THE JOURNAL OF COMPARATIVE NEUROLOGY 230:337-351 (1984)

Cortical Connections of Area 17 in Tree Shrews

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ABSTRACT

In order to better understand the organization of extrastriate cortex in tree shrews, injections in area 17 of wheat germ agglutinin or tritiated proline were used to reveal an intrinsic pattern of connections, ipsilateral connections with area 18 and two other subdivisions of cortex, and callosal connections with areas 17 and 18 of the opposite cerebral hemisphere. Areal patterns of connections were best seen in sections cut parallel to the surface of flattened cortex. Within area 17, periodic foci of labeled terminations and cells extended from and surrounded injection sites as described by Rockland et al. ('82). Single injections produced multiple foci of labeled terminations and cells in area 18. The foci tended to fuse into short bands that sometimes crossed the width of area 18. Double injections produced more foci, and multiple injections tended to produce more continuous regions of label. An overall retinotopic pattern was evident with rostral area 17 connected to rostral area 18 and caudal area 17 connected to caudal area 18. Terminations extended through layers II-VI, with some increase in density in layer IV. Cells in area 18 projecting back to area 17 were in layers III and V. The injections also allowed identification of previously undefined subdivisions of visual cortex in temporal cortex immediately adjoining area 18. Dense reciprocal connections were observed in a 13 mm^2 oval of cortex on the lateral border of the middle section of area 18 that we define as the temporal dorsal area, TD. Connections indicate a crude topographic organization with lower field represented rostrally and upper field caudally. Inputs were most dense in the middle cortical layers, and labeled cells were supragranular, and less frequently, infragranular. A 10-mm^2 oval of cortex near the posterior edge of the hemisphere, the temporal posterior area (TP), contained labeled cells after area 17 injections, but terminal labeling was only obvious in the dorsal part. Single injections sometimes produced quite separate dorsal and ventral zones of label in TP, suggesting a small separate dorsal division. A crude retinotopic order appears to exist within ventral TP, with the lower field most ventral. Labeled cells were largely supragranular. A fourth zone of ipsilateral connections was in posterior limbic cortex bordering area 17 on the ventromedial surface of the cerebral hemisphere. The callosal connections were reciprocal and included regions 1 mm wide on either side of the area 17 and area 18 border. Callosal connections were roughly homotopic. Callosal terminations included superficial layers, and projecting cells were both supragranular and infragranular. We conclude that extrastriate cortex in tree shrews contains at least three subdivisions, one of which (TD) may be the homologue of the middle temporal visual area of primates.

Key words: striate cortex, extrastriate visual cortex, corticocortical connections, visual representations

Accepted July 11, 1984.

Considerable progress has been made in understanding the organization of extrastriate cortex in cats and monkeys where a number of separate representations of the retina have been established in studies of patterns of connections and by electrophysiological mapping procedures (for review, see Van Essen, '79). Yet, little is known about the organization of extrastriate cortex in other mammmals (for review, see Kaas, '80). A greater understanding of the organization of extrastriate cortex in tree shrews would be important for several reasons. First, while phylogenetic affinities have been a matter of debate, tree shrews appear to be the closest living relatives of primates (e.g., Cronin and Sarich, '80). Thus, tree shrews can provide important information about the evolution of visual cortex in primates. For example, the middle temporal visual area (MT), is found in both simian and prosimian primates (see Weller and Kaas, '82), but it is not known if MT developed with primates or earlier. Investigations on tree shrews could help answer this question. Second, the visual system of tree shrews has many advanced features including a laminated lateral geniculate nucleus, a well-differentiated area 17, and a large and clearly laminated superior colliculus. It is of interest to determine if these features are associated with advances in the organization of visual cortex such as the presence of a number of subdivisions of extrastriate cortex. Third, tree shrews are born in an extremely altricial state and much of the development of the lateral geniculate nucleus occurs postnatally (Brunso-Bechtold and Casagrande, '82, '84). It is likely that much of the development of visual cortex also occurs postnatally and that studies of their cortical development would be valuable after normal adult organization became known.

One of the more productive ways of investigating the organization of poorly understood regions of the brain is to use the connections of known subdivisions to identify the locations, extents, and internal organizations of other subdivisions. In tree shrews, areas 17 and 18 are architectonically distinct, and both fields have been associated with systematic maps of the retina, V-I and V-II, respectively (Kaas et al., '72). We decided to start our investigations of the organization of extrastriate cortex in tree shrews by determining cortical connections of area 17. Patterns of area 17 projections have been used to subdivide extrastriate cortex in primates (e.g., Zeki, '69), and this approach was a logical first step.

Area MT in primates has a specific pattern of connections with area 17. In addition, uneven patterns of area 17 projections to area 18 (for a recent review, see Weller and Kaas, '83) and MT (e.g., Montero, '80; Weller and Kaas, '83) in primates suggest a nonuniform distribution of function and modular processing within these fields. Thus, revealing area 17 connections in tree shrews could both help subdivide extrastriate cortex and suggest the nature of processing units in these subdivisions. Finally, single locations in area 17 of tree shrews (Rockland and Lund, '82; Rockland et al., '82) and monkeys (Rockland and Lund, '83) have been shown to have an interesting periodic pattern of nearby lateral intrinsic connections. The present investigation of area 17 connections provided an opportunity to confirm and extend previous observations of the intrinsic pattern.

Since the subcortical connections of area 17 in tree shrews have been extensively described (Diamond et al., '71; Harting and Noback, '71; Harting et al., '73; Casagrande and Harting, '75; Hubel, '75; Carey et al., '79; Conley et al., '84; Huerta et al., '84), they are not detailed here. Some of our observations have been briefly reported elsewhere (Sesma et al., '83).

METHODS

The intrinsic and extrinsic connections of area 17 were investigated in nine adult tree shrews (*Tupaia belangeri*). In seven of these cases wheat germ agglutinin either tritiated (^{3}H-N-acetyl-WGA, [Steindler, '82]) or conjugated to horseradish peroxidase (WGA-HRP) was injected into area 17. The resulting patterns of anterogradely and retrogradely transported label were traced in sections cut parallel to the flattened hemisphere (see below). In four of the seven cases a single injection of WGA-HRP was made in one hemisphere (e.g., Fig. 4). In cases 83-44 and 83-69, two injections of WGA-HRP were made in the same hemisphere (Fig. 5, 8). In case 83-61, ten injections of WGA-HRP were made in the right hemisphere (Fig. 6) and three injections of ^{3}H-WGA were made in the left hemisphere. In the remaining two animals (77-11 and 78-23), bilateral injections of ^{3}H-proline and HRP were made and the pattern of anterogradely transported amino acid and retrogradely transported HRP was traced in sections cut in the coronal plane.

Surgical procedures were carried out with tree shrews anesthetized with an initial dose of 130 mg/kg of ketamine hydrochloride (White et al., '82) and supplemented with ketamine as needed. Striate cortex was exposed with aseptic procedures and 0.1% dilutions of WGA-HRP or ^{3}H-WGA in distilled water or ^{3}H-proline (35 μCi/μl) and 20% HRP in 0.9% saline were injected at 0.2–0.5 μl volume using calibrated micropipettes or a Hamilton microsyringe. After survival times of 24–48 hours, the tree shrews were deeply anesthetized and perfused through the heart with 0.9% saline followed by 1% paraformaldehyde and 1.25% glutaraldehyde in 0.1 M phosphate buffer (lectin cases) or 2% paraformaldehyde in 0.1 M phosphate buffer (^{3}H-proline cases). The two brains that received ^{3}H-proline/HRP injections were cut frozen at 30 μm and two sections in four were processed for autoradiography (Cowan et al., '72) or reacted for HRP using diaminobenzidine (LaVail and LaVail, '72). In the seven brains which received lectin injections, the cortex of each hemisphere was separated from the rest of the brain, submerged in 30% sucrose in phosphate buffer at 4°C, and flattened between glass plates (see Gould and Kaas, '81; Killackey et al., '83, for further details). The flattened cortical slabs were frozen and cut parallel to the surface the next day at 30–50-μm thickness. At least one of every three sections was reacted for HRP using tetramethylbenzidine (TMB) (Mesulam, '78) or processed for autoradiography (Cowan et al., '72). Other sections were stained using a silver procedure for myelin (Gallyas, '79) or processed for cytochrome oxidase activity (Wong-Riley et al., '78). The thalamus and brainstem of each case were cut in the coronal plane and processed as were the cortical sections.

