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Topographic Organization of Cortical Input to Striate Cortex in the *Cebus* Monkey: A Fluorescent Tracer Study

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ABSTRACT

Cortical afferents to area V1 were studied in seven *Cebus* monkeys by means of retrograde fluorescent tracers. Injections were placed in V1, under electrophysiological guidance, in the regions of representation of both the upper and lower visual quadrants, at eccentricities that ranged from 0.5 to 64 degrees.

In all cases retrogradely filled neurons were found in retinotopically corresponding portions of areas V2 and MT, as defined electrophysiologically (Rosa et al: J. Comp. Neurol. 275:326, 1988; Fiorani et al: J Comp Neurol 287:98, 1989). The results also revealed two other visual zones located anterior to V2 here named third and fourth visual areas. A topographical organization of the connections was observed in these areas, with upper quadrant located ventrally and lower quadrant located dorsally. A clear central-peripheral gradient, from the lateral to the medial cortical surface, was also observed in these areas.

Lower field injections revealed crude topographic organization in area DZ and a diffuse projecting zone in the annectent gyrus. Peripheral injections in V1 revealed a clear upper and lower field segregation in areas PO and prostriata as well as a complex topography in MST. In addition, another region of labeling revealed the presence of an area, the temporal ventral posterior region, with an organized topographic representation of the upper field, with a central to peripheral gradient, from the lateral to the medial cortical surface.

Three groups of cortical areas were distinguished according to the laminar distribution of neurons labeled from V1. In the first group, which is characterized by dense infra- and supragranular labeling, only V2 was included. The second group consists of areas V3, MT, and PO. These areas show dense labeling in the infragranular layers and occasionally sparse labeling in the supragranular layers. Finally, V4 and the other projecting areas, which are characterized by exclusive labeling of the infragranular layers were included in the third group.

Key words: V1, extrastriate cortex, connections, visual topography

Since the descriptions of multiple representations of the visual field in primate cortex (Cowey, '64; Cragg and Ainsworth, '69; Zeki, '69; Allman and Kaas, '71a,b; Van Essen and Zeki, '78), several studies have addressed the question of their connectivity. In primates, striate cortex (V1) is the main cortical target of the lateral geniculate nucleus (for a review, see Tigges and Tigges, '85) as well as the major source of afferents to several extrastriate areas (Lin et al, '82; Weller and Kaas, '83; Van Essen et al., '86). Recent retrograde tracer studies of cortical afferents of V1 in the macaque have reported that several regions of the occipital, parietal, and temporal lobes project back to V1. However, most of these studies have not identified the extrastriate areas that contain the labeled neurons (Rockland and Pandya, '81; Kennedy and Bullier, '85). More recently, Perkel et al. ('86) described, in the macaque, the specific areas that contribute afferents to foveal and parafoveal V1 and concluded that "all the presently known extrastriate visual cortical areas project to V1."

The reciprocity of connections between the visual areas is now widely understood as a basic organizational principle in the visual system. Several studies have, however, emphasized the differences in the laminar distribution of the forward and backward connections of cortical areas, implying a hierarchical processing of the visual information (Rockland and Pandya, '79; Tigges et al., '81; Maunsell and Van Essen, '83). Moreover, recent anatomical evidence shows that the "backward" projections may be able to

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integrate information from several levels of hierarchical processing, even from areas that process different aspects of visual perception (Shipp and Zeki, '89a,b; Zeki and Shipp, '89; Gattass et al., '90). This arrangement suggests that the backward projections may have an important role in the processing of visual information as suggested by Finkel and Edelman ('89) and shown by Sandell and Schiller ('82).

In order to build a model of processing of visual information for a New World monkey, we have started out by studying the connections of striate cortex with other visual areas in the *Cebus* monkey. Inasmuch as most of the connections between striate and extrastriate cortex are topographically organized (Van Essen, '79; Tigges et al., '81; Weller and Kaas, '83), a study with multiple injections in V1 could also provide information about the topographic organization of extrastriate cortex, in the *Cebus*. Therefore, we placed injections in V1 in the regions of foveal, intermediate, and peripheral representations of the visual field, both in the upper and lower quadrants. Here we describe the afferent connections of V1; the efferent connections will be described elsewhere. Preliminary results have been previously described (Rosa et al., '84, '88; Piñon et al., '86; Sousa et al., '87).

MATERIALS AND METHODS

Seven adult *Cebus apella* monkeys, weighing between 1.9 and 2.8 kg, were used in this study. In six animals, two injections of different fluorescent tracers were made in the left hemisphere, at different sites in V1 that were previously identified by electrophysiological recordings. In one of the animals (CBP-7—case 6) we injected only one fluorescent tracer, in the left hemisphere; the right hemisphere was used for another study. One of the animals (CB11) was also used for chronic electrophysiological recordings for other studies (Rosa et al., '88; Neuenschwander, '89), which covered most of the ventral and lateral extrastriate cortex as well as portions of the dorsal extrastriate cortex, in addition to the anatomical experiments here reported.

Abbreviations

An	annectent region
ca	calcarine sulcus
ce	central sulcus
ci	cingulate sulcus
col	collateral sulcus
DZ	area DZ
HM	horizontal meridian
io	inferior occipital sulcus
ip	intraparietal sulcus
la	lateral sulcus
lu	lunate sulcus
MST	area MST
MT	area MT
ot	occipitotemporal sulcus
PO	area PO
po	parietooccipital sulcus
pom	medial parietooccipital sulcus
PRO	area prostriata
st	superior temporal sulcus
TVP	temporal ventral posterior region
VM	vertical meridian
V1	striate cortex
V2	second visual area
V3	third visual area
V3v	ventral part of third visual area
V4	fourth visual area

Animal preparation and receptive field recording

The experimental procedures for multiunit recordings were described in detail elsewhere (Gattass and Gross, '81; Gattass et al., '87; Rosa et al., '88). Briefly, prior to the first recording session, under ketamine and pentobarbitone sodium anesthesia, the animal received a cranial prosthesis. This prosthesis consists of 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 halothane 2%, followed by a mixture of N_2O:O_2 (7:3). Muscular paralysis was induced by pancuronium bromide. Artificial ventilation was maintained by means of a respiratory pump, connected to a tracheal cannula. The level of the expired CO_2, the electrocardiogram, and the rectal temperature were continuously monitored and kept within the physiological range. The right eye was fitted with contact lenses, which focused the eye to the surface of a 57.3 cm radius transparent hemisphere placed in front of the animal. The positions of the blind spot and of the fovea were projected onto the hemisphere by means of a reversible ophthalmoscope and used to define the vertical and horizontal meridians of the visual field as previously described by Gattass and Gross ('81).

Varnish-coated tungsten microelectrodes were used to record from small clusters of neurons. The microelectrode was advanced through a 21 gauge guide tube, at 500 μm steps. Visual receptive fields were plotted by moving white or colored bars in front of the hemisphere, under light-adapted conditions, and by correlating the increments of neuronal activity followed by an audio monitor with stimulation of specific parts of the visual field.

Maps of the visual topography of V1 in the *Cebus* (Gattass et al., '87) were used to guide the electrode penetrations to specific portions of this area. In all cases exploratory recordings of V1 were carried out until the desired visual field representation for the injection site was located. The receptive fields recorded at the injection sites for the various cases are illustrated in the corresponding figures. The locations of the centers of the recorded receptive fields are usually a good estimate of the centers of the intended injection sites. However, in one case (case 4—Fig. 5) when replacing the microelectrode by the needle it did not reach the intended injection site in the upper bank (star in Fig. 5) and dispensed the tracer in the roof of the calcarine fissure (effective injection site). In another case (case 5—Fig. 6) there was significant leakage to the occipital operculum, resulting in a second effective injection site. In such cases the location of the recorded receptive field is meaningless. Therefore, in order to interpret the connectional data precisely we also determined the visuotopic extent of the effective injection sites by back-transforming to the visual field the region of V1 represented at the injection site, taking into consideration the retinotopic organization and the cortical magnification factor of V1 described for the *Cebus* (Gattass et al., '87).

The method used to define the visuotopic extent of the effective injection sites was shown to be precise based on the comparison of the topographical distribution of labeled cells in visual area V2 with the visuotopic map previously described for this area in the *Cebus* (Rosa et al., '88). Therefore the projections of the effective injection sites onto the visual field in cases with no electrophysiological defined receptive field (case 4 and opercular injection in case

5) seem to be a reasonable estimate of the topographical extent of the injection sites. We should, however, emphasize that these back-transformed fields are only approximations since there may be considerable individual variations in visual topography from case to case.

Injections of fluorescent tracers

Following recordings, injections were made either with a tapered micropipette (40–70 μm) (animals CB7, CB8, and CB9) or with a 1 μl Hamilton syringe with a 27 gauge needle (the remaining animals). The electrode guide tube was lowered to within 300 μm above the intended injection site. The electrode was then advanced again, and the retinotopic location of the injection site rechecked. The electrode was replaced either by the syringe or by the micropipette, the syringe needle was advanced through the guide tube to the same depth as the electrode, and 0.3–0.5 μl of a fluorescent tracer was injected. Three animals (CB7, CB8, and CB9) received injections of Bisbenzimide (5%) and Nuclear Yellow (2%). Three additional animals (CB11, CBF15, and CBF19) were injected with both Fast Blue (5%) and Diamidino Yellow hydrochloride (2%). The remaining animal (CBP7) was injected only with Fast Blue (5%). The guide tube was left in position for about 30 minutes after pulling out the syringe. In most cases this procedure allowed for precise positioning of the injections without leakage up the track.

Histological processing

After variable survival times (2 or 6 days) the animals, under deep anesthesia, were perfused transcardially with saline followed by formalin with increasing concentrations of sucrose (from 10% to 30%). The injected hemispheres were processed as previously described (Rosa et al., '88). Nonstained 40 μm sections, 400 μm apart, were mounted on glass slides, quickly dried and dehydrated (1 minute dip in absolute ethanol), defatted (1 minute dip in xylene), and then coverslipped with Eukitt. Alternate sections were postfixed in formalin and then stained for cell bodies with the Nissl method, and for myelin with either the Gallyas (animals CB7, CB8, and CB9) or the Heidenhein-Woelcke method (remaining animals).

