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Three Streams of Visual Information Processing in V2 of *Cebus* Monkey

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ABSTRACT

Gattass and collaborators (Gattass R, Rosa MGP, Souza APB, Piñon MCG, Neuenschwander S [1990a] Braz J Med Biol Res 23:375–393) proposed that the dorsal stream of visual processing, as defined by Ungerleider and Mishkin (Ungerleider LG, Mishkin M [1982] In: Ingle DJ, Goodale MA, Mansfield RJW, editors. Analysis of visual behavior. Cambridge: Massachusetts Institute of Technology. p 549–586), can be subdivided into dorsolateral and dorsomedial streams, and suggested that they may be involved in different aspects of the processing of motion and spatial perception, respectively. The goal of the present study was to provide additional evidence for this hypothesis by using cytochrome oxidase immunohistochemistry combined with retrograde tracing techniques. In Old World monkeys, the locations of visual area 4 (V4; ventral stream) and middle temporal area (MT; dorsal stream) projecting neurons in V2 supports the hypothesis that the cytochrome oxidase (CytOx)–rich thin stripes and the CytOx-poor interstripes are associated with the ventral stream, and that the CytOx-rich thick stripes belong to the dorsal stream. In this study we describe, in the New World monkey *Cebus*, the distribution of retrogradely labeled cells in V2 relative to the CytOx compartments after fluorescent tracers were placed in areas V4, MT, and the parietooccipital area (PO). We found PO-projecting neurons in CytOx-rich thick stripes and CytOx-poor interstripes in V2, whereas MT-projecting neurons appeared almost exclusively in thick stripes. In contrast, V4-projecting neurons were located mostly in CytOx-poor interstripes and CytOx-rich thin stripes. In addition, V4- and MT-projecting neurons were located mainly in supragranular layers, whereas PO-projecting neurons were located in supragranular and infragranular layers. These results support the hypothesis for the existence of three distinct streams of visual processing: ventral (including V4), dorsolateral (including MT), and dorsomedial (including PO). J. Comp. Neurol. 466:104–118, 2003.

Indexing terms: cytochrome oxidase stripes; visual area 2 modules; visual area 4; middle temporal area; parietooccipital area; New World monkey

The notion of two independent visual streams of information processing based on fragmented experimental evidence has been in the literature since the late 1960s (Trevarthen, 1968; Schneider, 1969). These investigators proposed segregation for focal and ambient vision (Trevarthen, 1968) or for a system to identify the stimulus (what) and another to localize it in visual space (where) depending on the geniculate striate and tectal systems (Schneider, 1969). Ungerleider and Mishkin (1982), based on anatomic and behavioral evidence, proposed that the topographically defined cortical visual areas of nonhuman primates (Van Essen, 1985; Gattass et al., 1990b) could be segregated into two functional streams of visual information processing. Areas of the ventral stream channel visual information about shape, texture, and color of objects to the inferior temporal cortex, and those of the dorsal stream process movement and spatial relationships

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of objects and project to the parietal cortex. Based on anatomic and electrophysiologic data Gattass et al. (1990a; Neuenschwander et al., 1994) suggested a subdivision of the dorsal pathway into two streams, which may be involved in different aspects of motion and spatial vision processing. These investigators proposed a dorsolateral stream involving the visual middle temporal area (MT), medial superior temporal area, and the ventral and dorsal lateral intraparietal areas and a dorsomedial stream involving the parietooccipital visual area (PO) in the anterior bank of the parietooccipital sulcus and the precuneate gyrus (Gattass et al., 1987; Rosa et al., 1988a; Fiorani et al., 1989; Neuenschwander et al., 1994; Piñon et al., 1998). A subdivision of the ventral stream has been proposed by Martin-Elkins and Horel (1992) based on afferent connections of different subregions in the anterior inferior temporal gyrus. They suggested a direct projection from visual area 4 (V4) to the temporal occipital externa area and the temporal externa area underlying visual discrimination and another indirect projection to the temporal externa area, via area temporal F of parahippocampal gyrus, involved in memory processes necessary for the correct performance on delayed matched-to-sample tasks. Goodale (1993), Goodale and Milner (1992) and Milner and Goodale (1993) proposed an alternate interpretation for the two visual processing streams, one involved in perceptual representation and the other in visuomotor control. More recently, Rosa and Tweedale (2001) also proposed the concept of two "dorsal streams" and suggested that the dorsolateral stream is important for the control of eye movements, whereas the dorsomedial stream provides signals that are important for the control of the skeletal musculature. Studies with magnetic resonance imaging and multidimensional scanning in humans also have suggested a segregation of the visual processing streams and that this organization may be present in all primates (Young, 1992).

In the present study, we provide additional evidence for two dorsal streams by using the well-characterized cytochrome oxidase (CytOx) profile of visual area 2 (V2) to show that this area is differentially connected with regions of the dorsomedial and dorsolateral streams of visual processing. It has been proposed that visual area 1 (V1) and V2 in primates can be subdivided into functionally distinct modules, such as those demonstrated by CytOx histochemistry (Carroll and Wong-Riley, 1984; Wong-Riley and Carroll, 1984; Tootell et al., 1985; Wong-Riley, 1988, 1989; Sincich and Horton, 2002a). The second visual area (V2), when stained for the mitochondria enzyme CytOx, shows a pattern of alternating thick and thin CytOx-rich stripes running perpendicular to the V1/V2 border and separated by CytOx-poor interstripes (Livingstone and Hubel, 1983; Wong-Riley and Carroll, 1984; Gattass et al., 1990a; De Yoe and Van Essen, 1985; Zeki and Shipp, 1989a). These three types of stripes differ in neuronal properties and connections (De Yoe and Van Essen, 1985; Zeki and Shipp, 1989a,b; Nakamura et al., 1993; Levitt et al., 1994a,b; Roe and T'so, 1995; Olavarria and Van Essen, 1997). Recently, Sincich and Horton (2002bb) reported an intermingling of visual information at early stages in the neocortex of macaque monkeys. After small injections into interstripe regions and viewing CytOx-rich thick stripes in V2, these researchers found double-labeled cells in interblob regions in V1. Although the projection from interblobs in V1 to CytOx-poor interstripe and CytOx-rich thick stripes in V2 arise from a common source, most neurons do project exclusively to a CytOx-poor or a CytOx-rich thick stripe. They proposed a rich intermingling of form, color, and motion signals between the ventral and dorsal streams of visual information processing.

In *Cebus*, the study of V2 in sections tangential to the cortical surface reacting to CytOx shows a pattern similar to the one described in *Saimiri* and *Macaca* (Rosa et al., 1988b; Wong-Riley and Carroll, 1984; Gattass et al., 1990a; Livingstone and Hubel, 1983; De Yoe and Van Essen, 1985; Zeki and Shipp, 1989a; Nakamura et al., 1993; Shipp and Zeki, 1995). Thus, to evaluate whether there is a segregation of the streams of visual information processing in CytOx modules of V2, we injected fluorescent retrograde tracers into V4, MT, and PO and studied the distribution of labeled cells in these modules. The distribution of labeled cells provided evidence for parallel pathways with origins in different CytOx modules in area V2. Preliminary reports of these data have been published elsewhere (Nascimento-Silva et al., 1995, 1997).

Abbreviations

Cortical visual areas	
MST	medial superior temporal area
MT	middle temporal area
PO	parieto-occipital area
TE	temporal externa area
TEO	temporal occipital externa area
TF	area temporal F of parahippocampal gyrus
V1	visual area 1 (primary visual cortex)
V2	visual area 2
V3	visual area 3
V4	visual area 4
Cortical sulciar	
ar	arcuate sulcus
ca	calcarine fissure
ce	central sulcus
ci	cingulate sulcus
io	inferior occipital sulcus
ip	intraparietal sulcus
la	lateral sulcus
lu	lunate sulcus
ot	occipitotemporal sulcus
p	principal sulcus
pmt	posterior middle temporal sulcus
po	parietooccipital sulcus
sl	lateral sulcus
st	superior temporal sulcus
tmp	temporal medial sulcus
Others	
CytOx	cytochrome oxidase
HM	horizontal meridian
VM	vertical meridian

MATERIALS AND METHODS

Nine adult *Cebus apella* monkeys, weighing between 1.8 and 2.9 kg, were used. Injections of two or three different fluorescent retrograde tracers were made into one or both hemispheres of each animal. We used previous topographic studies of V4 by Piñon et al. (1998), MT by Fiorani et al. (1989), and PO by Neuenschwander et al. (1994) to help place injections at similar eccentricities in all areas. Areas PO and MT received injections of Diamidine Yellow (Molecular Probes, Eugene, OR) and Fast Blue (Molecular Probes) and V4 was injected with Fluor Ruby (Molecular Probes) or Diamidine Yellow. We used 12 hemispheres: in

TABLE 1. Location of Injection Sites, Fluorescent Tracers, and Plane of Sections

Case	Animal	Plane of section	Injection site	Tracer RH	Tracer LH
			V4		DY
1	CB51	Flattened	MT	DY	
			PO	FB	FB
2	CB50	Flattened	V4	DY	DY
			V4	FR	
3	CB48	Coronal	MT	DY	
			PO	FB	
4	CB79	Flattened	MT		DY
5	CB 60	Flattened	V4	DY	
			PO	FB	
			V4		FR
6	CB52	Coronal	MT	DY	
			PO		FB
7	CB57	Flattened	MT		DY
			PO		FB
8	CB72	Flattened	MT		FB
			PO		DY
			V4		FR
9	CB47	Parasagittal	MT		DY
			PO		FB

DY, 5% Diamidine Yellow; FB, 10% Fast Blue; FR, 10% Fluor Ruby; LH, left hemisphere; MT, middle temporal area; PO, parietal occipital area; RH, right hemisphere; V4, visual area 4.

four hemispheres, we placed injections into a single area; in six, the injections were placed in two areas, PO and V4 or PO and MT; in the remaining two hemispheres, all three areas were injected. One hemisphere was sectioned in the parasagittal plane, three others in the coronal plane, and the remaining eight hemispheres were sectioned parallel to the pial surface by using flattened preparations of the cortex (Table 1).

