Cortical Connections of Areas V3 and VP of Macaque Monkey Extrastriate Visual Cortex

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ABSTRACT
The cortical connections of visual area 3 (V3) and the ventral posterior area (VP) in the macaque monkey were studied by using combinations of retrograde and anterograde tracers. Tracer injections were made into V3 or VP following electrophysiological recording in and near the target area. The pattern of ipsilateral cortical connections was analyzed in relation to the pattern of interhemispheric connections identified after transection of the corpus callosum. Both V3 and VP have major connections with areas V2, V3A, posterior intraparietal area (PIP), V4, middle temporal area (MT), medial superior temporal area (dorsal) (MSTD), and ventral intraparietal area (VIP). Their connections differ in several respects. Specifically, V3 has connections with areas V1 and V4 transitional area (V4t) that are absent for VP; VP has connections with areas ventral occipitotemporal area (VOT), dorsal prelunate area (DP), and visually responsive portion of temporal visual area F (VTF) that are absent or occur only rarely for V3. The laminar pattern of labeled terminals and retrogradely labeled cell bodies allowed assessment of the hierarchical relationships between areas V3 and VP and their various targets. Areas V1 and V2 are at a lower hierarchical level than V3 and VP; all of the remaining areas are at a higher level. V3 receives major inputs from layer 4B of V1, suggesting an association with the magnocellular-dominated processing stream and a role in routing magnocellular-dominated information along pathways leading to both parietal and temporal lobes. The convergence and divergence of pathways involving V3 and VP underscores the distributed nature of hierarchical processing in the visual system. J. Comp. Neurol. 379:21–47, 1997. © 1997 Wiley-Liss, Inc.

Indexing terms: neuroanatomy; pathway tracing; primate; cortical layers; hierarchy

More than two decades ago, Zeki (1969) and Cragg (1969) reported that striate cortex (V1) in the macaque projected to two distinct visual areas, V2 and V3, lying well within the belt of cortex previously known as Brodmann’s area 18. This discovery inspired a stream of studies identifying numerous visual areas in the occipital, temporal, parietal, and even frontal lobes (see Desimone and Ungerleider, 1989; Felleman and Van Essen, 1991; Colby and Duhamel, 1991, for reviews). Among the casualties to this process of splitting cortex into progressively more areas was V3 itself, as several studies suggest that V3 is not a single area adjoining the entire anterior border of V2. Rather, it can be subdivided into a dorsal half, still known as V3, that represents only the lower part of the visual field, and a ventral half, area VP (the ventral posterior area), that represents only the upper part of the visual field. V3 and VP differ from one another in their myeloarchitecture, their connections with V1 and the receptive field properties of their constituent neurons (Burkhalter et al., 1985; Newsome et al., 1986; Burkhalter and Van Essen, 1986). Alternative partitioning schemes for this region have been proposed, though. Some investigators (e.g., Gattass et al., 1988) prefer the terms dorsal V3 (V3d) and ventral V3 (V3v) to signify that these may be distinct subdivisions of a single area despite their differing characteristics. Krubitzer and Kaas (1993) support the notion of...
VP as a distinct area ventrally, but they suggest that 
(dorsal) V3 and the adjoining region, previously identified 
as V3A, should instead be regarded as a single visual area, 
which they suggest to be a homologue of the dorso-medial 
area (DM) of new world primates. We will use the V3/VP 
nomenclature in presenting our results, but will revisit the 
issue of terminology and partitioning schemes in the 
Discussion.

Relatively little has been published on the connections of 
V3 and VP with other extrastriate areas. Zeki (1971) 
reported on V3 projections at a time when many extrastri-
ate areas had yet to be identified, and he used a degenera-
tion technique that is less sensitive than anterograde and 
retrograde tracers now available. More recent studies 
involving tracers injected into other areas have reported a 
number of connections with V3 and VP (reviewed in 
Felleman and Van Essen, 1991; see Discussion). However, 
both V3 and VP are narrow areas buried within deep sulci, 
making them difficult targets for a systematic analysis of 
connectivity.

We were specifically interested in comparing the projec-
tions of V3 and VP in order to explore the nature and 
extent of dorso-ventral asymmetries in cortical organiza-
tion. This information provides a basis for comparisons 
with asymmetries in perceptual capacities and in visual 
representations in upper vs. lower visual fields (Van Essen 
et al., 1986; Previc, 1990). It is also instructive to analyze 
V3 and VP connections in relation to the different visual 
processing streams that have been intensively studied in 
many laboratories. These start with the subcortical magno-
cellular (M), parvocellular (P), and koniocellular (K) 
streams in the retina and lateral geniculate nucleus and 
continue with the magno-dominated (MD), b-lobo-
minated (BD), and interblob-dominated (ID) streams estab-
lished in V1 (see Casagrande, 1994; Casagrande and Kaas, 
1994; Van Essen and DeYoe, 1994; Van Essen and Gallant, 
1994). V3 has previously been linked to the MD stream by 
virtue of (i) its selective inputs from layer 4B of V1; (ii) its 
moderately high incidence of directional selectivity; and 
(iii) its heavy myelination and immunoreactivity for CAT-
301 (Burkhalter et al., 1985; Felleman and Van Essen, 
1987; DeYoe et al., 1990). VP has a high incidence of 
wavelength selective cells and orientation selective cells, 
and a low incidence of directional selective cells (Burkhal-
ter and Van Essen, 1986) and might therefore have a dorsi-
linkage to the BD and ID streams.

This study provides the first detailed characterization of 
a number of pathways linking V3 and VP with other 
cortical areas. We found that V3 and VP have similar but 
not identical patterns of connectivity with higher cortical 
areas. The laminar distribution of cells of origin and of 
efferent terminations permit an analysis of feedforward 
and feedback relationships between cortical areas which 
can be used to describe their hierarchical relationships 
(Rockland and Pandya, 1979; Maunsell and Van Essen, 
1983b; Felleman and Van Essen, 1991). In addition, the 
topographic organization of upper-field and lower-field 
connections provide a better understanding of a region 
previously considered to be a single area V3A (Van Essen 
and Zeki, 1978; Zeki, 1978a,b) but now regarded as two 
areas, V3A, and the posterior intraparietal area, PIP 
(Felleman et al., 1987; Colby et al., 1988). A preliminary 
report of some of these data has previously been published (Burkhalter et al., 1986).

**MATERIALS AND METHODS**

**Physiological recording and tracer injections.** Ex-
periments were carried out on eight hemispheres of seven 
juvenile macaque monkeys (Macaca fascicularis; 2–3 kg).
The location of V3 was determined during prior semi-
chronic single unit recording sessions in three hemi-
spheres or following multi-unit mapping of V3 and sur-
rounding cortex in two other hemispheres (see Felleman 
and Van Essen, 1987 for surgical and recording tech-
niques). Likewise, VP was localized during prior semi-
chronic recording from three hemispheres that established 
its location, extent and general topography (see Burkhal-
ter and Van Essen, 1986). In both sets of experiments, the 
splenial portion of the corpus callosum was transected 5–6 
days prior to perfusion, in order to provide an anatomical 
marker for the boundaries of several visual areas (Zeki, 
1970; Van Essen et al., 1982). Following 2–3 days of 
recovery from the callosal transection surgery, an acute 
recording session was begun. This started with a reconfi-
mation of the location of V3 or VP, followed by injection of 
tracers at one or more sites. During the post-injection 
transport period (2–3 days in all but one short-survival 
case of 12 hours) electrophysiological recordings unrelated
to the present study were carried out. All surgical and physiological procedures were carried out under the guidelines for animal use established by NIH, the Society for Neuroscience, and ARVO, and protocols were approved by the Animal Care and Use Committee of the California Institute of Technology.

Tracer injections were made using a modified 1 µl syringe (Hamilton Co., Reno, NV) which in seven cases contained 25–50 Ci of H-proline in 200 nl of 20% horseradish peroxidase (HRP, Boehringer Mannheim Biochemicals, Indianapolis, IN). In one case, the injection was 200 nl of a 2% suspension of the fluorescent retrograde tracer, Diamino Yellow. The syringe was modified to include a thinner barrel (30 ga.) at its end, and it was insulated except at the tip in order to permit multi-unit recordings in the vicinity of the injection site. V3 was approached posteriorly at an angle of approximately 30° from vertical in a roughly parasagittal plane. Injections were directed towards V3 on the annectant gyrus, where it typically is widest (Van Essen et al., 1986). VP was approached in an oblique plane that allowed recordings from several neighboring areas, including ventral V2, VP, and ventral V4. At the time of injections, the target area was identified based on receptive field size and the visual topography relative to other nearby penetrations. The locations of injection sites were subsequently confirmed by analyzing myeloarchitecture (for V3) and by their positions relative to callosal inputs (see Results).