Cell plotting, cortical reconstructions, and assignment of label to specific areas

The nonstained sections were scanned from the occipital pole to the central sulcus. The scanning was made with the aid of a Zeiss Axioplan fluorescence microscope, coupled to an X-Y plotter. The positions of the labeled neurons were then transferred from the drawings of the sections onto two-dimensional maps obtained from reconstructions of layer IV (Gattass et al., '87). The contours of layer IV from sections 1.2 mm apart were used to generate a three-dimensional wire model of striate and extrastriate cortices at 7.5× magnification. The border of striate cortex was then cut apart, and the whole model was flattened by hand to obtain a two-dimensional map. Myeloarchitectonic borders, as well as the recording sites, were also transferred onto the flattened maps, and used as reference guides to locate labeled cells with respect to specific areas. In two animals (CBF15 and CBF19) in which neither myeloarchitectony nor electrophysiology was available, label was assigned to specific visual regions based solely on their locations relative to the V1/V2 border as well as to the sulcal pattern.

RESULTS

Distribution of Labeled Cells in Extrastriate Cortex

After injections in different portions of V1, we observed labeled cells in portions of the occipital, parietal, and temporal lobes. Throughout this paper injections are referred to as central, intermediate, or peripheral, when the eccentricity of the centers of the receptive fields recorded at the injection sites, with respect to the fovea, was below 5°, between 5° and 20°, or beyond 20°, respectively. We shall first define the visual zones that project to V1, and next we shall consider the afferent connections to central, intermediate, and peripheral V1.

Assignment of label to specific visual regions. Figure 1 shows some cortical visual zones on a flattened reconstruction of the posterior cerebral cortex in the *Cebus* monkey. In this study, the location and borders of areas V2, MT, MST, DZ, PO, and prostriata were defined following the myeloarchitectonic or electrophysiological criteria used in previous studies. In five of the animals studied we were able to obtain a successful myelin stain. In these animals we used the myeloarchitectonic criteria described by Rosa et al. ('88) to define the borders of V2 and V3 and those described by Fiorani et al. ('89) to define areas MT, DZ, and MST. Area prostriata was defined based on the criteria defined by Sanides ('72) and by Gattass et al. ('87). The borders of area PO were defined based on the criteria defined by Colby et al. ('88) in the macaque and by Neuenschwander ('89) in the *Cebus*. Briefly, V2 shows two myeloarchitectonic patterns: one less stratified with a thick and homogeneous band of fibers extending from layer VI to the bottom of layer III, which resembles the pattern previously described for V2 in the macaque (Gattass et al., '81). The more stratified V2 is characterized by a less intense myelination of layer V so that the inner and outer bands of Baillarger become conspicuous. Throughout V2 the outer band of Baillarger is not sharply defined. This characteristic can be used to distinguish V2 from V3, located ventral and laterally, which is clearly stratified and presents a thin, sharply defined outer band of Baillarger. In addition, V3 presents a paler band between the inner band and the white matter, which is not observable in V2. Area MT shows two distinct myeloarchitectonic patterns: one with a dense and homogeneous pattern of fibers extending from layer VI to the bottom of layer III, observed in the posterior bank of superior temporal sulcus; the other, also homogeneous but less densely myelinated, found in the fold between the anterior and posterior banks of superior temporal sulcus. Area MST shows a dense and homogeneous pattern of fibers differing from MT by showing a conspicuous outer band of Baillarger. DZ shows two myeloarchitectonic patterns: one dense with a conspicuous outer band of Baillarger observed in the posterior bank of superior temporal sulcus, dorsolateral to MT; the other with a pale myeloarchitecture and visible outer band of Baillarger, found dorsal to MT. Area PO is densely myelinated and shows a sharp, heavily myelinated thick outer band of Baillarger. In addition, in two of the cases (animal CB11) areas V2, V3, V4, and PO were electrophysiologically defined.

The strip of cortex 4–5 mm wide located anterior to V2 is named here third visual area (V3). As previously described (Gattass et al., '90), this area contains an orderly representation of both visual quadrants and a distinct cytochrome-oxidase architecture. Its myeloarchitectonic characteristics

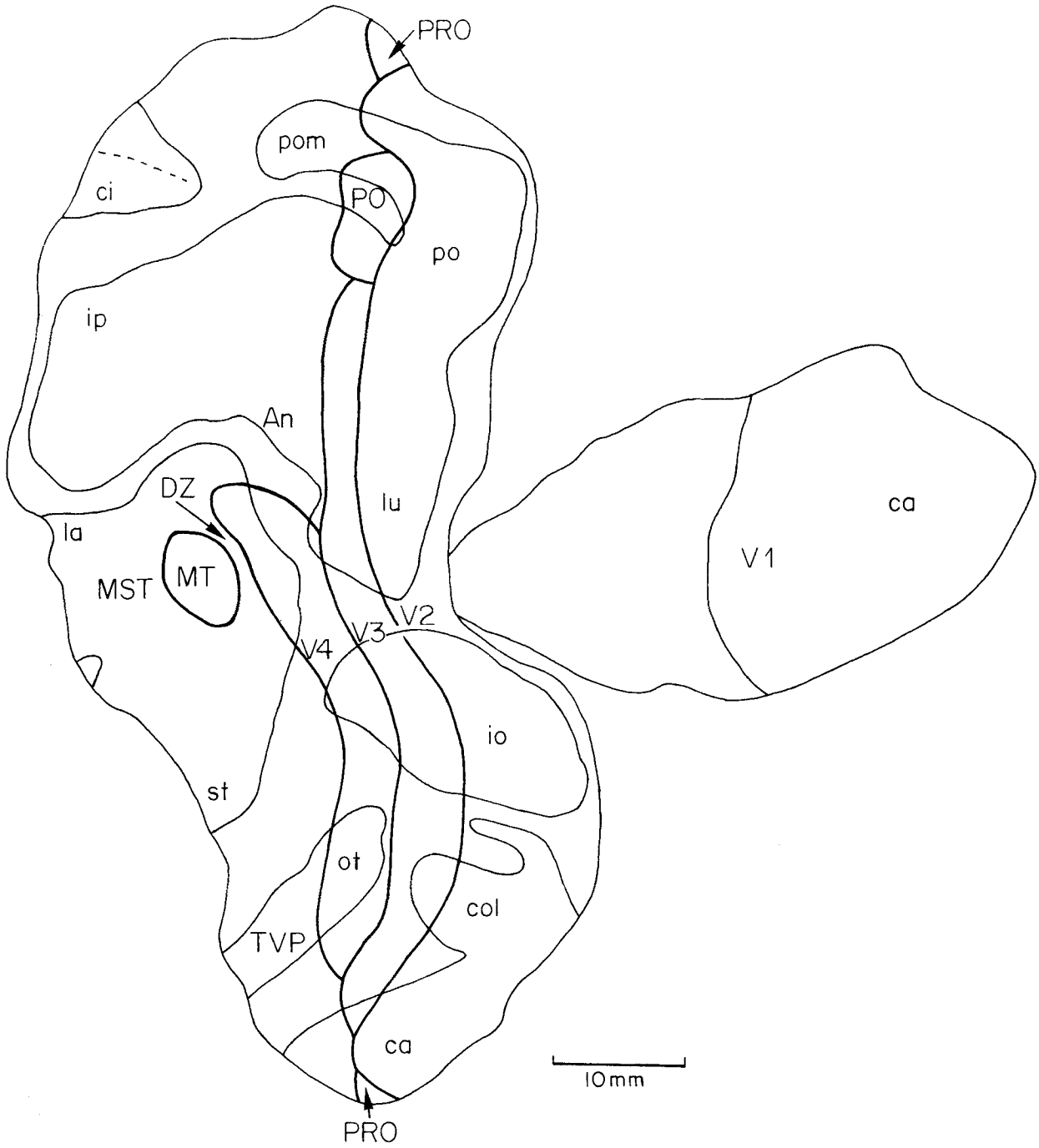

Fig. 1. Flattened reconstruction of the posterior cerebral cortex showing location and extent of the V1 projecting extrastriate visual regions. Thin lines indicate the lips of sulci. Thick lines indicate the borders of the extrastriate visual areas. For details see text.

in the ventral and dorsal cortical surfaces were described by Rosa et al. (88), although not named V3. Both these studies agree that the region containing the peripheral representation in dorsal V3 shows a heavier myelination, being different from the remaining portions of this area. Nevertheless, inasmuch as the study of V3 in the *Cebus* is still in progress and the present data do not show differences between the heavily and lightly myelinated portions as regards connections with V1, we provisionally consider V3 as a single area. The distribution of labeled cells in this strip of cortex after central, intermediate, and peripheral injections followed a progression from lateral to medial. The ventral portion of this area is coextensive with area V3v defined in the *Cebus* by Gattass et al. ('88b; '90), based on electrophysiological mapping experiments.

We also found labeled cells anterior to V3 following central, intermediate, and peripheral injections in V1. Labeled cells lie along a strip of cortex that includes part of

the posterior bank of the superior temporal sulcus and of the prelunate gyrus, the anterior tip of the inferior occipital sulcus, the posterior tip of the occipitotemporal sulcus, and parts of the adjoining tentorial surface. This region shows a central-peripheral organization similar to that described for area V4 of the macaque (Gattass et al., '88a); likewise the myeloarchitectonic pattern of this region is similar to that described in the macaque (Gattass et al., '88a); hence, we named this strip of cortex the fourth visual area (V4).

Finally, there are two regions that were named based only on their positions relative to the sulci. One lies anterior to V4 in the occipitotemporal sulcus and adjacent tentorial surface and is here named temporal ventral posterior region (TVP). The other, in the dorsal surface, extends from the paraoccipital sulcus into the tip of the superior temporal sulcus and is named here annectent region (An). The temporal ventral posterior region shows patches of labeled cells after central, intermediate, and peripheral injections in the upper quadrant in V1 (Figs. 3, 7, 9). Central injections involving the horizontal meridian also labeled cells in TVP (Figs. 2, 4). In the annectent region we only observed scattered cells. These cells were labeled solely after injections in the region of representation of the lower quadrant in V1 (Figs. 2, 5, 6).