Animal preparation and fluorescent retrograde tracer injections

The experiments were carried out in accordance with the Animal Care and Use procedures of the Guide for the Care and Use of Laboratory Animals by the National Institutes of Health (1995) and the guidelines of the Commission for Use of Experimental Animals of the Instituto de Biofisica Carlos Chagas Filho.

Animals were treated with dexamethasone (0.5 mg/kg; Decadron, Prodome, São Paulo, Brazil) for 3 days before surgery. On the day of surgery, animals underwent preanesthetic medication with atropine (0.15 mg/kg, intramuscularly; Atropina, Hypofarma, São Paulo, Brazil) and benzodiazepine (0.5 mg/kg, intramuscularly; Valium, Roche, Rio de Janeiro, Brazil). The animals were then anesthetized with ketamine hydrochloride (30 mg/kg, intramuscularly; Ketalar, Parke-Davis, São Paulo, Brazil) and maintained with sodium pentobarbital infusion (10 mg/kg, intravenously) or 2% Fluothane (Zenica, São Paulo, Brazil) in a mixture of N_2O_2:O_2 (70:30%). The level of the expired CO_2, rectal temperature, and heart rate were continuously monitored throughout the experiment and kept within physiologic range. Artificial ventilation, when needed, was maintained by means of a respiratory pump connected to a tracheal cannula. Under sterile conditions, craniotomies were made over the intended injection site(s) and the dura mater was sectioned to expose the cortical surface. All injections were placed under visual guidance. In the dorsal portion of V4, multiple injections were placed with a 1-liter Hamilton syringe with a 27-gauge needle. For injections into MT, we removed, by aspiration, the anterior bank of the temporal sulcus to expose the posterior bank and floor of the superior temporal sulcus, thus allowing the placement of multiple injections into the center of MT. For injections into PO, located in the medial surface, it was necessary to gently push the hemisphere laterally. Multiple injections were made into PO in the precuneate gyrus next to the border of the PO sulcus.

After the injections, the wound was closed in anatomic layers and, as a prophylactic measure, the animals received an intramuscular injection of G penicillin (300,000 IU; Benzetacil, Eurofarma, São Paulo, Brazil).

Histologic processing

After survival times of 14 to 21 days, six animals received a lethal dose of sodium pentobarbital (90 mg/kg, intravenously) and were perfused intracardially with 0.9% saline followed by 0.1 M phosphate buffer, pH 7.4. The brain was removed from the skull, and a block containing V1 and V2 was separated from the rest of the brain. The V1/V2 block was then flattened by using a method (method II) described by Tootell and Silverman (1985), which is similar to the method described by Olavarria and Van Sluyters (1985). The flattened preparation was fixed with a solution of paraformaldehyde (4%) in 0.1 M phosphate buffer for 12 hours and stored overnight in phosphate buffer and glycerol (10%). Frozen sections (40 μm) were cut in the tangential plane. Alternate sections were used for fluorescent analysis or stained for CytOx according to the procedure modified by Silverman and Tootell (1987). The other three animals were perfused with 0.9% saline followed by 4% paraformaldehyde in 0.1 M phosphate buffer, pH 7.4. The brains were removed from the skull, blocked, and stored overnight in phosphate buffer. The blocks were frozen and sectioned (40 μm) in the parasagittal or the coronal plane (Table 1). Alternate sections were stained for cell bodies (Nissl method), myelinated fibers (Gallyas method), and CytOx or were reserved for fluorescent analysis and stored, unstained, at 4°C in the dark.

Data analysis

Nonstained sections were scanned for the distribution of retrogradely labeled cells by using a Leitz Diaplan fluorescence microscope interfaced to a Minnesota Datamatrix X-Y System, Minnesota. The labeled neurons were plotted onto drawings of the section contours. Each section stained for CytOx histochemistry was photographed, and the prints, were used for the reconstruction of the stripe pattern in V2. Labeled cells were projected onto the photographic reconstruction of the CytOx compartments of V2 to allow the analysis of the relation of labeled cells in V2 to the CytOx modules. In single parasagittal, coronal, or tangential sections, we found it difficult to unequivocally distinguish the different CytOx modules because the stripes showed an irregular pattern, with bifurcation or nonhomogeneities similar to those described in *Macaca* by Levitt et al. (1994a) and Olavarria and Van Essen (1997). Thus, we analyzed serial sections and aligned the slides to help reconstruct the stripe pattern.

Injection sites

In cases in which the injection sites were contained in the flattened preparations, we performed measurements to confirm that the injection sites were restricted to the

intended area and were located within the gray matter. In the remaining cases, the brain was sectioned in the coronal or the parasagittal plane. We reconstructed the injection sites based on Nissl- or Gallyas-stained sections. The eccentricities of the injection site and label in V2 were estimated based on the distribution of labeled neurons in V1 and V2 as compared with published visuotopic maps (Gattass et al., 1987; Rosa et al., 1988a).

Two-dimensional reconstruction of the visual cortex

For cases sectioned in the coronal or parasagittal plane, we produced two-dimensional unfolding of the cortical surface by using three-dimensional wire models, based on contours of layer IV of sections (Gattass and Gross, 1981). Myeloarchitectonic borders of V1, V2, V4, MT, and PO, the injection sites, and the labeled cells were transferred onto the flattened two-dimensional maps.

RESULTS

In the present section, we first describe the locations of V4-, MT-, and PO-projecting neurons in relation to the CytOx modules in V2. Then we describe the laminar distribution of the labeled cells for each projection.

Projections from V2 to V4

We injected V4 in seven hemispheres at eccentricities varying from 2 to 30 degrees. In all cases, clusters of labeled cells in V2 were found in distinct stripes orthogonal to the V1/V2 border. By overlapping the plot of V4-projecting cells with the photographs of CytOx-stained adjacent sections, we were able to locate the cells in relation to the CytOx pattern of V2. Figure 1 shows that V4-projecting neurons were located in thin stripes and interstripe regions in central V2 (case 1, 2–7 degrees of eccentricity), whereas cells had no particular organization outside V2. In this case, the injection site, at 30 degrees of eccentricity, was more restricted than in other cases. In case 2, the labeled cells in the ventral part of V2 (Fig. 2) were organized in clusters that matched the morphology of the stripes and ran orthogonally to the V1/V2 border. In both cases, the cells avoided the thick stripes.

Projections from V2 to MT

Injections into MT of seven hemispheres resulted in a large number of labeled neurons restricted to the thick stripes in V2. Figure 3 shows the distribution of labeled neurons in V2 and neighboring areas after multiple injections into MT, on the floor of the superior temporal sulcus in cases 1 and 4. The labeled cells in V2 formed bandlike structures with the expected orientation of CytOx stripes. MT-projecting neurons were organized in clusters orthogonal to V1/V2 border, almost restricted to the thick stripes. No labeled neurons were found in CytOx-rich thin stripes, and few cells were located in the interstripes.

In case 3, injections into the upper field peripheral representations of PO and MT (Fig. 4) resulted in individually labeled neurons in thick stripes and interstripe regions of ventral V2. MT-projecting neurons in V2 were restricted to the thick stripes, whereas those projecting to PO also were found in interstripe regions. In coronal sections, MT-projecting neurons in V2 were intermingled with neurons projecting to PO; no double-labeled neurons were found.