Tissue processing and data analysis. At the termination of the experiment, the monkey was deeply anesthetized with Nembutal and perfused intracardially with 0.1 M phosphate buffer (pH 7.4) followed by fixative. In the V3 experiments, the fixative was 2% paraformaldehyde/2% glutaraldehyde, and it was washed out with 0.1 M phosphate buffer containing 10% sucrose. In the VP experiments, the fixative was 4% paraformaldehyde, and it was followed by a graded series of buffered fixative mixed with 10% and finally 20% sucrose. These perfusion conditions involved tradeoffs between the optimal conditions for the various anatomical procedures we used, including degeneration stains, myelin stains, autoradiography, cytochrome oxidase, and HRP histochemistry. The procedures used in the VP experiments were good for degeneration and autoradiography but were suboptimal for the detection of HRP; they resulted in relatively few retrogradely labeled cells, but were nonetheless consistent and robust enough to reliably assess the major inputs to VP.

After perfusion, the brain was removed, photographed, blocked, and immersed in buffered 30% sucrose. Hemispheres containing V3 injections were blocked in either the parasagittal or horizontal plane; hemispheres containing VP injections were blocked in an oblique plane, parallel to the angle of electrode penetrations that coursed from dorso-lateral to ventromedial cortex (Burkhalter and Van Essen, 1986). Connections with the frontal lobes and with subcortical structures were not examined in these experiments. Frozen sections were cut at 31 µm, collected in phosphate buffer (0.1 M), and immediately processed for HRP by using the tetramethylbenzidine (TMB) method of Mesulam et al. (1977) as modified by Shatz (see Maunsell and Van Essen, 1983b). Sections containing fluorescent, retrogradely labeled cells were mounted on glass slides, air dried, and observed under UV epi-fluorescence with a Leitz Orthoplan microscope (by using UV excitation from 340–360 nm and a barrier filter at 430 nm). The remaining brain sections were transferred into buffered 4% formaldehyde to be used for autoradiography, myelin, or degeneration stains. Autoradiography was prepared according to the procedure of Cowan et al. (1972) and involved exposures of 3–6 weeks. Degenerating fibers and terminals were visualized by using the protocol of Witanen (1969). The myeloarchitectonic borders of V3 and MT were determined from sections stained according to the protocol of Gallays (1979).

The locations of injection sites, labeled cells, silver grains, degenerating fibers, and myeloarchitecture were plotted on enlarged photographs of individual brain sections (5x or 8x). These section data were then used to generate two dimensional, unfolded maps of visual cortex (Van Essen and Maunsell, 1980). Architectonic borders were transferred to these maps by marking the transition regions for each section (generally about 1 mm), then drawing a partially smoothed border on the map that passed close to the midpoint of each transition region (Fig. 7, Van Essen et al., 1986). In one hemisphere (Case 1) a computer assisted microscope (DeYoe et al., 1990; Van Essen et al., 1990) was used to record the locations of labeled cells at high resolution. In addition, for some sections through V1, the outlines of cytochrome oxidase blobs and the borders of several cortical layers were scored by using this microscope and were aligned with nearby sections that were reacted for HRP or fluorescent labeled cells by using custom software on a computer graphics workstation (Silicon Graphics, Iris).

RESULTS

Connections of area V3

Figure 1 shows the multi-unit receptive fields recorded from each of the six V3 injection sites in five hemispheres. Receptive fields ranged from 2.5° to 9° in eccentricity, and receptive field sizes were appropriate for area V3, which on average are twice the linear dimensions of those at a corresponding eccentricity in V2 (Gattass et al., 1981; Felleman and Van Essen, 1987). All receptive fields were in the inferior contralateral quadrant, as expected for V3, ranging from near the horizontal meridian (close to the posterior border of V3) to near the inferior vertical meridian (close to the anterior border of V3).

In Cases 1–3, these physiological identifications were subsequently confirmed anatomically using previously established myeloarchitectonic criteria for recognizing V3 (Van Essen et al., 1986). For example, Figure 2A shows an autoradiographic section illustrating the combined HRP/proline injection in Case 2. The injection site was on the annectant gyrus (an internal fold between the lunate and parieto-occipital sulci), where V3 is widest and the eccentricity of the representation is convenient for mapping. In a nearby section stained for myelin, V3 is identifiable by its dense myelination within the infragranular layers and to a lesser extent, supragranular layers (Fig. 2B). The location of these borders and the degree of uncertainty of this transition are indicated by the asterisks within the white matter. In this and the other injections in Cases 1–3, the halo of label visible to the naked eye extended into white matter under the injection site and into some gray matter outside of myeloarchitectonic V3. However, evidence presented below, based on the laminar and topographic pattern of connections in V1, suggests that the effective size of the injection site (i.e., the region contributing substan-
ties to long-distance transport) in this and other cases was smaller than the visible tracer halo and was predominantly restricted to V3.

The bulk of our data regarding the connections of V3 come from the three injection sites in Cases 1 and 2. We will present these cases in detail, followed by brief summaries of the results for Cases 3–5.

**Case 1 (V3: HRP/Pro; DY).** Case 1 included one combined HRP/proline injection and a separate injection of DY. The overall distribution of label resulting from the HRP/proline injection is shown in Figure 3 on a two-dimensional cortical map and on a drawing of a horizontal section (upper left) that included the injection site (solid circle) plus patches of label in many different visual areas. In this and subsequent illustrations involving two-dimensional cortical maps, retrograde label is indicated by dots and anterograde label by hatching. The cortical map also shows the major cortical sulci (identified in italics, outlined with continuous lines, and with the fundus shown by dashed lines) and the myeloarchitectonic borders of V3 and MT (medium continuous lines). The contours of layer 4 from the illustrated section (fine dashed lines) are also shown, along with labels to denote the V1/V2 boundary (A,B), and the anterior limits of each contour (C,D). Regions receiving callosal inputs, as scored from sections stained for degenerating axons and terminals, are indicated by shading on the cortical map.

The HRP/proline injection site was centered within the myeloarchitectonic borders of V3 (lines in white matter in sections inset), and the halo of label around the injection site extended slightly beyond the boundaries of V3. Retrograde and anterograde label occurred as patches and elongated clusters extending over a large portion of dorsal cortex in the occipital and parietal lobes. Based on the relationship of these patches to architectonic borders and callosal inputs, we identified connections of V3 to nine different visual areas: V1, V2, V3A, PIP, V4, V4t, MT, MSTd, and VIP.

Before discussing the connections with extrastriate areas, we first consider the extent of labeling within V1, as this provides important constraints on the effective size of the injection site in Case 1. All of the anterograde labeling and the bulk of the retrograde labeling in V1 were concentrated in a region about 10 mm in mediolateral extent (horizontal on the map) and 7 mm in dorso-ventral extent (vertical on the map). The conclusion that the effective region of tracer uptake in V3 did not extend posteriorly to the V2/V3 border is consistent with the extent of the visual field involvement in V1 based on the cortical magnification factor. Specifically, at an eccentricity of 4° (the center of the injection site receptive field) the magnification factor in V1 is 2–3 mm/degree (Van Essen et al., 1984). At this magnification, the 10 mm labeled portion of V1 should encompass about 3°–5° of the visual field. This is about the size of the multi-unit receptive field plotted for the V3 injection site (see inset) and is smaller than the arc length between the horizontal and vertical meridians at this eccentricity. If, on the other hand, the effective region of tracer uptake had been as large as the tracer halo in Figure 2A, one would expect to see labeling in V1 extending ~15–20 mm on the cortical map. Most importantly, the limits of anterograde label were well away from the vertical meridian representation, along the dorsal margin of V1, and from the horizontal meridian representation, which runs midway through the V1 map along its long axis (Van Essen et al., 1984). This strongly suggests that the effective region of HRP/proline uptake in V3 did not reach the posterior border with V2 (horizontal meridian representation) or the anterior border with V3A (vertical meridian representation).

The extent of retrograde labeling was only slightly greater than the anterograde labeling in V1, thus, it is likely that the effective region of HRP uptake also did not exceed the full width of V3. This is supported by the fact that the vast majority (~95%) of retrogradely labeled cells throughout V1 were in layer 4B (see Fig. 7 below). If the HRP injection had substantially crossed the V2/V3 border, there should have been extensive labeling of layers 2 and 3 along the horizontal meridian representation of V1, unless the spread were by chance restricted to a V2 thick stripe, which receives its V1 inputs only from layer 4B (Livingstone and Hubel, 1984). If the injection had included extensive uptake from cut axons in the white matter under V3 (which could have led to spurious retrograde labeling but not of anterograde labeling), one would expect to see large regions of retrograde label lacking reciprocal anterograde label. In fact, the overall retrograde and anterograde patterns are similar throughout extrastriate cortex, with the exception of a patch of strong retrograde label and weak anterograde label in area MSTd. We conclude that the HRP/proline injection in Case 1 was largely if not entirely restricted to V3.