The patterns of retrograde and anterograde label were drawn from single sections magnified 40 times with a microscope and a drawing tube attachment. By carefully aligning blood vessels and artifacts in drawings of closely spaced sections, it was possible to summarize results from several sections on a single drawing and to include architectonic borders. The border of area 17 was particularly distinct, even in unstained sections (Figs. 2, 3). Laminar patterns of connections were best determined from coronal

sections (Fig. 7), although in tangential sections layer IV was usually apparent so that label could be characterized as either supra- or infragranular.

RESULTS

The results revealed a complex pattern of connections intrinsic to striate cortex, ipsilateral connections with at least four regions of extrastriate cortex, and callosal connections with striate and extrastriate cortex of the contralateral cerebral hemisphere. Figure 1 summarizes the major features of the ipsilateral projection pattern and indicates the retinotopic organization of striate cortex of the dorsolateral surface of the hemisphere as previously determined by electrophysiological mapping studies (Kaas et al., '72; also see Kaas, '80). The figure indicates that striate cortex connects topographically with area 18 or V-II, to a region we have defined as temporal dorsal (TD) cortex, and to a region we term temporal posterior (TP) cortex. Temporal posterior cortex appears to consist of two zones; the smaller dorsal region has reciprocal connections with area 17, the larger ventral region projects to area 17. Figure 1 also indicates that a single injection typically results in more than one focus of connections within a single connection zone, especially in area 18, and that connections vary in location in area 18, TD, and TP according to the location of the injection in striate cortex. Limbic cortex connections and callosal connections of area 17, which straddle the area 17/18 border, are not shown in Figure 1.

Figure 2 shows that much of the total areal pattern of cortical connections can be appreciated from even a single section when the flattening procedure is used and sections are cut parallel to the surface. Another example is shown in Figure 3. However, more details of the total pattern are apparent when the sections are viewed at higher magnification and when results from several sections are compiled on a drawing of a single section (e.g., Fig. 4). In addition, it is possible to consider only the retrogradely labeled cells or the diffuse label that largely or completely represents anterogradely transported WGA-HRP.

The intrinsic pattern

The intrinsic pattern of connections revealed by the present experiments corresponds closely with that described previously for striate cortex of tree shrews after HRP injections (Rockland and Lund, '82; Rockland et al., '82). Overlapping foci of terminals (Figs. 3, 4) and labeled cells protruded from the margin of a dense circle of label around single injection sites. In single sections these protrusions were sometimes elongated, forming short, varicose bands. Sometimes these were arranged in discontinuous, short rows of isolated clusters of terminals and cells. The banding was most evident after the total pattern was reconstructed from several sections, as shown for both anterograde and retrograde label in Figures 3 and 5. In addition, distinct foci of label were apparent at distances as far as 1.5 mm from the edge of the dense circle of label. These bands of

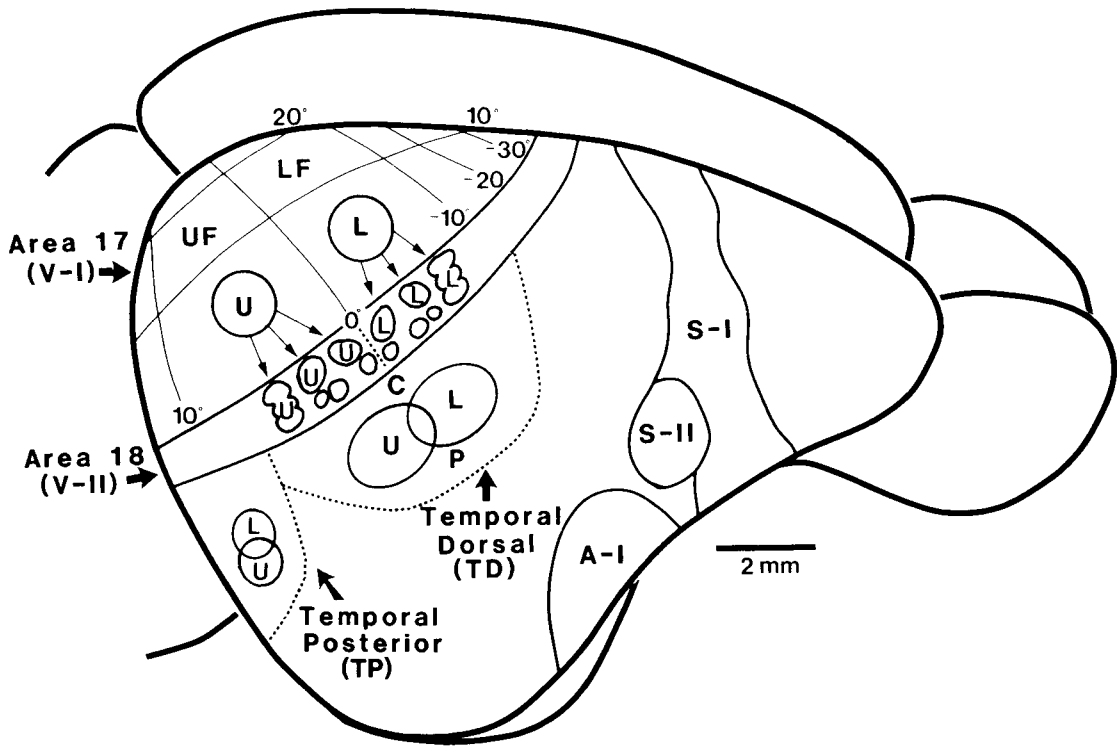


Fig. 1. The locations of area 17 (V-I), area 18 (V-II), and two extrastriate regions defined by their pattern of connections with area 17: temporal dorsal cortex (TD), temporal posterior (TP) cortex. The retinotopic organization of area 17 is from Kaas et al. ('72). The connections of the upper (U) and lower (L) central visual field are illustrated schematically for each visual area showing crude topographic organization. Note the connections between area 17 and 18 which are distinguished by the multiple foci that sometimes form bands in area 18. The dashed lines delimiting TD and TP are estimates based on myeloarchitecture. Not illustrated on this summary are connections with posterior limbic cortex and callosal connections of area 17. C, central vision; P, peripheral vision; UF, upper visual field; LF, lower visual field; S-I, first somatosensory area; S-II, second somatosensory area; A-I, first auditory area.