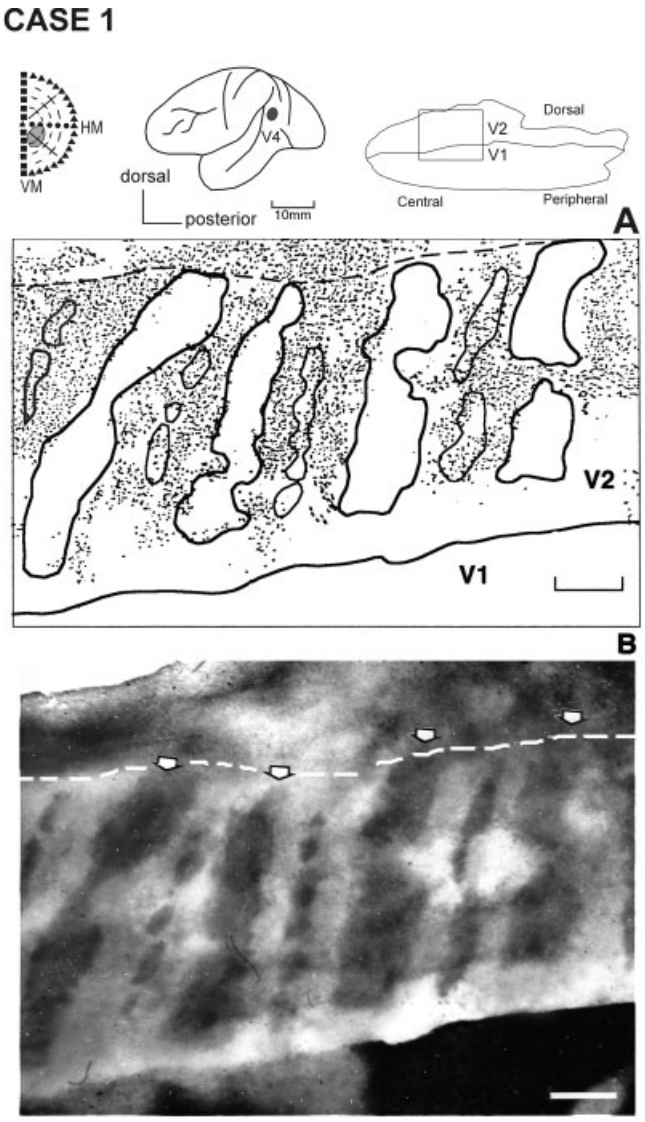

Fig. 1. Neurons in central visual area 2 (V2) projecting to visual area 4 (V4). Top left: Extent of the visual field represented at the injection site (2- to 15-degree eccentricities); top middle: lateral view of the hemisphere with the injection site indicated; top right: outline drawing of the flattened preparation of the dorsolateral portion of V2 in case 1. Boxed area indicates the region enlarged in A and B. **A:** Dots represent V4-projecting neurons, dashed lines (also in B) indicates the border between V2 and visual area 3 (V3), and the heavy solid line indicates the border between V2 and V1. Thin solid lines delineate the thin cytochrome oxidase (CytOx)–rich modules, and the heavy solid lines delineate the thick CytOx-rich modules. **B:** Photomicrograph of a tangential section of V2, with the thick striped regions indicated by arrows. Note that cells avoid the thick stripe regions. For abbreviations in all figures, see the Abbreviations list. Scale bars = 2 mm in A.

Projections from V2 to PO

After injections into PO in seven cases, we found a large number of labeled neurons in V2 in the region corresponding to the peripheral representation of the visual field, with eccentricities greater than 10 degrees. In all cases, the location of PO-projecting neurons in V2 included the

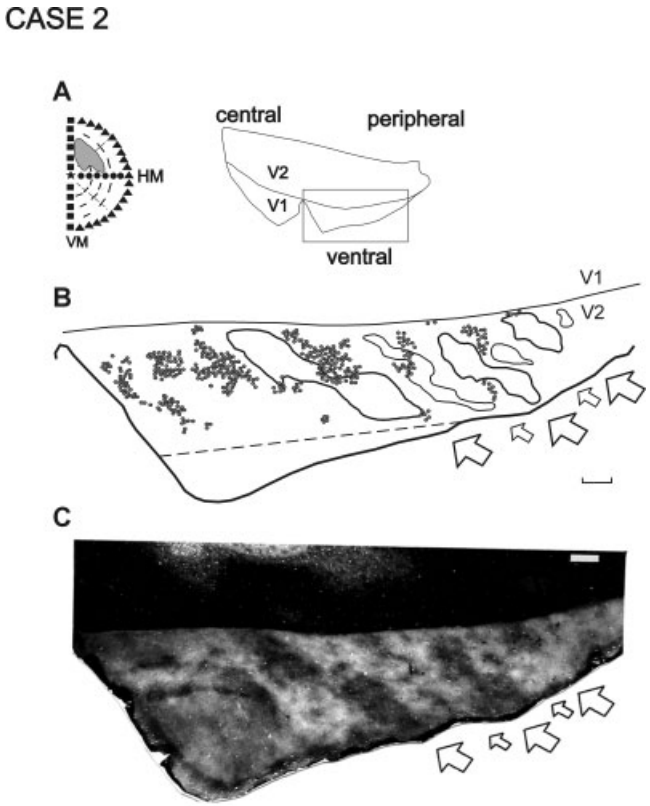

Fig. 2. Neurons in peripheral visual area 2 (V2) projecting to visual area 4 (V4). **A:** Left, extent of the visual field represented at the injection site into V4 (7- to 27-degree eccentricity). Right, outline drawing of the flattened preparation of the ventral portion of V2 in case 2. Boxed area indicates the region enlarged in B and C. **B:** Distribution of V4-projecting neurons (+) relative to cytochrome oxidase modules. **C:** Photomicrograph of the tangential section illustrated in B. In B and C, the small and large arrows indicate the thin and thick stripes, respectively. All other conventions as in Figure 1. Scale bar in B, C = 1 mm.

binocular and monocular representations of the visual field. In this respect, PO-projecting neurons were different from MT-projecting neurons, which were observed only in the region of binocular representation. In addition, labeled cells that projected to PO were located in CytOx-rich thick stripes and CytOx-poor interstripes of V2 in supragranular and infragranular layers. Figure 5 shows a photomicrographic reconstruction and enlarged photomicrographs of the lower bank of the calcarine sulcus in case 3 (also shown in Fig. 4) depicting PO-projecting neurons in supragranular (Fig. 5B,C) and infragranular (Fig. 5C) layers.

Figure 6 (case 5) shows clusters of labeled cells in the ventral portion of V2 after injections into the upper field representation of PO. In this case, the stain for CytOx revealed a clear pattern of alternate CytOx-rich and CytOx-poor zones, with groups of labeled cells in CytOx-rich and CytOx-poor zones.

Figure 7 (case 5) shows the resulting distribution of labeled cells in the dorsal portion of V2 in a case that received multiple injections into PO. After this large injection, most PO-projecting neurons of V2 were concentrated in thick CytOx-rich and CytOx-poor interstripe regions, with few cells in the thin stripes. In this case, labeled cells also were observed anterior to V2.

Overall, the injections into PO demonstrated that the origin of the dorsomedial stream in V2 is concentrated in the CytOx-rich thick and CytOx-poor interstripe modules in the peripheral representation of V2. The injections also showed that PO-projecting neurons of V2 coexist in the interstripes with V4-projecting neurons and in the thick stripes with MT-projecting neurons. Here again, no double-labeled neurons were found.

Laminar distribution of labeled cells

The laminar distribution of labeled cells in V2 after injections into V4, MT, and PO was analyzed in relation to the cortical layers. To identify the laminar distribution, we used adjacent sections stained for cell bodies to determine the location of the labeled cells relative to the granular layer.

Figure 8 (case 6) shows an example of laminar distribution in a series of coronal sections of V2 in a case that received multiple injections into PO. PO-projecting neurons were in the supra- and infragranular layers, but not in the granular layer. This pattern was observed in all cases in which we injected PO.

The resulting laminar distribution of labeled cells after multiple injections into V4, MT, and PO is shown in Figure 9 in a series of coronal sections. PO-projecting neurons showed a singular pattern in their location relative to the cortical layers (see also Figs. 8, 10). PO-projecting cells were in supragranular layers II and III and in infragranular layer VI, avoiding layer IV (Fig. 10), whereas V4- and MT-projecting neurons were found only in layers II and III.

Distribution of cells in CytOx modules of V2

To evaluate the relative distribution of the labeled cells within the CytOx modules of V2, we counted the cells in each module and across tangential cortical sections of two monkeys. Figure 11 shows that V4-projecting neurons were located mainly in the CytOx-poor interstripes (63%, 332 of 529) and less in the CytOx-rich thin stripes (31%, 164 of 529), whereas cells projecting to MT were concentrated in CytOx-rich thick stripes (97%, 394 of 404). PO-projecting neurons were equally distributed in CytOx-rich thick stripes (48%, 984 of 2,042) and CytOx-poor interstripes (45%, 937 of 2,042), and their distribution differed statistically from those of V4- and MT-projecting neurons ($P < 0.01$).

