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Cortical Connections of Areas 17 (V-I) and 18 (V-II) of Squirrels

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ABSTRACT

Connections of visual cortex in squirrels were investigated by placing WGA-HRP injections, and in some cases fluorescent dyes, into area 17 (V-I) or area 18 (V-II). Results were related to architectonic fields determined in brain sections cut parallel to the surface of manually flattened cortex and to limited microelectrode mapping data. Injections in area 17 provided evidence for 1) a patchy pattern of horizontal intrinsic connections extending 1–2 mm from the injection site; 2) uneven, widely distributed connections with area 18 (V-II) and adjoining occipital-temporal (OT) cortex; and 3) callosal connections of large portions of area 17 with the 17/18 border zone. While restricted locations in area 17 had uneven interconnections over several mm of area 18, more rostral locations in area 17 related to more rostral locations in area 18, demonstrating a topographic tendency. Injections in area 18 revealed 1) zones of discontinuous connections with area 17 that followed a topographic pattern, 2) patches of intrinsic connections that spread over distances of up to 6–8 mm from the injection site; 3) two zones of uneven connections with OT cortex suggesting the locations of at least two visual areas, OT_r and OT_c; 4) connections with limbic cortex rostromedial to areas 17 and 18; 5) sparse connections with regions of temporal cortex lateral to OT; and 6) uneven callosal connections with area 18 and OT cortex. The widespread and unevenly distributed intrinsic callosal interconnection patterns of areas 17 and 18 contrast with the restricted excitatory receptive fields of neurons and the retinotopic patterns of representation in these fields. Although physiological evidence is presently lacking, the patchy connections suggest that areas 17 and 18 in squirrels are modularly organized.

Key words: corpus callosum, intrinsic connections, rodents, visual cortex

While considerable progress has been made in understanding the anatomical connection patterns responsible for information processing in the visual systems of various primates (for reviews see Van Essen, '85; Kaas, '86; Maunsell and Newsome, '87; Kaas and Huerta, '88) and cats (see Rosenquist, '85), much less is known about the visual systems of other mammals including rodents. We studied two well-defined subdivisions of visual cortex in squirrels, areas 17 and 18, to see how these areas are interconnected and to see if their patterns of connections suggest the presence of additional subdivisions of cortex. In comparison to the more commonly studied rats, mice, and hamsters, squirrels offer the advantages of a larger brain and generally more distinct architectonic subdivisions of cortex (Kaas et al., '72). In particular, two subdivisions of visual cortex, areas 17 and 18, are obvious in brain sections stained for cells or myelin (see Hall et al., '71; Kaas et al., '72; Robson and Hall, '75; Weber et al., '77; Gould, '84; Krubitzer et al., '86). Area 17 has been shown to correspond to the primary representation of the visual hemifield, V-I, and area 18 has been related to the second representation of the visual hemifield, V-II (Hall et al., '71). In addition, area 17 receives a topographic projection from the dorsal lateral geniculate nucleus (Kaas et al., '72), whereas area 18 is characterized by dense input from an anterior subdivision of the pulvinar complex (Robson and Hall, '77). Thus, areas 17 and 18 appear to be valid and generally recognized subdivisions of visual cortex in squirrels (however, see Montero and Cliffer, '81) with clear homologies in other mammals (see Kaas, '80).

Our experiments were designed to answer several specific questions. First, widespread and discontinuously distributed horizontal intrinsic connections have been reported for

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area 17 and sometimes area 18 of tree shrews (Rockland and Lund, '82; Rockland et al., '82; Sesma et al., '84), monkeys (Rockland and Lund, '83; Livingstone and Hubel, '84a; Rockland, '85), galagos (Cusick and Kaas, '88b), and cats (Gilbert and Wiesel, '83; Matsubara et al., '85; LeVay, '88). The widespread patterns suggest that neurons even in these early stages of cortical processing are subject to influences of visual stimuli over relatively large regions of visual space, and the periodic distributions imply both a heterogeneous distribution of neuron classes and the presence of distinct processing modules within areas 17 and 18. Do such patterns of connections exist in rodents? Detailed descriptions of intrinsic connections in a range of mammals, including rodents, would help determine the prevalence of specific patterns. Experiments using WGA-HRP injections and brain sections cut parallel to the surface seem well suited for revealing intrinsic patterns (Sesma et al., '84; Livingstone and Hubel, '84a), and such preparations were used here.

A second question concerns the pattern of the interconnections between areas 17 and 18. Studies in cats (e.g., Wilson, '68; Symonds and Rosenquist, '84), monkeys (e.g., Wong-Riley, '79; Perkel et al., '86; Van Essen et al., '86), galagos (Symonds and Kaas, '78; Cusick and Kaas, '88b), and tree shrews (Sesma et al., '84) have revealed that the projections from restricted locations in area 17 are widespread and discontinuous in area 18 and yet conform to a crude topographic pattern that reflects the known retinotopic organizations of the two fields determined electrophysiologically. Such a projection pattern is consistent with the general concept that different subsets of processing modules in area 17 preferentially project to different subsets of processing modules in area 18 in a manner that complicates the local retinotopy of area 18 with repetitions but allows an overall retinotopy within the field (see DeYoe and Van Essen, '85; Van Essen et al., '86; Hubel and Livingstone, '87).

While there is widespread agreement on the significance of interconnection patterns of area 17 with area 18 in primates, cats, and tree shrews, the projection patterns of area 17 to area 18 in squirrels have been interpreted in two different ways. In preliminary reports, Cusick et al. ('80) and Johanson et al. ('86) concluded that even though the interconnections of area 17 with area 18 are patchy, the pattern is compatible with an overall retinotopic map in area 18. Montero and Cliffer ('81), in contrast, concluded that the projection pattern in squirrels revealed the existence of four visual areas in a rostrocaudal sequence in area 18 that correspond to visual areas proposed for peristriate visual cortex of rats (Montero et al., '73a,b; Montero, '80; Olavarria and Montero, '81, '84; Espinoza and Thomas '83) and rabbits (Montero and Murphy, '76). Detailed observations on the connection pattern of area 17 with area 18 in squirrels, where area 18 is architectonically distinct and appears to contain a single retinotopic pattern of activation, could help determine whether or not the organization of peristriate cortex in rodents is basically different from that in cats, tree shrews, and primates.

Another goal was to understand the organization of cortex lateral to area 18 where regional differences in cortical architecture are obvious (Kaas et al., '72). Cortex lateral to area 18 (V-II) receives input from area 17 in most or all mammals (Kaas, '80) including squirrels (Cusick et al., '80; Montero and Cliffer, '81; Johanson et al., '86). In addition, much of the lateral cortex caudal to auditory cortex (Luethke et al., '88) appears, from interconnections with the pulvinar complex (Kaas et al., '72; Robson and Hall, '75), to be associated with the visual system. Determining connection patterns between the lateral cortex and areas 17 and 18 could provide information about how lateral visual cortex is subdivided into areas and processing modules.

A final goal was to describe the callosal connections of restricted sites in areas 17 and 18. The total callosal projection pattern in squirrels has been described (Gould, '84). Terminations are concentrated in a periodic manner along the 17/18 border, as commonly reported for other mammals (e.g., Cusick et al., '85; Cusick and Kaas, '86). In monkeys, only the border zone of area 17 has callosal connections (e.g., Cusick et al., '84; Kennedy et al., '86). However, most mammals, including opossums (Cusick and Kaas, '86), rats and hamsters (Dursteler et al., '79; Olavarria and Van Sluyters, '83; Miller and Vogt, '84), tree shrews (Cusick et al., '85), and prosimian galagos (e.g., Weyand and Swadlow, '80; Cusick et al., '84), have additional widespread callosal connections within area 17. While widespread callosal connections were not revealed in area 17 of squirrels by studies of the total callosal pattern (Gould, '84), injections centered in area 17 of squirrels provide an alternative way of revealing such widespread callosal connections. Injections centered in areas 17 and 18 can also reveal if each of these fields has callosal connections with more than one field of the opposite hemisphere, if the connections are periodic, and if the connections are homotopic (mirror-symmetric) or heterotopic (see Miller and Vogt, '84). Observations on such details of callosal connection patterns would relate to concepts of interhemispheric transfer of information in rodents and other mammals.

Some of these results have been briefly presented elsewhere (Johanson et al., '86).

MATERIALS AND METHODS

Injections of one or more anatomical tracers were placed in area 17 or area 18 of ten grey squirrels (*Sciurus carolinensis*). Placements of injections were guided by microelectrode recordings in some cases. In all cases, results were related to myeloarchitectonic patterns observed in brain sections cut parallel to the manually flattened cortex. Recordings and injections were made with aseptic procedures in anesthetized animals.

Recording procedures

Limited microelectrode recordings were obtained in six squirrels in order to estimate the locations of physiological borders of area 17 (V-I) and area 18 (V-II). Procedures were modified from those used in a previous microelectrode mapping study of visual cortex in squirrels (Hall et al., '71). Each squirrel was anesthetized with ketamine hydrochloride (30 mg/kg) supplemented with acepromazine maleate (4.5 mg/kg). Additional doses of 10% of the original anesthetic were given as needed to maintain surgical levels of anesthesia (see White et al., '82). With aseptic precautions, the skull over part of the visual cortex was removed, the dura was reflected, and silicone fluid was used to protect the brain from drying. A high-magnification photograph of the brain was taken in order to cite electrode penetrations relative to the surface pattern of blood vessels. Recordings were obtained with low-impedance (0.9–1.3 MΩ) tungsten microelectrodes designed to record from small clusters of neurons. Receptive fields were plotted by hand with the aid of narrow bars of light projected onto the surface of a translucent plastic hemisphere centered to represent the visual field of the

contralateral eye. Changes in receptive field progressions for rows of recording sites, changes in receptive field size, and alterations in responsiveness to visual stimuli were used to estimate boundaries of V-I (area 17) and V-II (area 18). Small electrolytic lesions were placed at physiological boundaries by passing a 5–10-μamp current through the recording electrode for 5–10 seconds. Injections were placed in V-II relative to the estimated borders.

Injections

Most injections were 0.05–0.75 μl of 0.1% horseradish peroxidase conjugated with wheat germ agglutinin (HRP-WGA). In some cases additional injections were made with the 1–3% solutions of the fluorescent dyes diamidino yellow, fast blue, and rhodamine (0.2–0.5 μl). After the injections were complete, the skull opening was covered with an acrylic seal, and the skin was sutured.

Tissue preparation

After postinjection survivals of 2–3 days, each animal was given a lethal dose of anesthetic (sodium pentobarbital) and perfused through the heart with 0.9% saline followed by a mixture of 1.5% glutaraldehyde and 1% paraformaldehyde (for HRP-WGA) or 2% paraformaldehyde (for fluorescent dyes) in phosphate-buffered (pH 7.4) saline. The brain was removed from the skull, and cortex was separated from the rest of the brain. Cortex was then flattened between glass plates submerged in 30% sucrose in phosphate buffer for 15–18 hours (see Krubitzer et al., '86). The flattened cortical hemispheres were frozen and cut parallel to the surface into 40-μm sections. Alternate sections were either processed with tetramethylbenzidine to reveal HRP (Mesulam, '78) or mounted unstained for fluorescent microscopy for cases with fluorescent dye injections or stained for myelin by using the Gallyas ('79) silver procedure.

RESULTS

Injections of WGA-HRP and fluorescent dyes were used to determine the cortical connections of areas 17 and 18 in grey squirrels. Results are described in three major sections. The first section provides an overview of cortical organization in squirrels, includes new observations on the heterogeneous myeloarchitecture of area 18, and presents receptive field data from microelectrode recordings that are consistent with previous studies of the retinotopic organizations of areas 17 and 18. The second section describes the intrinsic, ipsilateral, and callosal cortical connections of area 17. The third section describes the intrinsic, ipsilateral, and callosal cortical connections of area 18.