Although tentative, this nomenclature shall be applied throughout this paper whenever assigning labeled cells to a specific visual zone.

Injections in central V1. Following injections in central V1 (Figs. 2–4), we observed densely packed labeled cells in retinotopically corresponding regions in V2 (Rosa et al., '88) and in MT (Fiorani et al., '89).

Figure 2 illustrates the results of an injection in the representation of the lower quadrant in central V1. Besides the patches found in V2 and MT, in the dorsal surface, there is also a large patch of densely packed labeled cells located in the anterior bank of the lunate sulcus (V3). This patch is continuous with the one located in V2. In addition, we also observed two other patches of labeled cells: one densely packed in the prelunate gyrus extending into the anterior bank of the lunate sulcus (V4); the other (DZ), with loosely packed cells, in the posterior bank of the superior temporal sulcus. The latter is continuous with the patch located in MT. The patch in the anterior bank of the lunate sulcus differs from that of V2 in the laminar arrangement of its labeled cells (see below). We also observed a few scattered labeled cells (dots in Fig. 2) in the dorsal portion of the prelunate and in the annectent gyri as well as in the lateral bank of the intraparietal sulcus (An) and in the superior temporal sulcus (in MT).

The injection depicted in Figure 2 also labeled cells in ventral extrastriate cortex. We observed two patches of densely packed cells: one in the anterior bank of the inferior occipital sulcus (V4) and another in the ventral convexity of the temporal cortex lateral to the occipitotemporal sulcus (TVP). Posterior to these patches we observed a patch of loosely packed labeled cells in the anterior bank of the inferior occipital sulcus (V2/V3 border).

In this case, as well as in case 8 (Fig. 9), the patches of label were found to be located in corresponding visuotopic regions in areas V2 (Rosa et al., '88), V3, V4 (unpublished results), and PO (Neuenschwander, '89) based on the electrophysiological recordings of this animal.

Injection in the upper quadrant representation of central V1 (Fig. 3) produced, in addition to the projections from V2 and MT, two patches of label in the ventral surface. They are located in the anterior bank of the inferior occipital sulcus, extending into the ventral convexity of the cortex (V3 and V4), and in the lateral bank of the occipitotemporal sulcus (TVP). Since myeloarchitectonic borders are not available for this animal, the assignment of label to specific areas must be regarded as tentative. Additionally, we found scattered cells in the anterior bank of the superior temporal sulcus, close to the border of MT. Based on the distance of these cells to the fundus of the superior temporal sulcus, some of these cells may belong to MST (Fiorani et al., '89). Scattered cells were also found in the collateral sulcus.

Six of the central injections included the region of representation of the horizontal meridian. The connections of V1 with V2 and V3 revealed by these injections were shown by Rosa et al. ('88). In order to illustrate the connections of other visual areas, in addition to V2 and V3, with central V1 we illustrate a representative case in Figure 4. Due to the involvement of the horizontal meridian, labeling occurred at the anterior border of V2, both dorsally and ventrally. These patches of label extended anteriorly into adjoining cortex (V3), albeit with different laminar involvement with respect to V2. We also observed intense labeling in a patch that extends from the anterior portion of the inferior occipital sulcus, through the prelunate gyrus (V4), into the posterior bank and floor of the superior temporal sulcus (DZ and MT). This injection also labeled three patches of densely packed cells in the lateral and medial lips of the occipitotemporal sulcus (TVP). In addition to these densely packed patches we also observed four sparse projections: one located in the posterior bank of the superior temporal sulcus, near the border of the foveal portion of MT (probably in DZ); a second one located anterior to the inferior occipital sulcus in the lateral surface (probably V4); and the remaining two located in the lateral bank of the occipitotemporal sulcus (V4/TVP). Medial to the occipitotemporal sulcus we also observed scattered cells.

Injections in intermediate V1. A V1 injection in the region representing 12° of eccentricity within the lower quadrant, close to the HM (Fig. 5), produced labeled cells in retinotopically corresponding regions of V2 and of MT. This injection also resulted in labeling anterior to V2, in the dorsal portion of the lunate sulcus (V3), in the prelunate gyrus, and beyond in the posterior bank of the superior temporal sulcus (DZ and V4). In addition, we also observed scattered cells in the region of the annectent gyrus (An) and in the anterior bank of the superior temporal sulcus.

Another V1 injection in a region of identical retinotopic representation (Fig. 6) leaked to the opercular striate cortex, a region representing about 5° of eccentricity (Gattass et al., '87). Although myeloarchitectony was not available in this case, the visual zones that project to V1 seem to be similar to those observed in the previously described cases (Figs. 2, 5). The leakage in the opercular surface resulted in a second effective injection site, as evidenced by the existence of two strongly labeled zones in retinotopically corresponding regions in V2. Label in MT was fairly uniform, being, however, more extensive than that observed in the cases illustrated either in Figure 2 or in Figure 5. Cells putatively assigned to MST were also more numerous, forming a patch of loosely packed labeled cells in the anterior bank of the superior temporal sulcus. Comparison of these two cases with the one illustrated in Figure 6 also demonstrates, in the latter, the presence of more scattered and spread label in the prelunate and annectent gyri.

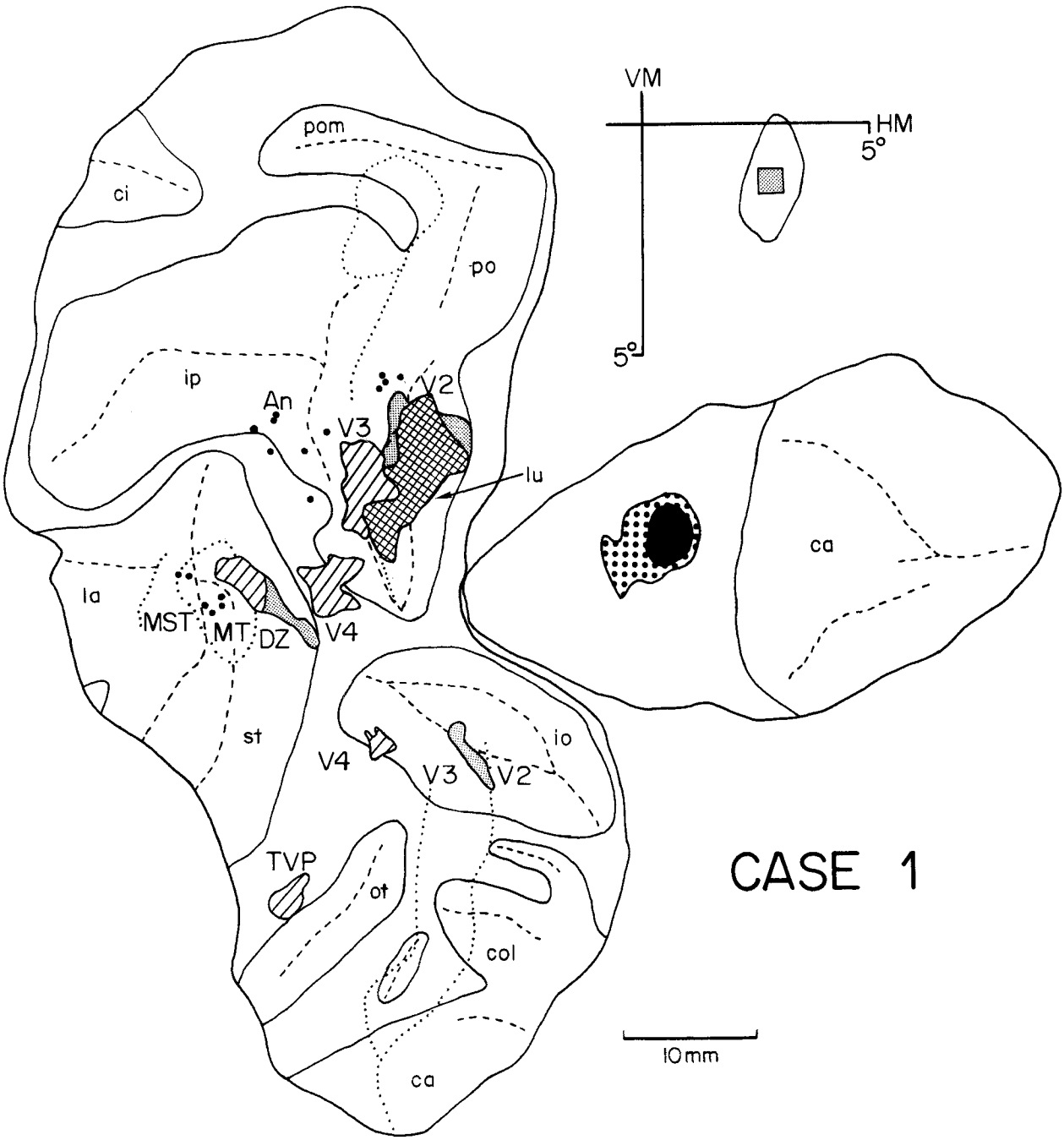

Fig. 2. Flattened reconstruction of the posterior portion of the cerebral cortex of *Cebus* (case 1—CB11). In this case, Fast Blue was injected at the central lower field representation in V1, with a small invasion of the upper field. In this and in subsequent figures area V1 (right) was separated from the extrastriate areas (left) to avoid distortions. Thin lines represent the borders and dashed lines the folds of the cortical mantle buried in the sulci. Dotted lines indicate myeloarchitectonic borders. In V1, black represents the injection site and large dots, intrinsic connections. In extrastriate, hatched areas indicate densely packed patches. Double hatching represents dense labeling of both infra- and supra granular layers. Gray represents loosely packed patches. Scattered cells are indicated by dots. The insert represents both the receptive field recorded at the injection site (gray) and the back projection of the injection site onto the visual field (outline).

