed in these cases corresponds to published maps of MT which show that lower fields are represented dorsally and posteriorly while upper fields are represented ventrally and anteriorly (Ungerleider and Mishkin, '79; Gattass and Gross, '81; Maunsell and Van Essen, '83). There were virtually no labeled cells in the lateral portion of area MT which represents the center of gaze.

Our observation of a retinotopically organized projection from MT to area PO is in accord with results obtained by Ungerleider and Desimone ('86b) following anterograde tracer deposits in MT. Injections into the peripheral lower field representation of MT (their case 6) labeled the lateral portion of area PO on the anterior bank of the parieto-occipital sulcus while injections into the peripheral upper field representation of MT (their case 4) labeled area PO on the medial surface of the hemisphere. These projections were not observed in an earlier study of connections of the central field representation in MT (Maunsell and Van Essen, '83).

Area MST. Area MST, is the dorsal bank of the superior temporal sulcus, contained a moderate number of labeled neurons in each case. Cells labeled from upper and lower field deposits were partially segregated. In case 1, label in MST was predominantly from the upper field injection (Figs. 5, 6G,H) though there was a separate patch of lower field label (Fig. 6I). In case 2, there was relatively more label from the lower field injection (Figs. 7, 8H). In case 3, there were relatively few labeled neurons within MST (Figs. 9, 10H). In each double label case there was evidence for some degree of local visuotopic organization but not for any overall retinotopy. The lack of global visual topography is consistent with recent mapping studies which show that MST contains a mosaic-type representation of the visual field (Desimone and Ungerleider, '86).

Area PP. In posterior parietal cortex (PP), both within the superior temporal sulcus and on the convexity of the inferior parietal lobule, there was sparse labeling after all five injections. In the double tracer cases there was incomplete segregation of the two tracers and no indication of global visuotopic organization (Figs. 6F, 8G). The lack of topographic ordering presumably reflects the absence of retinotopy in the inferior parietal cortex (Petersen et al., '82).

Intraparietal sulcus. Substantial labeling was seen in the intraparietal sulcus in each case. Labeled neurons were not distributed uniformly but appeared within specific zones. We have used myelin and anatomical landmarks to define separate labeled regions within the intraparietal sulcus. The status of these zones as distinct visual areas must remain uncertain until they can be defined physiologically.

PIP. The first of these zones is adjacent to area PO, near the point of confluence between the intraparietal and parieto-occipital sulci. We refer to this zone as the posterior intraparietal area (PIP). Area PIP is located between areas PO and V3d but is distinct from each in sections stained for myelin. Laterally, PIP borders on area V3A, though this border cannot be clearly demarcated in myelin-stained sections. PIP contained sparse to moderate numbers of labeled