In V2, the region containing label occupied a roughly triangular region on the two-dimensional map, 7 mm at its widest and 15 mm at its longest. The difference in overall shape of this region, compared to the more circular pattern in V1, is correlated with an overall anisotropy in the shape of V2, which is much longer (vertical on the map) than it is wide (Van Essen et al., 1986; 1990). Both the retrograde and anterograde patterns within V2 were distinctly patchy, but the patterns were not identical (see below).
Fig. 2. Location of injection site in V3, Case 2. A: Brightfield autoradiograph of a parasagittal brain section which shows an injection of $^3$H-proline and horseradish peroxidase (HRP) into V3 on the annectant gyrus. B: The myeloarchitectonic borders of V3 in a neighboring section, stained by the Gallyas method. Uncertainty limits for the posterior and anterior borders of V3 are indicated by asterisks in the white matter. Note that the dark halo of tracer near the injection site extends slightly beyond the posterior border of V3; however, the extent of cortex over which uptake led to detectible long-distance transport is likely to be much smaller and entirely within V3 (see text). Scale bar = 1 mm.
Fig. 3. Distribution of anterograde labeling (hatching) and retrograde labeling (dots) from an injection of \(^{3}H\)-proline and HRP into V3 (Case 1). Insets show the labeling in a single horizontal section (whose contour on the cortical flat map is indicated by dashed lines) taken at the level indicated in the hemisphere drawing alongside. On the cortical map, the myeloarchitectonic borders of V3 and middle temporal area (MT) are indicated by bold lines and the major sulci are shown as dotted lines. The pattern of callosal connections (shading) provides evidence for the borders of several visual areas. Visual areas to which label can be assigned are identified alongside each patch.
Anterior to V1 and V2, the detailed pattern of labeling is best discussed in relation to the pattern of callosal connections (shading). Note that the anterior border of myeloarchitectonic V3 is largely contained within a narrow strip of callosal-recipient cortex, as reported previously (Van Essen et al., 1986). A distinct patch of anterograde and retrograde label was present within myeloarchitectonic V3, about 3–5 mm antero-medial to the injection site and situated on the annectant gyrus. This is a reasonable distance over which to find patchy intrinsic connections, based on previous reports for areas V2 and V4 in the macaque (Yoshioka et al., 1992; Lund et al., 1993; DeYoe et al., 1994).

Immediately anterior to V3 (to the right on the map) is a large callosal-free zone surrounded by a callosal-recipient ring. In early studies, both the callosal-free zone and the margins of the callosal-recipient ring had been identified as a single visual area, V3A (Van Essen and Zeki, 1978; Van Essen et al., 1982). The HRP-proline injection labeled two sets of clusters within this region, one within the medial part of the callosal-recipient ring (up on the map) and the other involving both callosal-free and callosal-recipient cortex more laterally (down on the map). The center-to-center separation between the medial and lateral clusters is more than 1 cm and is much greater than the periodicity of patchiness known for other cortical areas known to have internal compartments (Van Essen et al., 1990; Lund et al., 1993; DeYoe et al., 1994). This suggests that two distinct areas exist within the region previously regarded as V3A. The lateral subdivision, contained mainly in the lunate sulcus and on the annectant gyrus, is the region emphasized in most previous studies of V3A, and we will continue to use the term V3A for this region. The medial subdivision around the junction of the intraparietal and parieto-occipital sulci, has been identified as the posterior intraparietal area, PIP (Felleman et al., 1987; Colby et al., 1988).

A smaller focus of label was present in an elongated, patchy strip near the fundus of the intraparietal sulcus, 5–10 mm anterior to the PIP focus. Its position on the lateral bank of the sulcus, within 2 mm of the fundus indicates that this focus lies within area VIP, the ventral intraparietal area, an area previously identified on the basis of its connections with MT (Maunsell and Van Essen, 1983; Ungerleider and Desimone, 1986). In between the main VIP and PIP foci were a few retrogradely labeled cells situated postero-medially in the intraparietal sulcus; these probably represent a minor connection with area PO and/or MIP.

In lateral extrastriate cortex, a nearly continuous swath of label spanned a 3 cm extent, from the lunate sulcus to the superior temporal sulcus (STS), including portions of areas V3A, V4, V4t, MT, and MSTd. There is some patchiness of both anterograde and retrograde label within this swath, but the patchiness does not correlate with areal boundaries inferred from callosal inputs or from myeloarchitecture. This swath extends from the callosal-free portion of V3A, across the callosal-recipient band that separates V3A from V4, and into the callosal-free portion of V4 on the prelunate gyrus and posterior bank of the STS (Van Essen et al., 1982). Area V4t is much narrower (~2 mm wide) and is contained within a callosal-recipient strip between V4 laterally, and area MT medially (Desimone and Ungerleider, 1986). Given that V4t and dorsal V4 represent only lower visual fields (Van Essen and Zeki, 1978; Van Essen et al., 1981; Gattass, et al., 1985), it is not surprising that the labeling was largely continuous across this region. MT, on the other hand, contains a complete representation of the contralateral hemifield, and it is therefore puzzling at first glance that the label in MT extended across its full width. However, the upper field is known to be underrepresented in MT, and examples have previously been published of recording sequences traversing the full width of MT yet containing receptive fields restricted to the lower quadrant (Maunsell and Van Essen, 1987; Van Essen et al., 1981). The label on the anterior bank of the STS includes area MSTd as delineated by Komatsu and Wurtz (1988) and may extend into polysensory area STPp (Bruce et al., 1981; see Felleman and Van Essen, 1991).

Results for the DY injection in Case 1 are shown in Figure 4, which includes two representative brain sections along with the two-dimensional cortical map. The injection site was contained within myeloarchitectonic V3 in the fundus of the lunate sulcus, about 4 mm lateral to the HRP/proline injection. As expected from the known topography of V3, the receptive field at the injection site (1-DY in Fig. 1) was more central (2 eccentricity) than for the HRP/proline injections. As expected, the region of labeling in V1 is displaced about 5 mm lateral to that from the HRP injection previously illustrated in Figure 3. The region of DY labeling extended ventrally to the representation of the horizontal meridian in V1, suggesting that the effective injection site extended to the V2/V3 border. However, the labeling did not reach the vertical meridian representing in either V1 or V2, suggesting that the effective injection did not reach the anterior border of V3. The retrograde labeling in V1 was restricted to layer 4B, implying that any transport arising from tracer leakage into V2 was by chance restricted to its thick stripe compartment (see above). There was a patch of label near the medial limit of myeloarchitectonically identifiable V3 (up on the map), approximately 7 mm from the injection site. It is unclear whether this represents (i) genuine intrinsic label unusually distant from the injection site but within the range reported in the literature; (ii) a connection with area VIP, just outside V3; or (iii) artifactual label in V3 arising from involvement of white matter under the injection site. Altogether, we conclude that the DY injection site in Case 1 was largely restricted to V3 but with possible involvement of V2 and/or subjacent white matter.

Outside V1, label was present in all of the major target zones identified from the HRP/proline injection. In V2, there was some clustering of DY-labeled cells in V2, but this was not as pronounced as for the companion HRP/proline injection. Throughout extrastriate cortex there was extensive overlap of label from the two injection sites, but in most areas there were systematic differences in the center of each focus. Since these differences allow assessment of the topographic organization of different areas, they are illustrated in Figure 5 in an overlaid pattern that uses different hatching for the two injection sites and also includes the pattern of callosal inputs. For areas V3A, V4, V4t, and MT, the DY-labeled cells from the more central injection (horizontal hatching) occupy a slightly lower position on the cortical map than the HRP-labeled cells from the more peripheral injection (vertical hatching). This pattern corresponds with the known topographic organization of extrastriate areas (Van Essen and Zeki, 1978; Desimone and Ungerleider, 1986; Van Essen et al.,
Fig. 4. Cortical flat map from Case 1-DY, which illustrates the distribution of retrogradely labeled cells following an injection of Diamidino Yellow (DY) into V3. In addition to the nine cortical connections described from Case 1-HRP/Pro, this injection produced three labeled foci in ventral extrastriate cortex. Conventions as in Figure 3. The DY injection site is shown by a solid circle; for reference, the open circle shows the location of the companion HRP/proline injection illustrated in the preceding figure. A: Horizontal section through the injection site in dorsal cortex. B: Section through ventral cortex indicating labeling on the anterior bank of the IOS. This section is flipped horizontally to conform to the orientation of its contour on the 2-D map.
Fig. 5. Combined connections of Case 1. Cortical map which illustrates the relationship between the retrograde labeling from the two injection sites in Case 1. Vertical stippling indicates labeling from the HRP/proline injection; horizontal stippling indicates DY labeled cells; shading indicates interhemispheric connections. The DY injection was more centrally located (2° eccentricity) than the HRP injection (4° eccentricity), so the differences between the two patterns is a useful indicator of the topographic organization of each labeled area.