Finally, the injection site located in the calcarine fissure involved the representation of the horizontal meridian resulting in label at the V2/V3 border at the ventral surface. Therefore, the invasion of white matter by the injection did not seem to invalidate these data.

A large injection in the upper field representation of V1, at 10° of eccentricity, is illustrated in Figure 7. In addition to the patches located in V2 and MT we found three additional regions of labeling in the ventral cortical surface. These patches lie in the ventral convexity of the cortex: one,

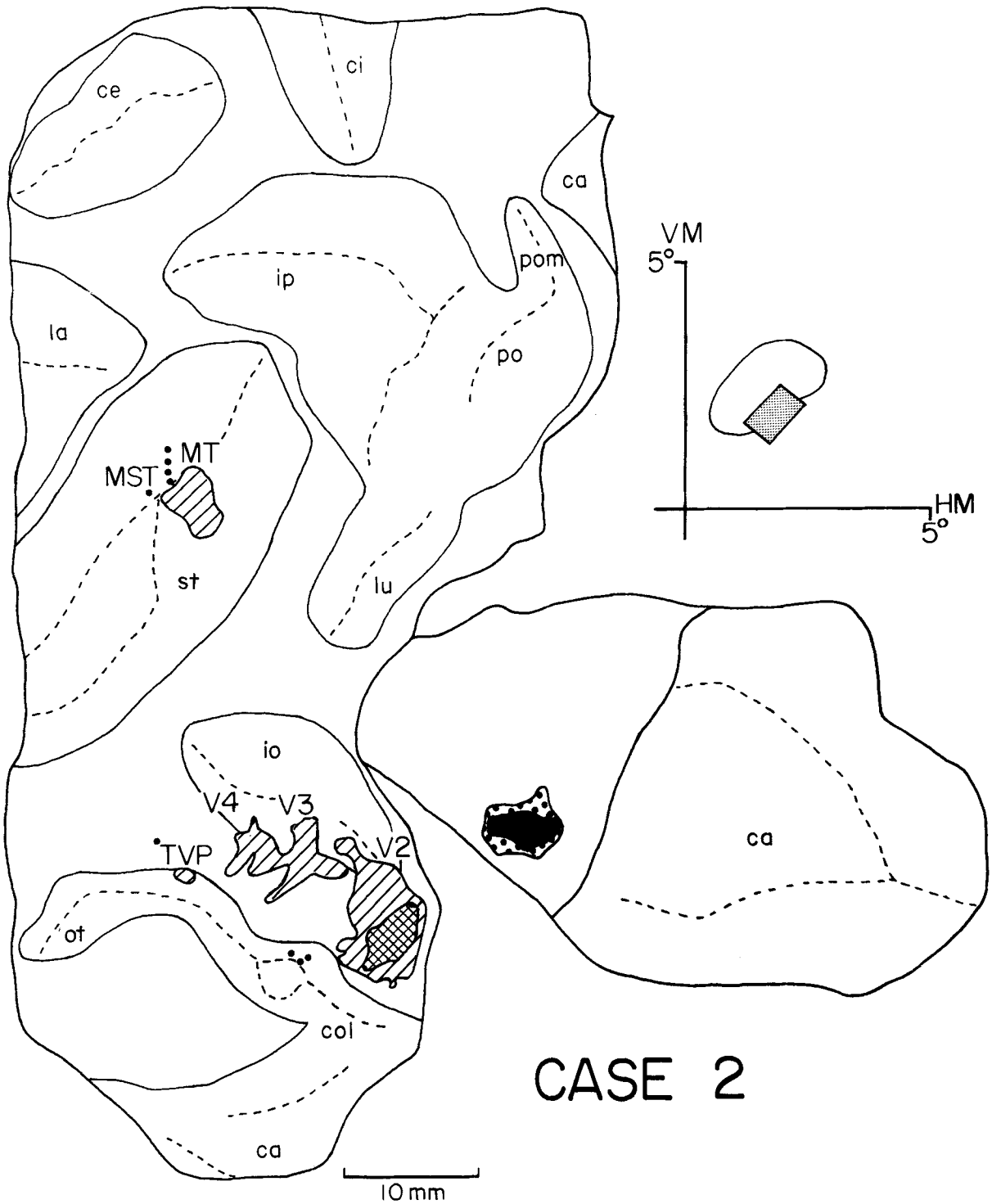

Fig. 3. Flattened reconstruction of the posterior portion of the cerebral cortex of *Cebus* (case 2—CBF19) showing the injection of Fast Blue at the central upper field representation in V1 and patches of labeled cells in extrastriate cortex (see also legend to Fig. 2).

continuous with that of V2, extends into the lateral bank of the collateral sulcus and into the medial bank of the occipitotemporal sulcus (V3, V4); a second one is located anterior to the collateral sulcus and the remaining one in the medial bank of the occipitotemporal sulcus. The latter two probably belong to TVP. We also observed scattered cells in the ventral convexity of the temporal cortex.

Injections in peripheral V1. An injection in V1 at the region representing the lower quadrant periphery (Fig. 8) resulted in four main patches of labeled cells, in addition to

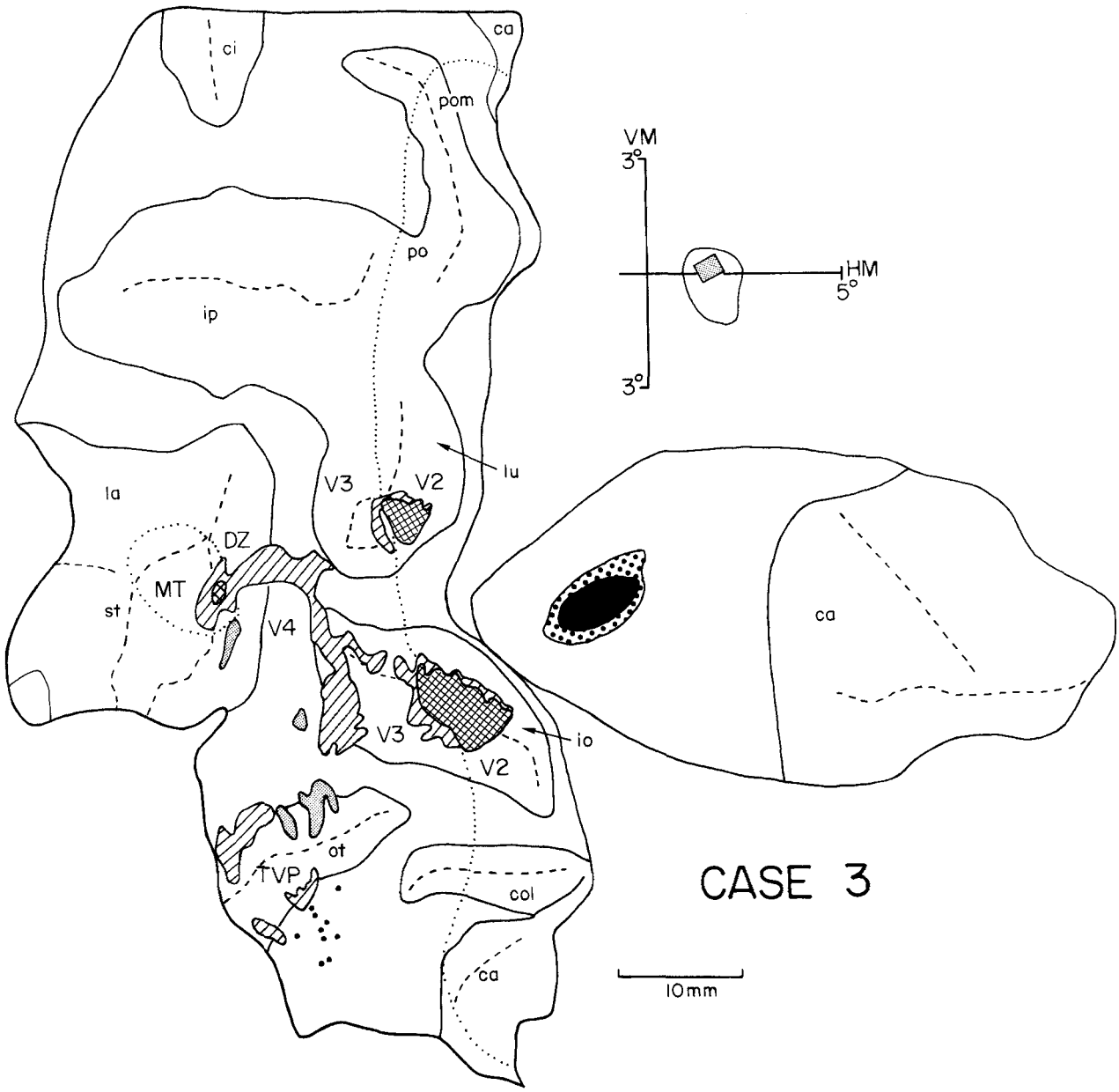

Fig. 4. Flattened reconstruction of the posterior portion of the cerebral cortex of *Cebus* (case 3—CB7) showing the injection of Bisbenzimide at the representation of the central portions of the horizontal meridian. Coarse double hatch in this and in following figures represents dense infragranular and sparse supragranular labeling (see also legend to Fig. 2).

those found in V2 and MT. One of these patches extends from the anterior bank of the parietooccipital sulcus into the medial bank of the intraparietal sulcus (PO/V3) and shows infra- and supragranular labeling. Anterior to this patch there is a region of loosely packed labeled cells, near the medial lip of the intraparietal sulcus. The remaining two patches (MST and V4) are in the posterior and anterior banks of the superior temporal sulcus. Scattered cells were also found anterior to V2, in area prostriata, as defined based on cytoarchitectonic criteria, and in the prelunate gyrus, in a region that probably corresponds to V4.