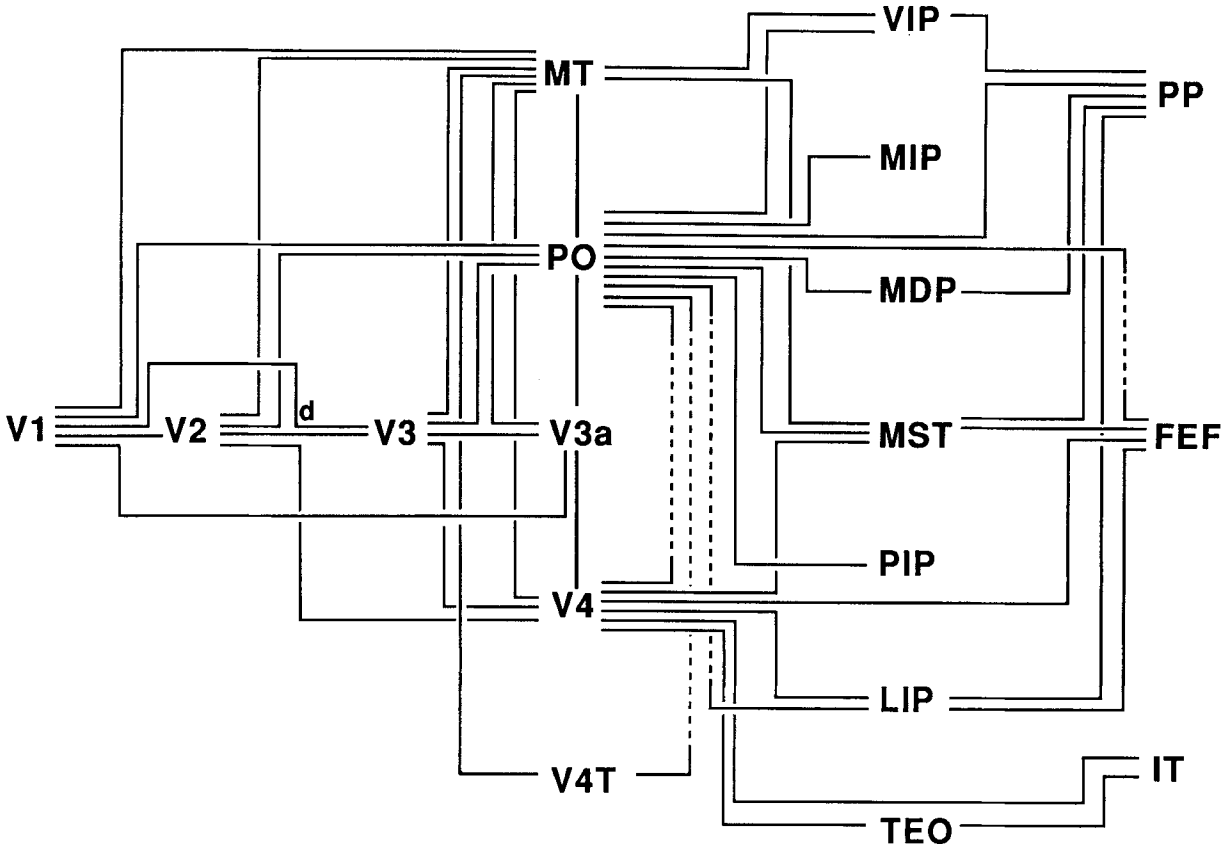

Fig. 12. Area PO and visual areas to which it is connected. In order to highlight the connections of area PO not all known visual cortical pathways are shown. Areas are arranged in left-to-right order by hierarchical level, determined on the basis of laminar patterns of interconnecting pathways as characterized in this and previous studies (see text). Solid lines indicate consistent projections; dashed lines indicate weak or inconsistent projections. Area PO is connected to several dorsal stream areas (MT, MST, VIP, PP) but has weak or no connections with ventral stream areas (V4, TEO, IT).

neurons after all five injections (Figs. 6B–E, 8C, 10D). Neurons labeled from the upper and lower field injections were segregated, as shown in the flattened maps (Figs. 5, 7). The variability in the arrangement of upper and lower field neuronal labeling may reflect variability in retinotopic organization (Van Essen and Zeki, '78).

MIP. We were surprised to observe a second zone of labeled cells located in the posterior portion of the medial bank of the intraparietal sulcus, a region generally regarded as somatosensory in function. We refer to this zone as the medial intraparietal area (MIP). Neurons in MIP were labeled after all five injections (Figs. 6E–G, 8B, 10C). Separate tracer deposits labeled populations of cells that were segregated in case 1 but intermingled in case 2 (Figs. 5, 7).

LIP/VIP. In each case, substantial labeling occurred in a third zone composing the lateral bank and fundus of the intraparietal sulcus. This zone is partially coextensive with two previously defined areas, VIP and LIP. Within LIP/VIP neurons labeled from upper and lower field deposits were partially segregated, though there was no consistent pattern across cases (Figs. 5, 7).

MDP. In four of the five cases, sparse to moderate labeling occurred on the medial surface of the hemisphere, in a region dorsal and partly anterior to area PO which we call the medial dorsal parietal area (MDP) (Figs. 6A–E, 8A). In the case with moderate labeling from both tracer injections, cells labeled from separate deposits were segregated (Fig. 7).

Frontal cortex. Two of the five injections (1-U and 2-L) produced sparse neuronal labeling in the frontal eye fields and adjacent cortex. In each case the zone of labeled neurons extended from the posterior bank of the superior limb of the arcuate sulcus to the principal sulcus (Figs. 6J, 8I).