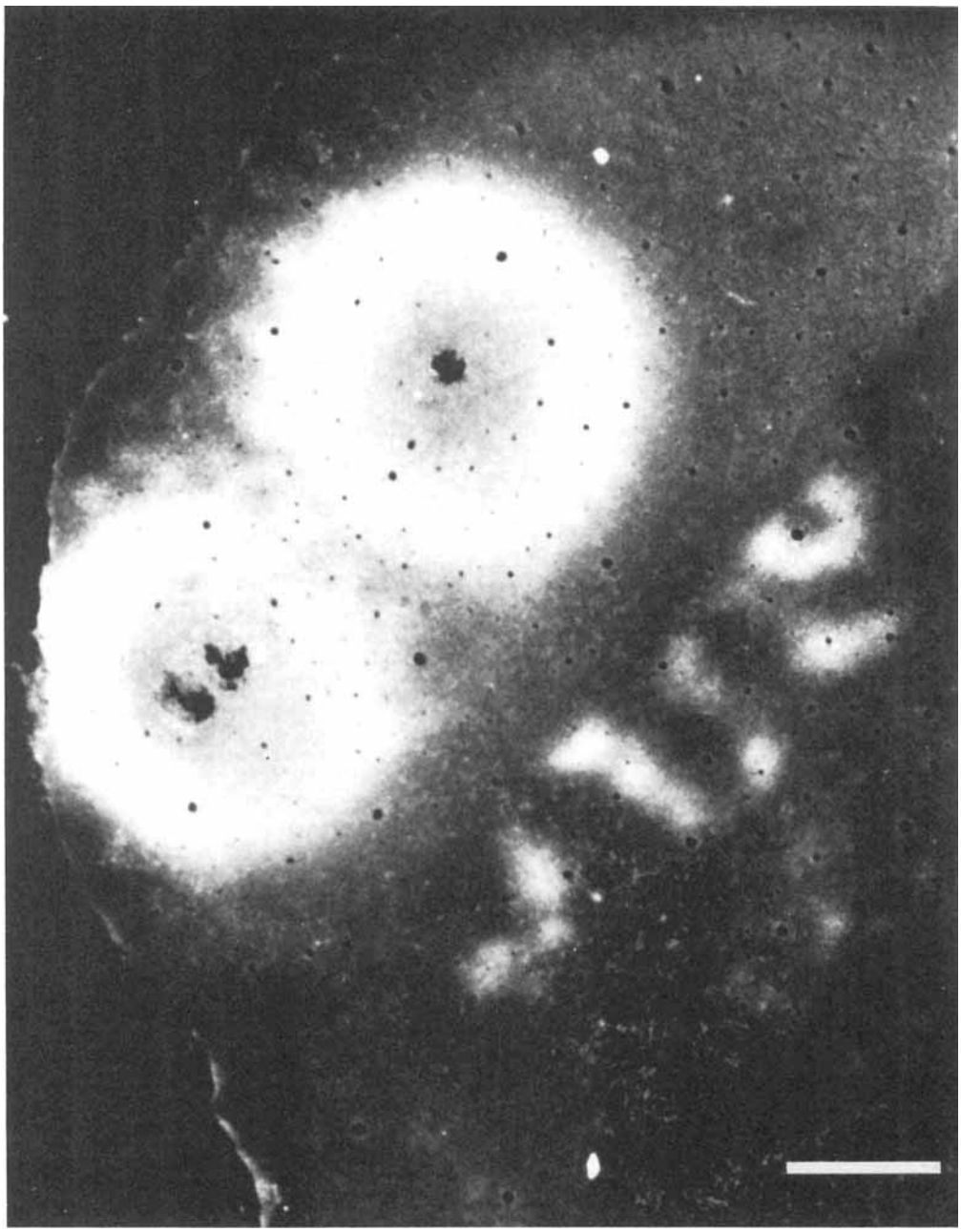


Fig. 2. A dark-field photomicrograph of a single section showing two striate injection sites of WGA-HRP and the overall areal pattern of intrinsic and extrinsic connections (case 83-44). Patches of labeled cells and terminals extend from the injection sites except between them, where the pattern of labeling is more uniform. The extent of area 17 can be delimited by a lighter background than adjacent area 18. The width of area 18 is distinguished in this case by the length of the bands of label. Rostral to the area 18 label several fainter foci of label are seen in temporal dorsal cortex. Rostral is on right, medial at top. Scale = 1 mm.

label had center-to-center separations of 400–600 μm (uncorrected for shrinkage).

The present cases provided evidence that all locations in striate cortex may be subserved by lateral intrinsic connections. When two injection sites were placed in striate cortex of the same cerebral hemisphere, periodic patterns of intrinsic label surrounded each injection site (Figs. 2, 5). However, in the supragranular layers the region between the two injection sites was more evenly labeled so that the periodic pattern was largely obscured. In deeper layers the region between the injection sites contained fewer labeled cells and terminals between the injection halos. An even more uniform labeling pattern was seen around the multiple injections in striate cortex (Fig. 6), even though the foci of labeled cells and terminals were not fused in the lateral geniculate nucleus. This result suggests that the relatively

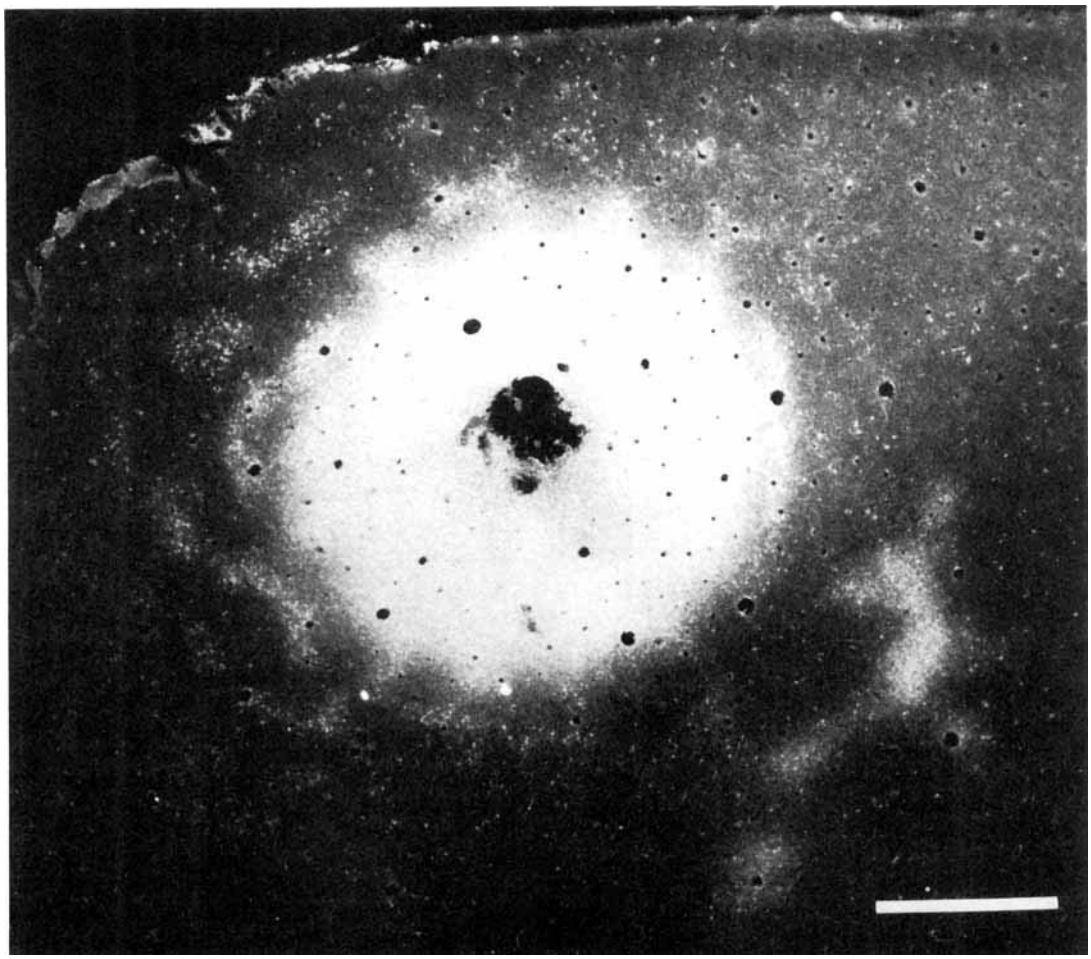


Fig. 3. A single injection site (case 83-41) in the lower visual field representation of area 17. This dark-field photomicrograph shows in greater detail the intrinsic connections around the injection site as well as the multiple foci of labeled cells and terminals in area 18. Again the extent of striate cortex can be delimited by the lighter background of the tissue. This section is about 500 μm (supragranular) from the pial surface. Rostral is on the right, medial at the top. Scale = 1 mm.

uniform cortical labeling between injection sites was due to more even labeling of lateral intrinsic connections, rather than direct diffusion of the tracer.

The distribution of filled cells and terminals within specific cortical layers was difficult to evaluate in tangential sections. However, even in these sections, it was apparent that the foci of labeled cells and terminals were most obvious in the supragranular layers. In coronal sections of brains with ^{3}H-proline injections (Fig. 7), separate puffs of anterograde label were apparent in layers I–IIIb near the injection site, while dense, continuous label spread out from the region of the injection site in layer IIIc and to some extent in layers V and VI. These observations correspond closely with those of Rockland et al. ('82).

Area 18 or V-II

In tree shrews, area 18 is a visual area on the outer border of striate cortex that is easily defined by physiological mapping and cytoarchitectural criteria (Kaas et al., '72). As in other species, area 18 in tree shrews corresponds to a representation of the contralateral visual hemifield, V-II. Area 18 can be identified cytoarchitecturally by a lighter myelin stain in sections from flattened cortex, and in Nissl-stained coronal sections, by lower density cell packing in layers IV and VI than seen in adjoining cortex. In sections from the flattened brains, the border with striate cortex was obvious in Nissl-stained sections or sections reacted for cytochrome oxidase, but it was usually necessary to extrapolate the outer border from the known width of area 18. Comparisons with adjacent sections stained for fibers were sometimes used to help define the outer border.