After an injection in V1 in a region representing the upper quadrant periphery (Fig. 9) we found patches of labeled cells both in the dorsal and ventral extrastriate cortical surfaces, in addition to those found in V2 and MT. In the ventral surface, we observed a patch of densely packed labeled cells (V3) continuous with the labeling in V2. Note that, in this case, it was possible to observe that the label in V3 was located in a region representing the same portion of the visual field as the injection site (see Fig. 11). We also observed four additional regions of loosely packed labeled cells located anterior and medial to this patch (V4, TVP, and PRO). While label in V4 was assigned based on myeloarchitectonic grounds as well as on electrophysiological recordings, using the criteria defined by Gattass et al. ('88a) in the macaque, area prostriata was defined based on

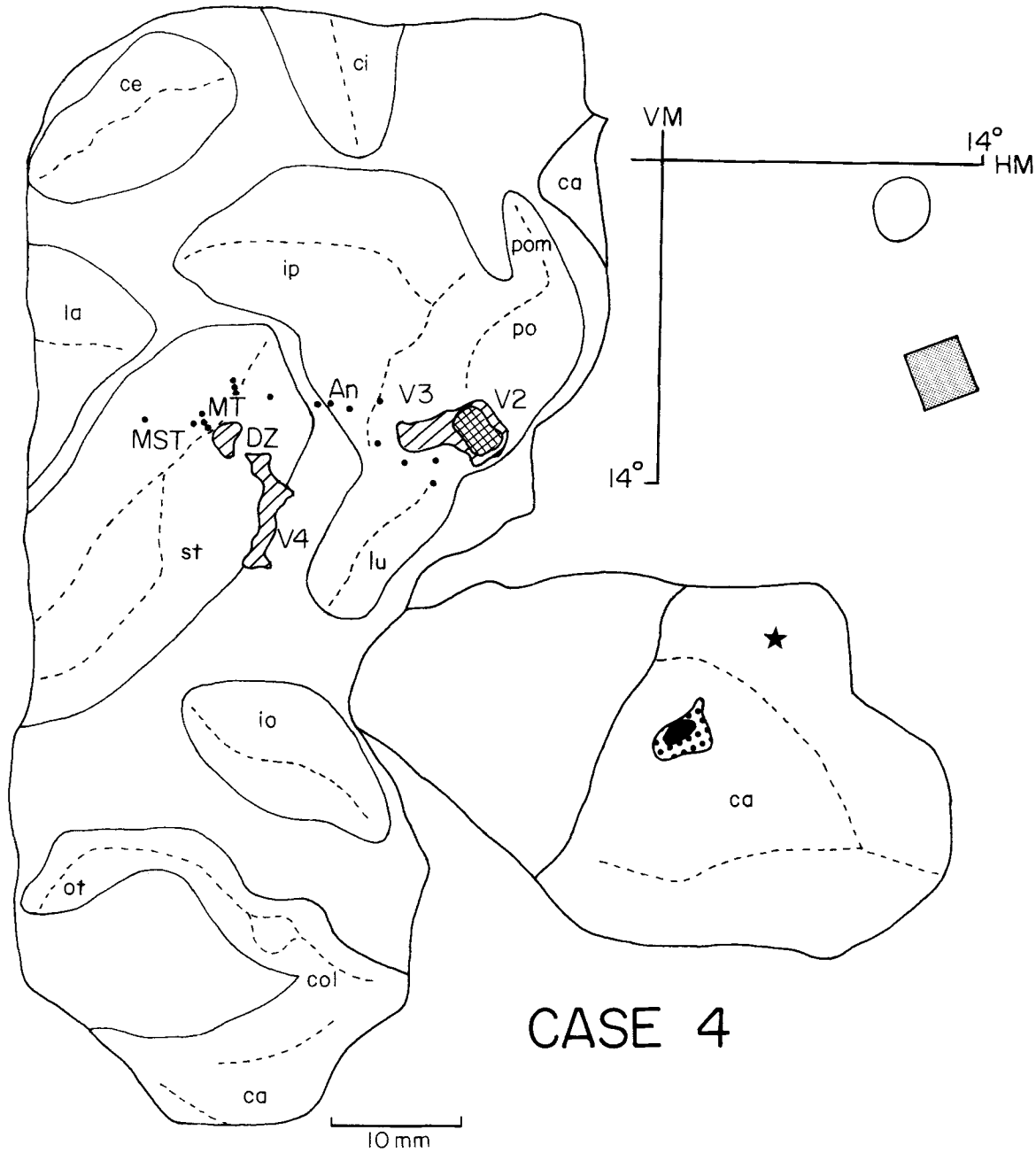

Fig. 5. Flattened reconstruction of the posterior portion of the cerebral cortex of *Cebus* (case 4—CBF19) showing injection of Diamidino Yellow at intermediate lower field representation. Star in the flattened reconstruction represents the intended injection site, which corresponds to the recorded receptive field illustrated in the insert (see also legend to Fig. 2).

architectonic criteria only (Gattass et al., '87). Scattered labeled cells were also observed in the ventral surface.

In the dorsal surface we found a patch of densely packed labeled cells in the medial parietooccipital sulcus, extending into the medial surface. Myeloarchitectony and electrophysiological recordings revealed that these cells are located at the region of representation of the peripheral upper quadrant in area PO, thus in retinotopic register with the injection site. In this patch we found labeled cells both in the infra- and supragranular layers. Here again, similar to the case illustrated in the previous figure, we found a patch of labeled cells in the anterior bank of the superior temporal sulcus, close to the MT border. In this case we were able to assign this label to area MST, as defined by Fiorani et al. ('89) based on myeloarchitectonic grounds.

Evidence of visual topography in extrastriate areas

The location of the extrastriate projection regions was consistent with the topographic organization that has been revealed for the various areas. In order to visualize this

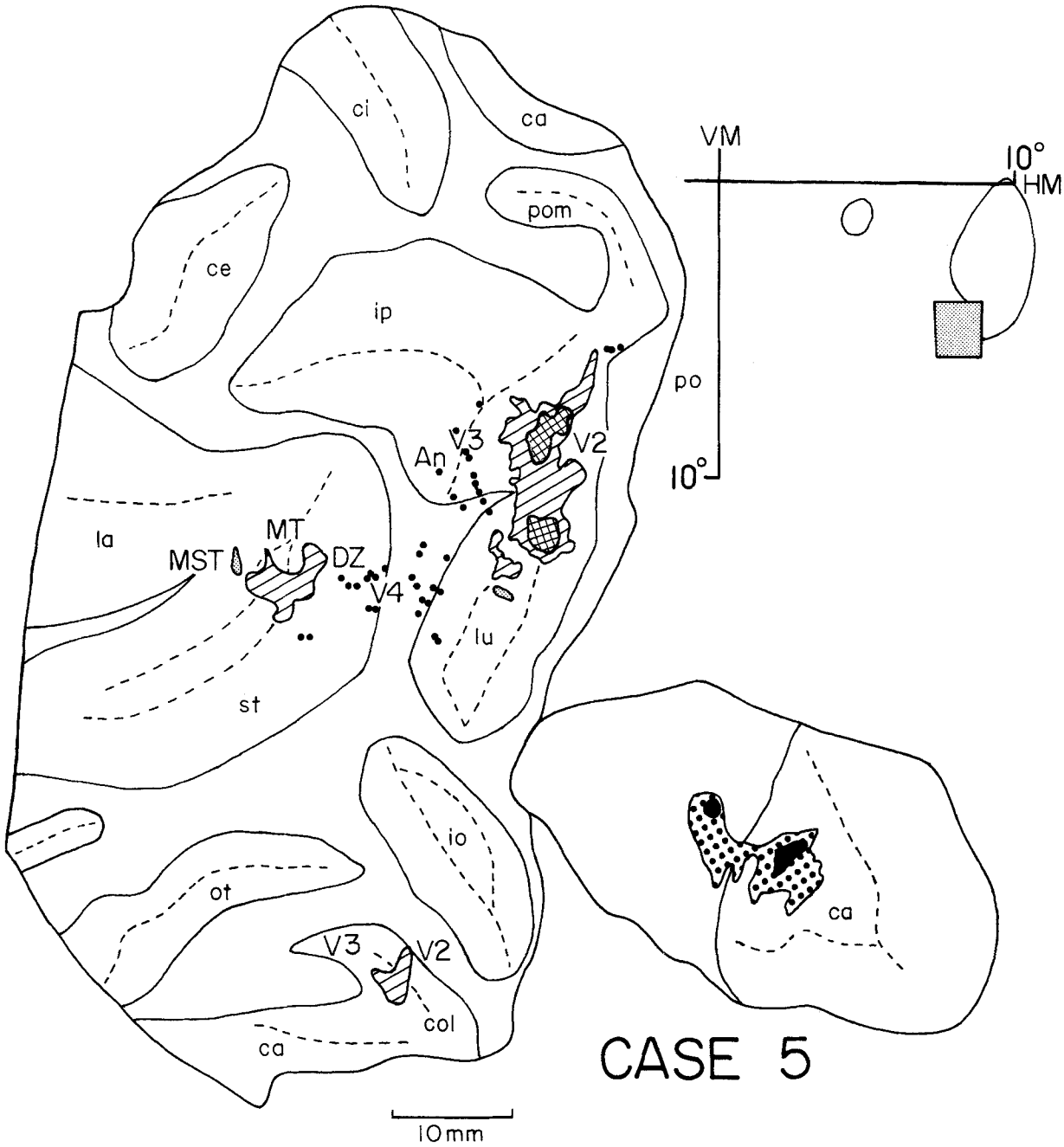

Fig. 6. Flattened reconstruction of the posterior portion of the cerebral cortex of *Cebus* (case 5—CBF15) showing injection of Diamidino Yellow at central and intermediate lower field representations (see also legend to Fig. 2).

organization we drew, with different symbols, the injection sites and the corresponding projection regions, for representative cases, on a standard flattened reconstruction of striate and extrastriate cortices (Fig. 10). This figure shows two trends of the visual topography in most areas of the extrastriate cortex of *Cebus:* first, the existence of a segregation between the representation of the lower (filled symbols) and the upper (open symbols) quadrants; and second, a central-peripheral gradient in which the representation of the central visual field lies laterally and that of the peripheral visual field medially.

In V2, as well as in V3 and V4, the central-peripheral gradient is evident both in the dorsal and ventral cortical surfaces. These surfaces represent the lower and upper quadrants, respectively.