We searched for double labeling in 18 superimposed projection fields in V2 in the seven cases studied. Although we found MT- and PO-projecting neurons in the thick stripes and PO- and V4-projecting neurons in the interstripes, there were no double-labeled cells in V2 after multiple injections into V4, MT, and PO.

DISCUSSION

First, we discuss the relationship between our results and those obtained in other species. Second, we reevaluate the visual information processing streams and their relation to the CytOx modules of V2. Third, we discuss the laminar distribution of these projections in *Cebus* in relation to the hierarchical location of the extrastriate visual areas.

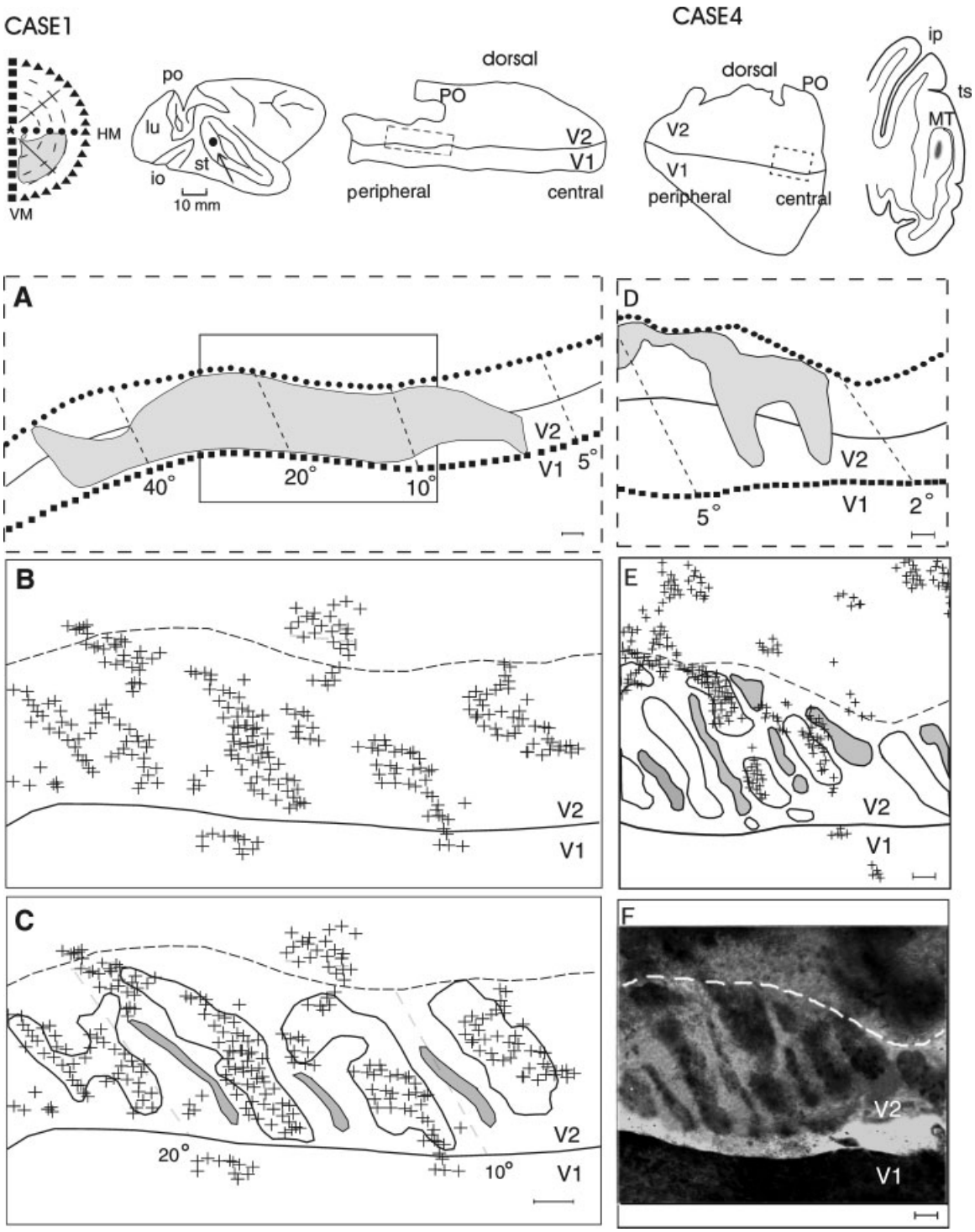

Fig. 3. Neurons in visual area 2 (V2) projecting to the middle temporal area (MT) in cases 1 and 4. **A, D:** Regions containing labeled cells (shaded areas) in relation to the visual topography of V2. The extent of the visual field (upper left) represented at the injection sites (upper middle) includes eccentricities from 7 to 60 degrees in case 1 and from 2 to 6 degrees in case 4. **B, C, E:** The distribution of labeled cells (+) after injections of Diamidine Yellow into MT is shown on flattened preparations of dorsal V2. MT-projecting neurons are organized in regular patches orthogonal to the V1/V2 border (solid line) extending to the anterior border of V2 (dashed line). **F:** Photomicrograph of the tangential section shown in E. The horizontal meridian (HM) is represented by solid circles, the vertical meridian by squares, and the eccentricity lines by dashed lines. See also Figures 1 and 2. Scale bar = 1 mm.

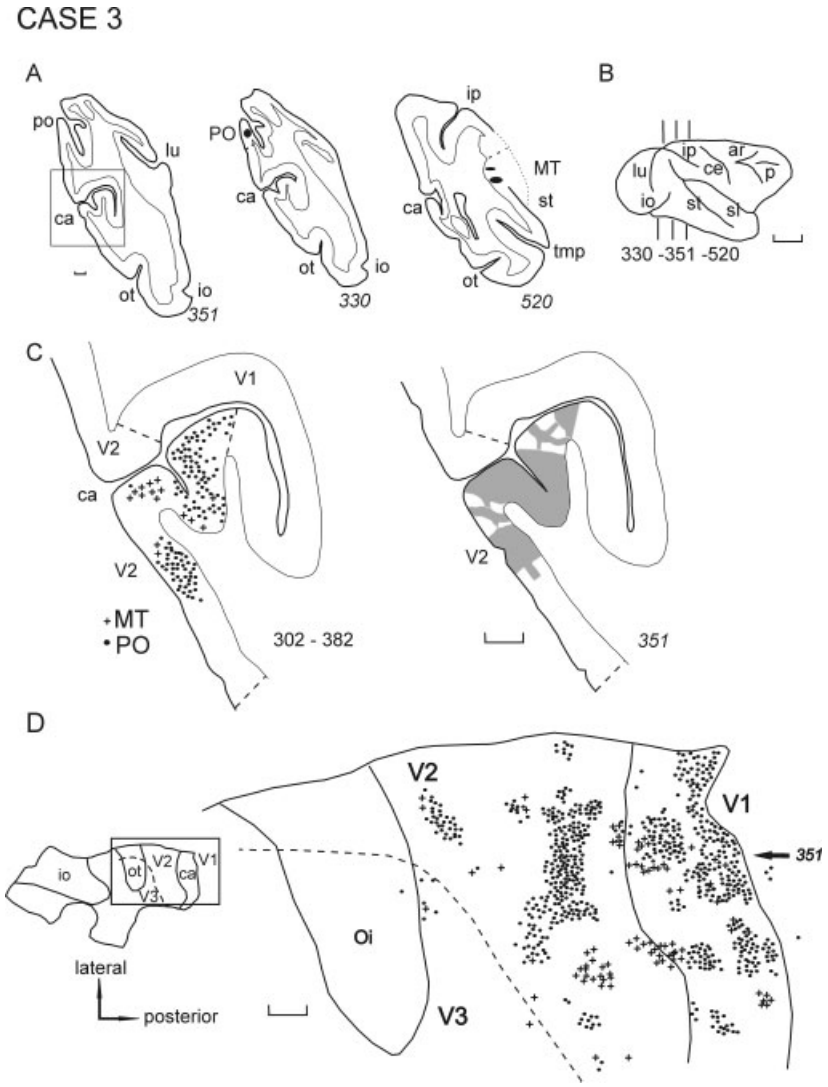

Fig. 4. Projection from visual area 2 (V2) to the middle temporal area (MT) and the parietooccipital area (PO) in case 3. **A:** Coronal sections at the levels indicated in the lateral view of the hemisphere (**B**) show the projection zone (boxed area) and the injection sites into PO (middle) and MT (right). **C:** The calcarine fissure is enlarged to show the labeled cells from nine overlaid sections (left) and the drawings of the cytochrome oxidase modules in V2 (right). PO- (dots) and MT- (+) projecting neurons are intermingled in thick stripes. **D:** Enlarged portion of the flattened map of V2 and surrounding areas (boxed area at left) shows the distribution of labeled cells. An arrow indicates the level of section 351. Scale bars = 2 mm in A, C, D; 10 mm in B.