The locations, myeloarchitectures, and retinotopic organizations of areas 17 and 18

The locations of areas 17 and 18 in grey squirrels are shown relative to other subdivisions of cortex in Figure 1. Areas 17 and 18 are easily distinguished subdivisions of visual cortex. The architectonic boundaries of these fields have been illustrated previously, both in standard coronal and sagittal planes of section (e.g., Hall et al., '71; Kaas et al., '72) and in sections cut parallel to the surface of manually flattened cortex (Krubitzer et al., '86; Luethke et al., '88). As pointed out in these studies, area 17 is characterized

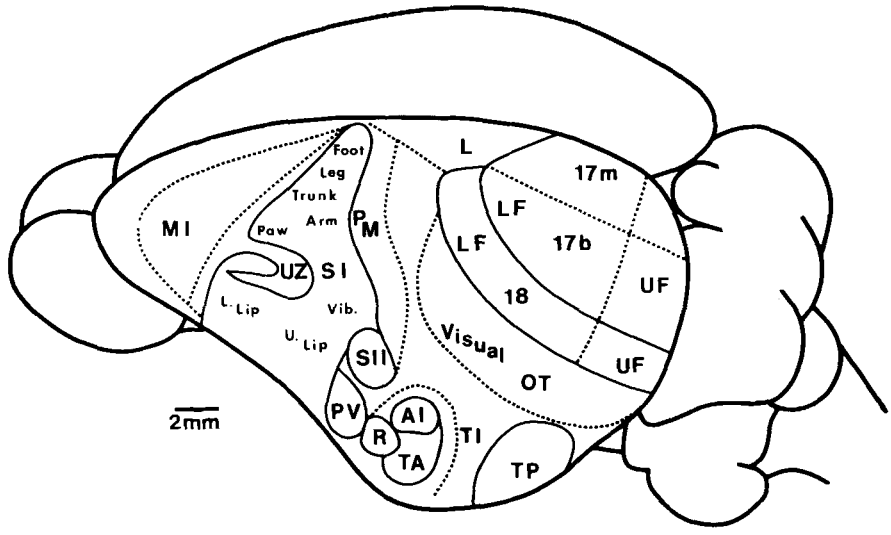


Fig. 1. A dorsolateral view of the brain of a grey squirrel summarizing our current understanding of cortical organization. Previous microelectrode mapping studies of visual cortex show that two architectonic fields, areas 17 and 18, correspond to separate representations of the contralateral visual hemifield, the first (V-I) and second (V-II) visual areas (Hall et al., '71). A lateral portion of area 17 (17b) is thicker and is activated by both eyes (binocular); a medial portion (17m) is monocular, activated only by the contralateral eye. The lower visual field (LF) is represented rostrally in areas 17 and 18, while the upper visual field (UF) is caudal. A dotted line indicates the approximate location of the zero horizontal meridian through the horizontal streak of high ganglion cell density in the central retina. The 17/18 border corresponds to the zero vertical meridian or line of decussation of the retina. Connections with area 17 (Cusick et al., '80) and with the visual thalamus (Kaas et al., '72) identify the occipital-temporal zone (OT) lateral to area 18 as part of visual cortex. Temporal anterior (TA), temporal intermediate (TI), and temporal posterior (TP) are architectonic subdivisions from Kaas et al. ('72). The auditory fields (the primary field, A-I, the rostral field, R, and the auditory fringe marked by a dashed line, as well as TA) are from Luethke et al. ('88) and Merzenich et al. ('76). The somatosensory fields (the primary area, S-I; the second area, S-II; the parietal ventral area, PV, the parietal medial field, PM, and the unresponsive zone, UZ) are based on Sur et al. ('78), Nelson et al. ('79), and Krubitzer et al. ('86). Vib., vibrissae; L Lip, lower lip; U Lip, upper lip. The primary motor field, M-I, is based on unpublished microstimulation results by L.A. Krubitzer and studies of myeloarchitecture and connection patterns with somatosensory cortex (Krubitzer et al., '86).

by a distinct layer IV that is densely packed with small, darkly stained granule cells, while area 18 is less conspicuously laminated and has no layer of darkly stained, closely packed cells. In myelin-stained sections, both areas 17 and 18 have middle layers of dense myelination, but the myelination of area 17 is more sharply confined. As a result, in selected supragranular sections from flattened cortex just superficial to the dense myelination in area 17, area 17 may appear moderately and nearly uniformly myelinated while area 18 exhibits bands of dense myelination separating patches or ovals of moderate myelination (Fig. 2). In such sections, the 17/18 border is marked by a 300–400-μm-wide band of dense myelination. The outer border of area 18 features a wider, less even zone of dense myelination. Zones of dense myelination 300–700 μm wide bridge these two darkly staining bands at intervals of 300–700 μm. The zones of dense myelination surround 300–700-μm ovals of light myelination at semiregular intervals. Given the approximate 15-mm length of area 18, some eight to 12 ovals probably occur in area 18. However, the most caudal portion of area 18 extends around the caudal curvature of the hemisphere and slightly onto the ventral surface. This portion of cortex is difficult to unfold in the flattened preparations, and therefore we do not have complete observations on the myeloarchitecture of caudoventral area 18.

In six experiments, microelectrode recordings were made to provide information on the retinotopic organization of areas 17 and 18 and to guide the placements of injections in area 18. Figure 3 shows typical results from two rows of recording sites which began in area 17, proceeded toward the 17/18 border, and crossed the width of area 18. Both rows produced sequences of receptive fields that moved toward the zero vertical meridian and then sharply reversed direction for successive sites across area 18. The outer border of area 18 was marked by a profound reduction in responsiveness to visual stimuli in these anesthetized squirrels. However, occasional recordings from sites immediately lateral to area 18 revealed a sequence of receptive fields that

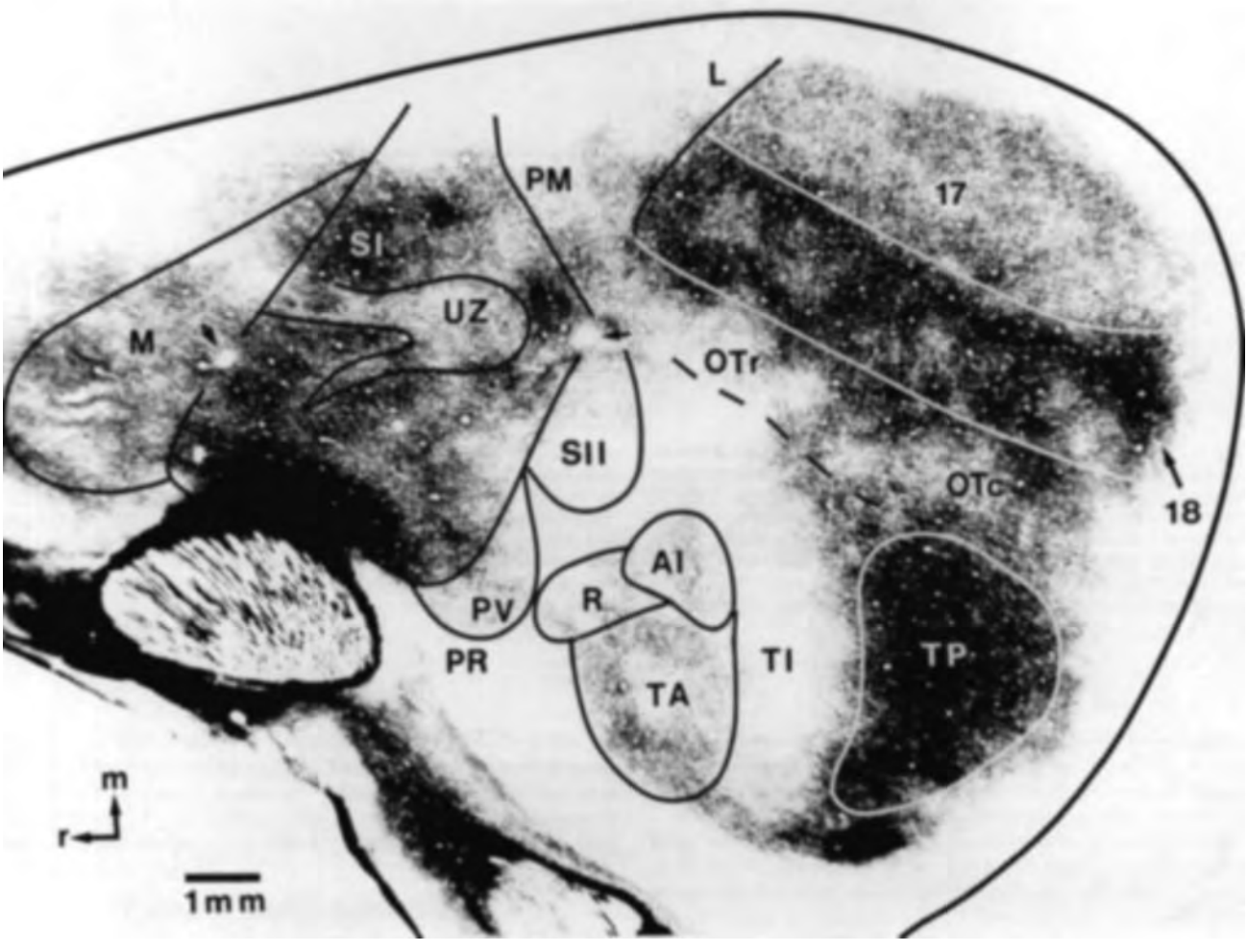


Fig. 2. The myeloarchitecture of area 18 and other fields in a "surface-view" brain section cut through the middle layers of cortex parallel to the surface. Area 18 is apparent as a densely myelinated band containing semiregularly spaced "holes" of light myelination. Caudal occipital-temporal cortex (OT_c) is more densely myelinated than rostral occipital-temporal cortex (OT_r), while area 17 is moderately myelinated. Other fields include the densely myelinated temporal posterior area, TP, the lightly myelinated temporal intermediate area, TI, subdivisions of auditory cortex (AI, R, and TA; see Luethke et al., '88), somatosensory areas (S-I, S-II, PM, PR, PV, and UZ; see Krubitzer et al., '86), and motor (M) cortex. Microlesions (arrows) mark the physiologically determined rostral and caudal boundaries of S-I. L, limbic cortex; compare with Figure 1. r, rostral; m, medial.