The temporal ventral posterior region (TVP) shows an organized representation of the upper visual field with a large emphasis in the representation of central vision. In the posterior portion of TVP there is a clear central-peripheral gradient with the central representation located laterally and the peripheral one medially. It is worth noticing that a lower field injection (case 2) labeled cells in TVP. How-

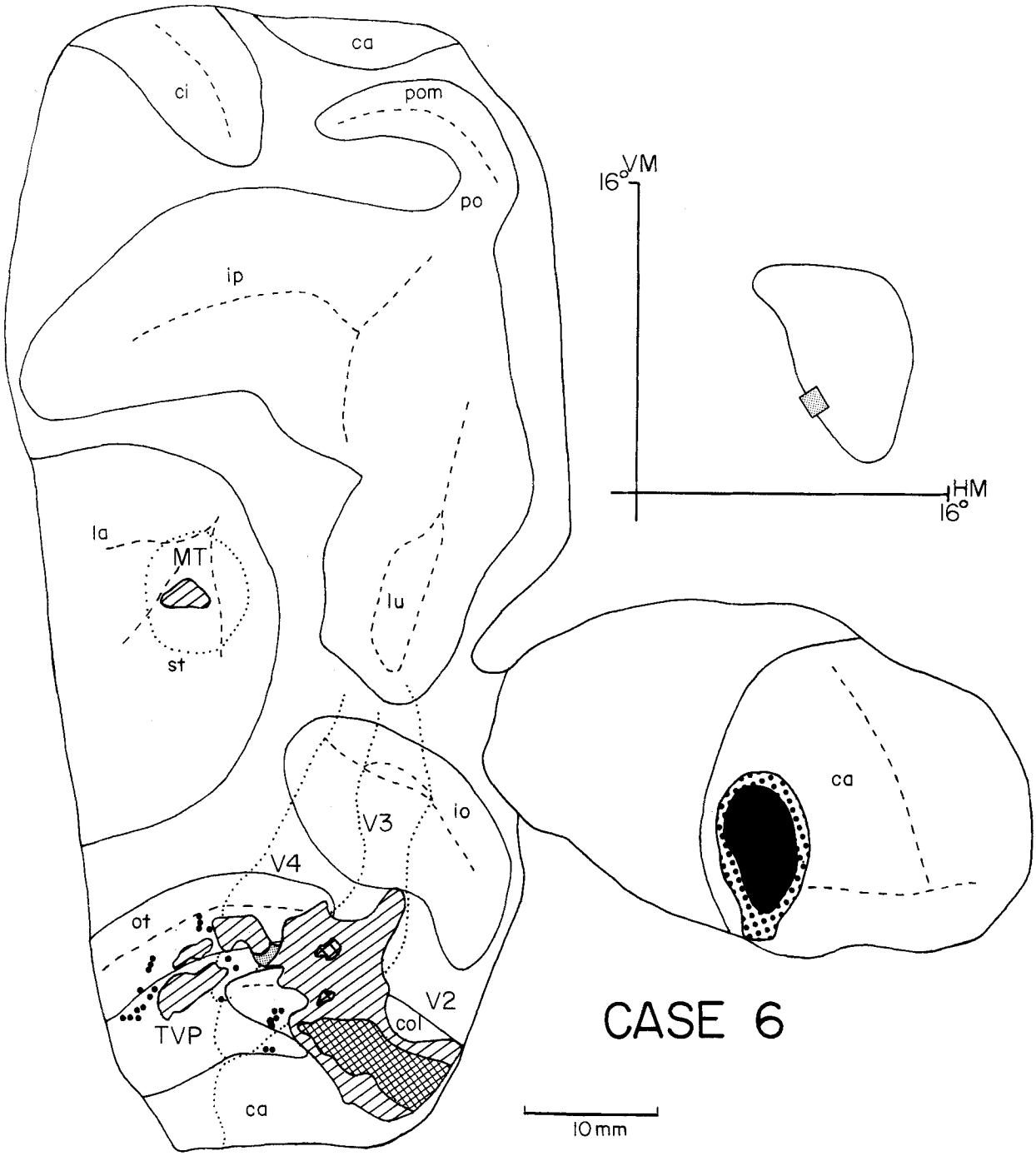

Fig. 7. Flattened reconstruction of the posterior portion of the cerebral cortex of *Cebus* (case 6—CBP7) showing injection of Fast Blue at intermediate upper field representation (see also legend to Fig. 2).

ever, this injection also labeled cells ventrally in the V2/V3 border, as well as in V4, indicating that this injection must have involved the horizontal meridian representation. Therefore, there are no lower field cases that show label in TVP.

Area PO and area prostriata only project to peripheral V1. Area MST also showed distinct patches of labeled cells after peripheral injections in V1; however, some of the central injections (cases 2, 4, and 5) may have also labeled sparse cells in this area. In the absence of independent criteria in these cases we regard the evidence of central projections from MST to V1 as tentative. However, while in PO and area prostriata there is a clear segregation of the lower and upper visual quadrants the lateral portion of area MST shows patches of labeled cells after injections in the lower and upper field peripheries in apparently the same regions (Figs. 8, 9, 10, insert).

In the annectent region (An) we found no central-peripheral gradient; in addition, in this region we only

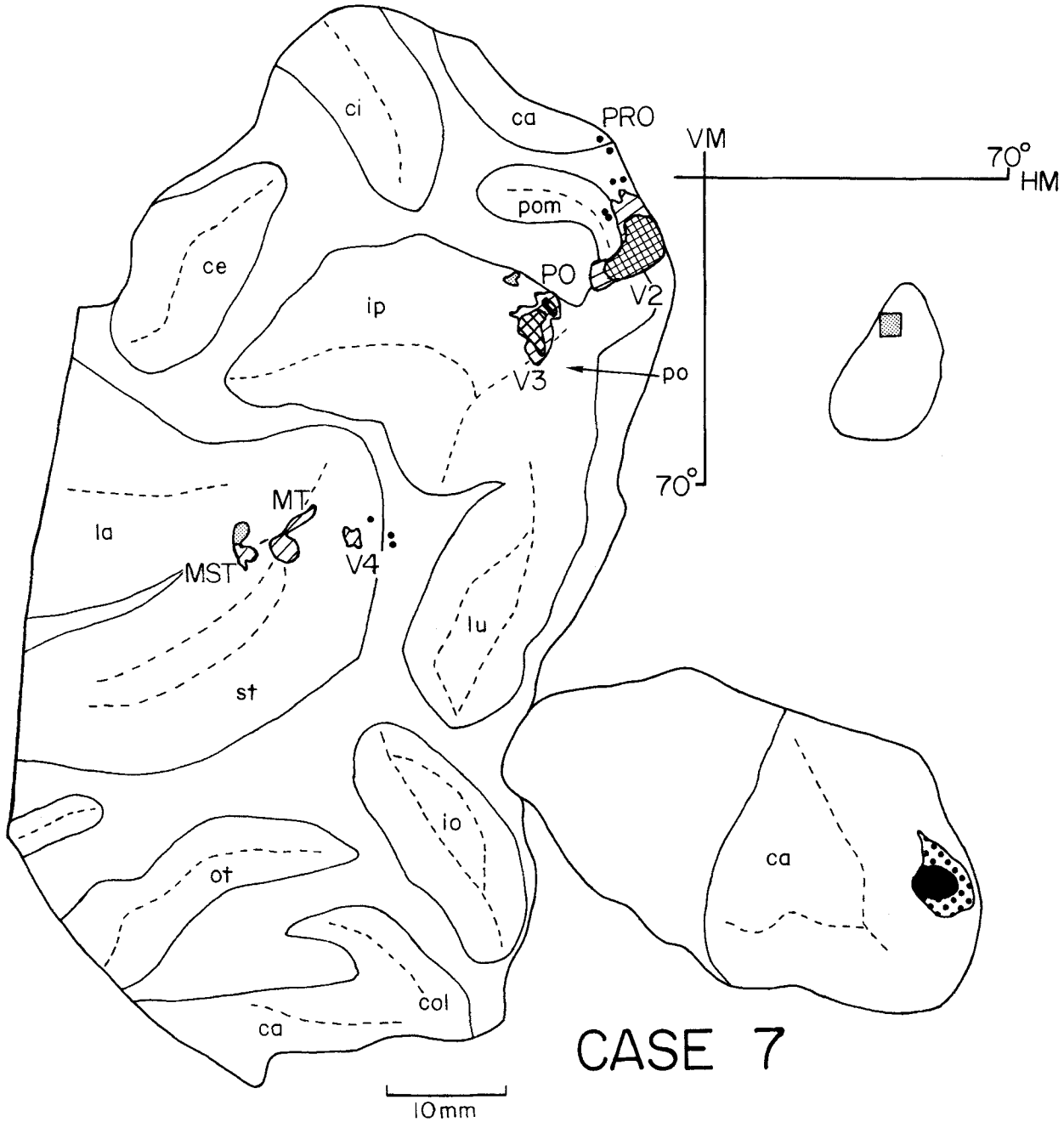

Fig. 8. Flattened reconstruction of the posterior portion of the cerebral cortex of *Cebus* (case 7—CBF15) showing injection of Fast Blue at lower field periphery (see also legend to Fig. 2).

found labeled cells following injections in the lower quadrant representation of V1 (Figs. 2, 5, 6).

Laminar distribution of labeled cells

The foci of label found in this study can be subdivided into three different groups based on the pattern of laminar distribution of the labeled cells. The first group of V1 afferents shows densely packed heavily labeled cells located in both the infragranular and supragranular layers. We found this pattern of laminar distribution in all projections from V2. The second group was characterized by the presence of densely packed strongly labeled cells in the infragranular layers and occasionally sparse labeled cells in the supragranular layers. This is the pattern in MT, V3, and area PO. The third group of V1 afferents was characterized by exclusive labeling of the infragranular layers. This pattern was found in the remaining zones described in this study.