Single injections of WGA-HRP always produced a number of separate foci of labeled cells and terminals in area 18 (Figs. 3, 4). As a rule, labeled cells and terminals were coextensive. A single injection with a dense central core of about 1 mm in diameter would typically produce five to eight foci of label that clustered in the same region of area 18, and often partially fused. The total area encompassed by the foci of label appeared to be slightly larger in surface area than the core of the injection site. Our measurements indicate that striate cortex ($\sim$66 mm^2) is about three times as large as area 18 ($\sim$21 mm^2), so locations in area 17

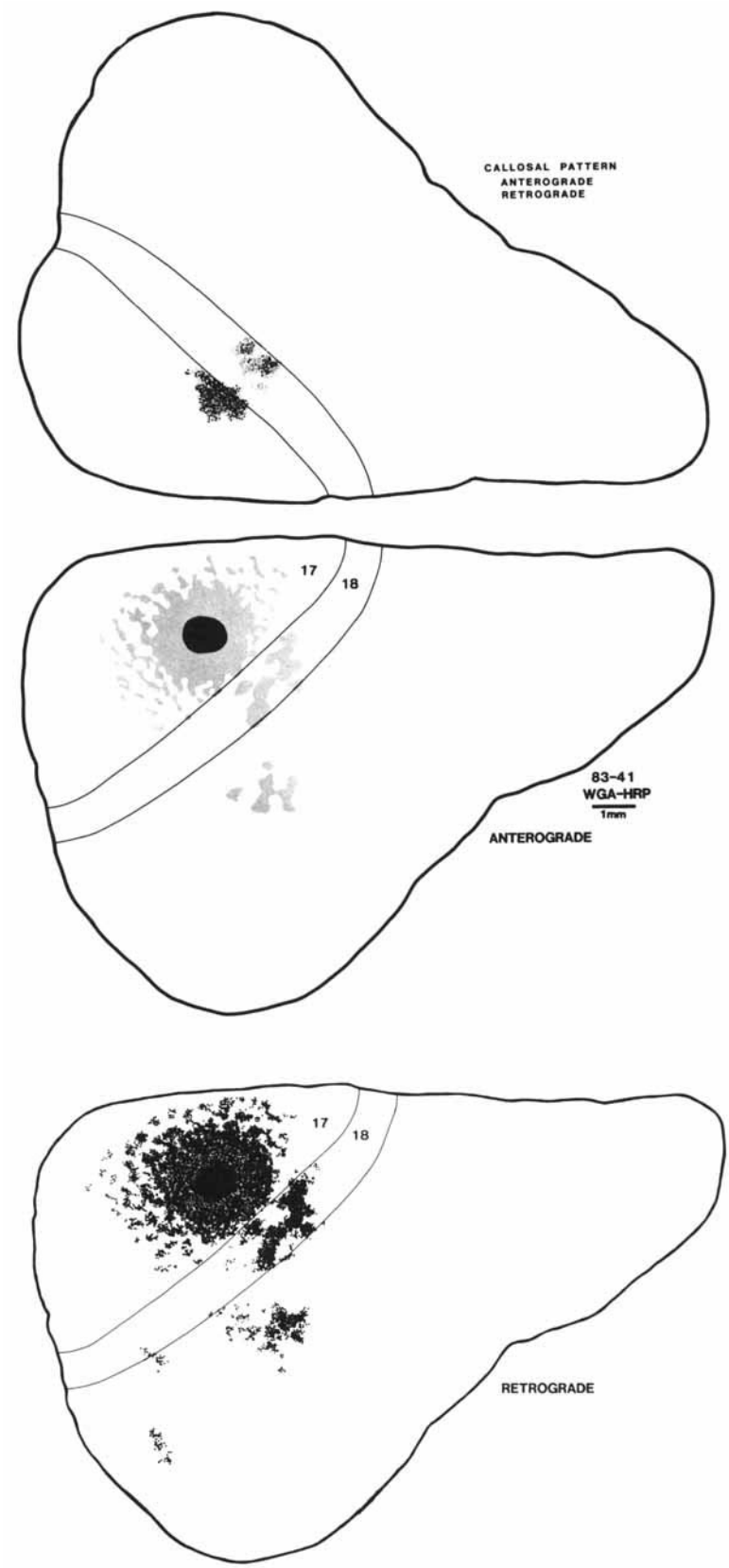
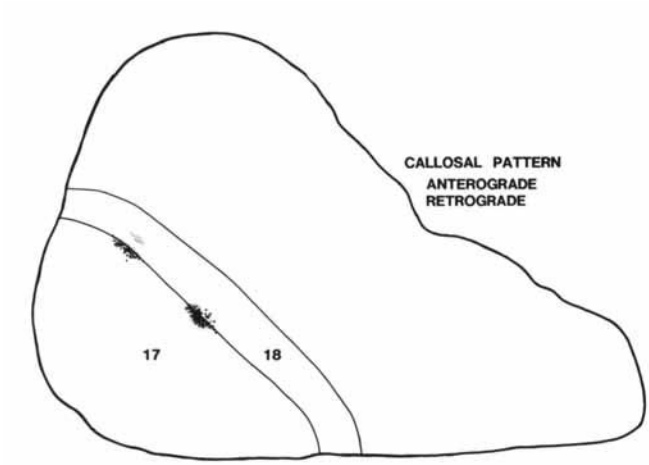
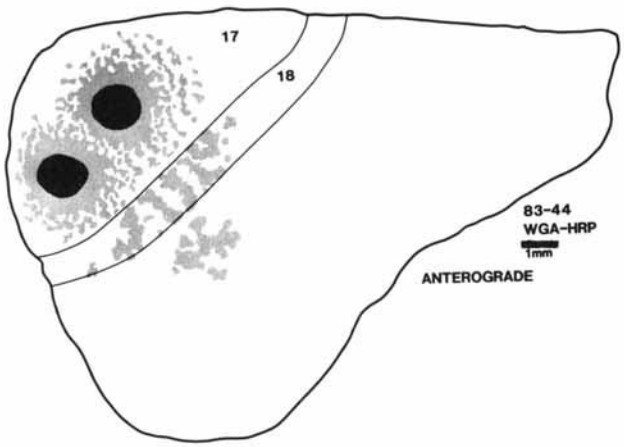


Fig. 4. A reconstruction through six sections of the contralateral and ipsilateral connections of area 17 revealed by a single injection of WGA-HRP. Ipsilateral anterograde and retrograde label are shown on separate reconstructions. Contralateral anterograde and retrograde label are shown on the same figure. The borders of area 17 and 18 were determined using sections stained for cytochrome oxidase.





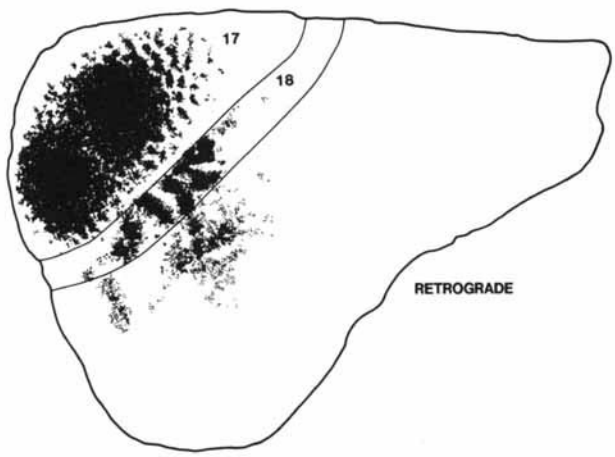
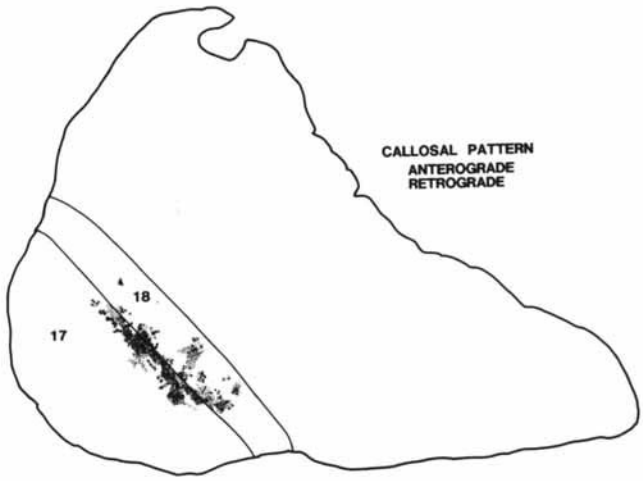
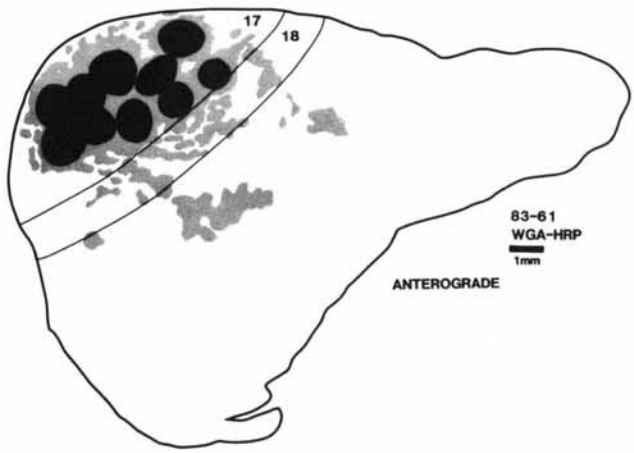


Fig. 5. A reconstruction of the pattern of connections of area 17 revealed by two injections of WGA-HRP.