Emphasis on peripheral visual field

Area PO is unique among the currently known visual areas in macaque in its emphasis on the visual field periphery. This unusual retinotopy is reflected in its connections. All of our injections were made at locations representing the visual field periphery, and only peripheral field regions were labeled. The exclusion of labeled cells from zones representing the central visual field is best appreciated on a flattened map (Fig. 11). There is no overlap between the extensive zone containing the central 10° representation in each visual area and the zone containing labeled cells. While we assume that cells in the central field representation in area PO must receive input from central representations in other areas, these results suggest that area PO is specialized for processing peripheral visual field information.

Laminar pattern of connections

In V1, cells projecting to PO were found both in layer IVB

and in the supragranular layers. In V2, V3d, and V3v, cells projecting to PO were concentrated in the supragranular layers. In contrast, labeled cells in the intraparietal sulcus, the superior temporal sulcus, and frontal cortex occupied the supra- and infragranular layers in roughly equal numbers. These results suggest that area PO receives an ascending input from V1, V2, and V3 and should be placed above them in the hierarchy of visual areas (Maunsell and Van Essen, '83). Area PO occupies an intermediate position in the hierarchy and is most strongly connected to dorsal stream areas (Fig. 12).

DISCUSSION

Area PO is a newly recognized and relatively inaccessible visual area. No previous studies have focused specifically on its connections. Further, most of area PO represents the peripheral visual field and relatively few connectional studies have been concerned with the parts of prestriate areas representing the peripheral visual field.

We have identified sources of cortical input to area PO and have analyzed the visual topography of these pathways by injecting distinguishable retrograde tracers at specific retinotopic loci under physiological guidance. We have found that area PO receives retinotopically organized projections from several areas known to contain maps of the visual field, including V1, V2, V3, V4, and MT. Area PO also receives projections from higher-order visual areas which do not appear to be retinotopically organized. Area PO is suited by its connections to serve as a link between low-order visual areas and high-order association areas, expecially those of the parietal lobe.

Area PO receives a direct projection from striate cortex

There is a direct and moderately strong projection from striate cortex to area PO. This pathway arises primarily from the peripheral field representation in striate cortex, in keeping with the emphasis on the periphery in area PO. This restriction may serve to explain why this projection has not been noted in most previous studies of the efferent connections of V1 in macaque. A recent study, in which the connections of peripheral V1 were carefully examined, does show evidence for a projection to area PO (Van Essen et al., '86).

Prestriate cortex projections to area PO

We have confirmed previous reports that area PO receives retinotopically organized input from areas V2 (Ungerleider et al., '83) and MT (Ungerleider and Desimone, '86b) and we have demonstrated previously unreported projections from areas V3d, V3v, V3A, V4, V4T, MST, and MDP. Of these areas, V2 is the strongest source of input to area PO. This finding strengthens the interpretation, based on the existence of direct input from V1, that PO has significant access to visual information in early stages of transcortical processing.

Visual areas of the intraparietal sulcus

There are substantial projections to area PO from the intraparietal sulcus. Little is known concerning the organization of visual areas in intraparietal sulcus: neither the number of distinct areas nor their topographic organization has been established physiologically. On the basis of the present results and those of others, we suggest that there are four visual areas within the intraparietal sulcus. Two of these areas, VIP and LIP, have been defined previously on connectional grounds (Maunsell and Van Essen, '83; Andersen et al., '85) and may overlap to a considerable degree. Two additional areas, termed here MIP and PIP, are also connected to PO.

PIP. PIP is located in the posterior fundus of the intraparietal sulcus where it joins the parieto-occipital sulcus. It is adjacent to areas PO and V3d and can be distinguished from them on the basis of myeloarchitecture. Laterally, PIP extends to the annectent gyrus where it borders on area V3A. In the literature on connections of the intraparietal sulcus, this area has not been given explicit consideration though a projection from V3 to PIP has been observed (Felleman et al., '87). Electrophysiological mapping studies in this region reveal an area of relatively small receptive fields, comparable in size to those in V3A (Gattass and Covey, unpublished results). Also, Van Essen and Zeki ('78) reported an anomalous "second" central field representation at the medial edge of V3A which may be coextensive with PIP. This representation included receptive fields out to 20° eccentricity and was distinct from the central field representation in V3A proper.