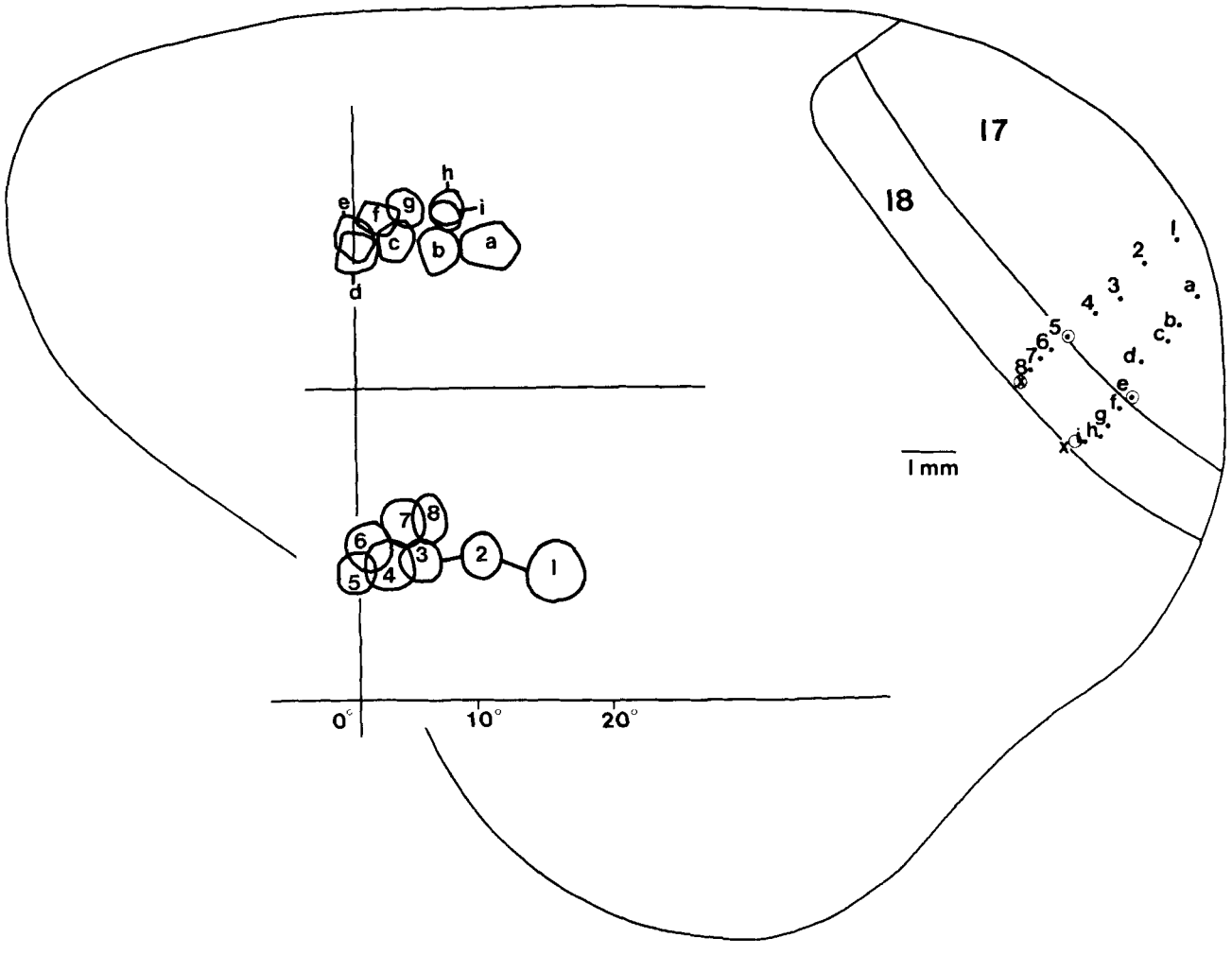


Fig. 3. Receptive fields for two representative rows of recording sites extending from area 17 across area 18. Sites where marker lesions were placed are circled. Sites 5 and e were judged to be on or near the V-I/V-II border by being at the point of reversal for receptive field sequences. The Xs mark sites where a reduction in responsiveness to visual stimuli suggested the outer border of area 18. The borders of areas 17 and 18 were determined from the myeloarchitecture in brain sections cut parallel to the surface as in Figure 2. Note the close correspondence of the physiological and architectonic boundaries. The receptive fields were determined in the contralateral hemifield of the contralateral eye with moving spots and bars of light. The vertical line represents the line of decussation as estimated from the recordings. Each horizontal reference line is about 10° into the lower visual field, but the zero horizontal was not accurately determined. Row 1–8 is in the expected location of the zero horizontal, while receptive fields in row a–i are about 2° above the zero horizontal. Compare with Figure 1.

reversed direction and progressively moved toward the zero vertical meridian as recording sites moved laterally. This second reversal suggests that cortex lateral to area 18 has a different pattern of retinotopic organization than area 18.

Most of our recordings were across the midportion of area 18. In each case, receptive fields progressed only 10–15° horizontally from the zero vertical meridian before a change in responsiveness marked the lateral border of area 18. Although receptive fields for sites in area 18 were sometimes about the same size as those for sites in area 17 (Fig. 3), more typically, receptive fields for sites in area 18 were larger. Receptive fields for sites in central-lateral area 17 were 2–5° in diameter, while receptive fields for sites in the midportion of area 18 ranged from 2 to 10° in diameter. Often, the transition of a progression of recording sites from area 17 to area 18 was marked by the cessation or reversal of the nasalward progression of receptive fields, an increase in receptive field size, and a slight to moderate reduction in responsiveness to visual stimuli. Recording sites in rostral area 17 and area 18 had receptive fields lower in the visual field than caudal sites.

Cortical connections of area 17

The cortical connections of area 17 were determined from three cases in which injections of WGA-HRP were confined to area 17, two cases in which two (fast blue and diamidino yellow) or three (fast blue, rhodamine, and WGA-HRP) tracers were injected, and one case in which three larger injections of WGA-HRP were placed on the 17/18 border. The results revealed patterns of intrinsic connections, ipsi-

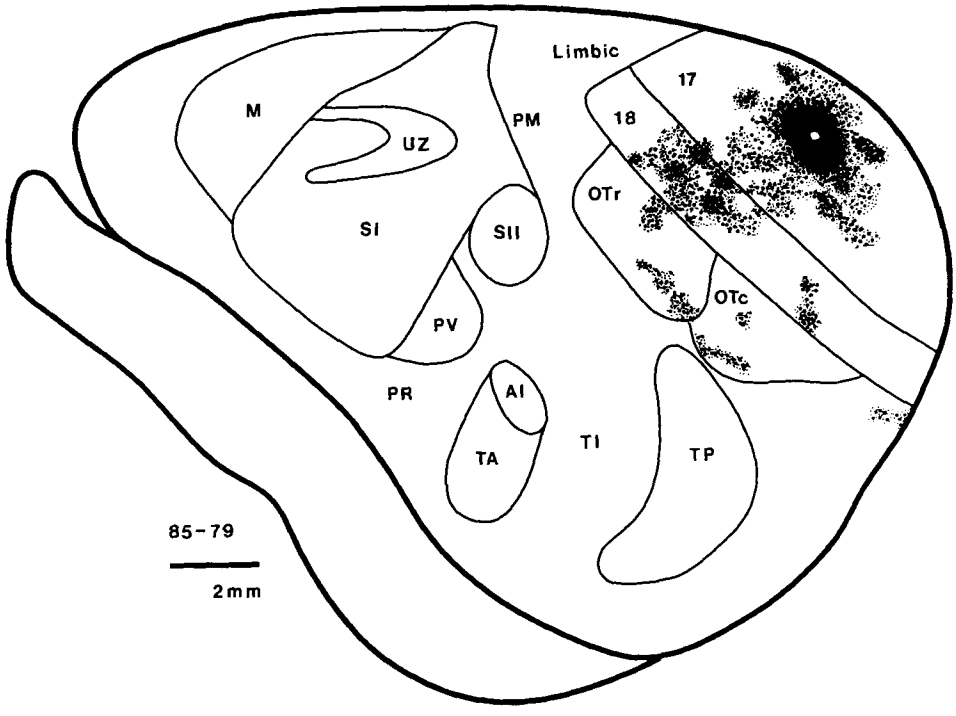


Fig. 4. The distribution of labeled neurons (large dots) and fine processes (fine dots) after an injection of WGA-HRP in area 17. The black oval indicates the core of dense, uniform label, and the white center indicates the injection tract. The surface view of the left cerebral hemisphere was drawn from a single section from cortex that had been removed, flattened, and cut parallel to the surface. Label from deeper and more superficial sections was added after careful alignment by blood vessels. Outlined fields were apparent in adjacent sections stained for myelin. PR, parietal-rhinal cortex. Other abbreviations as in Figure 1.

lateral connections with area 18 and occipital-temporal cortex, and callosal connections with areas 17 and 18.

Intrinsic connections. Injections of WGA-HRP produced a dense core of label immediately surrounded by a less dense ring of labeled cells and fine processes. Beyond this ring of label, scattered clumps and short bands of labeled cells and processes were located within 1–2 mm of the margins of the dense injection core (Figs. 4, 6, 7, 9). Injections of fast blue, diamidino yellow, and rhodamine (case 86-66, Fig. 9, and case 87-63, not shown) also revealed uneven halos of labeled cells around injection sites; most of these labeled cells were within 2 mm of the margin of the injection core. Thus, lateral intrinsic connections were evenly and densely distributed over very short distances, much less dense and more unevenly distributed over larger distances up to 2 mm, and sparse or absent over longer distances. The 1–2-mm connections tended to be with an array of separate clumps of cells.

Ipsilateral connections. The major ipsilateral connections of area 17 were with area 18. Each WGA-HRP injection in area 17 produced a zone of unevenly distributed labeled cells and processes in area 18 that usually included a larger focus and one or more smaller foci separated by 200–1,500-μm zones of unlabeled cortex (Figs. 4, 6, 7). Similar distributions of labeled cells were produced by injections of fluorescent tracers (Fig. 10).

The locations of the clumps of label in area 18 varied with the location of the injection site in area 17. Injection sites along the lateral margin of area 17 tended to label the immediately adjacent medial portions of area 18, although some of the foci of label were farther away (Figs. 6, 18). More central injections in area 17 produced a zone of label which extended across the width of area 18 (Fig. 4). Rostral injections in area 17 tended to label more rostral foci and caudal injections more caudal foci in area 18. The topography of the ipsilateral connections was most obvious in case 86-66 (Fig. 9) in which three different tracers were injected in area 17. The most rostral injection was fast blue. The resulting clumps of label were distributed over the most rostral third of area 18. A more caudal injection of WGA-HRP produced two major clumps of label collectively centered about 1 mm more caudal than the collective center of the clumps resulting from the injection of fast blue. Nearly 3 mm more caudal in area 17, an injection of rhodamine produced a wide array of clumps centered some 2 mm more caudal than the center of WGA-HRP clumps in area 18. Thus, single injections in area 17 produced clumps of label over as much as a third of area 18, and injections separated by as much as 5 mm (Fig. 9) in area 17 produced a partial overlap of the zones of transported tracer as well as an overlap of some clumps of label. Yet within this topographic divergence, there was topographic order. The most dense interconnections appeared to be roughly between corresponding retinotopic locations in the maps in V-I and V-II (see Fig. 3; Hall et al., '71). Finally, injections of fast blue and diamidino yellow made 1 mm apart in area 17 produced two overlapping zones of label in area 18 but little overlap in labeled cell clusters (case 87-63, not shown). This separation of connections in overlapping

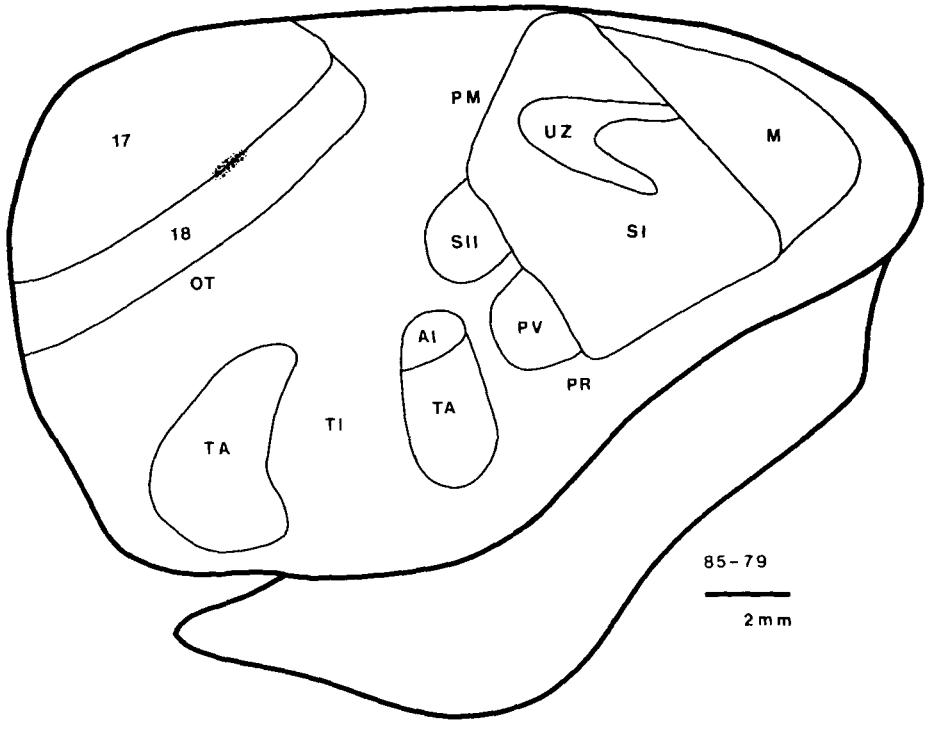


Fig. 5. The distribution of cortical label in the right hemisphere after the injection of WGA-HRP in the left hemisphere shown in Figure 4. Abbreviations and conventions as in Figure 4.

zones suggests that separate classes of cells in modules in areas 17 and 18 are interconnected in parallel.