In PIP, there is one region where the two sets of label overlap strongly and another (more lateral) involving only label from the more central injection. This suggests that PIP may have a cruder and more irregular topographic organization than does V3A. In areas MSTd and VIP there is more extensive overlap of labeled regions, supporting previous indications that there is little topographic organization of these areas (Komatsu and Wurtz, 1988, Desimone and Ungerleider, 1986; Colby et al., 1988). In the intraparietal sulcus, the DY labeling extended from the fundus of the sulcus to 3-4 mm up the lateral bank of the sulcus. We infer that the labeling involved not only VIP but also area LIPv as delineated in Blatt et al. (1990).

The DY injection led to several additional foci not seen with the HRP/proline injection. Modest labeling was present ventral to MSTd on the anterior bank of the STS and ventral to MT on the floor of the STS. This labeled region includes area MST (Komatsu and Wurtz, 1988) and probably also area FST more ventrally (Desimone and Ungerleider, 1986). In addition, there were two prominent foci in ventral extrastriate cortex, whose identification is facilitated by comparison to the callosal inputs in this region (Fig. 4, section B and Fig. 5). The more posterior focus (to the left) includes both sides of a callosal-recipient zone that runs along the border between area VP and ventral V4 (Newsome et al., 1986). The more anterior focus is located in a callosal-free zone that includes ventral V4 posteriorly and the ventral occipito-temporal area (VOT) anteriorly (Van Essen et al., 1982; 1990). Bearing in mind that the effective DY injection site (unlike the HRP/proline site) extended to the horizontal meridian representation (see above), and that the horizontal meridian representation is known to be interconnected between dorsal and ventral extrastriate cortex (Zeki, 1971), it is parsimonious to attribute these ventral foci to connections associated with the split representation of the horizontal meridian. However, we cannot exclude the possibility that part or all of these ventral foci are associated with uptake from white matter or cortex adjoining V3. In any event, the relationship to the callosal pattern suggests that some label is present in all four of these ventral areas (V2, VP, V4, and VOT). Finally, there was a small focus (indicated by a question mark) on the medial bank of the occipito-temporal sulcus in an unassigned location that might be area VOT, the ventral subdivision of posterior inferotemporal cortex (PITv) or the visually responsive portion of area TF (VTf; Gattass et al., 1988).

**Case 2 (V3: HRP/Pro).** In this experiment, a combined HRP/proline injection was made at an eccentricity of 7° in the inferior quadrant, away from both the horizontal and vertical meridians. The patterns of retrograde and anterograde labeling are shown on a flat map of occipital, parietal, and temporal cortex (Fig. 6), along with the pattern of anterograde transport indicated on two representative sections (A–B). As with Case 1, the labeling pattern in extrastriate cortex is described in relation to the distribution of callosal inputs illustrated by shading. Connections were seen with areas V1, V2, V3A, PIP, VIP, LIPv, V4, V4t, MT, and MSTd, in a pattern that is similar but not identical to the HRP/3H-proline injection in Case 1. The labeling in V1 was slightly elongated (11 mm × 7 mm on the map) along the axis of changing polar angle (vertical on the map), and it extended farther into the calcarine sulcus than in Case 1. This fits with the greater eccentricity associated with the injection site (7° vs. 4°). The anterograde labeling extended to the vertical meridian representation but was well away from the presumed location of the horizontal meridian representation in V1. The retrograde labeling avoided both the horizontal and vertical meridian representations in V1. As with Case 1, these observations, combined with the fact that the retrograde labeling in V1 involved only layer 4B, indicates that the effective injection sites for both HRP and 3H-proline in Case 2 were largely if not exclusively restricted to V3.

In V2, there was a patchy distribution of label across a 10 mm by 6 mm region on the map. Immediately anterior to V3 were two prominent foci, a medial anterograde and retrograde focus at the juncture of the intraparietal and parieto-occipital sulci (area PIP; see section A, Fig. 6) and a lateral anterograde-only focus on the anterior bank of the lunate sulcus (area V3A, see section B, Fig. 6). The interhemispheric connections in this region did not show a large, well-defined callosal-recipient ring surrounding a single callosal-free zone as occurred in Case 1. This is attributable in part to the individual variability in the pattern of interhemispheric connections (Van Essen and Zeki, 1978; Van Essen et al., 1982) but also to the lower quality of degeneration staining in this particular hemisphere. Nonetheless, the geographical locations of the two foci is sufficiently similar to that of Case 1 that we are confident in assigning the medial and lateral ones to PIP and V3A, respectively.

Another focus of combined anterograde and retrograde label was present on the lateral bank of the intraparietal sulcus, 6-12 mm anterior to the PIP focus. The label in this region is likely to include both VIP and LIPv. The foci in
Fig. 6. Cortical flat map from Case 2 that illustrates the distribution of anterograde (stippling) and retrograde (dots) from an injection of \(^{3}H\)-proline and HRP into V3. Labeling was widespread and included V1 and eight other extrastriate targets. Same conventions as Figure 3.

Insets A and B show anterograde labeling patterns in two parasagittal sections, one passing through the injection site and the other more lateral.
V4t and MT contained robust labeling in both anterograde and retrograde directions. Interestingly, the labeling in area MSTd was exclusively retrograde, whereas that in V4 and V3A was exclusively anterograde. A weak patch of anterograde label was present more ventrally in the STS, in area MSTl or FST.

Cases 3-5. In Case 3, the injection site was centered in myeloarchitectonic V3, but included modest tracer spillage into nearby V2. Because the animal survived only 12 hours after the tracer was injected, transport to distant cortical areas was minimal, and this case was used only to examine the laminar pattern of retrograde labeling in V1 and V2. In Cases 4 and 5, injections of 3H-proline were made into physiologically identified V3, close to the horizontal meridian representation and therefore presumably near the border with V2. Unfortunately, the quality of myelin staining in these hemispheres was inadequate to reliably identify V3 in the vicinity of the injection site, and we therefore consider these to be examples of combined V2/V3 injections. In Case 4, anterograde label was present in six dorsal visual areas (V1, V2, V3A, PIP, V4, and MT). In Case 5, anterograde label was present in the same six areas and in V4t. In both cases, the injections produced labeling in ventral extrastriate cortex (along the presumed V2/V5 border in both cases, and also along the presumed V4/VOT border in Case 5). This similarity with the labeling in Case 1-DY (but not with the other Case 1 and Case 2 injections) supports the argument that the ventral extrastriate labeling is specifically associated with the connections along the horizontal meridian representation.

Summary of V3 connections. Table 1 summarizes the connections with different visual areas that were identified for each injection in Cases 1-5. Connections that were convincingly present are denoted by a ‘+’ when there was reasonably robust labeling and by a ‘w’ when the labeling was weak. Those whose existence was questionable are denoted by a '?', and those that were demonstrably lacking are denoted by a ‘-’. (n.d. signifies connections that were not tested for because of the short survival time.) Cases 4 and 5 produced relatively weak labeling patterns overall, and we consider the absence of label in areas where label was present in other cases to reflect technical inadequacies of the Case 4 and 5 injections rather than biological variability.

Altogether, these results indicate that V3 has robust, reciprocal connections in most or all cases with areas V1, V2, V3A, PIP, V4, V4t, MT, MSTd, and VIP. In addition, there is evidence for sparse or inconsistent connections with areas LiPv, MSTI, FST, and STPp, and also with VP, V2v, V4v, and VOT in relation to the horizontal meridian representation.

Laminar and modular patterns of connectivity. As already noted, retrogradely labeled cells in V1 occurred predominantly in layer 4B. Figure 7 shows a photomicrograph of HRP filled cells extending throughout layer 4B of V1 from Case 2-HRP. The labeling was distinctly patchy in some sections in this case. In Case 1-HRP, the retrograde labeling of V1 was more uniform in layer 4B, and some labeled cells were observed in supragranular layer 3. Figure 8 is a computer reconstruction of four brain sections from Case 1, illustrating the locations of HRP labeled cells in V1 relative to the pattern of cytochrome oxidase activity in the immediately adjacent sections. The observed supragranular labeling is unlikely to be due to the inadvertent involvement of V2, since the observed labeled cells were centered within a larger field of exclusive labeling of layer 4B. Comparable numbers of labeled cells were present in blobs and in interblob regions, indicating that there is little or no specificity for either compartment. In this

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**TABLE 1. Areal Distribution of Label Following Tracer Injections Into Area V3**

<table>
<thead>
<tr>
<th>Case</th>
<th>V1</th>
<th>V2</th>
<th>V3A</th>
<th>PIP</th>
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<th>V4t</th>
<th>MT</th>
<th>MSTd</th>
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1Consistency of V3 Connections. Overview of the patterns of cortical connections observed following six different V3 tracer injections in 5 hemispheres. -, label absent; +, label present; +?, label probably present; w, weak labeling; ?, label probably absent; n.d., not determined; this case was only scored for V1 and V2.