MIP. MIP is defined here as the posterior portion of the medial bank of the intraparietal sulcus. This region has classically been considered part of area 5 (Brodmann, '05). The major connections ascribed to the medial bank of intraparietal sulcus include inputs from primary somatosensory cortex, from somatosensory association cortex (gyral area 5), and from premotor cortex (Jones and Powell, '70; Jones et al., '78). Inputs have also been described from parietal cortex on the medial surface of the hemisphere (Pandya and Seltzer, '82; Seltzer and Pandya, '86) and from the principal sulcus (Pandya et al., '71). While visual connections have not been reported previously for this area, there is physiological evidence for visual responsiveness in MIP. In 2-DG studies, Macko et al. ('82) and Macko and Mishkin ('85) have demonstrated that MIP is activated metabolically by visual stimuli. In a single-unit recording study, Covey and Gattass (unpublished observations) have noted the presence of visually responsive neurons with peripheral, vertically elongated receptive fields.

VIP. VIP was defined by Maunsell and Van Essen ('83) as the MT projection zone within the intraparietal sulcus. In addition to its distinctive myeloarchitecture (Ungerleider and Desimone, '86b) and input from MT, area VIP differs from other intraparietal area in that it receives an input from peripheral V2 (Ungerleider and Desimone, '86b). VIP is thought to have at least some degree of retinotopic organization in that projections from the central and peripheral parts of the retinal map in MT terminate in separate subdivisions of VIP, distinguished on the basis of myelination (Ungerleider and Desimone, '86b).

LIP. LIP was described by Andersen et al. ('85) as that portion of the lateral bank of the intraparietal sulcus which projects to the frontal lobe. This zone may overlap in part with the MT-projection zone (VIP) described above. LIP has previously been shown to project to cortex in the vicinity of area PO (Pandya and Seltzer, '82, case 16). LIP receives substantial projections from other extrastriate visual areas including V3, V4, and TEO and from adjacent area 7 (Rockland and Pandya, '79; Seltzer and Pandya, '80, '86; Burkhalter and Van Essen, '83; Felleman and Van Essen, '83, '84; Fenstemaker et al., unpublished results) and projects to the fundus and lower bank of superior temporal sulcus (Seltzer and Pandya, '78, '84). The lateral bank of the intra-

parietal sulcus is also strongly linked by reciprocal pathways to dorsolateral prefrontal cortex (Pandya et al., '71; Jacobson and Trojanowski, '77; Goldman-Rakic and Schwartz, '82; Schwartz and Goldman-Rakic, '84) and the frontal eye fields (Barbas and Mesulam, '81; Andersen et al., '85). Subcortically, LIP projects strongly to the deep layers of the superior colliculus (Lobeck et al., '83; Lynch and Graybiel, '83; Lynch et al., '85) and to the pons (May and Andersen, '86). Physiological studies of LIP indicate that it contains cells with eye movement-related activity as well as active reach and hand-eye coordination cells (Mountcastle et al., '75) and that microstimulation in this region produces saccadic eye movements (Shibutani et al., '84).

Projections from medial and frontal cortex

We observed moderate labeling on the medial surface of parietal cortex in a zone dorsal and anterior to area PO, in a region we refer to as MDP. Cells in this region have large receptive fields and habituate quickly to visual stimulation (Covey, unpublished results). This region has received relatively little attention in previous studies of parietal connectivity. It has recently been shown, however, that area PO projects to MDP (Cavada and Goldman-Rakic, '86). Medial parietal cortex itself projects to the caudal portion of the inferior parietal lobule (Mesulam et al., '77). MDP may thus serve as one of the areas through which area PO relays visual information to inferior parietal cortex.

In frontal cortex we found a sparse projection to area PO. While this projection has not been described previously, the reciprocal projection from the region of area PO to frontal cortex has been noted (Jacobson and Trojanowski, '77; Barbas and Mesulam, '81, '85; Barbas, '85, '86). Within the frontal eye fields (FEF) it is specifically the rostral portion which receives input from PO (Barbas and Mesulam, '81, injection X). These findings are consistent with the present results in that area PO receives a sparse input from the FEF and that input arises from the rostral FEF. This rostral region receives a few other inputs from visual cortex, and stimulation at this site produces large saccadic eye movements (Robinson and Fuchs, '69). Barbas and Mesulam ('81) suggest that this rostral zone may be involved in orienting to peripheral visual stimuli. Assuming that there is a reciprocal projection from PO to FEF, area PO may be one of the areas which supplies information on peripheral visual stimuli to the rostral FEF.