Other interconnections of area 17 were with cortex lateral to area 18. Single injections of WGA-HRP in area 17 typically produced several (three to six) distinct clusters of labeled cells and processes in occipital-temporal (OT) cortex lateral to area 18 (Figs. 4, 6, 9). The interconnections with area 17 were within a strip of cortex 1–2 mm wide extending 10 mm or more along much of the border of area 18. A topographic pattern of connections within this strip was not obvious. The distribution of label in OT cortex allows for the possibility that cortex lateral to area 18 contains several subdivisions of visual cortex with inputs from area 17. The connection patterns of area 18 with OT cortex more clearly suggests the existence of at least two separate fields, rostral and caudal OT cortex or OT_r and OT_c.

Callosal connections. Injections in area 17 produced zones of label along the 17/18 border of the opposite cerebral hemisphere. Figure 5 shows the location of label over a restricted region of the 17/18 border resulting from an injection of WGA-HRP displaced about 10° from the representation of the zero vertical meridian into area 17. The injection produced a confined zone of label involving adjoining parts of both area 17 and area 18 in a rostrocaudal location that corresponds with the rostrocaudal level of the injection site in the other hemisphere. The strip of label contained both neurons and fine processes. No label was apparent in either area 17 or 18 away from common border, or in OT cortex.

Similar results were obtained from a case in which injections of rhodamine and WGA-HRP labeled the contralateral hemisphere (Fig. 9). Labeled neurons from the rhodamine injection were within area 17, but along the 17/18 border. The WGA-HRP injection labeled both cells and processes near the 17/18 border. The injection sites were 3 mm apart while the centers of two clusters of callosally transported label were 4 mm apart.

More extensive label in the contralateral hemisphere was produced in one case by an injection of WGA-HRP that was placed within area 17 near the 17/18 border (Figs. 6, 8). In this case, a strip of label was found along the 17/18 border of the right hemisphere that matched the rostrocaudal location of the injection in the left hemisphere, as in cases described above, but the strip extended into area 18, and four additional foci of label were scattered over area 18. Finally, a small focus of label was noted lateral to area 18.

Cortical connections of area 18

Connections of area 18 were investigated in four cases with injections confined to area 18 and in one case with injections overlapping the 17/18 border in OT_c.

Intrinsic connections. The intrinsic connections of area 18 were quite broadly distributed (Figs. 11, 14, 16, 18). An injection of WGA-HRP in the rostral half of area 18 produced a dense halo of labeled cells and processes in the surrounding 500 μm of cortex, and dense clumps of label distributed rostrally and caudally as far as 4 mm from the margins of the injection core (Fig. 11). A smaller WGA-HRP injection resulted in clumps of label as distant as 3 mm from the core (Fig. 14). Similar results were obtained with an injection of fast blue (Fig. 18). Labeled neurons were distributed over 6 mm of cortex and as far as 3 mm from the injection core. In all cases the intrinsic label was not uniformly distributed but formed clumps that were especially obvious away from the injection site.

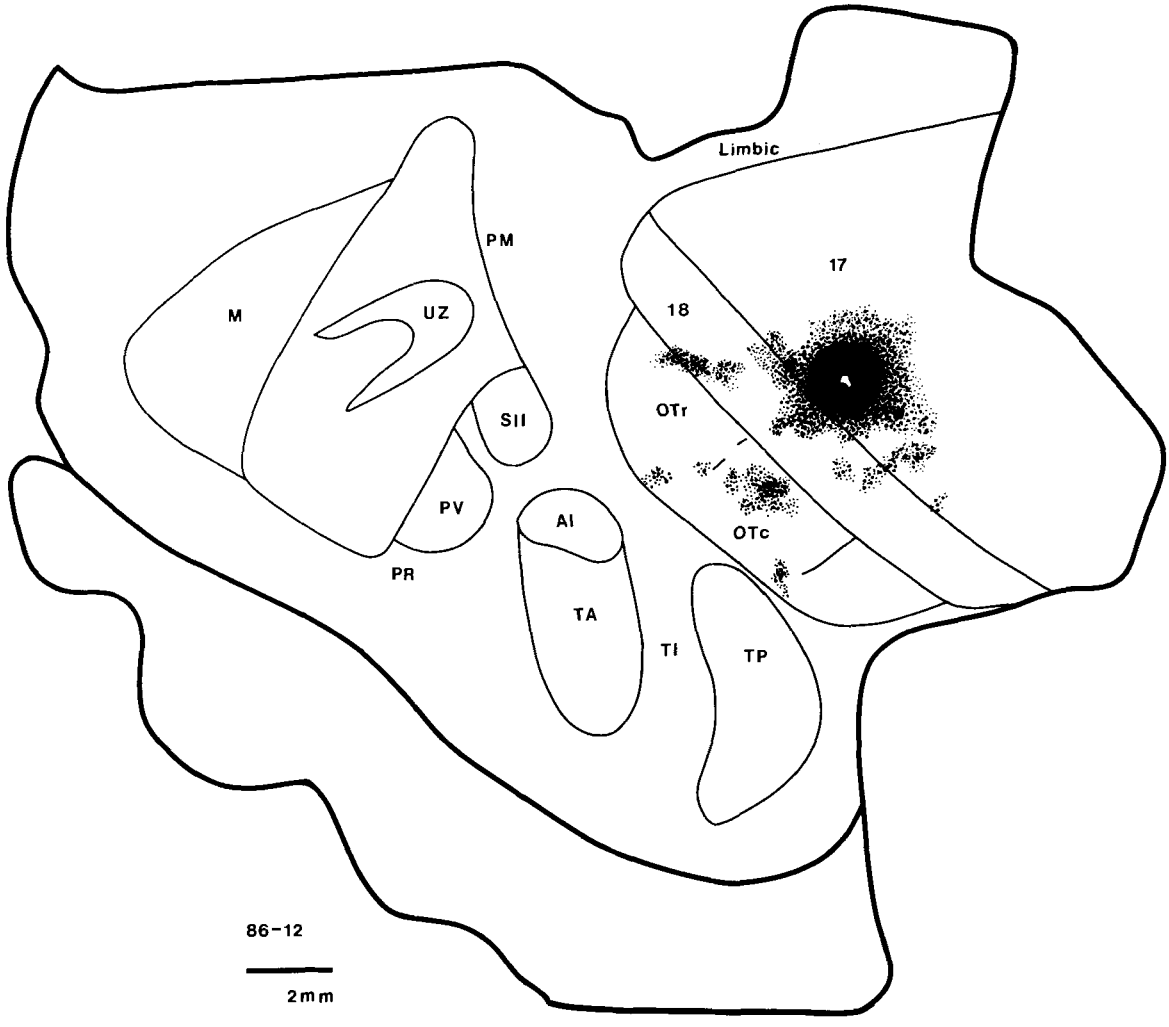


Fig. 6. The distribution of cortical label after one injection of WGA-HRP in area 17 near the 17/18 border. Abbreviations and conventions as in Figure 4.

Ipsilateral connections with area 17. Injections in area 18 generally produced zones of label in area 17 that were smaller than might be expected from the widespread patterns of label in area 18 after injections in area 17. In case 86-54, for example, labeled cells and cell processes were rather uniformly distributed near the 17/18 border along the margin of the injection site (Figs. 11, 12). A separate zone of label, starting about 1 mm within area 17, formed a 3 × 1.5 mm oval. Within this oval, labeled neurons formed clusters and short bands separated by zones with little label. Even more restricted patterns occurred in cases 86-45 (Fig. 14) and 86-24 (Fig. 16). In these cases, most of the label in area 17 was adjacent to the injection site and within 2 mm of the 17/18 border. Only the injection of fast blue in area 18 (Fig. 18) labeled neurons scattered over a considerable extent of area 17. This more extensive distribution included both a 7 mm × 3 mm oval of cortex along the 17/18 border and a more distant clump of cells in more medial area 17.

Interconnections with OT cortex. Injections in area 18 consistently produced patches of labeled cells and processes in cortex immediately lateral to area 18 (Figs. 11, 14, 16, 18). The largest injection in area 18 (Fig. 11) resulted in patches of label over 8 mm of the length of occipital-temporal cortex (OT). Smaller injections produced fewer patches and provided evidence that OT cortex contains more than one visual area. In case 86-45 (Fig. 14), for example, the patches of label were in two distinct locations, and labeled axons could be followed from the injection site to both locations. In each location, labeled cells formed two somewhat separate patches. A similar separation of patches within two distinct locations was observed in case 86-24 (Fig. 16), which had a more caudal injection in area 18. Patches of label were found in two ovals of slightly different myelination (see Fig. 2), which we refer to as the rostral and caudal divisions of occipital-temporal cortex, OT_r and OT_c. Finally, a case with an injection of fast blue in area 18 (Fig. 18) resulted in labeled cells in both the rostral and caudal locations in OT. The rostral location also had input from area 17. (Note the label resulting from the WGA-HRP injection in area 17.) Thus, both the pattern of connections and the myeloarchitecture provide evidence for at least two distinct visual areas in OT cortex.

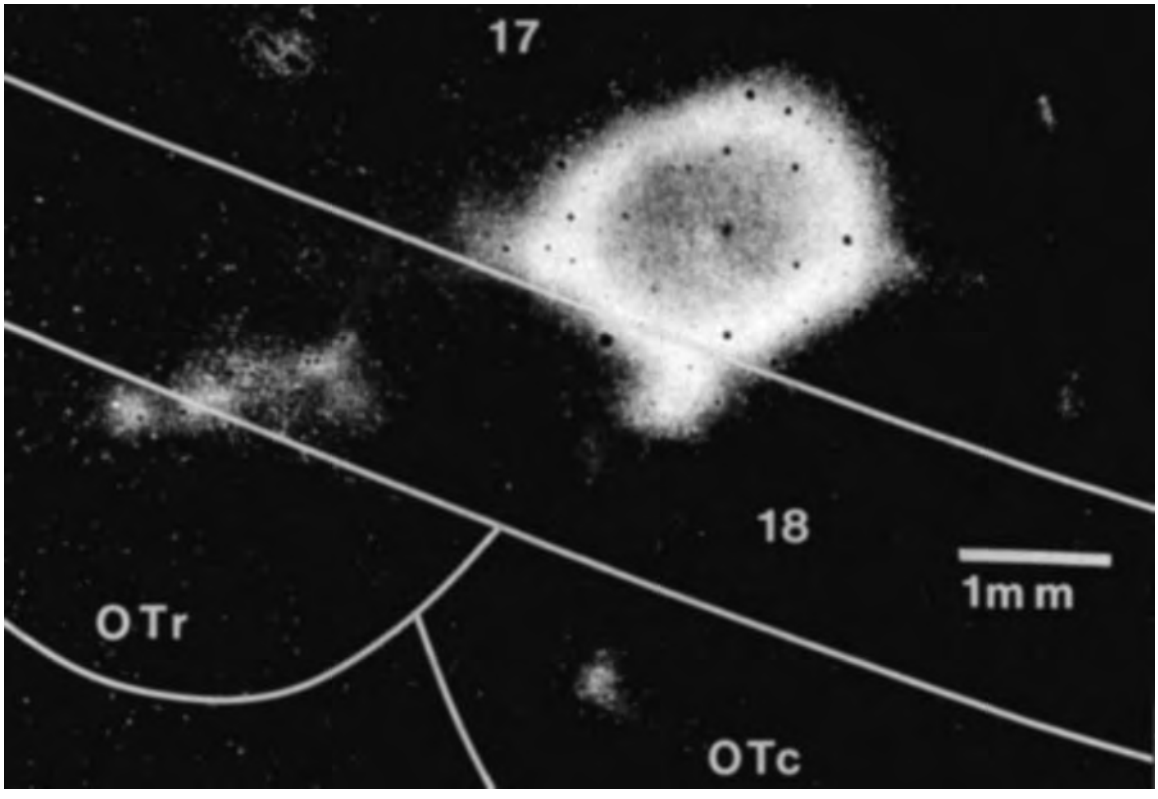


Fig. 7. A darkfield photomicrograph of a WGA-HRP injection in area 17 and transported label in area 17, area 18, and rostral and caudal divisions of occipital-temporal cortex (OT_r and OT_c). Case 86-12. Compare with Figure 6.