2See list of abbreviations.
Fig. 8. Exploded, three-dimensional computer reconstruction of four horizontal brain sections through V1 that contained retrogradely labeled cells in supragranular layers and layer 4B (Case 1). The pattern of cytochrome oxidase staining from nearby sections is plotted along with the location of HRP labeled cells. Thick lines indicate the pial and white matter-layer six borders. The thin lines indicate layer 4A and the 4C/5 border. Scale bar = 2 mm.
hemisphere, approximately 5% of the labeled cells in V1 were found outside of layer 4B. In the remaining retrograde injection (Case 3), virtually all labeled cells in V1 were restricted to layer 4B.

In Cases 2 and 4, anterograde labeling in V1 was seen in three tiers, corresponding to layers 1, 4B, and 6 (Fig. 9). In Case 1, the anterograde labeling was only seen in layer 4B, whereas Case 5 had weak labeling only in layers 1 and 6. In Case 2, the labeling was patchy in layers 4B and 1 and to a lesser extent in layer 6 (Fig. 9). Individual patches were approximately 250 µm in width and had an average separation of 500–600 µm. There was no obvious correlation between these patches and the cytochrome oxidase blobs in the superficial layers of V1 that were identified in nearby sections. The retrograde labeling in layer 4B was less patchy than the anterograde labeling pattern.

The laminar pattern of connections between V2 and V3 showed a characteristic asymmetry, with retrogradely labeled cells occurring predominantly in layer 3 of V2 and anterograde label terminating mainly in superficial and deep layers, avoiding layer 4. The anterograde projection to V2 is illustrated in a darkfield photomicrograph from Case 1 (Fig. 10). The patchiness of anterograde label evident in this single section was reconstructed over a 3 mm dorso-ventral extent of V2 (Fig. 11). Each section displays anterograde label (hatching) and retrograde label (dots) taken from nearby sections. The thin contour lines in each section indicate layer 4 in order to facilitate the distinction between superficial vs. deep layers. The anterograde label appears as a few discrete patches separated by distances ranging from 0.7 mm to 4 mm. The retrograde labeling was highly patchy in some sections and nearly continuous in others, albeit with significant fluctuations in density.

Figure 12 shows two-dimensional maps reconstructing the pattern of anterograde labeling in V2 (in Case 1) and of both retrograde and anterograde labeling in V2 (Case 2). In both examples, particularly in Case 2, the patches of anterograde label form stripe-like regions running roughly orthogonal to the V1/V2 border. The periodicity of the anterogrady labeled stripes in Figures 11 and 12 (1.5–2.5 mm) is roughly half of the 4 mm periodicity reported for a complete set of cytochrome oxidase thick, thin, and interstripes in V2 (Tootell and Hamilton, 1989; Zeki and Shipp, 1989; DeYoe et al., 1990), but in the absence of cytochrome oxidase staining in these hemispheres, we cannot identify which stripe(s) were actually labeled. For both cases, many of the retrograde and anterograde clusters coincide with one another, but the correspondence is not perfect even in regions where there is extensive label of both types.
The projections to areas anterior to V3 (i.e., all targets besides V1 and V2) shared several important characteristics in terms of the laminar pattern of labeling, but there were significant differences as well. The most consistent characteristic was that anterograde connections terminated most densely in layer 4 but usually extended significantly into layer 3 and often into layer 2. This is illustrated in darkfield photomicrographs of anterograde labeling in V4 (Fig. 13A) and PIP (Fig. 13B).

Figure 13 also reveals patchiness of anterograde labeling within individual areas. To analyze this pattern in more detail, Figure 14 shows 10 horizontal sections spaced at 0.25 mm intervals through the prelunate gyrus and anterior bank of the lunate sulcus in Case 1. In the most dorsal sections (a,b), V4 contains only a single patch of label about 1 mm in width. In progressively more ventral sections (e–g) this patch splits into multiple foci, and additional foci emerge in V4 and in V3A. The relationships among patches are better seen on an unfolded cortical map (inset, Fig. 14, at the same scale), where they coalesce into a series of stripes that course roughly dorso-ventrally down the prelunate gyrus and anterior bank of the lunate sulcus. Stripes are typically 0.5 to 1.0 mm wide and 1–5 mm long, and they are separated by distances of 0.5 to 2 mm.

The retrograde labeling in areas besides V1 and V2 generally appeared as one of two distinct laminar patterns (insets in Fig. 3, 4). In areas V3A, V4, MSTd, LIPv, and VIP the labeling was predominantly in infragranular layers, including layers 5 and 6. In areas MT and V4t, the retrograde labeling was bilaminar, being extensive in both supragranular layers (mainly layer 3) and infragranular layers (layers 5 and 6). In area PIP, the labeling was predominantly infragranular in Case 2 and in the DY injection for Case 1 (Fig. 4), but was bilaminar for the HRP injection in Case 1 (Fig. 3). In Figure 4, the transition from bilaminar to predominantly infragranular labeling occurred quite sharply, 1.5–3 mm lateral to the midpoint of the MT myeloarchitectonic transition zone (solid bar in the white matter). This is consistent with the width of V4t estimated on physiological and myeloarchitectonic criteria by Desimone and Ungerleider (1986). Although we did not have independent evidence to confirm the V4/V4t border in this hemisphere, this finding nonetheless suggests that...
the laminar pattern of connections may be useful in distinguishing areal boundaries even when the labeling is continuous across the border.

**Connections of area VP**

Combined injections of HRP and ³H-proline aimed at physiologically identified VP were made in three hemispheres. As with the V3 injections, the evaluation of the extent of injection sites is best considered separately for each case.

**Case 6 (VP HRP/Pro).** Figure 15 shows the results from Case 6. The cortical map shows both retrograde and anterograde label; the accompanying individual section drawings show either anterograde label (sections A–D) or retrograde label (section E). The injection site (solid circle) was at the fundus of the occipito-temporal sulcus (OTS), on the lower left of the map. The multi-unit receptive field recorded at this site was located half-way between the vertical and horizontal meridians at an eccentricity of 10°, as shown in the inset to the left of the cortical map. A nearby, slightly more posterior recording site (asterisk), had a receptive field closer to the horizontal meridian, consistent with its position closer to the V2-VP border. These receptive fields are appropriate in size for VP, whereas they are larger than those expected for V2 and smaller than those expected for V4 at a corresponding eccentricity (Newsome et al., 1986; Gattass et al., 1981, 1988). Immediately anterior to the injection site is a callosal-recipient strip previously shown to delineate the border between VP and ventral V4 (Newsome et al., 1986). Although there are no reliable architectonic criteria for identifying the borders of VP, these topographic relation-
Fig. 13. Darkfield photomicrograph of two parasagittal brain sections which illustrate patchy feedforward projections from V3 (Case 2). Dense patches of silver grains were found centered over layer 4 and extended into deep layer 3. A: Patchy projections to V4 on the prelunate gyrus. Arrows indicate layers 1 and 6. B: Patchy projections to area PIP. Scale bar = 1 mm.
ships indicate that the injection was centered approximately within the 3-4 mm width of VP. Posterior to the diffuse halo surrounding the injection site was a large patch of anterograde label in V2, at a location appropriate to be in topographic correspondence with the receptive field at the injection site (Gattass et al., 1988; Newsome et al., 1986). The extent of the labeled V2 patch on the cortical map (9 mm maximum diameter) is similar to that encountered in V1 and V2 after the V3 injections described above. Moreover, the anterograde label in Case 6 did not extend to the vertical meridian representation, suggesting that the effective extent of the 3H-proline injection did not reach the VP/V4 border. The retrograde labeling in V2 was somewhat greater in extent, raising the possibility that the HRP injection site might not have been completely restricted to VP. The density of retrograde label in individual sections (cf. section E, Fig. 15) was not as great as for the V3 injections (cf. Figs. 3 and 4), which is attributable to the different fixation conditions for the two sets of injections (see Methods). Nonetheless, the degree of retrograde labeling in Case 6 was adequate to identify the major inputs to VP.