The transition in the laminar pattern of labeled cells between V2 and V3 was found to be an useful criterion for delimiting the anterior border of V2 (Rosa et al., '88). In animal CB11, the border between V2 and V3v based on the

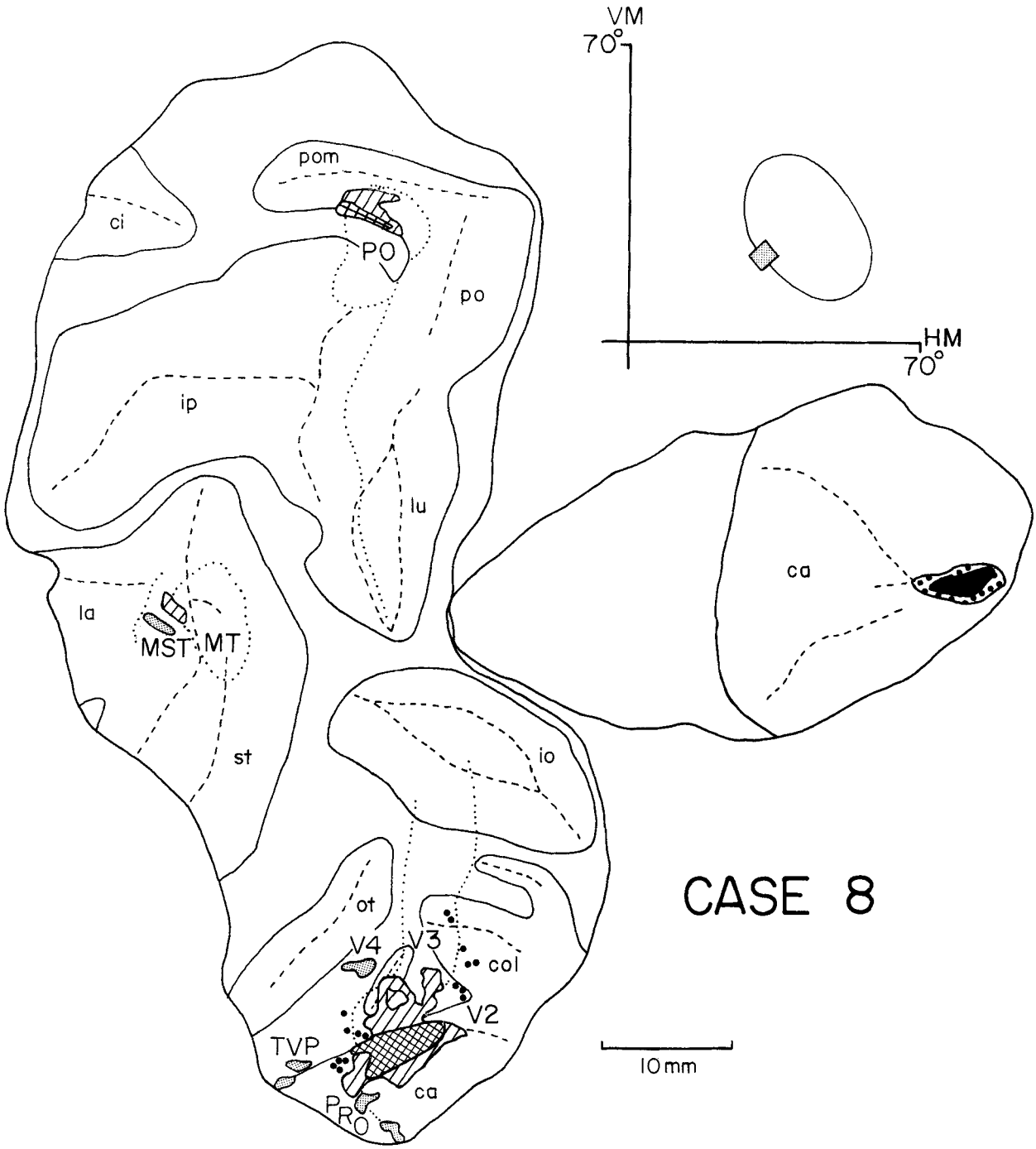

Fig. 9. Flattened reconstruction of the posterior portion of the cerebral cortex of *Cebus* (case 8—CB11) showing injection of Diamidino Yellow at upper field periphery (see also legend to Fig. 2).

transition in the laminar pattern of labeled cells was found to be coincident with both the myeloarchitectonic and electrophysiological borders of V2, as shown in Figure 11. In this figure, the myeloarchitectonic border (dashed line) and the transition in the laminar pattern (arrowhead) coincide with the cortical site where one observes a reversion in the progression of receptive fields, in a penetration across V2 and V3v. This reversion, which occurs at the horizontal meridian representation (sites 5–6), characterizes the anterior border of V2 as defined by Rosa et al. ('88).

DISCUSSION

The pattern of connections, the myeloarchitecture, and, in some animals, the electrophysiological data allowed us to subdivide the extrastriate cortex in various areas, as illus-

Fig. 10. Topography of the afferent cortical projections to V1. Thin lines indicate the borders of the sulci. Dotted lines are myeloarchitectonic borders based on animal CB11. The injection sites and corresponding projecting zones are represented by the same symbols. The region inside the box is shown at a higher magnification in the insert (for details see text).

trated in Figure 1. In previous anatomical descriptions of the cortical afferents of V1, using horseradish peroxidase (HRP) as tracer, Rockland and Pandya ('81) described in the macaque only two projecting zones. The same observation was made by Tigges et al. ('81) in the squirrel monkey. Other studies using HRP as retrograde tracer such as those of Lin et al. ('82), in the owl monkey, and of Van Essen et al. ('86), in the macaque, concluded that three extrastriate areas, namely V2, MT, and DM or V3 project to V1. Our evidence argues in favor of other extrastriate areas projecting back to V1 besides those already described by these authors. The difference between their results and ours could be attributed to the sensitivity of the tracers used in the various studies. Using fluorescent tracers, other authors have described several V1 projecting zones, in the macaque (Kennedy and Bullier, '85; Perkel et al., '86).

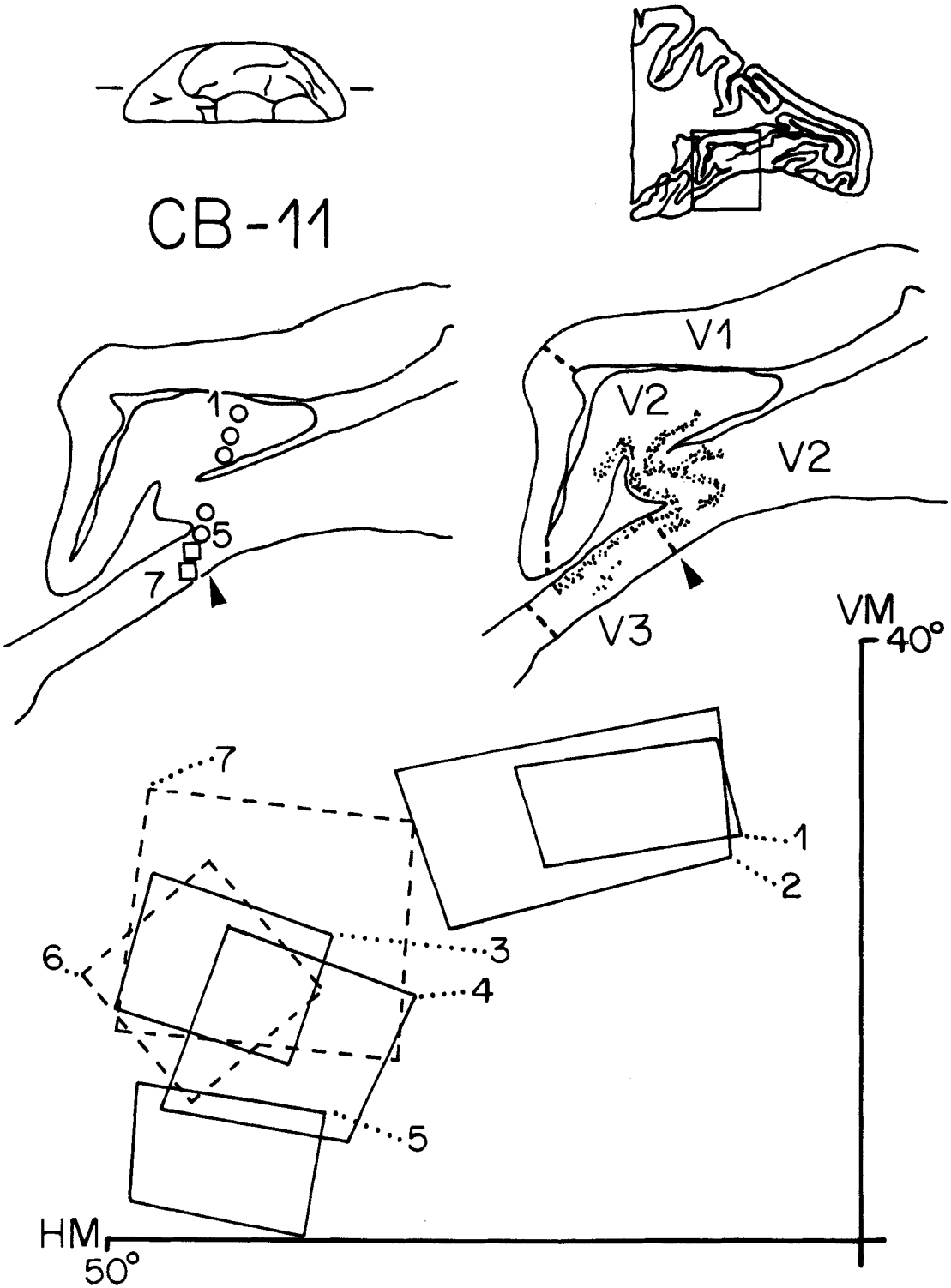

Fig. 11. Coincidence of the transition of distinct laminar patterns of labeled neurons with the electrophysiological and myeloarchitectonic transitions at the border between V2 and V3. Ventral view of the left hemisphere (upper left) showing the level of the section illustrated at upper right. The region inside the box is enlarged and illustrated in the middle. Middle left: Sequence of recording sites along a penetration across V2 and V3. Middle right: Dots represent labeled neurons in V2 and V3; dashed lines, myeloarchitectonic borders; and arrowhead the transition of the laminar pattern of projections. Lower: representation of the upper quadrant showing receptive fields recorded at the sites indicated in the section (middle left).