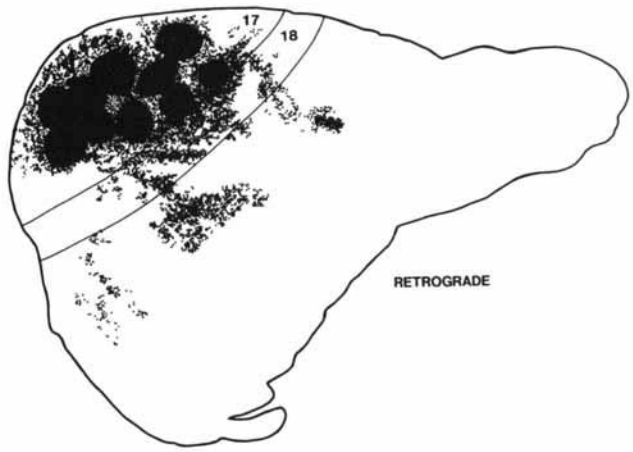
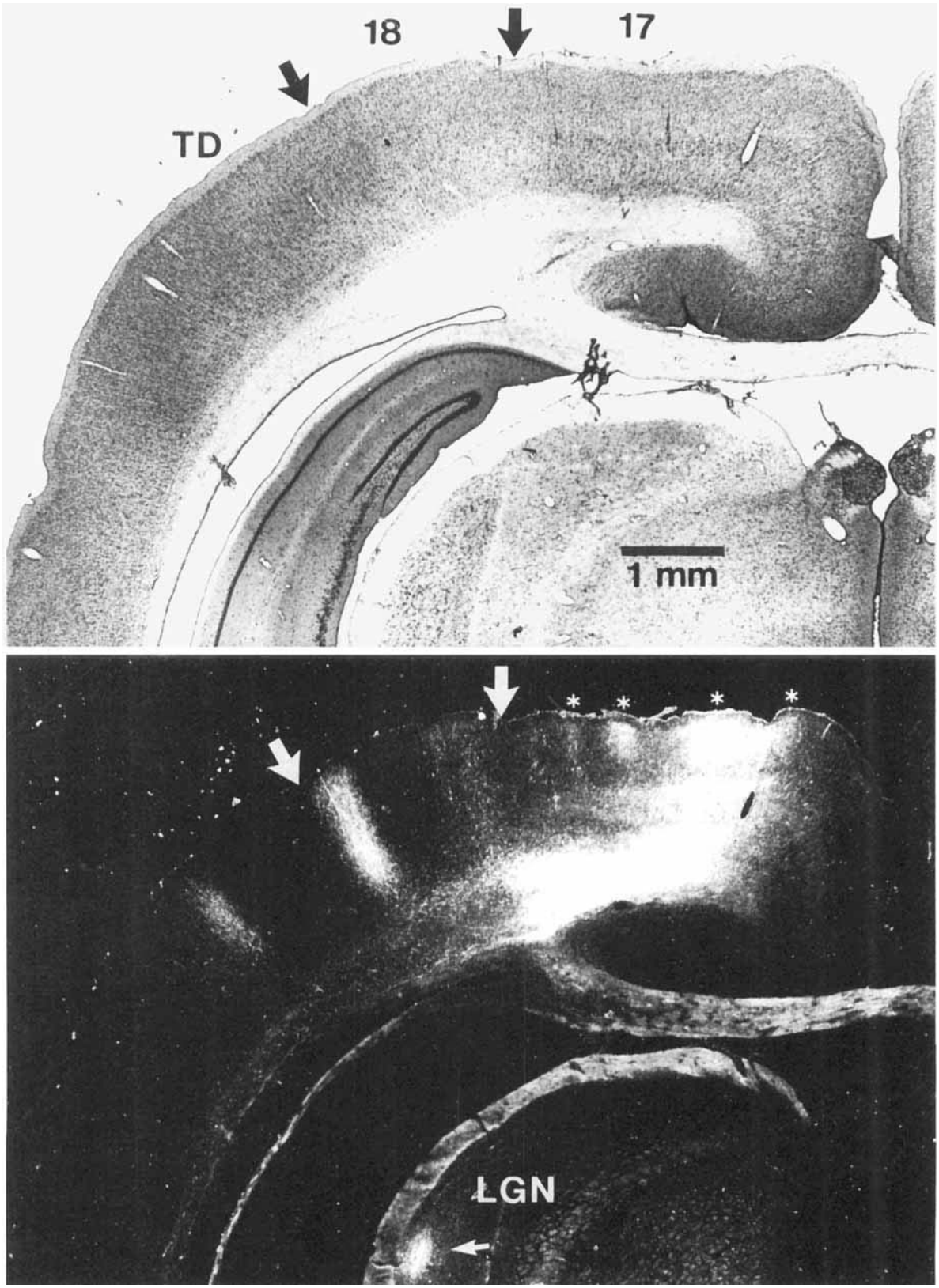


Fig. 6. A reconstruction of the pattern of connections of area 17 revealed by ten injections of WGA-HRP. The most rostral patches of label are probably connections of area 18 which resulted from the most rostral injection straddling the 17/18 border. Label was not seen in this region in any other case. Architectonic borders were determined using sections stained for myelin.


18
17
TD
1 mm
LGN

apparently project to a larger proportion of area 18. The partially fused foci of label in area 18 sometimes formed bands that crossed the entire width of area 18 (Figs. 3, 4).

When more than one injection was made in area 17, the number of foci of label in area 18 increased. The two injection sites illustrated in Figures 2 and 5, for example, produced five or six clusters of label that were subdivided into ten to 15 distinguishable foci of label. After ten injections in area 17, the number of foci of label was still greater (Fig. 6), but clearly not ten times greater than after a single injection. Instead, the unlabeled regions between foci were smaller than after single or double injections, although discontinuities were still apparent. By encircling the portion of area 18 with foci of label after one (Figs. 3,4) two (Figs. 2, 5), or ten (Fig. 6) injections, it is apparent that the labeled region almost doubled in area after two separate injections, but only increased by roughly another third after ten closely spaced injections. This observation indicates that there is both convergence and divergence of inputs from area 17 to area 18.

The projections from area 17 to area 18 also follow a retinotopic pattern. Both area 17 and area 18 represent the upper field caudally and the lower field rostrally. The zero vertical meridian is represented along the common lateral border of areas 17 and 18, and more peripheral vision is represented ventrally in area 17, and at the rostral and caudal extremes of area 18 (see Fig. 1 and Kaas et al., '72). Injections placed rostrally in area 17 produced foci of label that were more rostral in area 18 (Figs. 3, 4), while injections placed caudally (caudal injection in 83-44, cases 83-35 and 83-59 not shown) resulted in label that was caudal in area 18. In case 83-44, with two injections in area 17 (Figs. 2, 5), labeled axons were traced from each injection site to foci of label in area 18, and the caudal three clusters of label related to the caudal injection site, while the rostral three clusters related to the rostral injection site. In this case, the middle clusters received projections from both injection sites. Injections in striate cortex that included sites on both the dorsal and ventral surfaces of the cerebral hemisphere (case 84-69) resulted in foci of label from central to caudal area 18 (Fig. 8). The label in caudal area 18 could represent connections with ventral area 17, which represents the peripheral visual field.

While the projections of area 17 to area 18 appear to be at least crudely retinotopic, there is evidence that some disparities in retinotopic positions of connections occur. The outer border of area 18 represents the visual hemifield some 15–30° from the zero vertical meridian in the central portion and visual field as far as 60° or more toward the ends of the outer margin of the belt (Kaas et al., '72). The injection in Figure 2 includes cortex that would appear to represent a portion of the visual field from 2 to 7° from the zero vertical meridian. The resulting label in area 18 appears to include cortex representing 0–15° or more from the zero vertical meridian. All cases studied had labeled clusters next to the 17/18 border even if the injection center was displaced from this border by 3–4 mm. In this and other cases, the projection zone in area 18 appears to include a somewhat larger portion of the representation than the injection sites.