Relationship of area PO to other visual areas

Reciprocity. In a recent review of extrastriate cortical connectivity, Van Essen ('85) concluded that there were no convincing counterexamples to the principle of reciprocal connectivity in cortex. We may expect that area PO will ultimately be shown to project to each of the areas from which it receives cortical input. While the efferent projections of area PO have not yet been directly investigated, several of the areas from which we have observed projections to PO have been reported to receive inputs from the medial surface of the hemisphere and anterior bank of the parieto-occipital sulcus, i.e., in the region of area PO. These include projections ot MT (Ungerleider and Desimone, '86b), VIP (Seltzer and Pandya, '80), LIP and PP (Seltzer and Pandya, '80; Hedreen and Yin, '81), MDP (Cavada and Goldman-Rakic, '86), and frontal cortex (Jacobson and Trojanowski, '77; Barbas and Mesulam, '81).

Hierarchical position of area PO. Studies of the laminar organization of transcortical pathways have revealed consistent patterns in visual cortical connectivity (Kuypers et al., '65; Tigges et al., '73, '74, '81; Rockland and Pandya, '79; Maunsell and Van Essen, '83; Van Essen and Maunsell, '83). Rostrally directed (or feed-forward) projections typically originate in the supragranular layers of a lower-order area and terminate in layer IV of a higher-order area. Caudally directed (or feedback) projections originate in both the supra- an infragranular layers of a higher-order area and terminate outside of layer IV in a lower-order area. On the basis of this principle, Maunsell and Van Essen ('83) have proposed that there is a hierarchy of visual areas in which each area is placed one level above the "highest" area from which it receives a forward-going projection.

Area PO receives projections from the supragranular layers of areas V1, V2, and V3. From all other areas, it receives projections from both supra- and infragranular layers. Although information on the layers of termination for PO projections would be necessary to establish the hierarchical position of area PO with certainty, the present results suggest that area PO should be placed above the level of V3 and below that of MST, VIP, and LIP, i.e., at a level comparable to that of MT and V4 (Fig. 12). This placement agrees with that suggested by the pattern of laminar origin in the projection from area PO to frontal cortex (Barbas, '86).

Functional streams. Ungerleider and Mishkin ('82) have distinguished two functional "streams" originating in striate cortex. The dorsal stream, leading to parietal cortex, is primarily concerned with spatial vision and visuomotor functions whereas the ventral stream, leading to inferior temporal cortex, is primarily concerned with pattern recognition. Anatomically, the pathways leading to parietal and inferior temporal cortex are at least partially distinct, and analysis of connections allows many visual areas to be assigned to either the dorsal stream or the ventral stream (Mishkin et al., '83; Ungerleider, '85). Physiologically, the two streams appear to receive distinct inputs. The magnocellular and parvocellular divisions of the lateral geniculate nucleus contribute differentially to striate cells visual responses (Malpeli et al., '81), and these channels remain segregated through several levels of processing in extrastriate cortex (Maunsell and Schiller, '84; Maunsell, '87). Cells in dorsal stream areas which receive magnocellular input are particularly suited to the analysis of visual motion (Van Essen and Maunsell, '83).

Area PO is clearly related connectionally to the dorsal stream, which includes areas MT, MST, and VIP. It appears to provide visual areas in the intraparietal sulcus with relatively direct access to peripheral visual field information from areas V1 and V2. The emphasis on the periphery in area PO fits well with the observation that ventral stream areas heavily represent the central visual field while dorsal stream areas are relatively more concerned with the peripheral visual field (Ungerleider and Desimone, '86b).