Retrograde and anterograde label associated with this injection site were absent in V1. This is in accord with our earlier report (based on V1 injections and lesions) of an absence of connections between V1 and VP (Van Essen et al., 1986). Moreover, it provides confirmatory evidence that the effective injection site did not encroach significantly into area V2, because the powerful connections between these two areas would otherwise have been evident.

There was a small patch of retrograde label within VP, about 1 cm lateral to the injection site (up on the map). This is larger than the range of intrinsic connection distances reported for V2 and V4 after biocytin injections (Yoshioka et al., 1992; Lund et al., 1993), but it is within
Fig. 15. Ventral posterior area (VP) connections in relation to callosal connections (Case 6). The cortical flat map illustrates the anterograde (stippling) and retrograde (dots) labeling following a combined HRP/3H-proline injection into VP. Shading indicates regions of degeneration caused by transection of the corpus callosum. Myeloarchitectonically identified area MT is indicated by solid outline. Other conventions as in Figure 3. Insets show the pattern of anterograde label (A–D) and retrograde label (E) from selected obliquely oriented sections whose positions are indicated on the cortical map.
the range seen in V4 after fluorescent tracer injections (DeYoe et al., 1994), and it is also within the range of patchy projections to area VP determined from V2 injections (Newsome et al., 1986). We consider it likely that this patch represents a genuine intrinsic connection but cannot rule out the alternative that it arose from HRP uptake by cut fibers in white matter somewhere along the injection track.

Anterior to the injection site, two major foci of label were found in the callosal-free zone and surrounding callosal-recipient region that help to delineate area VOT and ventral V4. The position of these foci in relation to callosal-recipient cortex suggests that much of the label is within VOT, but the more posterior focus probably includes ventral V4. A more medial focus of anterograde label was present on the parahippocampal gyrus, in a region likely to be part of area VTF, as described by Gattass et al. (1988).

Several patches of anterograde and retrograde label were observed within the superior temporal sulcus. Two distinct patches of anterograde label were present in widely separated locations within the myeloarchitectonic borders of MT. Similar patchiness has also been reported in the projections from V1 to MT (Van Essen et al., 1986) and may be related to the topographic irregularities previously described in MT (Maunsell and Van Essen, 1987). Anterograde and retrograde label were present dorsal and medial to area MT, corresponding to area MSTd.

In dorsal occipital cortex, there was a combined anterograde and retrograde focus in area V3A, along the margins of callosal-recipient cortex on the anterior bank of the lunate sulcus. A separate focus was present at the juncture of the parieto-occipital and intra-parietal sulci, medial to the V3A focus but contained within the same callosal-recipient ring; we interpret this second focus to be in area PIP. Both the V3A and PIP foci associated with VP injections were lateral to the V3A and PIP foci after V3 injections (see Figs. 3, 4, 6). This is consistent with the known topography of upper-field vs. lower-field representations in this region (Van Essen and Zeki, 1978). Lateral to the V3A focus was a small patch of anterograde label on the prelunate gyrus, which is likely to correspond to a representation of the upper visual field previously identified as the dorsal prelunate area (DP) (Maguire and Baizer, 1984). Anterior to the PIP focus were several small patches of anterograde label in the intraparietal sulcus. Most of this label was within area VIP near the fundus, but some of the label on the lateral bank of the sulcus may have extended into adjoining area LIPv.

**Case 7 (VP HRP/Pro).** In this experiment, a combined HRP/proline injection was made into area VP on the medial bank of the OTS. The locations of the injection site and labeled projection fields relative to sulcal and callosal borders are illustrated on a two-dimensional map in Figure 16, along with the anterograde labeling pattern in two representative brain sections (A and B). The receptive field associated with this injection was at an eccentricity of 12° and was closer to the vertical meridian than the horizontal meridian (inset, Fig. 16). Anterograde and retrograde label occurred in a discrete focus at an appropriate topographic location in V2. The labeled region in V2 was 8–10 mm across and did not reach the vertical meridian representation at the V3/V2 boundary; as argued above, this suggests that the effective injection site did not extend to the VP/V4v boundary. However, the overall density of degenerating terminals was weak throughout ventral occipital cortex in this hemisphere, possibly because the corpus callosum had been incompletely transected, and there was no well-defined strip of callosal-recipient cortex to allow a convincing anatomical delineation of the VP/V4v boundary. In V1 (not shown on the cortical map) there was a small focus of HRP labeling in the anterior part of the calcarine sulcus, where the far periphery is represented. This was attributable to tracer leakage and uptake by cut axons where the electrode track passed through the immediately underlying optic radiation.

Connections with nine visual areas were observed in Case 7, in a pattern similar to that found for Case 6. Retrograde and anterograde label from this injection site were absent in V1. Anterograde projections were observed to a large cortical region within the lateral and medial banks of the OTS approximately 10 mm anterior to VP. This projection field, like that observed in Case 6, is located within the ventral callosal region which helps to delineate ventral area V4 and area VOT. The observed projections to this region include both callosal-free and callosal-recipient cortex and are likely to involve VOT and perhaps also V4v. (The absence of robust anterograde label more posteriorly in V4 is puzzling, but may reflect the relatively high background labeling surrounding the injection site in this case). A third ventral projection field was located in area VTF on the parahippocampal gyrus. Scattered retrograde label was present anterior to the OTS, perhaps in central inferotemporal cortex (CIT).

In the superior temporal sulcus, reciprocal connections were found with MT and MSTd. In dorsal extrastriate cortex, combined retrograde and anterograde labeling was present in area PIP, and patches of anterograde label were present in areas V3A and DP. As in Case 6, anterograde label in the intraparietal sulcus was present in area VIP near the fundus and may have extended into area LIPv along the lateral bank of the sulcus.

**Case 8 (VP /V4v HRP/Pro).** In Case 8, the injection site was at the vertical meridian representation along the VP/V4v border; because of the likelihood that the injection substantially involved both areas we mention the results only briefly. Major foci of retrograde and anterograde label were present in V2v (concentrated along the border with V1), VTF, PIP, and VIP. In addition, anterograde labeled foci were present in V4v/VOT and MT, but there was no discernible label in V3A.

**Summary of VP connections.** Tables 2 summarizes the results for the retrograde and anterograde label for Cases 6–8. Connections in at least one direction occurred in most or all cases with nine areas, and connections with two additional areas were likely in at least some cases.

**Laminar patterns of VP connectivity.** Area VP receives feedforward input from cells located in the supragranular layers in area V2. It provides feedback whose axons terminate most strongly in layers 1 and 6 of V2. The remaining cortical targets received feedforward inputs from VP that terminated most densely in layer 4. Retrogradely labeled cells in these regions were found predominantly within the infragranular layers, consistent with a feedback projection from higher areas.

Some of the connections of VP showed distinct patchiness within the target area, particularly in the anterograde direction (see Fig. 16, Section A). Patchiness in the projection to V2 is illustrated in Figure 17, which shows multiple anterograde patches in V2 with a periodicity of 1–2 mm. Although cytochrome oxidase histochemistry was
not available in this hemisphere, this periodicity is suggestive of projections arising from more than one cytochrome oxidase compartment of V2.

**DISCUSSION**

**Comparison of V3 and VP connections.** Like all other neocortical areas that have been studied in primates, areas V3 and VP have numerous connections with other cortical areas, including more distant targets as well as immediate neighbors. For some of these pathways, this is the first detailed documentation of their existence. For others, we provide additional characterization of pathways whose existence was already established from tracer injections in other visual areas, (Maunsell and Van Essen, 1983b; Newsome et al., 1986; Perkel et al., 1986; Unger-
CONNECTIONS OF MACAQUE V3 AND VP

TABLE 2. Areal Distribution of Label Following Tracer Injections Into Area VP

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1Consistency of VP Connections. Overview of the patterns of cortical connections observed following combined HRP and 3H-proline injections into VP in three hemispheres. Conventions as in Table 1: –, label absent; +, label present; +?, label probably present; w, weak labeling; ?, label probably absent.

2See list of abbreviations.

leider and Desimone, 1986; Van Essen et al., 1986; Andersen et al., 1990; Boussaoud et al., 1990). Some of these connections can also be inferred from the original lesion study of V3 projections by Zeki (1971), even though at the time of his study most of the areas in our current partitioning scheme had not yet been identified.

As a framework for discussing these connections, it is useful to display the overall pattern as part of an anatomically based hierarchy that places each visual area at a particular level in relation to other areas (Felleman and Van Essen, 1991). This hierarchy was generated using the laminar distribution of the cells of origin and the axonal terminations to categorize each pathway as ascending, descending, or lateral (Rockland and Pandya, 1979; Maunsell and Van Essen, 1983b; Felleman and Van Essen, 1991). Figures 18 and 19 show the areas specifically connected with V3 and VP, respectively, in “subhierarchies” that have been extracted from the overall cortical hierarchy. In each subhierarchy, solid lines indicate a linkage between areas (in one or both directions) that was present in all cases of our study involving robust tracer injections (cases where the overall pattern of labeling was not strong are excluded). Bold dashed lines indicate linkages present in some, but not all of such cases. Light dashed lines indicate pathways that have been reported in other studies on the basis of tracer injections into target areas of V3 or VP but were not observed in the present study.