The projections from area 17 to area 18 extended as vertical columns from layer VI to layer II with a greater density in layer IV (Fig. 7). The cells projecting from area 18 to area 17 were most dense in layer III, but some were also located in infragranular layers. In flattened sections, the cells seen in deeper sections (infragranular) were more broadly distributed than those located superficially, which occurred in discrete foci. The areal pattern of labeled cells closely matched the areal pattern of anterograde label, with the exception that a few labeled cells were sometimes apparent in regions without obvious anterograde label (Figs. 3, 4). This difference, however, might be the result of different thresholds for detecting sparse levels of retrograde and anterograde label.

The temporal dorsal area

A second projection zone of striate cortex was to an oval of cortex on the lateral border of the middle of area 18 (Fig. 1). We term this previously undefined subdivision of cortex the temporal dorsal area (TD) for its dorsal location in temporal cortex. It appears to be about 5 or 6 mm long and 2 or 3 mm wide for a surface area on the order of 13 mm^2. In sections stained for myelin this region was somewhat lighter than area 18 but darker than other surrounding regions.

There is evidence for both the divergence and convergence of connections to TD. A single injection in area 17 (Figs. 3–5) produced a zone of label in TD somewhat smaller than the zone in area 18. As in area 18, the label is clustered into several partially joined foci. Two separate injections in area 17 produced only a slightly larger zone of anterograde label, although a scattering of labeled cells occurred over a larger region (Figs. 2, 5). Ten clustered injections in area 17 did not produce a much larger region of label and the labeling was still discontinous (Fig. 6).

While a single injection in area 17 labeled a large portion of TD, there was evidence for a retinotopic pattern. Rostral injections in area 17 produced more rostral label in TD (Fig. 4) while caudal injections produced caudal label (Fig. 5). Also, the injection placed in ventral area 17 representing peripheral vision produced label in a more lateral zone of TD (Fig. 8). Thus inputs from area 17 to TD converge and overlap and yet appear to preserve a rough retinotopic pattern with the lower field represented rostrally, the upper field caudally, and peripheral vision laterally.

As was the case for area 18, the labeled cells and terminals in TD were highly overlapping in areal extent. Projections were concentrated in granular and supragranular layers (Fig. 7), while labeled cells projecting back to area 17 were located in layer III, and in infragranular layers.

Temporal posterior cortex

A region of temporal cortex near the posterior margin of the hemisphere projects to area 17, and at least the dorsal portion receives input from area 17. We call this zone of connections the temporal posterior area (TP). TP is smaller than TD and has a rostrocaudal width of about 1.5 mm and a dorsoventral length of about 4 mm for an area of about 10 mm^2. In sections stained for myelin, TP appeared to consist of a more densely myelinated oval, the dorsal part being more lightly myelinated and distinct from the area 18 strip.

Fig. 7. A light-field and a dark-field photomicrograph of the same coronal section from case 77-11, in which ^{3}H-proline and HRP were injected into area 17. The arrows mark the cytoarchitectonic borders of area 17, 18, and TD. Superficial patches of intrinsic label in area 17 are marked by asterisks. The focus of cells and terminals in the LGN (small arrow) indicates that the injection site was quite restricted.

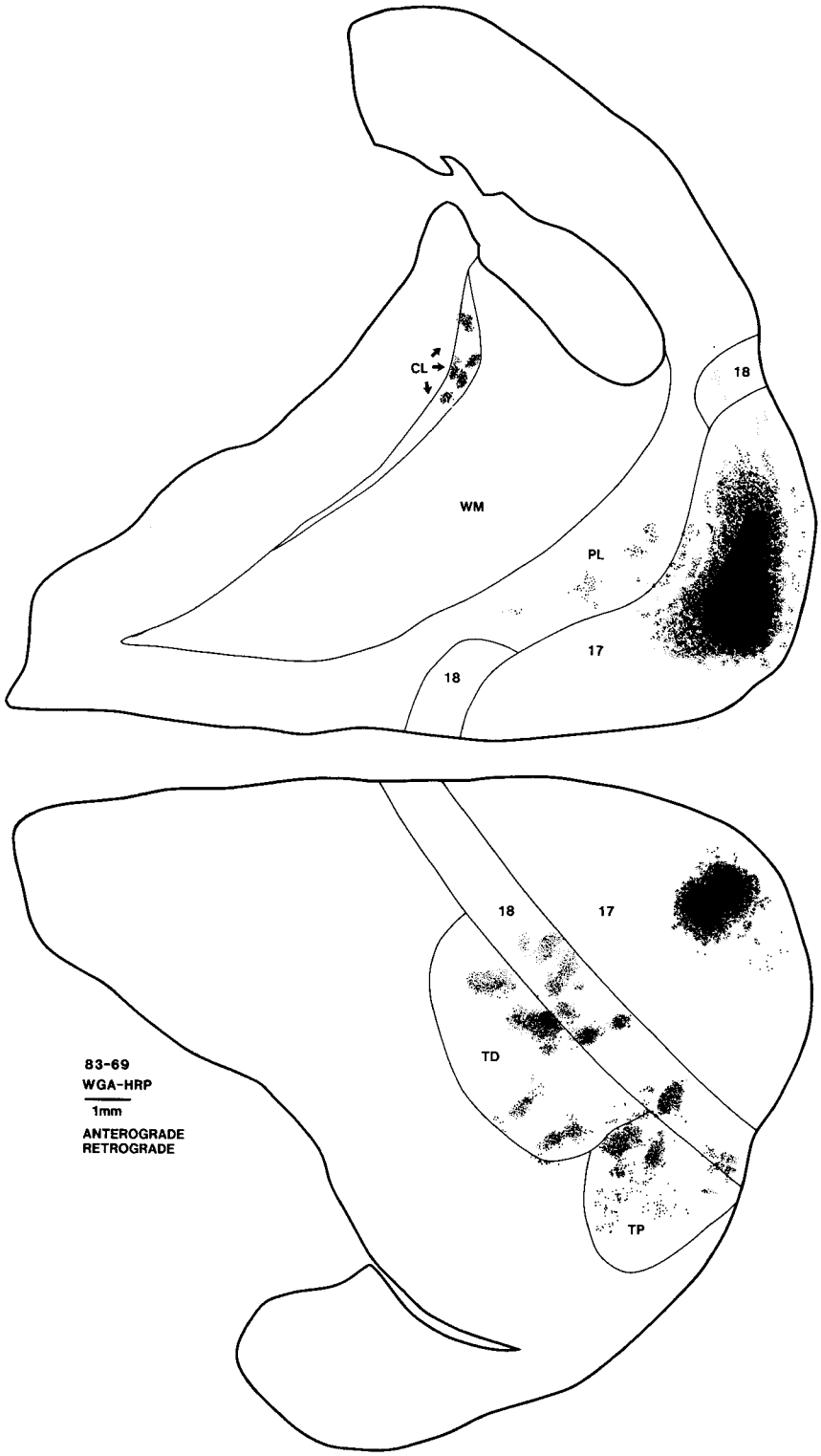


Fig. 8. Reconstructions of the pattern of connections of area 17 revealed after injections of WGA-HRP in the dorsal (lower) and ventral (upper) striate cortex. Each reconstruction is based on three to six sections from the flattened hemisphere. The upper reconstruction is reversed to show the ventral surface as a foldout. There was no apparent label in the contralateral hemisphere in this case. Fine dots represent anterograde label; large dots represent labeled cells. In the ventromedial reconstruction posterior limbic cortex lies between the two wings of area 18. Areal and architectonic borders were determined from sections stained for myelin. The large ventral injection also involved dorsal cortex and a second injection was slightly displaced laterally on the dorsal surface. PL, posterior limbic cortex; WM, white matter; CL, claustrum.

Results typical of a single injection in area 17 are shown in Figures 3 and 4. Such an injection resulted in a cluster of about 20 labeled cells found in the dorsal portion of TP along the area 18 border and a second cluster of 40 or more labeled cells in the ventral portion of TP about 1.5 mm away. Following single injections in area 17, other distinguishing features of the TP connections were as follows: (1) anterograde label was sparse or in some cases absent in dorsal TP and never apparent in ventral TP; (2) the density of label was much less than that observed in area 18 or TD; and (3) fewer cells were labeled in dorsal TP but these were grouped in a single focus, while in ventral TP many more cells were scattered over a wider area. Projections to TP were not apparent after injections of ^{3}H-proline (cases 77-11, 78-23) or ^{3}H-WGA (cases 83-35, 83-61L) in area 17.