Visual areas emphasizing the periphery

Previous reports have described visual areas which emphasize the peripheral visual field in a number of species. In carnivores, such an area has been found in the splenial sulcus of both cat (Kalia and Whitteridge, '73) and mink (McConnell and LeVay, '86). In both species this area borders on striate cortex, adjacent to the representation of the far periphery in area 17, and contains primarily cells with receptive fields in the periphery. In the mink, this area receives projections from areas 17 and 18.

Among primates, there is evidence for a peripheral visual area in *Galago*, squirrel monkey, and owl monkey (see below). In *Galago*, the dorsal area adjoins V2 along the horizontal meridian representation and has an expanded representation of the peripheral visual field as compared to other extrastriate areas (Allman et al., '79). In the squirrel monkey, there is a projection from V1 to the medial surface of the hemisphere at the parieto-occipital sulcus, in a location similar to that of area PO (Martinez-Millan and Hollander, '75). This projection is seen only after injections into the peripheral field representation of striate cortex. These results, and those described below for the owl monkey, suggest that an extrastriate area emphasizing the visual periphery may be a consistent feature across several species.

Homology with owl monkey area M?

Allman and Kaas ('76) have described in the owl monkey a visual area ("M") on the medial surface of the hemisphere with an unusual visual topography: 96% of the cortex in area M represents portions of the visual field more than 10° away from the fovea. Thus, as compared to other visual areas, there is an over-representation of the visual periphery in area M. In the macaque, area PO appears to be equally dominated by the peripheral field representation (Covey et al., '82; Gattass et al., '85). Moreover, in both M and PO, receptive fields are large compared to those in other prestriate areas (Baker et al., '81; Covey et al., '82).

The location, borders, and overall topography of areas M and PO are similar. Area M, like PO, is located just anterior to V2 and adjoins V2 along a split representation of the horizontal meridian. In area M, as in PO, there is a discontinuity across this border with V2 such that the upper field representation in M or PO abuts the lower field representation in V2. In both M and PO, the representation of the lower vertical meridian forms another border—that with DM in the owl monkey and with V3A in the macaque.

Our findings support the view that areas M and PO are homologous by providing evidence that M and PO are connected to comparable sets of cortical areas. One of the major projections from area M is to V2 (Graham et al., '79). Other prominent projections go to DM, DI, posterior parietal cortex, and cortex rostral to area M on the medial surface. Sparser projections go to DL, MT, and ST (adjacent to area MT) (Graham et al., '79). A projection from area M to V1 may also exist (Weller, personal communication). In macaque, we have shown that a very similar set of connections exists (see Allman et al., '81; and Weller and Kaas, '81, for discussion of homologies). Our findings thus constitute further evidence for a homology between area M and area PO. The validity of this proposed homology will ultimately depend on how the physiological properties of cells in area PO compare with those described for area M (Baker et al., '81; Petersen et al., '88).

Possible functions of area PO

Area PO appears to be connected primarily to peripheral field representations in other extrastriate areas. This finding is consistent with its topography, which empahsizes the visual field periphery (Covey et al., '82). Area PO may make special contributions to visual functions that make use of peripheral information. The visual periphery is known to be important for detection of linear and circular vection (Dichgans et al., '72; Held et al., '75) and for spatial orientation (Malcolm, '84). Peripheral vision is also important for selecting targets in visual search tasks (Williams, '67), suggesting that visual areas concerned with the periphery may be involved in the visuomotor system. The present connectional results support the notion that area PO may be involved in the visual guidance of eye movements. Visual areas in the intraparietal and superior temporal sulci that project to PO contain neurons activated in relation to eye movements (Lynch et al., '77; Newsome and Wurtz, '82), and it would not be surprising if such cells were also found in area PO. All three of these cortical zones share common outputs to visuomotor structures such as the visual pons (Brodal, '78; Glickstein et al., '80; May and Anderson, 86) and the superior colliculus (Colby and Olson, '85). Finally, peripheral vision is important in reaching for nonfoveated targets. The emphasis on the visual field periphery in area PO, apparent both connectionally and physiologically, suggests that it is well suited to contribute to visuospatial functioning.

ACKNOWLEDGMENTS

We thank Maria Carmen Pinon for her help with the cortical maps. This research was supported by NIH grants EY06126, NS07230, EY04685, MH19420, NSF grant BNS 8200806, FINEP/FUJP grant 4386083100, and CNPq 300188/80.

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