We found consistent connections between V3 and nine other visual areas, as evidenced by pathways that were seen in one or both directions in the majority of cases, including several that involved robust tracer injections (Table 1). There is also a connection between V3 and the frontal eye fields (FEF) that was reported by Barbas and Mesulam (1981) but was not tested in the present study because we did not examine the frontal lobes. Connections between V3 and five additional areas occurred in a minority of cases (including two pathways that occurred only in association with injections that involved the horizontal meridian representation). Finally, a connection between V3 and area PO was reported by Colby et al., 1988, which we might have missed because our V3 injections involved relatively central visual field representations, whereas PO mainly involves a representation of the visual periphery.

We found consistent connections between VP and nine different visual areas. There is also a connection between VP and FEF reported by Barbas and Mesulam (1981) but not tested here. In addition, there are several additional connections that were inconsistent in occurrence, and also a connection reported between PO and VP (Colby et al., 1988) but not evident in our results.

All but a few of the identified pathways are reciprocal, in that they occurred after both anterograde and retrograde tracer injections. The apparent exceptions include a linkage from FST to V3 (but not the reverse), from VP to VIP (but not the reverse), and several others indicated in Table 1. The apparent absence of reciprocity may in some cases reflect technical factors, such as the different sensitivity of particular tracer injections, or enroachment into an adjoining area by one tracer and not the other even when injected at the same site. On the other hand, a few cortico-cortical pathways appear to be genuinely non-reciprocal (Perkel et al., 1986; see Felleman and Van Essen, 1991; Salin and Bullier, 1995). Also, there is likely to be some genuine individual variability in the occurrence of certain pathways, particularly ones that are relatively minor, that transcend any technical factors.

Among the many connections that are reciprocal, most showed an approximate correspondence in the spatial extent of anterograde and retrograde labeling, but the patterns often differed in detail. It has been suggested that descending connections generally extend over a larger region than the reciprocal ascending connections (Zeki and Shipp, 1989; Krubitzer and Kaas, 1989; see Salin and Bullier, 1995). Because of technical limitations already discussed, our results neither support nor argue strongly against this hypothesis.

**Alternative partitioning schemes for V3 and VP.** Our results provide important evidence relating to the schemes for partitioning visual cortex in the vicinity of V3 and VP. In general, visual areas can be distinguished from one another on the basis of a variety of criteria relating to architecture, connectivity, visual topography, and function. However, the evidence obtained using any single approach often involves complexities or subtleties that can make it hard to distinguish unequivocally between areas (Felleman and Van Essen, 1991; Colby and Duhame, 1991; Sereno et al., 1994).

The distinction between V3 and VP was originally based on differences in myeloarchitecture, receptive field properties, and connections with V1 (Van Essen et al., 1986; Burkhalter et al., 1986; Newsome et al., 1986). Here we have confirmed the asymmetry of connections with V1, which were consistently seen after V3 injections but not after VP injections. In addition, we found indications of differences in V3 and VP connections with a number of extrastriate areas, including VTF, FST, V4t, DP, and VOT. Connections between VP and VTF occurred in nearly all cases, whereas connections between V3 and VTF were rare or absent altogether, even though VTF is reported to contain a representation of the lower visual field (Gattass et al., 1988). We found no connections between VP and FST, consistent with the finding by Boussaoud et al. (1990) that projections from VP to FST are rare. In contrast, both studies found connections between V3 and FST (mainly in the direction from FST to V3 in the present study; mainly from V3 to FST in the Boussaoud et al. study). Area V4t is connected with V3 but not VP, which is in accord with the
Fig. 17. Patchy VP connections with V2 (Case 6). Darkfield autoradiograph of an oblique section that demonstrates multiple dense clusters of labeled terminals in a bilaminar pattern in ventral V2 within the inferior occipital sulcus from a \(^{3}H\)-proline injection in VP. Layers 1, 4, and 6 are indicated by thin arrows. Broad arrows indicate clusters of silver grains overlying layers 1 and 6. Layer 4 is unlabeled. Scale bar = 1 mm.
evidence that V4t represents only the lower quadrant. Likewise, areas DP and VOT are connected with VP but not consistently with V3, which correlates with the evidence that DP and VOT represent only the upper quadrant (Maguire and Bazier, 1984; Van Essen et al., 1990). Altogether, these findings add to the collection of asymmetries between V3 and VP and enhance the plausibility of considering them as separate areas that contain only partial representations of the contralateral hemifield. Nonetheless, it can still be argued that V3 (V3d) and VP (V3v) are asymmetric components of a single visual area that is internally heterogeneous in its organization and connectivity (Gattass et al., 1988). The main argument favoring the unified (V3d/V3v) scheme is that together the two regions constitute a complete representation of the contralateral hemifield. However, as already noted, other areas in the macaque (including V4t, VOT, and DP) appear to contain incomplete representations of the visual field. Additional examples indicative of incomplete visual representations have been obtained in a recent detailed mapping study in the owl monkey (Sereno et al., 1994).

Krubitzer and Kaas (1993) have proposed a different scheme, in which (dorsal) V3 and the adjacent part of V3A together correspond to the dorsomedial area (DM) in the owl monkey. If correct, their hypothesis would substantially affect how we interpret some of the present results. However, we consider the available data (including V4t, VOT, and DP) to appear to contain incomplete representations of the visual field. Additional examples indicative of incomplete visual representations have been obtained in a recent detailed mapping study in the owl monkey (Sereno et al., 1994).

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Krubitzer and Kaas (1993) suggest that the reported myeloarchitectonic distinctions between V3 and V3A might instead reflect artifactual variations that are primarily related to the pattern of cortical folding. In our experience, myeloarchitectonic V3 can be reliably recognized when well-stained sections using the Gallyas (1979) method are available. It has a consistent appearance that is not attributable to the local cortical folding pattern (see also Girard et al., 1991), and this has allowed myeloarchitectonic V3 to be completely mapped in seven hemispheres besides those reported here (Van Essen et al., 1986). Moreover, its location correlates well (albeit not perfectly; see below) with V3 as identified using several independent criteria, including Cat-301 immunoreactivity (DeYoe et al., 1990), the pattern of V1 projections, and the pattern of callosal inputs (Van Essen et al., 1986). Hof and Morrison (1995) have suggested that the pattern of immunoreactivity for SMI-32 provides another basis for distinguishing V3 from V3A, although the borders of V3 and V3A shown in their Figure 1 do not appear to correspond to the borders delineated in the present study or by Van Essen et al. (1986).

A second issue relates to the topographic organization of V3 and V3A as assessed by receptive field mapping and by the pattern of callosal connections. Krubitzer and Kaas (1993) suggest that the lower-field representation of V3 directly adjoins the upper-field representation of V3A, jointly constituting a single visual field representation. However, this interpretation is difficult to reconcile with the reported topographic organization of this region. Even though there is some local topographic disorder in this region, two studies have reported (i) a progression from the horizontal meridian representation along the V2/V3 border to receptive fields at or near the inferior vertical meridian at the anterior border of V3, and (ii) a separate, mirror-image representation that progresses from the inferior vertical meridian at the V3/V3A border, across the horizontal meridian, and into the upper-field representa-
tion of V3A (see Figs. 8, 9, 11 of Van Essen and Zeki, 1978; Fig. 13 ofGattass et al., 1988). Moreover, this topographic organization correlates with the pattern of callosal inputs (Van Essen and Zeki, 1978; Van Essen et al., 1986). A related point is that if there were only a single lower-field representation between V2 and the upper-field representation of V3A, there would necessarily be a topological discontinuity somewhere in the mapping. No convincing illustration of such a discontinuity has been reported in this region. More generally, it is noteworthy that recent fine-grained mappings in the owl monkey indicate that overt topographic discontinuities occur rarely if at all in visual cortex (Sereno et al., 1994), even though apparent discontinuities had previously been described at some boundaries between visual areas in earlier studies carried out with sparser spacing of recording sites (Allman and Kaas, 1971; 1975). Given that topographic discontinuities have been convincingly demonstrated in the somatosensory cortex of primates (Merzenich et al., 1978), there may be important differences across sensory modalities in certain principles of topographic mapping. 