Two or more injections in striate cortex produced larger regions of label and more labeled cells in TP (Figs. 5, 7, 8), and obvious levels of anterograde label (Figs. 6, 8) in dorsal TP indicating a reciprocal connection with area 17. The noticeable anterograde label in dorsal TP was usually very close to the area 18 border, so that some of this label could be in area 18. However, following an injection in the ventromedial striate cortex, the anterograde label in dorsal TP was clearly lateral to area 18 (Fig. 8). Because anterograde label was obvious only in dorsal TP, and single injections sometimes produced separate foci of label in dorsal and ventral TP (Fig. 4), TP possibly contains two separate visual areas.

The following observations also suggest that a crude retinotopic map exists in the larger ventral portion of TP. Injections in rostral area 17 produced label in more ventral TP (Fig. 4), while injections in middle and in caudal area 17 produced label in more dorsal TP (Fig. 8). This, together with evidence from other cases, suggests that the lower visual quadrant is represented ventrally and the upper visual quadrant is represented dorsally in TP. These cases also produced label which did not obviously shift in location within the most dorsal portion of TP.

The sparse anterograde label and the labeled cells in dorsal TP were supragranular whereas in ventral TP labeled cells were both superficial and deep to layer IV.

Limbic cortex

An extensive region of cortex on the ventromedial surface of the hemisphere lies rostral to the ventral striate border. This cortex has been termed calloso-marginal (Le Gros Clark, '24; Diamond et al., '70) and posterior limbic (Kaas et al., '72). Posterior limbic cortex is identified by the absence of a distinct fourth layer of cells, and a merging of the fifth and sixth cortical layers (Diamond et al., '70). It merges into the retrosplenial cortex rostrally and both fields are unresponsive to visual stimuli (Kaas et al., '72). In the present flattened material, posterior limbic cortex was identified by position relative to the area 17 border.

Following injections of WGA-HRP into the lateral striate cortex labeled cells were scattered in a broad focus within the ipsilateral posterior limbic cortex. These cells appeared to be in the deeper layers of this agranular zone. Sparse anterograde label, where present, was located within the same layers as the labeled cells. Although labeled cells were scattered, a crude retinotopic organization was suggested by these connections with upper-field caudal and lower-field rostral. When a large injection was made in the ventromedial striate cortex (Fig. 8) the labeled cells in the limbic cortex appeared in more punctate and denser clusters than those seen in any other cases involving other regions of striate cortex. This result suggests that posterior limbic cortex is more strongly connected to portions of area 17 representing the peripheral visual field.

Other ipsilateral connections

Large injections in area 17 also revealed terminations and labeled cells in the dorsal claustrum, as previously reported (Carey et al., '79, '80; Huerta et al., '84). Subcortically, labeled cells and terminals were seen in dorsal lateral geniculate nucleus (Diamond et al., '70; Florence and Casagrande, '78; Huerta et al., '84), the pulvinar (Harting et al., '73; Carey et al., '79, Huerta el al. '84), the ventral lateral geniculate nucleus (terminals only) (Harting and Noback, '71; Huerta et al., '84), and the superior colliculus (terminals only) (Casseday et al., '79; Harting et al., '73; Huerta et al., '84). Connections of striate cortex with the dorsal lateral geniculate and superior colliculus related matching parts of the retinotopic maps in the three structures (Kaas et al., '72; Lane et al., '71).

Callosal connections

Injections within area 17 centered as far as 1.5 mm from its lateral border (within 10° of the vertical meridian) produced coextensive foci of anterograde and retrograde label within contralateral areas 17 and 18 (Figs. 4–6). However, an injection site centered at the medial pole of striate cortex, some 2.5 mm from the lateral border, did not produce appreciable contralateral label. Furthermore, callosal connections appeared to be most dense for injections closest to the lateral border of striate cortex (Figs. 4, 6). Thus, although striate cortex in tree shrews projects callosally, these connections appear to be concentrated near the lateral border of striate cortex. Positions in striate cortex over 1–2 mm from the border (i.e., beyond 10° from the vertical meridian) have few or no callosal connections. This conclusion is consistent with the total pattern of interhemispheric connections revealed by multiple injections of HRP (Cusick et al., '84b).

Interestingly, the label in area 17 did not correspond precisely with the location of the injection site in the opposite hemisphere. While the callosal connections were roughly homotopic (Figs. 4–6), foci of connections were always on the lateral border of area 17 (the vertical meridian representation), even when the injection sites were 1-1.5 mm (around 10°) from the border. This suggests that the injections did not reveal the full extent of callosal terminations and projecting cells in area 17 (see Cusick et al., '84b).

Injections in area 17 also revealed connections with area 18 of the opposite hemisphere. These connections roughly matched the area 17 injections in retinotopic location in that rostral injections produced rostral label, and caudal injections produced caudal label. Some of the callosal label in area 18, however, was clearly displaced from the 17/18 border and was found in portions of lateral area 18 that would be expected to represent visual field locations 10–20° from the zero vertical meridian (Kaas et al., '72). In some instances, a single injection in area 17 produced several patches of label in contralateral area 18 (Fig. 6). In case 83-61, three closely spaced injections of ^{3}H-WGA were made close to the 17/18 border in striate cortex contralateral to the multiple WGA-HRP injections. The callosal projection revealed by autoradiography was densest at locations corresponding to the injection sites, but in between the label was continuous along the 17/18 border. The middle of the

callosal patch was broader and extended further into area 17, corresponding to the middle injection which was slightly more displaced from the border than the other injections.

Callosally projecting cells in area 17 were in supragranular layers with a few larger cells in infragranular layers. Callosal terminals in area 17 were also found in infra- and supragranular layers, with a suggestion of label in layer IV. A similar laminar distribution of cells and terminals was observed in area 18. These findings are consistent with the results of Cusick et al. ('84b).

DISCUSSION

Injections of anatomical tracers into area 17 of tree shrews revealed a periodic pattern of intrinsic connections, a pattern of bandlike connections in area 18, two regions of connections in temporal cortex, connections with limbic cortex, and callosal connections with areas 17 and 18. These connections are discussed and compared with those reported for other mammals, including primates.

The intrinsic pattern

The intrinsic pattern of connections in tree shrews is characterized by vertical connections between layers (e.g., Nauta et al., '73) and horizontal connections within layers (Rockland and Lund, '82; Rockland et al., '82). The horizontal spread of transported label extended over 1 mm from the edge of the injection site in the supragranular layers, and it consisted of labeled pyramidal cells and surrounding axons. The label formed short, fingerlike extensions from the continuously labeled zone that became less dense and more punctate with distance. Our results are basically similar to those reported by Rockland et al. ('82) for tree shrews, with the exception that the pattern of intrinsic connections in their material was described as forming two or three stripelike arrays after a single injection. In our material, separate foci of label were much more obvious, although there was an alignment of foci into strips. Overall, the pattern in tree shrew appears to us to be similar to the periodic, patchlike pattern of intrinsic connections described by Rockland and Lund ('83) for area 17 of monkeys, and the difference between tree shrews and monkeys does not appear to be as marked as previously described.

An important issue is whether the punctate pattern of intrinsic connections represents a pattern of fixed locations with horizontal connections, or if single injections reveal only certain locations in a system of continuous horizontal connections (Rockland et al., '82; Rockland and Lund, '83). The tendency for the horizontal label to be more continuous after double (Fig. 5) or multiple (Fig. 6) injections suggests that the horizontal connections are continuous and that small, single injections selectively label only part of the total system. One possibility is that the horizontal connections are related in some way to the pattern of orientation-selective neurons (Mitchison and Crick, '82; Rockland and Lund, '83) that has been observed in tree shrews (Humphrey and Norton, '80; Humphrey et al., '80) and other mammals. The grouping of foci of intrinsic connections in tree shrews tends to form bands that are perpendicular to the lateral border of striate cortex (Figs. 3, 8), and bands of orientation-specific cells tend to course in the same direction (Humphrey and Norton, '80, Humphrey et al. '80; Rockland et al., '82). In support of the theory that intrinsic connections relate to orientation bands, there is evidence that intrinsic inhibitory connections in area 18 of cats are concentrated in orientation bands containing neurons most sensitive to stimuli that are orthogonal to the stimuli most effective for neurons at the injection site (Cynader et al., '83; Matsubara and Cynader, '83).