Comparison with data from other species

There are similarities between the pattern of projections of V2 to PO and V4 in New and Old World monkeys. In the New World monkey *Aotus trivirgatus*, the dorsomedial area (DM) receives topographically organized projections from V1 and V2 (Krubitzer and Kaas, 1993; Casagrande and Kaas, 1994) similar to the macaque, in which PO (or V6) receives topographically organized projections from V1 and V2. The projections from V2 to PO originate predominantly from the supragranular layers, whereas those from V1 originate from layer IVb and supragranular layers (Colby et al., 1988; Rosa and Tweedale, 2001). In *Cebus*, the projections to PO arise from supra- and infragranular layers of V2 and from supragranular layers of V1. The projections from V1 and V2 to MT differ from those to PO. The projections to MT arise from the supragranular layers of V1 (Rosa et al., 1993) and V2, whereas those to PO arise from supragranular and infragranular layers (no labeled cells in layer IV).

The similarities with regard to the topographic organization, connectivity, and relative location of PO and DM also suggest a homology between these two areas (Neuenschwander et al., 1994). This area was characterized in *Macaca* as an area with a distinct myeloarchitecture containing a complex visuotopic map with no emphasis of the central field representation (Covey et al., 1982; Colby et al., 1988). Based on its location, pattern of connections, and basic topographic arrangements, Gattass et al. (1990b) suggested a possible homology to visual area M as described by Allman and Kaas (1976) in the owl monkey.

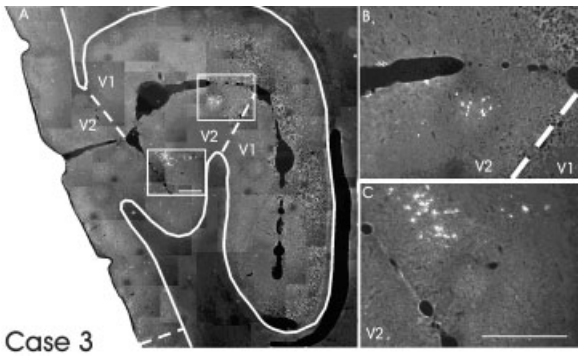

Fig. 5. Neurons in visual area 2 (V2) projecting to the parietooccipital area (PO) in case 3. **A:** Photomicrographic reconstruction of a coronal section (section 362 in Fig. 4) through the calcarine fissure shows areas containing PO-projecting cells in V2, enlarged in **B** and **C** (boxed areas). The continuous line indicates the limit between the gray and white matter, and the dashed lines represent the myeloarchitectonic borders. Scale bars = 1 mm in A, C.

However, the study of the afferent connections of PO (Colby et al., 1988) showed that peripheral V1 and peripheral V2 project heavily to this area, as they do to DM in the owl monkey (Krubitzer and Kaas, 1993). Based on the relative location, connections with V1 and V2, and its myeloarchitecture, Neuenschwander and collaborators suggested a homology of PO with DM of *Aotus* (Neuenschwander, 1989; Neuenschwander et al., 1994). In addressing the connection of the visual areas in primates, Casagrande and Kaas (1994) termed the region of the anterior bank of the parietooccipital cleft in macaque as *DM*. In the owl monkey, Krubitzer and Kaas (1993) proposed that PO could be part of dorsal V3 inasmuch as both areas receive direct projections from V1. The visual topography, location, and continuity of portions of dorsal V3 was shown to vary from animal to animal in macaque (Gattass at al., 1988). However, upper and lower central V2s project to V3 and dorsal V3, whereas upper and lower peripheral V2s project to PO (Gattass et al., 1997). In

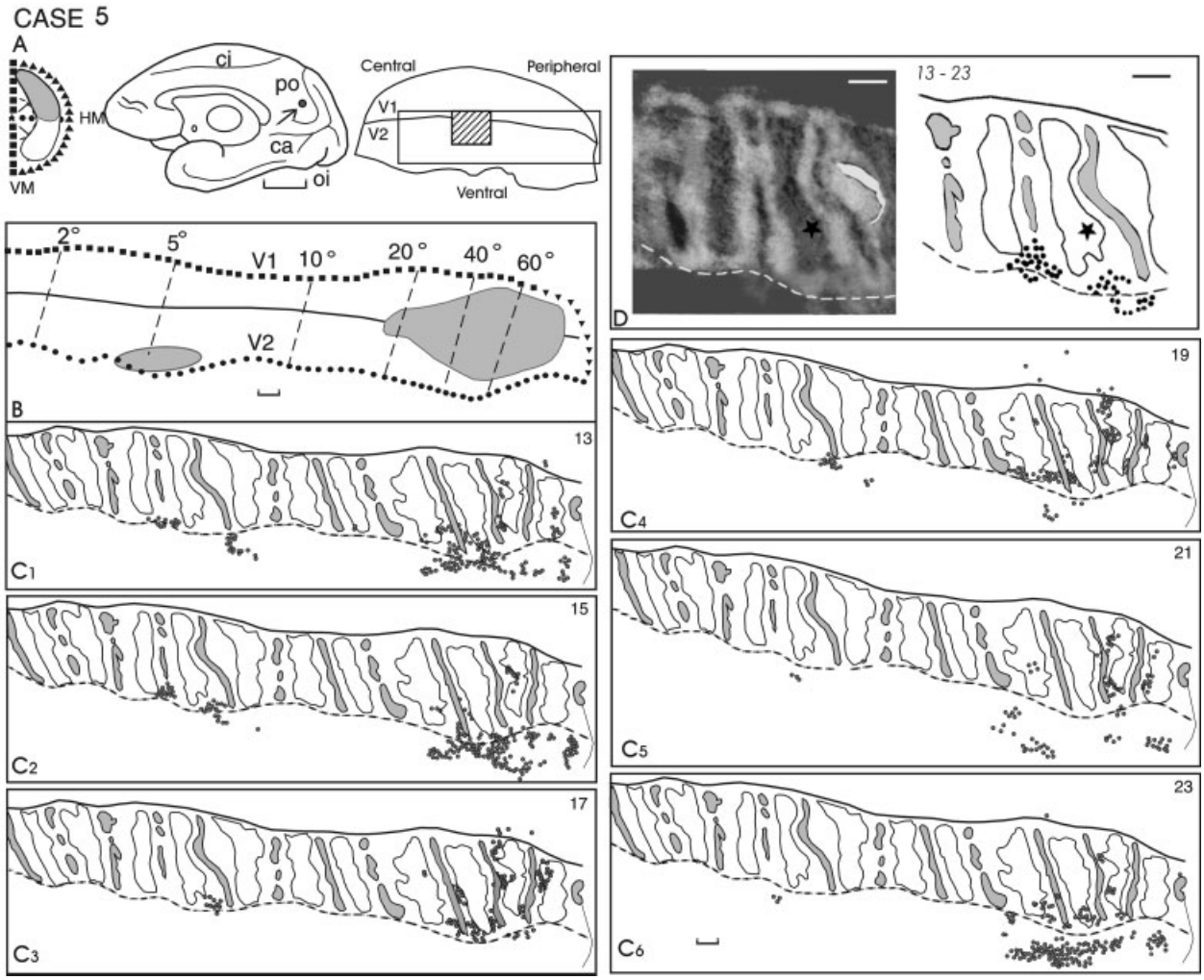

Fig. 6. Neurons in ventral visual area 2 (V2) projecting to the parietooccipital area (PO) in case 5. **A:** The distribution of labeled cells (dots) after injections of Fast Blue into the PO is shown on a flattened preparation of the ventral portion of V2 (upper right). **B:** Regions containing labeled cells (shaded areas) are related to the visual topography of V2. **D:** The hatched box in A is enlarged to show the relation of labeled cells (right) to the cytochrome oxidase (CytOx) modules of V2 (left). PO-projecting neurons avoid the thin CytOx-rich stripes (light gray) of V2. **C_1–C_6:** Tangential sections parallel to the pial surface show the distribution of labeled cells (dots; section numbers are indicated on the upper right corner). Stars indicate the same location in the cortex. See also Figures 1–3. Scale bars = 10 mm in A; 1 mm in B, D, C_6.