Similarly, in this study, we have also found several V1 projecting areas. Of these at least six showed topographically organized projections to V1.

Topographic distribution of label

The projections from V2 and MT seem to obey the principle of visuotopic connectivity in which interconnected regions must represent the same parts of the visual field. The clear central-peripheral gradient and upper-lower quadrants segregation revealed by the projections from V2 in this study are consistent with the topography proposed by Rosa et al. ('88). Following the same principle the topography revealed by the projections in MT (see Fig. 10) is also in agreement with the visuotopic organization proposed by Fiorani et al. ('89) for this area. The topographic distribution of the projection zones in MT, however, shows a larger overlap of the patches of labeled cells than in V2. This overlap could be the result of the larger receptive field sizes and scatter of MT as compared to V2 as well as of its smaller magnification factor (Fiorani et al., '89). Perkel et al. ('86) have shown, in the macaque, a similar overlap after two separate injections in V1. These authors attributed this overlap to the wide axonal arborization and scatter in the projections from MT to V1. Similar overlap was also observed in the forward projections from V1 to MT in macaque, in *Aotus,* and in marmoset (Zeki, '71; Spatz, '77; Montero, '80; Tigges et al., '81; Weller and Kaas, '83; Van Essen et al., '86). In *Cebus,* as in macaque, area V2 and MT are reciprocally connected to area V1. Piñon et al. ('90) using tritiated amino acids have shown topographically organized projections from V1 to V2 and to MT in the *Cebus.*

Based on single unit studies, myeloarchitecture, and connections of V1 in macaque, Van Essen et al. ('86) described a dorsoventral asymmetry that led to the proposition of two distinct areas, V3 and VP, anterior to V2. Our data, however, show that unlike the macaque (Newsome et al., '86), in *Cebus* both the dorsal and the ventral portions of V3 project to V1 with a clear gradient of the central-peripheral as well as of the upper-lower quadrant representations. The central-peripheral gradient observed in the region anterior to ventral V2 after upper field injections confirms the visual topography proposed by Gattass et al. ('88b) for ventral V3 in the *Cebus.* The existence of a similar gradient anterior to dorsal V2 after lower field injections, as well as the similar pattern of laminar distribution of labeled cells, led us to name this region as area V3. This area would therefore have a central-peripheral organization similar to that of area V3 described by Zeki ('69) and by Gattass et al. ('88a) in the macaque. This observation, therefore, does not support the notion of a dorsoventral asymmetry in the *Cebus.* Whether this discrepancy is to be attributed only to the different sensitivities of the tracers employed in these studies is doubtful, inasmuch as *Cebus* and macaques are members of different lineages of simians that have been separated for at least 30 million years (Fleagle, '88). Therefore, this may be a real difference between these species. Another observation is that injections placed at the representation of the horizontal meridian resulted in two patches of label in V3, one located dorsally and another ventrally. Thus, like in V2, these data suggest the existence, in the *Cebus,* of a split representation of the HM in this area, as described in the macaque (Zeki, '69; Gattass et al., '88a).

A similar gradient of labeled cells was found in a strip of cortex anterior to V3, allowing us to define another afferent zone of V1, which was named area V4. This area borders V3 for most of its extent, except for the peripheral dorsal component that is separated from V3: it crosses the prelunate gyrus and enters the superior temporal sulcus. The fourth visual area may have a proportionally larger representation of the central regions than other visual areas (see, for example, Fig. 4).

The central-peripheral and upper-lower gradients of V3 and V4 in the *Cebus* are similar to those described for areas V3 and V4 in the macaque (Gattass et al., '88a). In addition the data is also consistent with the existence of a compressed representation of the lower quadrant relative to the upper quadrant in V4, as described in the macaque (Gattass et al., '88a).

In the myeloarchitectonically defined DZ we only observed labeled cells after lower field injections. This projection had, however, a crude central-peripheral gradient, similar to that observed in MT. This crudeness in the representation may also, as in MT, be related to receptive field sizes as well as to the low magnification found in DZ (Fiorani et al., '89). The location and the central-peripheral gradient of area DZ in the *Cebus* are similar to those of area V4t (Desimone and Ungerleider, '86; Gattass et al., '88a) in the macaque. Significant differences in the myeloarchitecture, however, exist between DZ and V4t (Fiorani et al., '89).

We observed a greater involvement of the anterior bank of the superior temporal sulcus after injections in peripheral V1 than after injections placed at the representation of central vision. In both case 7 and case 8, which had injections placed at the representation of the periphery, two patches of labeled cells were found in the superior temporal sulcus (Figs. 8, 9). The more posterior one may correspond to the representation of the periphery in MT. The anteriorly located patch, however, may correspond to a second patch in area MT or may lie in area MST. In case 8 (animal CB11) the most anterior patch is undoubtedly outside myeloarchitectonically defined MT. In both cases the patches of labeled cells in the anterior bank of the superior temporal sulcus were assigned to area MST of the *Cebus* (Fiorani et al., '89). Note, however, that the portion of MST that projects to V1 is somewhat more restricted than the myeloarchitectonic region called MST by these authors. This fact may suggest the existence of functionally distinct areas within this region, as suggested by Komatsu and Wurtz ('88).

After injections in the regions of representation of the upper and lower periphery in V1 we observed labeled cells in the medial parietal cortex in the region corresponding to area PO of the PO complex defined by Neuenschwander ('89) in the *Cebus.* The projections to this area showed a crude retinotopy: a lower quadrant injection labeled neurons along the parietooccipital cleft (Fig. 7), while an upper quadrant injection labeled neurons in the dorsal bank of the medial parietooccipital sulcus and medial surface (Fig. 8). The locations of the upper and lower quadrant projections in PO are in agreement with the visual topography described by Neuenschwander ('89) in the *Cebus.* These projections are also compatible with the representation of upper and lower field in the macaque (Colby et al., '88). In addition, the projecting zones in the *Cebus* are similar to those that receive projections from peripheral V1 in the macaque (Colby et al., '88).

In the anterior portion of the calcarine sulcus and adjacent cortex we observed another area that projects, very

sparsely, to peripheral V1. This region, presumably homologous to the architectonically defined area prostriata (Sanides, '72), showed only a few labeled cells after peripheral injections. A crude retinotopy, with at least a segregation of upper and lower quadrants, appears to be present.

Anterior to V4 in the ventral convexity of the cortex, in both banks of the occipital-temporal sulcus within cytoarchitectonic areas TEO and TF (Von Bonin and Bailey, '47), we found several patches of labeled cells after central, intermediate, and peripheral upper field injections. These observations suggest that the region defined as TVP has a representation of the upper visual field. The peripheral representation of this area borders the peripheral representation of both V2 and V3. The posterior portion of TVP may overlap in part with area TEO as defined in the macaque (Fenstemaker et al., '85; Boussaud et al., '88, '90) and possibly also with area VF (Gattass et al., '86).

Extent of the visual field representation

The injections in V1 reveal distinct ratios of central-peripheral representation in the areas studied in this investigation. In addition, not every injection labeled all visual areas. Some areas, like V2, V3, and V4, showed extensive projections after central injections while others (PO, MST, and PRO) showed labeled cells only after peripheral injections.

The distribution of label in V2 and MT shows that these areas contain nearly a complete representation of the binocular visual field, as previously reported by Rosa et al. ('88) and Fiorani et al. ('89), respectively. The same appears to be true of V3 except for the fact that the projections of the extreme periphery of the lower quadrant can not be clearly distinguished from those of the neighboring area PO. On the other hand, V4 has a proportionally larger representation of the central region. After injections at the representation of the far periphery only a few cells were labeled in this area. This finding suggests that V4 might not have a complete representation of the visual field, a result similar to that described by electrophysiological recordings, in the macaque (Gattass et al., '88a).

Laminar pattern of projections

Similarly to Perkel et al. ('86), in this study we have subdivided the visual areas in three groups according to the laminar distribution of labeled neurons from V1. These authors, however, included V2, V3, and the posterior region of V4 in one group, which, among other characteristics, shows labeling in the infra- and supragranular layers. Our results in the *Cebus* led us to propose a different subdivision from that adopted by Perkel et al. ('86). In one group, which is characterized by dense infra- and supragranular labeling only V2 was included. Dense infra- and sparse supragranular labeling set apart in a second group V3, MT, and PO; V4 and the other projecting areas have been included in a third group characterized by exclusive labeling of the infragranular layers. Since our results were consistent among specimens the differences between our results and those described by Perkel et al. ('86) could be due to distinct organization of extrastriate cortex in *Cebus* and macaque monkeys.

We have not characterized the laminar patterns of projections described in this study as forward, backward, or intermediate inasmuch as it is difficult to classify connections based solely on data obtained with retrograde fluorescent tracers, as previously discussed by Boussaud et al. ('90). Tigges et al. ('81) state that in a pair of interconnected areas the association neurons lie predominantly in the infragranular layers, in anteriormost located areas, while in posteriormost areas they lie in the supragranular layers. In *Cebus* the association neurons of areas that project back to V1 are predominantly located in the infragranular layers. This result is similar to those described by Rockland and Pandya ('79) in macaque and by Tigges et al. ('81) in squirrel monkey.

In areas V3, MT, and PO, however, we occasionally found labeled neurons in the supragranular layers. The existence of supragranular labeling in MT was also described in the marmoset (Spatz, '77) and in the squirrel monkey (Wong-Riley, '79) after injections of HRP in V1. In V2, after injections in V1, Tigges et al. ('81—squirrel monkey) found that most labeled neurons were concentrated in the infragranular layers. This result is in disagreement with those of the present study (*Cebus*) and of Perkel et al. ('86—macaque) in which both infra- and supragranular layers are densely labeled. This unique distribution of label assigns a special status to area V2 that may give support to the hypothesis of Allman and Kaas ('71b) in which areas V2 and V1 would work as a diad.

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