Area 18 connections

Area 18 is architectonically distinct in tree shrews, and it is coextensive with the second visual area (V-II) (Kaas et al., '72). It appears that area 18 or V-II is a subdivision of visual cortex in all mammals, and in all mammals V-II receives input from area 17 (Kaas, '80). The most interesting present observation is that single locations in area 17 project to multiple foci in area 18, and that these foci tend to coalesce into bands that sometimes cross the complete width of the field.

While such a projection pattern has not been widely reported, it may exist in other mammals. An almost identical pattern has been found in area 18 of the rather distantly related grey squirrel (Cusick et al., '80; unpublished observations), and multiple foci of projections from single locations in area 17 to the region of area 18 have been reported in rats (Montero et al., '73; Olavarria and Montero, '81) and rabbits (Montero and Murphy, '76). A patchy distribution of projections to area 18 has been reported for cats (Montero, '81), and Wong-Riley ('79) first stressed the "columnar" distributions of such label in area 18 of monkeys (also see Curcio and Harting, '78; Maunsell et al., '80; Lin et al., '82; Livingstone and Hubel, '82; Weller and Kaas, '83). While such multiple foci of terminals have been interpreted as evidence for multiple visual areas within the V-II region (Montero, '81), it seems more reasonable to interpret the pattern as an uneven or modular distribution of function. Such a concept is consistent with the banding pattern of cytochrome oxidase- and myelin-dense regions that have been reported for area 18 of monkeys (Tootell et al., '83; Livingstone and Hubel, '83), and unevenly distributed callosal projections (Cusick et al., '84a, '84b) in area 18 of monkeys and tree shrews. We feel that the banding pattern of projections to area 18 may be more distinct in tree shrews than many mammals, but it probably reflects a basic and widespread organization.

The observation that multiple, closely spaced injections in area 17 produced a more continuous zone of label in area 18 suggests that all parts of area 18 receive area 17 inputs and that the banding is not a result of a subdivision of area 18 into regions with and without area 17 inputs. The results suggest instead that a given location in area 17 projects to a series of grouped locations in area 18, with some fixed periodicity, and that nearby locations in area 17 project to similar, partially offset locations in area 18. That several locations in area 17 project to the same location in area 18 is suggested by the consistently observed larger receptive fields in area 18 (e.g., Gattass et al., '81). In tree shrews, the receptive fields in V-II are about four to five times larger than those in V-I, when matched for visual field eccentricities (Kaas et al., '72; Kaufman and Somjen, '79). However, the projection of one location in area 17 to several locations in area 18 should produce considerable receptive-field scatter, and even repetitions and disruptions of retinotopic order if this divergence is entirely excitatory. Such complications of retinotopic organization have not yet been observed in mapping studies of V-II in tree shrews (Kaas et al., '72) and other mammals (see Kaas, '80).

A related puzzle is that the pattern of interconnections only roughly corresponds to the retinotopic order of the two representations. While rostral area 17 projects rostrally, caudal area 17 projects caudally, and ventral area 17 proj-

ects toward the ends of the area 18 belt as expected, small disparities appear to result when the two maps are considered in more detail. For example, injections in parts of area 17 representing the first 10° of visual field project to bands crossing the width of area 18, which represents 15° or more of visual field, depending on location (Kaas et al., '72).

It is noteworthy that results of filling single, physiologically defined axons in monkeys and cats pose a similar puzzle. In monkeys and cats, it has been shown that Y-like axons from the LGN, with relatively small receptive fields, distribute clumps of arbors to more than one ocular dominance column. The same axons have terminal arbors which extend well outside the zone of their physiologically defined receptive fields (Gilbert and Wiesel, '83; Blasdel and Lund, '83). In addition, many callosal connections of visual areas in primates do not appear to be reflected in the excitatory receptive fields (Weller and Kaas, '82; Cusick et al., '83). Thus, all area 17 inputs to area 18 in tree shrews may not be reflected in the excitatory receptive fields and the retinotopic maps. Another possibility is that a detailed map would reveal complexities not seen in a limited exploration of the organization of V-II in tree shrews (Kaas et al., '72).

The laminar pattern of connections of area 17 with area 18 in tree shrews appears to be typical of other mammals (Weller and Kaas, '81, '82). Terminations in area 18 were more dense in layer IV, as is characteristic of an activating pathway (see Maunsell and Van Essen, '83), but the supragranular and infragranular terminations appear to be more dense than in primates (see Weller and Kaas, '81, for review).

Connections with limbic cortex

Sparse reciprocal connections were found between area 17 and cortex bordering area 17 on the ventromedial surface of the cerebral hemisphere. Previously we referred to this cortex as posterior limbic cortex (Kaas et al., '72). Such connections were somewhat surprising, since they have not been noted in studies of striate cortex connections in primates using HRP or ^{3}H-proline as an anatomical tracer (see Weller and Kaas, '83, for review). However, part of limbic cortex (area 29 or cingulate cortex) has reciprocal connections with area 17 in rats (Vogt and Miller, '83) and squirrels (Cusick et al., '81). An effort should be made to determine if this pathway is present or absent in other mammals, since it represents a direct link between primary visual cortex and the limbic system.

The TD and TP areas

Connections of area 17 revealed two previously unidentified subdivisions of temporal cortex. At present, it is unclear whether these subdivisions represent true visual areas. As previously defined (see Kaas, '82), a visual area should contain a systematic representation of the visual hemifield, a distinctive pattern of extrinsic connections and architectonic characteristics, and evidence of functional uniqueness. The TD and TP subdivisions in tree shrew appear to at least partially fulfill the anatomical criteria. Both zones show evidence of topographic connections with area 17 and they are distinct in myeloarchitecture. However, TP does not have a single connection pattern with area 17, and thus TP could represent two areas, TPd (dorsal) and TPv (ventral). Ventral TP is unusual in that it appears to lack reciprocal connections with area 17; it may only send input to area 17. Such a situation is similar to what has been described for the physiologically defined medial visual area in owl monkeys which appears to project to area 18 without receiving information from area 18 in return (Graham et al., '79). Another possibility is that the present procedures were inadequate to reveal sparse anterograde label in ventral TP.

Dorsal TP is so close to area 18 that it could be argued that dorsal TP simply represents part of area 18. However, placing TP dorsal in area 18 would make part of area 18 unusually wide, not in keeping with cyto- and myeloarchitectonic differences. Differences in laminar position of labeled cells give further support for distinguishing dorsal TP from area 18.

Homologies of TP and TD with known visual areas in other mammals are uncertain. However, an area 17 projection to cortex roughly in the location of dorsal TP has been reported in rodents (Olavarria and Montero, '81) and rabbits (Montero and Murphy, '76). Nothing similar to ventral TP connections has been reported. There is more evidence for a region comparable to TD. Area 17 projections to cortex immediately lateral to the middle sector of area 18 (V-II) have been reported for a number of mammals (see Kaas, '78). Thus, TD may be a basic mammalian visual area such as V-II. TD also may be the homologue of the middle temporal (MT) visual area (see Weller and Kaas, '81) of primates. Both MT and TD are aligned in cortex with the middle section of area 18, and both areas receive similar retinotopic projections from area 17. There are, however, two main differences between TD and MT. TD lies adjacent to area 18 (V-II) while MT is separated from area 18 by another visual area, the dorsolateral visual area (DL) or V4. In addition, TD is less densely myelinated than MT. Thus, TD is an attractive candidate as a homologue of MT, but it will be necessary to demonstrate further similarities (e.g., thalamic connections [Diamond et al., '70; Harting et al., '73] and functional properties of cells) and account for the differences before firm conclusions are possible.

ACKNOWLEDGMENTS

The authors are grateful to Ms. Judy Ives and Ms. Aurora Buck for their technical and histological assistance and Ms. Pat Burns and Ms. Joan Couch for typing the manuscript. We thank Dr. D.A. Steindler for the ^{3}H-WGA and suggestions on its use, Dr. S.L. Florence for the use of case 77-11, and Drs. C.G. Cusick, M.F. Huerta, T.T. Norton, and J.T. Wall for helpful comments on the manuscript. Supported by NIH grants EY-02686 (J.H.K.) and 1-K04-EY00223 and EY05038 (V.A.C.).

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