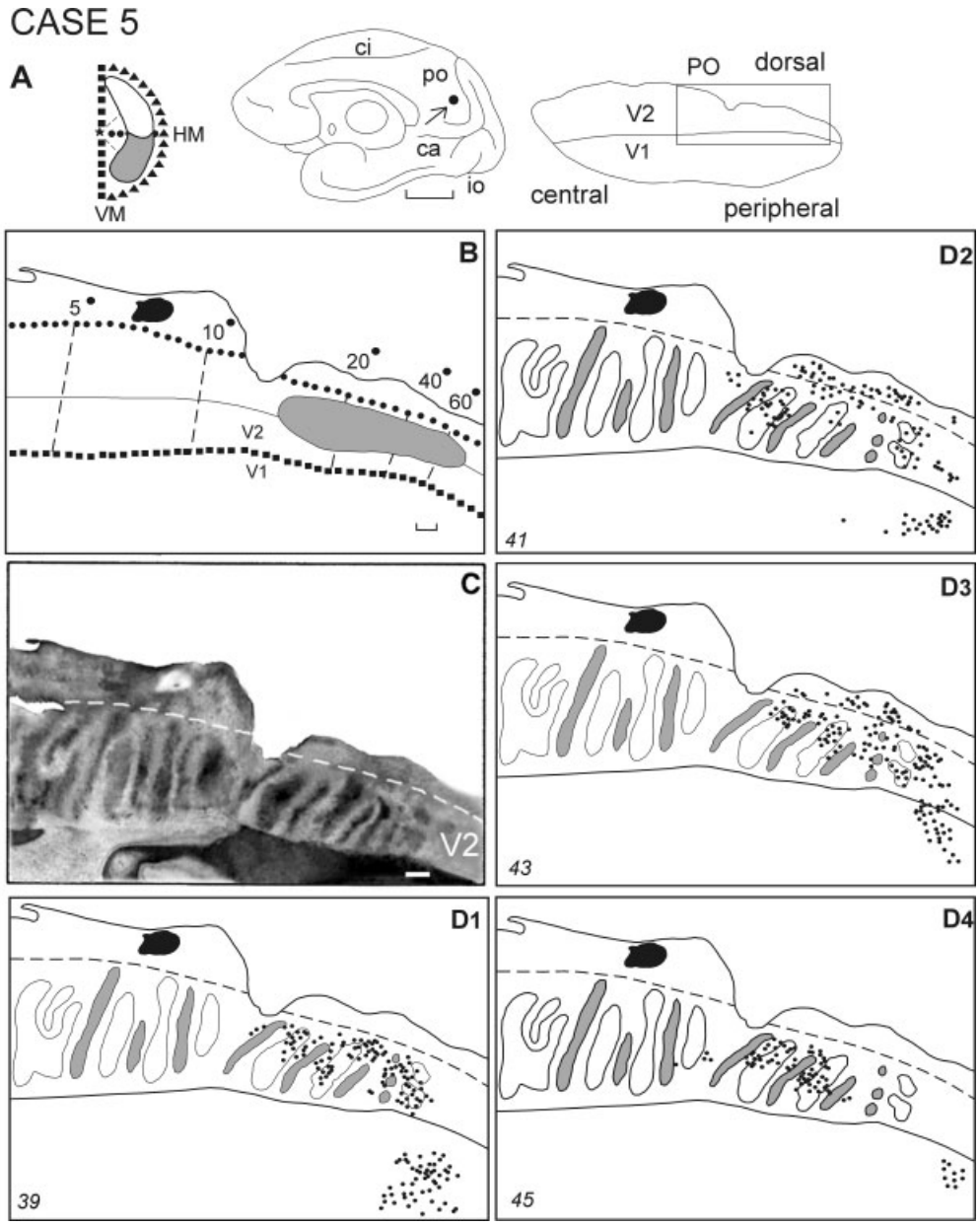

Fig. 7. Neurons in dorsal visual area 2 (V2) projecting to the parietooccipital area (PO) in case 5. **A:** The extent of the visual field (left) represented at the injection site includes eccentricities from 15 to 70 degrees. **B, D:** The injection site is indicated in black and corresponds to the pale region in C. The region containing the labeled cells (shaded area) is related to the visual topography of V2 in B. **C:** Photomicrograph montage of sections parallel to the pial surface stained for the cytochrome oxidase (CytOx) enzyme. **D_1–D_4:** Flattened preparations of V2 and surrounding areas show the relation of the labeled cells to the CytOx-rich modules of V2. PO-projecting neurons avoid the thin CytOx-rich stripes (thin solid line) of V2. Section numbers are indicated in the lower left corner. See also Figures 1–3. Scale bars = 10 mm in A; 1 mm in B (applies to B–D4).

addition, Sousa et al. (1991) found that in *Cebus* dorsal and ventral V3s project back to V1. Thus, the distinction of PO from V3 and V3A is based on myeloarchitecture, connections with V2 (Gattass et al., 1997), and immunohistochemistry for SMI-32 (Hof and Morrison, 1995). Based on visual topography, receptive field size, and myeloarchitecture in *Cebus*, Neuenschwander et al. (1994) showed two distinct areas in the anterior bank of parietooccipital sulcus and named them *PO* and *POd*. POd has larger receptive fields and a distinct myeloarchitecture. For Krubitzer and Kaas (1990b, 1993) and Casagrande and Kaas (1994), the projections to DM in primates arise from CytOx-rich stripes, with virtually no cells in the interstripes. However, in five of the five cases injected, we found that in *Cebus* CytOx-rich thick stripes and CytOx-poor interstripes of V2 project to PO (Figs. 4, 6, 7). Thus, a more conservative interpretation of the connectional data suggests that the differences in the connectivity of V2 to DM

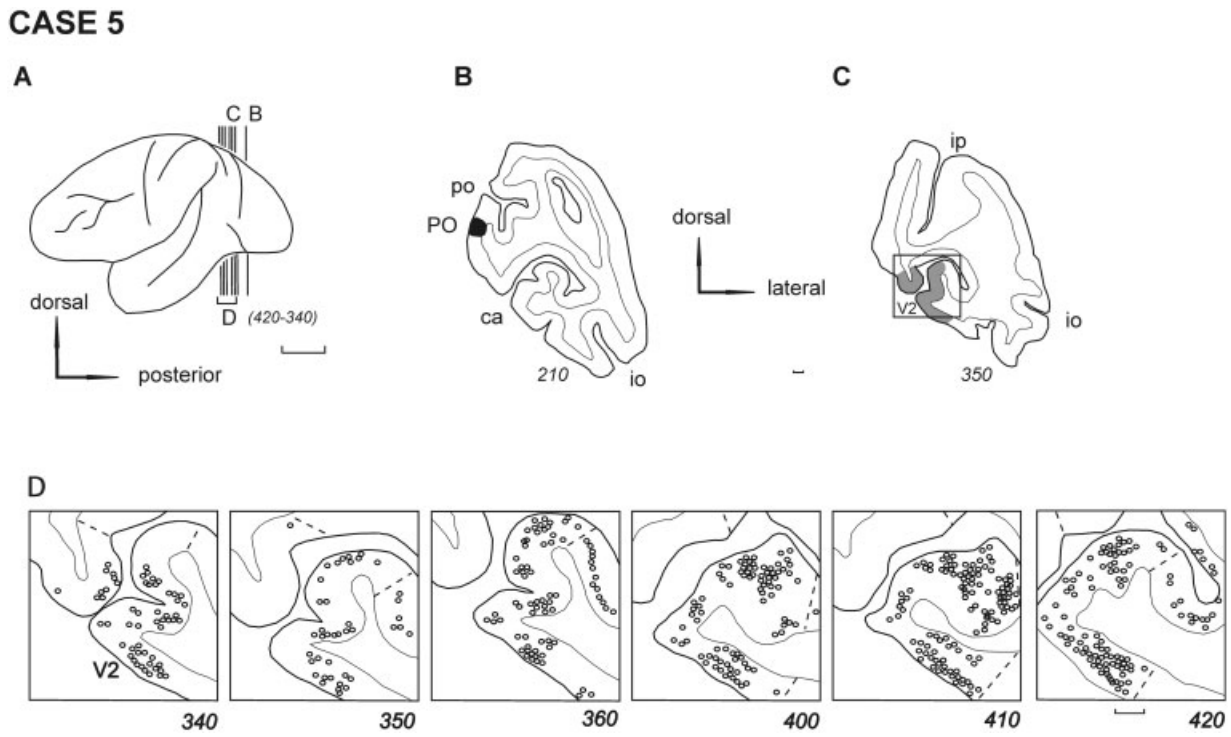

Fig. 8. Laminar distribution of neurons in visual area 2 (V2) projecting to the parietooccipital area (PO) in case 5. A series of coronal sections (**D**) at the levels indicated in the lateral view of the hemisphere (**A**) shows labeled cells (open circles) after injections of Fast Blue into PO (**B**). **C:** The target zone in ventral V2 (boxed area) is enlarged in D to show labeled cells in supra- and infragranular layers. Scale bars = 10 mm in A; 2 mm in B, C; 1 mm in D.

and to PO may be related to interspecies differences, probably related to the differences in the circadian habits of these monkeys. Adding to the diversity in nomenclature, more recently, Galletti et al. (1996) proposed the name of *V6* to PO of the macaque. Recently, POd was renamed *V6A* by Galletti et al. (2001).