Other ipsilateral connections. Most cases with an area 18 injection resulted in label in limbic cortex (see Kaas et al., '72) rostral and medial to area 17 (Figs. 11, 16, 18). The larger injections (Fig. 11) produced large, dense patches of label in limbic cortex, while small foci of label (Figs. 14, 16, 18) resulted from the smaller injections. Most of the area 18 injections also resulted in label in cortex lateral to the OT zone. Case 86-45 (Fig. 14) produced none; case 86-24 (Fig. 16) resulted in two small patches in cortex caudal to TP; and the large injection in case 86-54 (Fig. 11) had label in cortex caudal to TP, a small focus in TP, and some label rostral to TP. The injection of fast blue (Fig. 18) labeled neurons in TP and in cortex caudal to TP. Finally, a large injection core resulting from three fused injection cores involving both areas 17 and 18 produced dense label in cortex caudal to TP, a small focus in TP, and a focus rostral to TP. Thus, it appears likely that area 18 projects to cortex caudal to TP and perhaps to TP and cortex rostral to TP (TI, see Fig. 1) as well.

Callosal connections of area 18

All injections in area 18 resulted in labeled neurons and processes in area 18 of the opposite hemisphere (Figs. 13, 15, 17). This label formed several dense clumps in the region closely matching the injection site location, and—especially for the larger injection sites—in other locations in area 18 as well (Fig. 13). The labeled patches of callosal connections were not as widespread as the ipsilateral intrinsic label, but callosal patches from a single injection were distributed over as much as 6 mm of area 18.

Other label on the contralateral side extended slightly into area 17 in some (Figs. 15, 17) cases but not others (Fig. 13). In two cases, callosal label was found in caudal but not rostral OT (Figs. 13, 17). Finally, the very large injection which involved both areas 17 and 18 (case 86-4, not shown) resulted in contralateral label in both areas 17 and 18. The label extended across the width as area 18 as far as 3 mm into area 17 and in addition included cortex caudal to TP and limbic cortex rostral to area 17.

DISCUSSION

The cortical connections of areas 17 and 18 in squirrels were investigated with restricted injections of WGA-HRP and fluorescent dyes. The results (Fig. 19) support a number of conclusions: 1) Area 18 or V-II in squirrels is a single visual area containing repeating modules or processing units. 2) A belt of occipital-temporal cortex just lateral to area 18 receives inputs from both areas 17 and 18. 3) Area 18 has direct interconnections with limbic cortex. 4) Callosal terminations from areas 17 and 18 are concentrated along the 17/18 border, but more central regions of area 17 contribute to this pattern. 5) Area 18 has additional callosal connection with occipital-temporal cortex. These and other conclusions are discussed and related to other findings below.

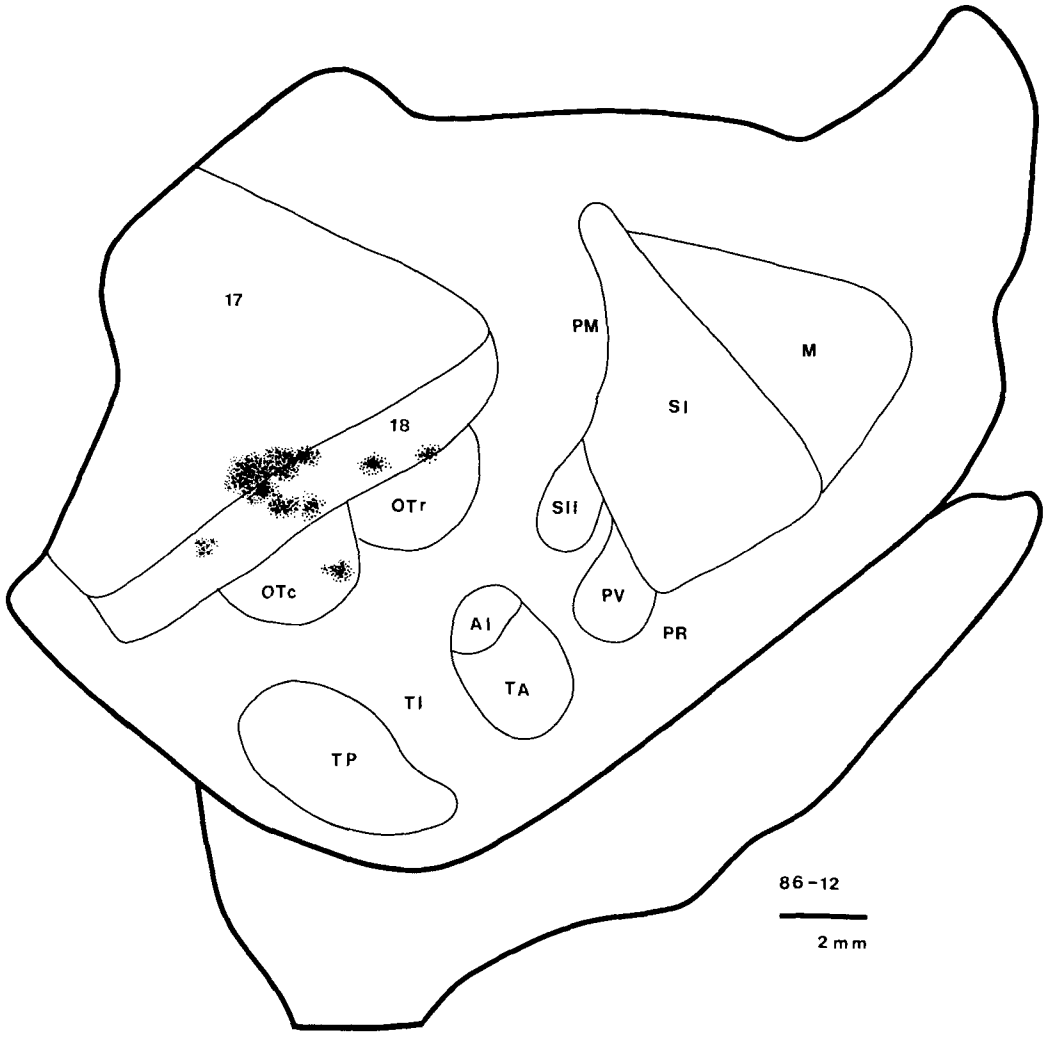


Fig. 8. The distribution of cortical label after an injection of WGA-HRP into area 17 of the opposite hemisphere. Abbreviations and conventions as in Figure 4.

The organization of area 18 in squirrels

Area 18 is a distinct architectonic subdivision of visual cortex that extends as a narrow belt along the lateral margin of area 17. Although recognized by modern investigators (e.g., Abplanalp, '70; Hall et al., '71; Kaas et al., '72; Weber et al., '77; Gould, '84), the less-developed medial monocular portion of area 17 was curiously misidentified as area 18 by Brodmann ('09) in squirrels. This error persisted in squirrels and other rodents (e.g., Volkmann, '26), with either the medial portion of area 17 or the medially adjoining limbic cortex being incorrectly labeled as area 18. Krieg ('46) partially corrected this error by identifying a lateral "area 18a," which was recognized as not resembling "area 18" on the medial side of area 17.

Our present contribution to the study of the architecture of area 18 in squirrels is to show that the field is not uniform in the areal distribution of dense myelination. Instead, a strip of dense myelination forms the border of area 18 with area 17, and thick bands of dense myelination extend across the width of area 18 at semiregular intervals. More evenly distributed myelination occurs on the lateral border of area 18. The overall appearance is that of a sequence of lightly myelinated ovals along the length of area 18, each surrounded by dense myelination.

While the functional significance of the lightly myelinated ovals is uncertain, they appear to roughly correspond to the spacing of ovals of cortex that are relatively free of callosal connections in area 18 of squirrels (Gould, '84). Callosal terminations along the lateral border of area 17 produce an even more pronounced rostrocaudal sequence of ovals in rats (Cusick and Lund, '81; Olavarria and Montero, '84), but it is uncertain if the myelination pattern in this species also reveals ovals. Dense myelination along the 17/18 border and alternating myelin dense and myelin light bands which extend across area 18 are present in monkeys (Krubitzer and Kaas, '89). The myelin dense and the myelin light bands, which also differ in cytochrome oxidase activity (e.g.,

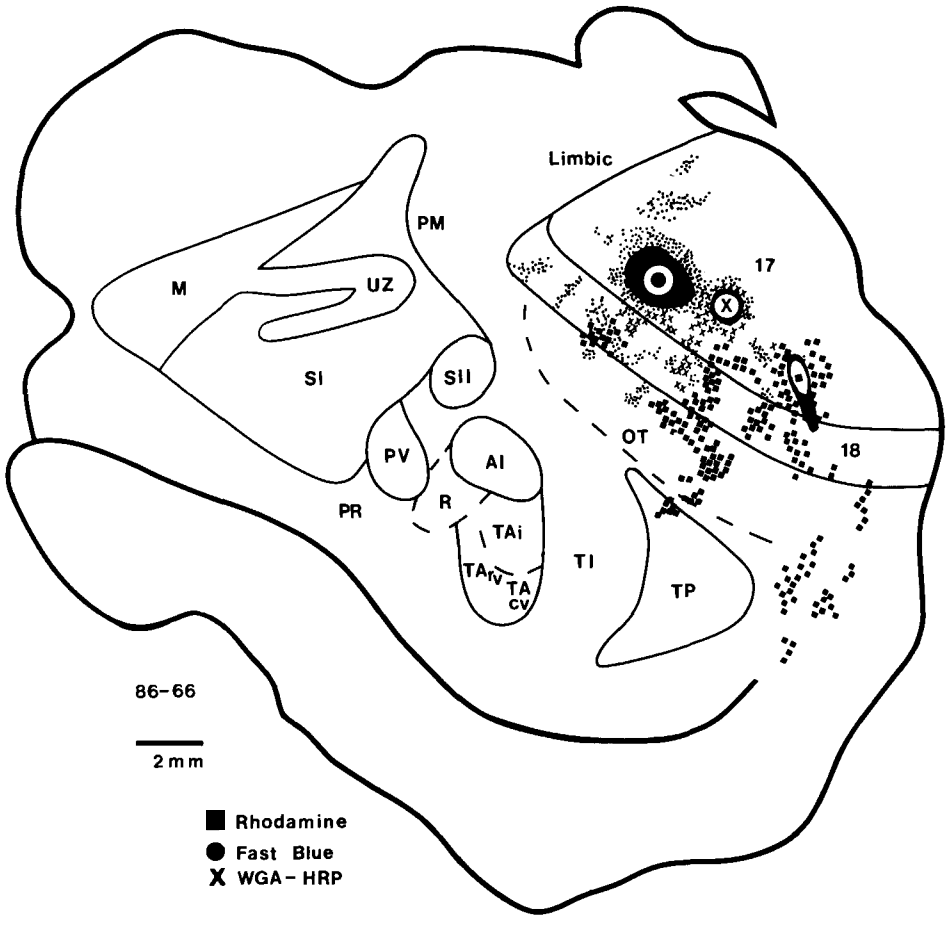


Fig. 9. Patterns of label after injections of three different tracers in area 17. Black ovals mark the zone of dense label around the injection sites and the probable maximum extent of the injection sites. Dots = fast blue; Xs = WGA-HRP; squares = rhodamine. Subdivisions of TA are based on Luethke et al. ('88). Conventions as in Figure 4.

Tootell et al., '83), correspond to sets of connectionally and functionally distinct processing modules (e.g., Livingstone and Hubel, '84a; DeYoe and Van Essen, '85; Shipp and Zeki, '85; Krubitzer and Kaas, '89; Hubel and Livingstone, '87). Thus, the repeating pattern of lightly myelinated ovals surrounded by dense myelination in squirrels suggests a functional heterogeneity that plausibly could be related to alternating modules which receive either callosal or ipsilateral cortical and thalamic inputs, or the segregation of different functional streams from area 17 within area 18. Other unidentified factors may also contribute to the heterogeneity.

Single restricted injections in area 17 consistently resulted in a patchy distribution of label in area 18. This is the common projection pattern in other mammals, including rats (Cusick et al., '80; Montero and Cliffer '81), monkeys (e.g., Perkel et al., '86; Livingstone and Hubel, '87), prosimians (Cusick and Kaas, '88b), tree shrews (Sesma et al., '84), and cats (e.g., Symonds and Rosenquist, '84). The usual interpretation of such a pattern is that single locations in one field project to separate groups of neurons of related function in another field (e.g., Kaas, '88).