Krubitzer and Kaas (1993) suggest that the existence of V1 projections to both V3 and V3A constitutes an argument for considering them as a single area, DM. However, the connection between dorsal V1 and V3 is robust and consistent (occurring in all 13 cases tested by Van Essen et al., 1986), whereas that between V1 and V3A is sparse and inconsistent (definite or probable occurrence in 5 of 21 cases in the same study). A possible physiological correlate of this difference in connectivity is that cooling of V1 completely blocks visual responses of neurons in V3 but leaves many neurons in V3A still responsive to visual stimulation (Girard et al., 1991).

Finally, the laminar pattern of connectivity between V3 and V3A shows a characteristic asymmetry indicative of areas at different hierarchical levels. As illustrated in Figures 3, 4, and 6, the anterograde label from V3 to V3A terminates mainly in layer 4 (the forward pattern), whereas the retrograde label from V3A to V3 originates mainly from layers 5 and 6 (a feedback pattern), suggesting that V3A is at a higher hierarchical level than V3 (Fig. 18). If V3 and V3A were part of the same area, one would expect an intrinsic pattern having columnar anterograde label and bilaminar retrograde label (Felleman and Van Essen, 1991).

Altogether, we consider it unlikely that V3 and V3A are parts of a single visual area in the macaque. While rigorous proof on such matters is difficult given the complexity of the different types of data, we consider it parsimonious to retain the distinction between V3 and V3A as separate visual areas.

Most of the areas with which V3 and VP are connected have previously been identified using multiple anatomical and/or physiological criteria. However, the present study has provided important new evidence regarding the partitioning of two regions of extrastriate cortex, namely, the V3A/PIP region dorsally, and the region of VOT and surrounding cortex ventrally.

**Areas V3A and PIP.** Our anatomical evidence that the region previously identified as V3A contains two distinct areas is consistent with observations from two previous studies. Complexities in the topographic organization of V3A, including a possible double representation of central visual fields, were noted in the original study of V3A (Van Essen and Zeki, 1978), but the characterization was not sufficiently detailed to warrant a designation as two separate areas. Colby et al. (1988) reported projections to area PO arising from two separate regions that they identified as V3A and PIP, in a pattern that is largely in accord with our findings. In terms of topographic organization, our evidence suggests that central fields are represented ventro-posteriorly and peripheral fields dorso-anteriorly in both V3A and PIP. However, our results suggest a mirror-symmetry in the representation of lower vs. upper fields, with upper fields represented along the V3A-PIP border and lower fields represented laterally in V3A and medially in PIP. This is roughly consistent with the topography for upper vs. lower fields suggested by results of Colby et al. (1988) for their Case 2. It differs from the description they provide for their Case 1, in which it appears that upper fields are represented posterior to lower fields in PIP and dorsal to lower fields in V3A. However, there are plausible alternative assignments for the areal boundaries in their Case 1 that would be more consistent with our interpretation of the location and topography of these areas.

**Areas VOT, PITv, and TEO.** Area VOT was previously identified in a physiological mapping study as an upper-field representation adjoining ventral V4 (Felleman et al., 1985; Van Essen et al., 1990). Ventral V4 and VOT lie largely within a large callosal-free region, but they extend into a surrounding callosal-recipient ring, much as occurs for other pairs of extrastriate areas such as VP/ventral V2, V3/dorsal V2, and V3A/PIP. In our partitioning scheme (Felleman and Van Essen, 1991) the principal area adjoining VOT on its anterior side is area PITv. In the present study, we found no projection from either V3 or VP to PITv, nor have such connections been encountered in a study involving tracer injections into PITv (Felleman and McClendon, 1991; Felleman et al., 1992). PITv has a crude topographic organization and receives inputs from lower-field as well as upper-field subdivisions of V4 (Felleman and McClendon, 1991; DeYoe et al., 1994). PITv also differs from VOT in having more extensive interhemispheric connections (Van Essen et al., 1982), although for technical reasons this difference was not apparent in the present study.

An alternative partitioning scheme for this region is that a single area, TEO, occupies the region we regard as VOT and PITv and includes a representation of both upper and lower fields (Boussaoud et al., 1991). TEO is reported to have connections with area VP and ventral V2, but this would be consistent with the present study if the relevant part of the tracer injection in TEO included what we regard as VOT (Nakamura et al., 1993). TEO as defined is an area whose upper-field and lower-field components differ in their connectivity, and we therefore consider the VOT/PITv distinction to be a more parsimonious accounting of the available data. However, either scheme is reasonable, as long as the criteria for identification are made clear (see above).

**Processing streams.** During the past 15 years there have been numerous studies of the different processing streams that course through the primate visual system. As noted in the Introduction, these streams start with the magnocellular, parvocellular, and koniocellular streams at the subcortical level (Casagrande, 1994). They continue with the magnno-dominated (MD), blob-dominated (BD), and interblob-dominated (IB) streams that are established in V1 and can be traced through several levels of extrastriate cortex (Van Essen and DeYoe 1994; Van Essen and Gallant, 1994). V3 is preferentially linked to the MD
stream by virtue of its inputs from layer 4B of V1. We found its connections with V2 to be distinctly patchy, but the periodicity of the patches suggests an involvement of more than one type of stripe compartment of V2. Hence, there may be convergence from different streams in the ascending inputs from V2 to V3. This interpretation is consistent with the physiological characteristics of V3 neurons (Felleman and Van Essen, 1987). The 40% incidence of direction selectivity reported for V3 is high enough to suggest an association with the MD stream, but it is consistent with influences from other streams as well, as it is much lower than the 90% incidence of direction selectivity reported for MT (Maunsell and Van Essen, 1983a).

The connections between V2 and VP were also patchy, and as with the V2–V3 pathway, the periodicity of these patches suggests involvement of more than one V2 compartment. Physiologically, direction selectivity is relatively rare in VP, whereas there is a high incidence of wavelength selectivity and orientation selectivity (Burkhalter and Van Essen, 1986). Accordingly, one might suspect that VP is more closely associated with the BD and ID streams than with the MD stream, but our anatomical evidence does not bear directly on this issue.

At higher levels of the hierarchy, there is a basic distinction between areas in inferotemporal cortex that are implicated in object recognition (the “what” pathway) and posterior parietal areas that are implicated in the analysis of spatial relationships (the “where” pathway) (Ungerleider and Mishkin, 1982; Desimone and Ungerleider, 1989). Our results demonstrate that V3 and VP both have close associations with posterior parietal cortex, by virtue of direct projections to VP and LIPv and indirect projections via MT and MSTd. However, they are also associated with the inferior temporal stream by virtue of their projections to V4, which is the main source of inputs to inferotemporal cortex. Similar arguments have been made that area V4 also links the parietal and temporal processing streams (Baizer et al., 1991; Morel and Bullier, 1991).

V4 is anatomically heterogeneous, with segregated regions receiving inputs from the BD and ID compartments (thin stripes and interstripes) of V2 and from specific subdivisions of inferotemporal cortex (Zeki and Shipp, 1990; Felleman andMcClenond, 1991; DeYoe et al., 1994; Felleman et al., 1992). Given our observations that the projections from V3 to V4 are highly patchy, it is intriguing to wonder whether this patchiness is correlated with the BD and ID subregions of V4 or whether it reflects an independent aspect of cortical modularity.

**Comparison with other primates.** Visual cortex in all primate species studied to date, from prosimians to humans, includes two large areas, V1 and V2, surrounded by a mosaic of smaller extrastriate areas, one of which is area MT (Allman, 1981; Van Essen, 1985; Kaas, 1988; Sereno and Allman, 1991; Krubitzer, 1995; Sereno et al., 1995). Numerous other possible homologies have been proposed, particularly between the New World owl monkey and the Old World macaque monkey, but in general the evidence is fragmentary and less compelling. Of particular relevance to the present study are possible homologies of V3 and VP in the macaque. The ventral posterior area (VP) of the owl monkey (Newsome and Allman, 1980) is similar in position (relative to ventral V2) and topographic organization to VP in the macaque, and is therefore a strong candidate for a homologue. As noted already, area DM in the owl monkey has been suggested as a homologue of a combined V3/V3A in the macaque (Krubitzer and Kaas, 1993); however, we consider this an unlikely possibility because of the aforementioned evidence that V3 and V3A are indeed separate areas. Alternatively, DM might be homologous with just one of these areas, either V3 or V3A. A homology between DM and V3 seems unlikely, given their differences in topographic organization and laminar pattern of inputs from V1. A homology with V3A seems more plausible, although owl monkey DM and macaque V3A differ in how central vs. peripheral visual field representations are oriented in relation to neighboring areas. A more extensive anatomical and physiological characterization of these regions in a variety of primates is needed to resolve this issue and to attain a better understanding of the commonalities in cortical organization across primate species.

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**LITERATURE CITED**


CONNECTIONS OF MACAQUE V3 AND VP