In *Cebus* and macaque, the V4-projecting neurons are located in thin CytOx-rich stripes and CytOx-poor interstripes (Nakamura et al., 1993). This remarkable similarity of the origin of the V4-projecting neurons in V2 in both monkeys contrasts with the long period of phylogenetic segregation of New and Old World monkeys.

Streams of visual information processing

The functional segregation in V2 that has been suggested by different anatomic studies (De Yoe and Van Essen, 1985; Livingstone and Hubel, 1988; Burkalther and Bernardo, 1989; Levitt et al., 1994a,b; Abel et al., 1997; Sincich and Horton, 2002a) has been confirmed by electrophysiologic studies with complex visual stimuli (Levitt et al., 1994a,b; Roe and Ts'o, 1995). These studies showed that the visual information that is processed in V1 is sent to distinct functional domains in V2, represented by distinct CytOx modules that contain separate representations of the visual field and is involved in processing different visual attributes (Malach et al., 1994; Shipp and Zeki, 1995). The data also indicated that a group of modules defined on anatomic and physiologic grounds may also represent a basic processing unit of the topographically organized V2.

Ventral stream. V4 in *Macaca* receives direct projections of V1 only from the foveal region (Shipp and Zeki, 1986); however, it receives direct projections from thin CytOx-rich stripes and interstripes of the entire binocular representation of V2 (Nakamura et al., 1993; Felleman et al., 1997). Nakamura et al. (1993) used flattened preparations of V2 to emphasize that the cells that project to V4 avoid the thick stripe regions. Our results in *Cebus* confirmed the segregation of the connections reported for macaques, inasmuch as V4-projecting neurons are located in thin CytOx-rich stripes and in CytOx-poor interstripes of V2. This projection was restricted to the central 30-degree eccentricity in V2, even after multiple injections into the region of the far peripheral representation of V4 (Piñon et al., 1998).

Dorsolateral stream. In the Old World monkey *Macaca*, MT receives direct projections from V1 (Maunsell and Van Essen, 1983; Desimone and Ungerleider, 1986) and contains a complete representation of the binocular visual field (Gattass and Gross, 1981). In the New World monkey *Cebus*, MT receives from and projects to the binocular region of V1 (Sousa et al., 1991; Rosa et al., 1993) and contains a complete representation of the binocular visual field (Fiorani et al., 1989). As in other primates, in *Cebus*, V2 projections to MT originate mainly (>90%) from thick CytOx-rich stripes of V2 (Krubitzer and Kaas, 1990a; Levitt et al., 1994b).

In Old World primates, the vast majority of neurons in the thick CytOx-rich stripes of V2 shows movement selectivity (Shipp and Zeki, 1985; Levitt et al., 1994a) similar to

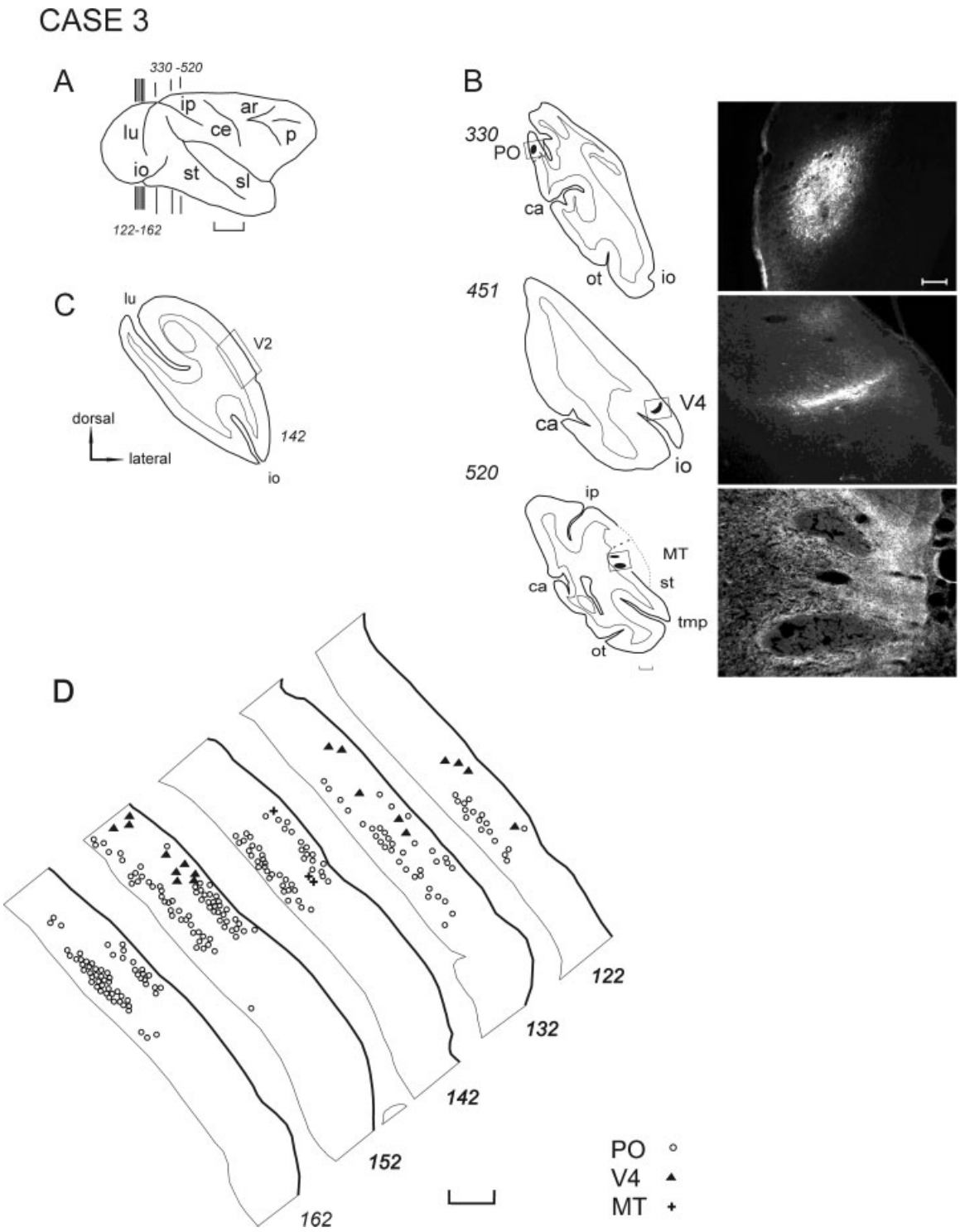

Fig. 9. Laminar distribution of neurons in visual area 2 (V2) projecting to visual area 4 (V4), the middle temporal area (MT), and the parietooccipital area (PO). Series of coronal sections (**D**) at the levels indicated (122–162) in the lateral view of the hemisphere (**A**) show PO- (open circles), MT- (crosses), and V4- (triangles) projecting neurons after injections of retrograde tracers in case 3. **B:** Left, coronal sections at the levels indicated (330–520) in the lateral view of the hemisphere show injections sites (black areas). Right, photomicrographs of the region inside the boxed area show the injections sites. **C:** The target zone in dorsal V2 (boxed area) is enlarged in a series of sections (D) to show PO-projecting neurons in supra- and infragranular layers and MT- and V4-projecting neurons in supragranular layers. Scale bars = 10 mm in A; 2 mm in B (left); 100 μm in B (right); 1 mm in D.