The distribution of label transported from area 17 to area 18 was patchy in the present cases; the patches varied in location and number in relationship to the location and size of the injection. The projection pattern did not appear to relate to the series of four visual areas in area 18 proposed by Montero and Cliffer ('81). Instead, the transported label followed a single topographic pattern with rostral injections in area 17 producing more rostral patches in area 18 and caudal injections producing more caudal patches (Fig. 19). This topographic pattern was most apparent in one case where three different tracers were injected in a rostrocaudal sequence in area 17 and the resulting zone of label, though partially overlapping, formed a matched rostrocaudal sequence in area 18 (Fig. 9). Cusick et al. ('80), in a series of cases including some with ^{3}H-proline injections, found a comparable topographic projection pattern.

In other rodents, Montero et al. ('73a) and Olavarria and Montero ('81, '84) concluded that the discontinuous projection pattern of area 17 to lateral cortex (area 18a of Krieg, '46) corresponds to foci in four visual areas. However, the patterns they described as well as the patterns of label in cortex lateral to area 17 after injections in area 17 reported

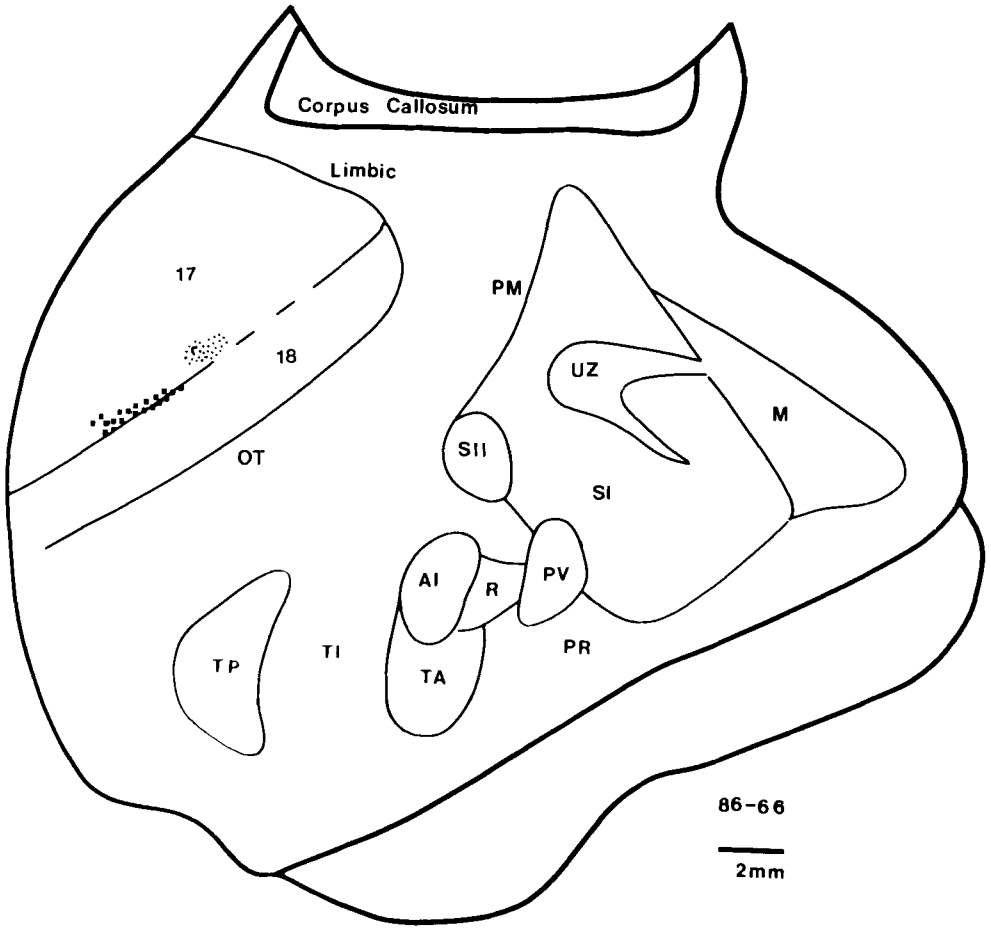


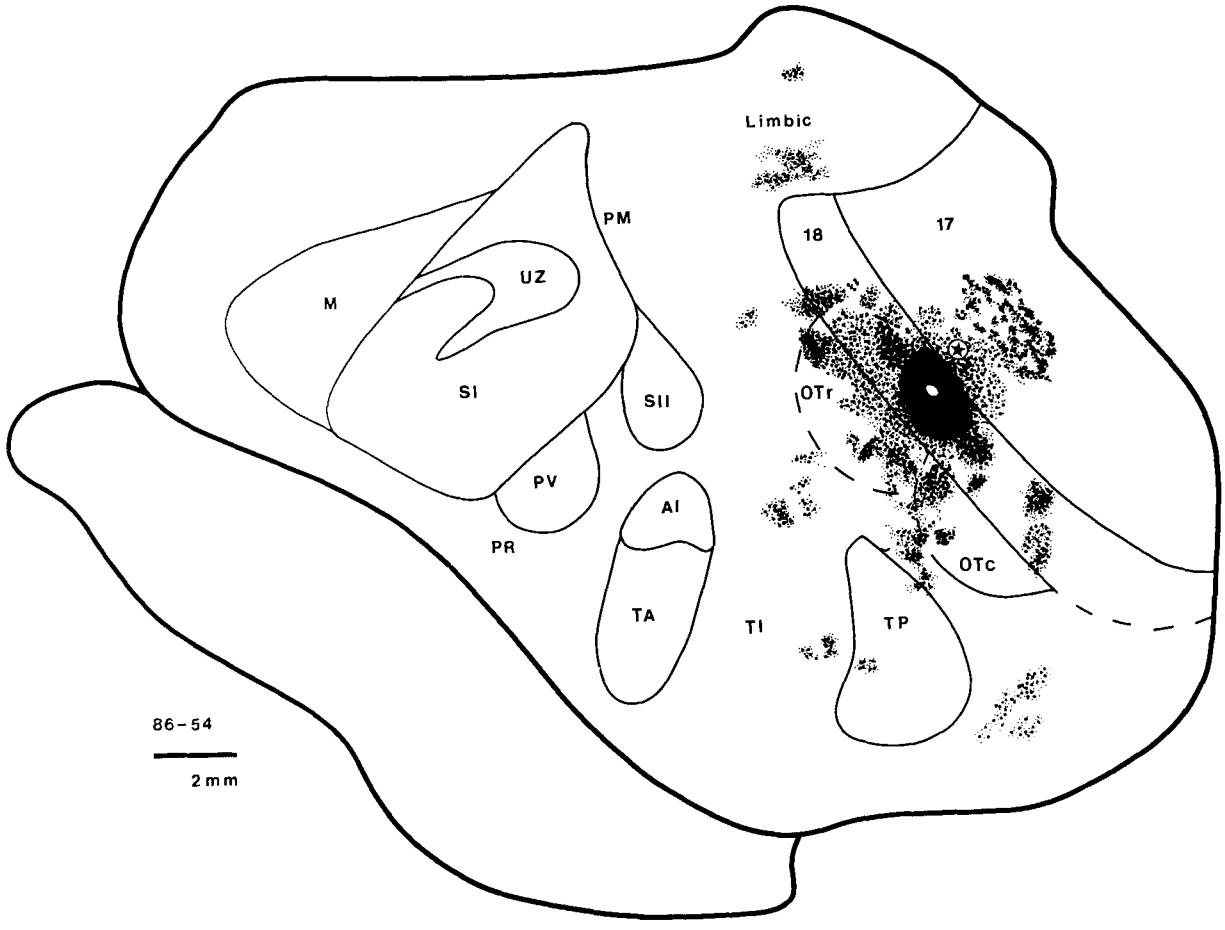
Fig. 10. Distribution of label resulting from injections of rhodamine (squares) and WGA-HRP (dots) in area 17 of the opposite hemisphere (see Fig. 9). The fast blue injection did not produce callosal label. Conventions as in Figure 4.

by others in rats (Miller and Vogt, '84), mice (Simmons et al., '82; also see Olavarria et al., '82), and hamsters (Dursteler et al., '79) seem compatible with the concept of a single visual area, V-II, along the lateral border of area 17 with repeating modules.

The present electrophysiological results are consistent with the view that there is a single overall retinotopic organization within area 18 in squirrels. Previously, Hall et al. ('71) reported that rows of microelectrode recording sites extending mediolaterally from area 17 across area 18, resulted in a continuous sequence of receptive fields progressing toward the zero vertical meridian (line of decussation) and reversing at the 17/18 border to extend some 10–15° into the contralateral hemifield for the midportion of area 18 and as far as 60° for rostral area 18. Rostrocaudal sequences of rows consistently revealed a shift in receptive field locations from the lower to the upper visual field. Thus, area 18 appeared to contain a single systematic representation of the contralateral hemifield, V-II, as in other mammals, with a roughly mirror-image organization of that in V-I, and differing from V-I mainly in a displacement of temporal vision toward the ends of area 18. Subsequently, Gould ('84) used microelectrode recordings to identify the V-I/V-II border in squirrels and confirmed the reversal of retinotopic organization at the border. Thus, electrophysiological results from three studies in squirrels support the conclusion that area 18 contains, at least roughly, a single systematic representation of the visual hemifield that mirrors that in V-I. This conclusion conforms to most (Drager, '75; Tiao and Blakemore, '76; Choudhury, '78; Olavarria and Mendez, '79; Wagor et al., '80), but not all (Montero et al., '73b; Espinoza and Thomas, '83), of the electrophysiological mapping results in other rodents and with those in many other mammals (see Kaas, '80). It is surprising, however, that the patchy mixture of the projections of area 17 to area 18 is not reflected in any obvious way in the retinotopic activation pattern. Recent fine-grain mapping studies of area 18 in monkeys have revealed that the overall retinotopic map is discontinuous and repetitive at the local level (DeYoe and Van Essen, '85; Shipp and Zeki, '85; Hubel and Livingstone, '87). More detailed mapping studies in squirrels might reveal similar features. Another possibility is that some of the inputs from area 17 are not reflected in the restricted excitatory receptive fields of most area 18 neurons (see Allman et al., '85).

The intrinsic connections of areas 17 and 18

Injections in area 17 and in area 18 revealed widespread horizontal connections in both fields. In area 17, the horizontal connections were uniformly distributed for a short



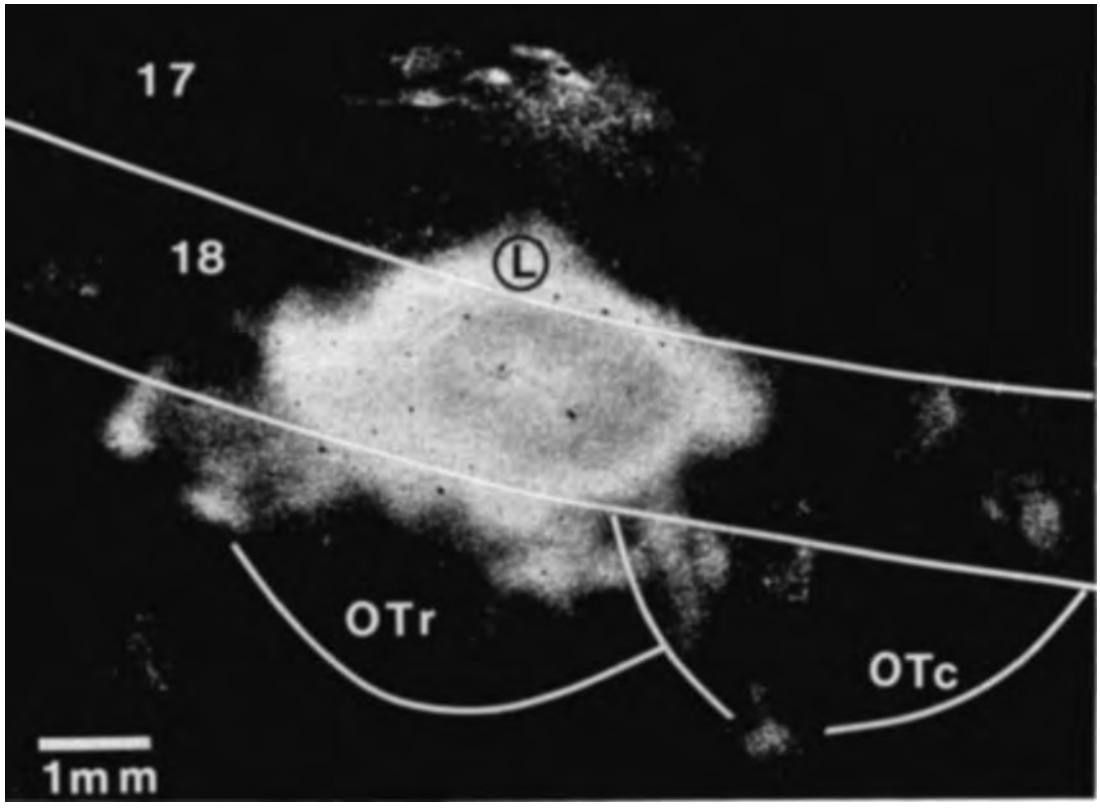


Fig. 11. (Top) The distribution of cortical label after an injection of WGA-HRP into area 18. The starred circle indicates a microlesion placed just inside the V-I border with V-II as judged from a progression of receptive fields for a row of recording sites approaching and crossing the 17/18 border. The architectonic borders were determined from brain

Fig. 12. (Bottom) A darkfield photomicrograph of a WGA-HRP injection in area 18 and transported label in area 17, area 18, and rostral and caudal divisions of occipital-temporal cortex (OT_r and OT_c). L marks a lesion placed at the physiological border of V-I. Case 86-54. Compare with Figure 11.

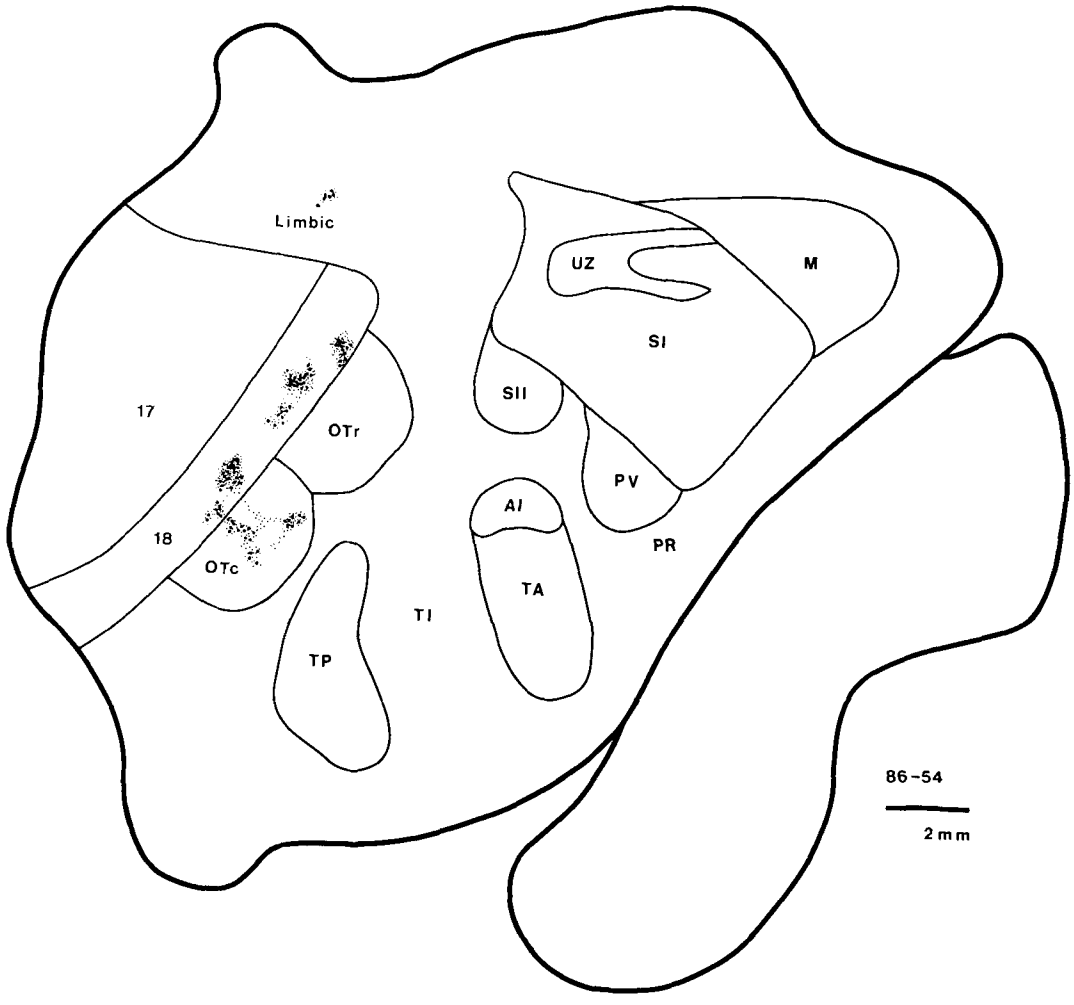


Fig. 13. The distribution of cortical label after an injection of WGA-HRP into area 18 of the opposite hemisphere (see Fig. 11). Conventions as in Figure 4.

distance around the injection core and became patchy and semiregular over a range of 1–2 mm from the injection site. Such widespread and periodic intrinsic connections in area 17 may be common in mammals (see Gilbert, '83, for review). They were first demonstrated in tree shrews (Rockland and Lund, '82), where they are particularly well developed (also see Sesma et al., '84). Markedly periodic patterns have been described in monkeys (Rockland and Lund, '83; Livingstone and Hubel, '84) and in prosimian galagos (Cusick and Kaas, '88). In these primates, the longer, periodic horizontal connections appear to be between functional subunits characterized by high cytochrome oxidase activity, the CO blobs. However, such blobs have not been reported for area 17 of tree shrews and, in our CO preparations of cortex in squirrels, we failed to detect blobs. The general concept is that the widespread, periodic intrinsic connections are between modules of cells with similar properties (e.g., Mitchison and Crick, '82; Livingstone and Hubel, '84b; Ts'o et al., '86), but there is support for the alternative that such connections are inhibitory between cells differing in a critical parameter (Matsubara et al., '85; however, see LeVay, '88). The widespread intrinsic connections in area 17 of squirrels suggests that physiological studies of modular organization might be productive.

In area 18 of squirrels, the intrinsic connections appeared to have both short, somewhat evenly distributed components, and longer discontinuous components. Separate patches of label were found up to several millimeters from injection sites. Area 18 is a long, narrow belt, and the longest intrinsic connections are along the length. Both local and distant horizontal connections also have been described in area 18 of cats (Matsubara et al., '85; LeVay, '88b), monkeys (Tigges et al., '74; Wong-Riley, '79; Livingstone and Hubel, '84a; Rockland, '85), and galagos (Cusick and Kaas, '88). Matsubara et al., ('85) point out that the retinotopic map in area 18, V-II, is anisotropic. That is, there is much greater cortical magnification along the length than across the width of V-II. These investigators suggest that the longer intrinsic connections along the length of the field compensate for the anisotropy by allowing cells with receptive fields in one location to more equally relate to cells with receptive fields in surrounding visual space. In the midsection of area

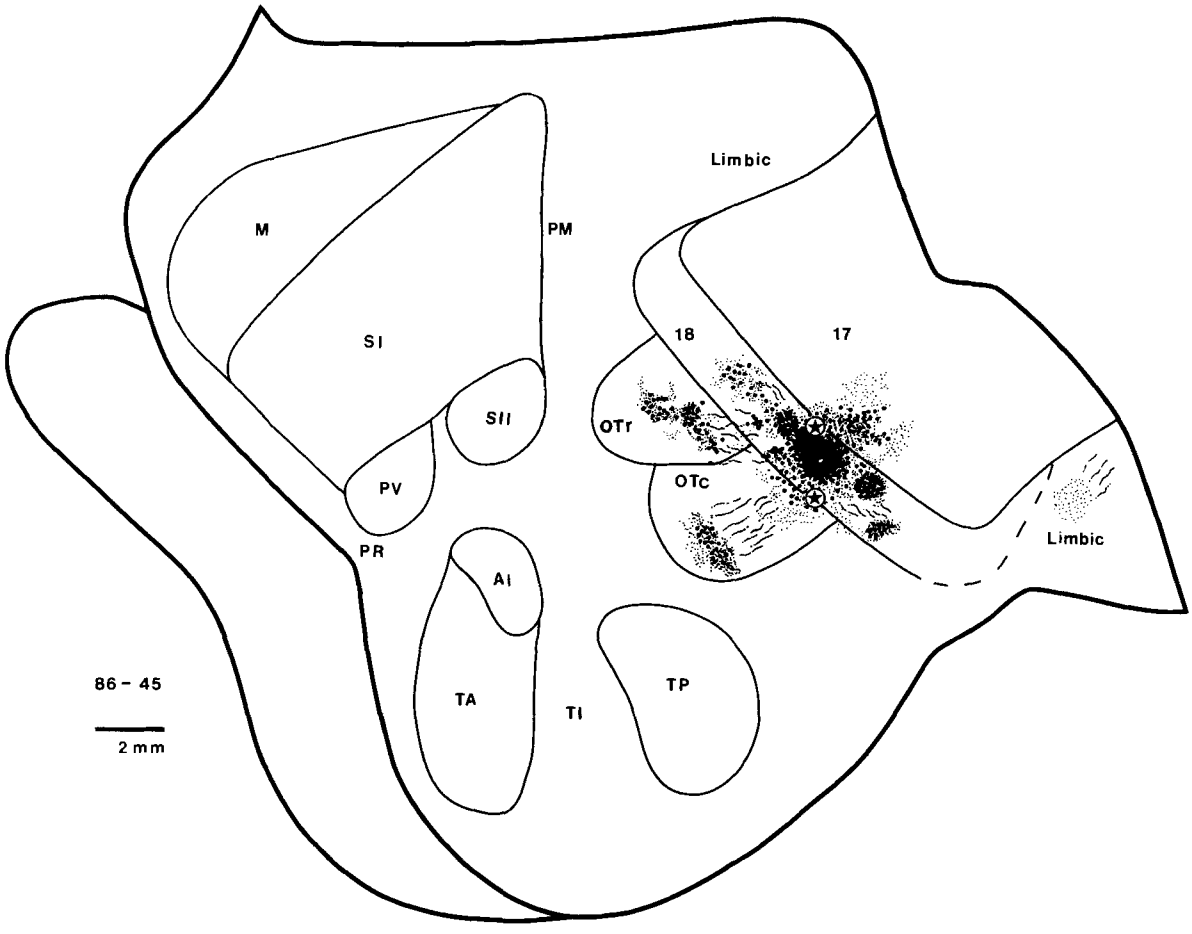


Fig. 14. The distribution of cortical label after an injection of WGA-HRP into area 18. The starred circles indicate microlesions made at the inner and outer borders of V-II as determined from recording sites extending from V-I across V-II. Conventions as in Figure 4.

18 of squirrels, the anisotropy of V-II is quite pronounced so that roughly twice the distance is required to move 10° in the visual field along the length as compared to across the width of area 18 (see Hall et al., '71). Thus, as for area 18 of cats, the longer intrinsic connections along the length of area 18 of squirrels may relate to the anisotropy of the representation.

Connections of areas 17 and 18 with occipital-temporal (OT) cortex

Areas 17 and 18 project to a broad band of cortex along the lateral border of area 18 (Fig. 19). The label resulting from single restricted injections was distributed in discontinuous patches which were often spaced over much of the rostrocaudal extent of this cortical band. Some of the injections, especially those in area 18 (e.g., Fig. 14), suggest the existence of two distinct projection fields, one rostral to the other. Callosal connections of areas 17 and 18 also support this conclusion since only one of the two myelinated ovals, OT_c, is connected with the contralateral areas 17 and 18.