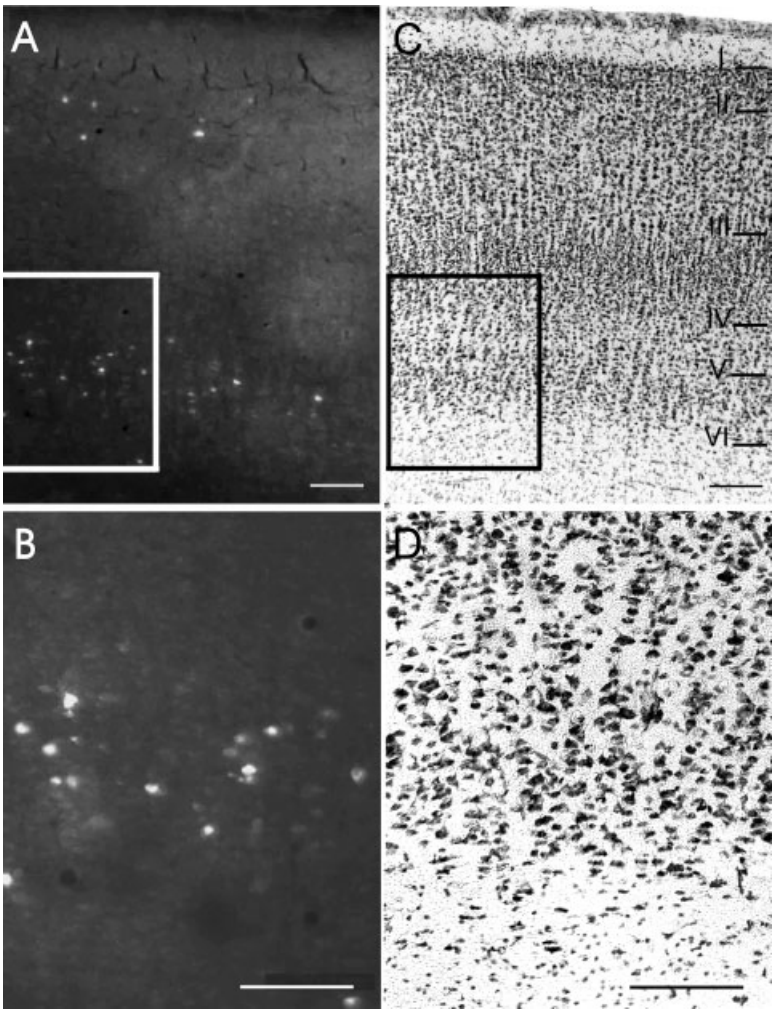

Fig. 10. Laminar distribution of neurons projecting the parietooccipital area. Photomicrographs of dorsal V2 in coronal sections (case 3) under fluorescent microscopy (**A, B**) and stained for cells (**C, D**) show labeled cells in supra- and infragranular layers. Boxed areas in A and C are enlarged in B and D. Scale bars = 150 μm in A, C; 500 μm in B, D.

those of MT (Albright et al., 1984). In addition, cells projecting to MT are located mainly in thick CytOx-rich stripes in V2 (Shipp and Zeki, 1985). The present results in *Cebus* monkeys are similar to the results reported by Nakamura et al. (1993) and Levitt et al. (1994b) in Old World monkeys. In addition, the observation that no labeled cells are found in thick CytOx-rich stripes after injections into V4 separates the ventral stream from the dorsolateral one.

Dorsomedial stream. The segregation of the streams of visual information processing went one step further when we found that PO-projecting neurons, in addition to being in thick CytOx-rich stripes as MT-projecting neurons, were found in CytOx-poor interstripes, regions of origin of the ventral stream. Thus, the distribution of cells in V2 after injections into PO corroborates a subdivision of the dorsal stream into dorsolateral and dorsomedial subdivisions, with origins in MT and PO, respectively. This distribution of cells of the dorsomedial stream in V2 is complementary to those of the ventral and dorsolateral streams. The vast majority of the cells of origin of the dorsolateral and ventral streams is located in the region of representation of the central visual field, albeit in distinct CytOx compartments. The number of PO-projecting neurons in peripheral regions of V2 is higher than that of V4-projecting neurons. This distribution matches the expected distribution based on the topography of PO (Neuenschwander et al., 1994). Thus, based on the site of origin in V2, we can characterize three completely segregated streams of visual information processing.

No double-labeled cells were found in V2 after injections into PO and V4 or PO and MT. The segregation of the dorsolateral and dorsomedial streams relative to the topography of their projections is such that the dorsolateral stream includes the representation of central and peripheral regions of the binocular visual field, whereas the dorsomedial one represents predominantly the binocular and monocular peripheral representations of the visual field. In contrast, although the distribution of projecting neurons is different in terms of topographic location, the projections from the thick CytOx-rich stripes are common

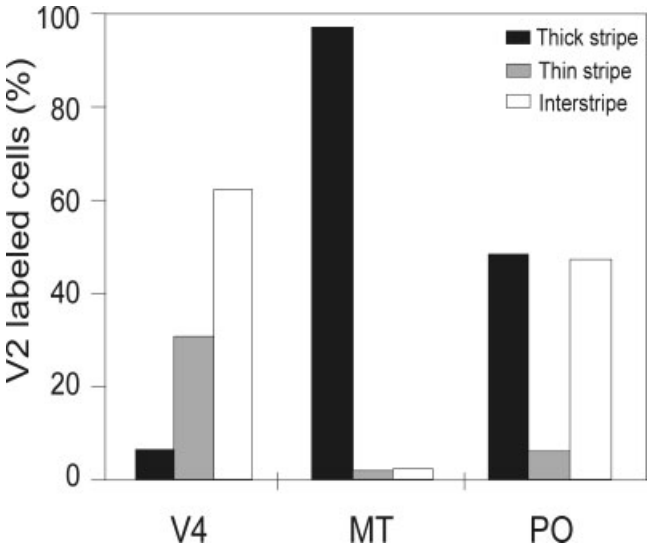

Fig. 11. Efferent neurons and cytochrome oxidase (CytOx) modules of visual area 2 (V2). Histograms of labeled cells in CytOx modules of V2 after injections into visual area 4 (V4), the middle temporal area (MT), and the parietooccipital area (PO). Bars corresponding to thick stripes are shown in black, those to thin stripes are shown in gray, and those to interstripes in are shown in white.

to both streams. The segregation of the V2 compartment observed in this study contrasts with the intermingling of visual information at early stages in the neocortex of macaque monkeys (Sincich and Horton, 2002b). After small injections of retrograde tracer into CytOx-poor interstripe regions and CytOx-rich thick stripes in V2, Sincich and Horton found double-labeled cells in interpatch regions in V1. This datum suggests a rich intermingling of visual information between the ventral and dorsal pathways.

The distribution of cells that project to V4, MT, and PO follow the morphology of the CytOx compartments in V2. The segmental appearance shown by thin CytOx-rich stripes and by the clustering of V4-projecting neurons in *Cebus* is similar to that described in *Macaca* (Tootell and Silverman, 1985; Zeki and Shipp, 1989a; Nakamura at al, 1993; Xiao et al., 1999) and *Saimiri* (Livingstone and Hubel, 1984; Krubitzer and Kaas, 1989).

Although the segregation of the central connections into two or three streams of visual information processing are currently accepted, other connectional schemes have emerged, such as those of the fast and slow streams defined by Kennedy and Bullier (1985) or the one based on the output connections leading to visuomotor modules for reaching out or for grasping an object (Milner and Goodale, 1993). The notion of segregated streams of visual information processing is compatible with models proposed on the basis of connectional data (Kennedy and Bullier, 1985). The asymmetry on the pattern of central versus peripheral connectivity (Gattass et al., 1988) raises the possibility that the modular segregation of V2 is used differentially by the different streams.

Laminar organization of the connections of V2

The models of hierarchical organization of visual cortical areas suggest that projections can be classified as feedforward, feedback, or intermediate projections. A connection is considered feedforward if it projects from lower-order to higher-order areas, with cells of origin located mainly in layer III and projecting to layer IV of the target region. Feedback projections originate in higher-order areas and terminate in lower-order ones. In this case, the cells are mainly in the infragranular cortical layers V and VI and project above or below layer IV, avoiding layer IV (Rockland and Pandya, 1979; Maunsell and Van Essen, 1983). A pattern is considered intermediate when the distribution of cells of origin and of the projections is homogeneous across all layers. The bilaminar pattern is characteristic of the feedforward projections and is present in all connections of a higher-order area. A bilaminar pattern of projecting neurons also could characterize a connection of the intermediate type, feedforward, or feedback, as described by Felleman and Van Essen (1991).

Neurons of V2 projecting to V4 and MT were found in supragranular layers, whereas PO-projecting neurons were found in supra- and infragranular layers. These results suggest that V4 and MT are located in the same hierarchical position and higher than V2, whereas PO is in an intermediate hierarchical position in relation to V2. These data support the subdivision of the dorsal stream proposed based on the tangential analysis of V2. It also suggests that the ventral and dorsolateral components, V4 and MT, are located in the same hierarchical level in relation to V2.

The distribution of V4-, MT-, and PO-projecting neurons is unique with regard to the different cortical layers and the different sets of CytOx modules of V2. The projections to V4 with their origins in thin stripes and interstripes of V2 arise from cells in the supragranular layers. The cells in thick stripes of V2 that project to MT also are in the supragranular layers, whereas the projections to PO, with origins in thick stripes and interstripes of V2, arise from cells in the infra- and supragranular layers, avoiding layer IV. In addition, there is no superimposition in the streams of visual information processing, inasmuch as no double-labeled cells were found.

The data obtained thus far can favor or be against the segregation of the streams of visual information processing. Against segregation is the fact that there are V4- and PO-projecting neurons in interstripes of V2 and in supragranular layers. Also, that there are MT- and PO-projecting neurons in thick stripes. In contrast, the absence of double-labeled cells after simultaneous injections into MT and V4, MT and PO, or V4, MT, and PO favor a total segregation of the dorsomedial and dorsolateral streams. In addition, in this study we found that only PO-projecting neurons arise from infragranular layers. In conclusion, the present results support an anatomic segregation of the dorsal stream into two streams of visual information processing in *Cebus*, a dorsolateral one and a dorsomedial one.

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