We refer to the lateral projection zone of areas 17 and 18 at the junction of occipital and temporal cortex as the occipital-temporal (OT) region. Previously, we identified much of OT cortex as "area 19" (Kaas et al., '72), a term that now seems inappropriate since homologies in cortex lateral to area 18 are uncertain, and quite different organizations for cortex lateral to area 18 have been described in cats (e.g., Tusa et al., '79) and monkeys (see Kaas, '86). The OT region of squirrels is not homogeneous in architecture and connections. We previously distinguished a lateral portion with somewhat denser myelination as "19p" (Kaas et al., '72), and the present sections from flattened cortex reveal separate rostral and caudal ovals of somewhat different myelination (Fig. 2). Separate parts of OT have connections with different subdivisions of the pulvinar complex (Robson and Hall, '77) and, as noted above, patterns of connections with areas 17 and 18 are compatible with the view that the OT region contains more than one visual area. However, the possibility also remains that OT cortex in squirrels is a single functional subdivision of the visual system with roughly the location and organization of V-III (area 19) of cats. Support for this relation is also provided by the limited recordings just outside the lateral border of area 18 in squirrels, which suggests a retinotopic organization for OT that is much like that of V-III in cats (Hall et al., '71).

Projections from areas 17 and 18 to cortex along the lat-

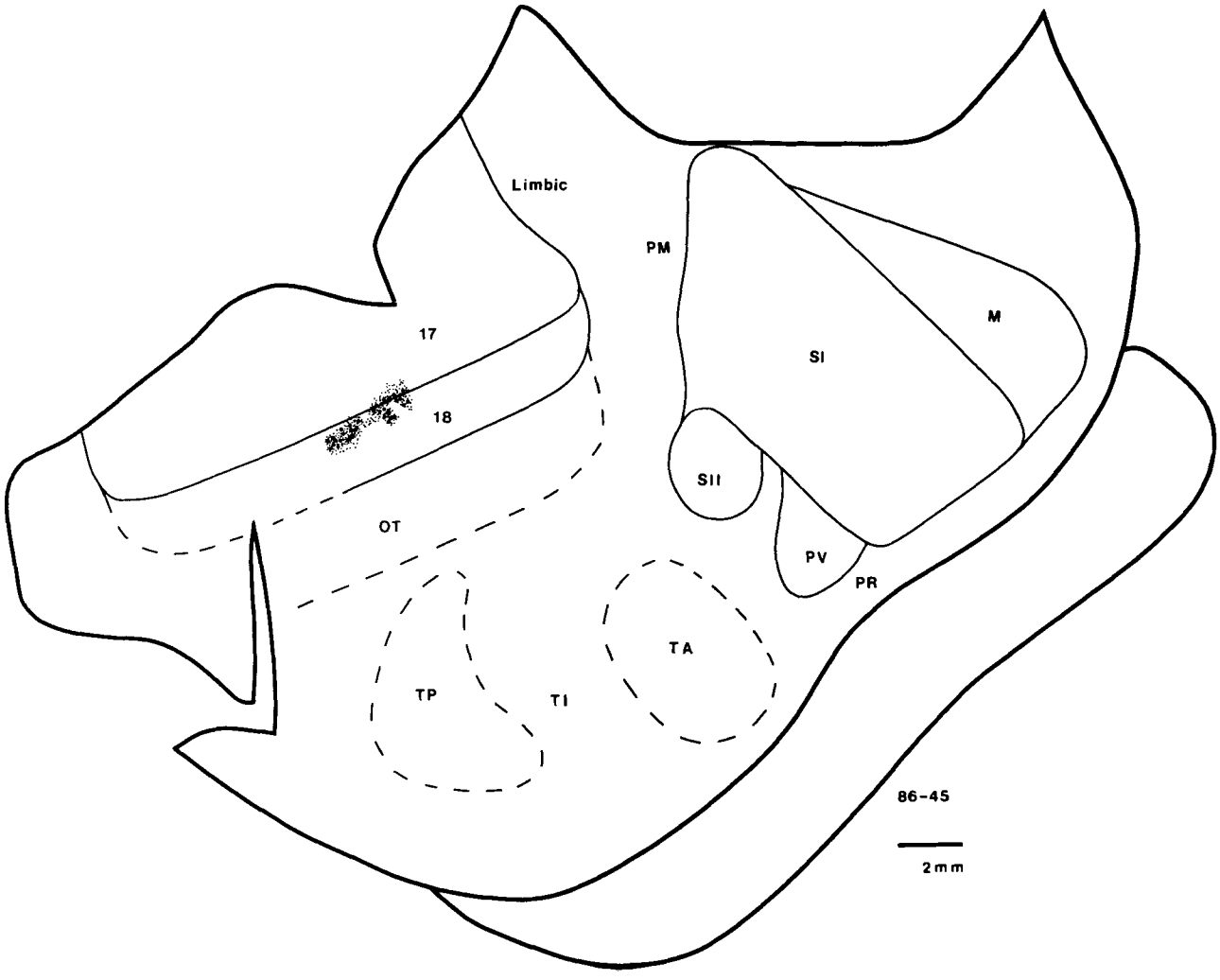


Fig. 15. The distribution of cortical label after an injection of WGA-HRP into area 18 of the opposite hemisphere (see Fig. 14). Conventions as in Figure 4.

eral border of area 18 have been reported for a number of mammalian species (see Kaas, '80), and such connections may exist in all mammals. In tree shrews (Sesma et al., '84), there is evidence for more than one projection field along this border. The existence of area 17 projections to OT cortex in a wide range of mammals is consistent with the possibility that a homologue of the middle temporal visual area, of primates, which receives inputs from areas 17 and 18 but is displaced from the area 18 border, exists along the area 18 border in other mammals (see Sesma et al., '84, for discussion).

Injections of area 17 sometimes produced sparse label in cortex lateral to OT. In a previous study (Cusick et al., '80), interconnections were sometimes demonstrated between area 17 and limbic cortex, although they were not apparent in the present investigation. Differences in survival time, tracer, and size of injection could account for these differences in observations. Area 18 injections more consistently revealed connections with cortex lateral to OT cortex, and often resulted in label in limbic cortex.

Although limbic cortex (L) receives visual input from area 18 and perhaps area 17 (Cusick et al., '80) in squirrels, and cortex in a comparable location receives input from area 17 in other rodents (e.g., Montero et al., '73a; Dursteler et al., '79; Simmons et al., '82; Olavarria and Montero, '81, '84; Miller and Vogt, '84), limbic cortex was not found to be responsive to visual stimuli in anesthetized squirrels (Hall et al., '71). Architectonically, L is quite different from area 18 (Kaas et al., '72), and area 18, but not L, has connections with the pulvinar complex (Robson and Hall, '77). In other rodents, cortex in the region of L receives input from the "lateral" (lateral dorsal) nucleus of the thalamus rather than from the lateral posterior or pulvinar complex (see Dursteler et al., '79), supporting the view that this cortex is part of the limbic system.

Callosal connections

The results led to several conclusions about the callosal connections of areas 17 and 18 of squirrels. First, much of area 17 has interconnections with the other hemisphere. All

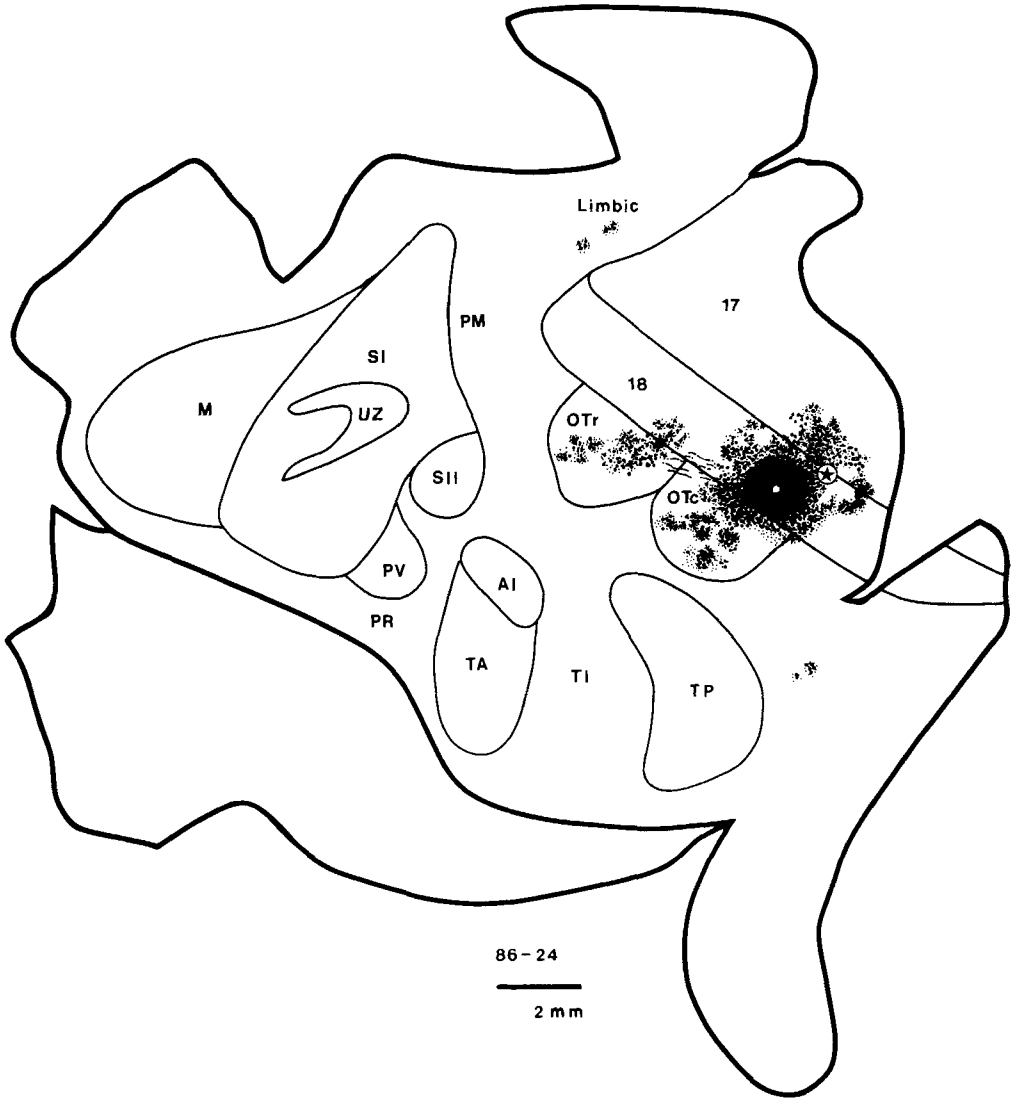


Fig. 16. The distribution of cortical label after an injection of WGA-HRP into caudal area 18. The starred circle marks a microlesion placed at the physiologically defined V-I/V-II border. Conventions as in Figure 4.

injections in area 17 resulted in label in the other hemisphere, even when injections were displaced centrally in area 17, away from the lateral border representing the zero vertical meridian. However, since no injections were placed in medial area 17, we are uncertain if the monocular portion of area 17 has callosal connections. In monkeys, callosal connections are restricted to the border of area 17, but such connections are widespread over much of area 17 in most investigated mammals, and even in prosimian primates (see Cusick and Kaas, '86, for review). In general, the callosal connections are dense along the 17/18 border and decrease markedly in density away from the border. In rats, callosal connections originate throughout area 17 (Olavarria and Van Sluyters, '83), but the more typical finding is that few or no callosal connections stem from the medial, monocular portions of area 17 (e.g., Cusick et al., '85).

Remarkably, the widespread callosal connections in area 17 were demonstrated by the locations of the injection sites producing callosal label but not by the locations of the transported label. Injections both at and away from the 17/18 border produced contralateral label, but the label was apparent only along the 17/18 border and not centrally in locations corresponding to the injection sites (Fig. 19). Thus, our second conclusion is that some of the callosal connections are not mirror symmetrical or homotopic but are heterotopic. The callosal connections of central locations in area 17 appear to be concentrated at the border region of the same retinotopic elevation. Since injections near or away from the area 17 border failed to demonstrate labeled neurons or terminals in central parts of area 17, we interpret the results as indicating that central locations in area 17 of squirrels have callosal connections that are dense along the 17/18 border and sparse more centrally in area 17, including the homotopic locations. Injections within area 17 apparently produce enough transported label to reveal the dense connections along the 17/18 border but not the sparse, more

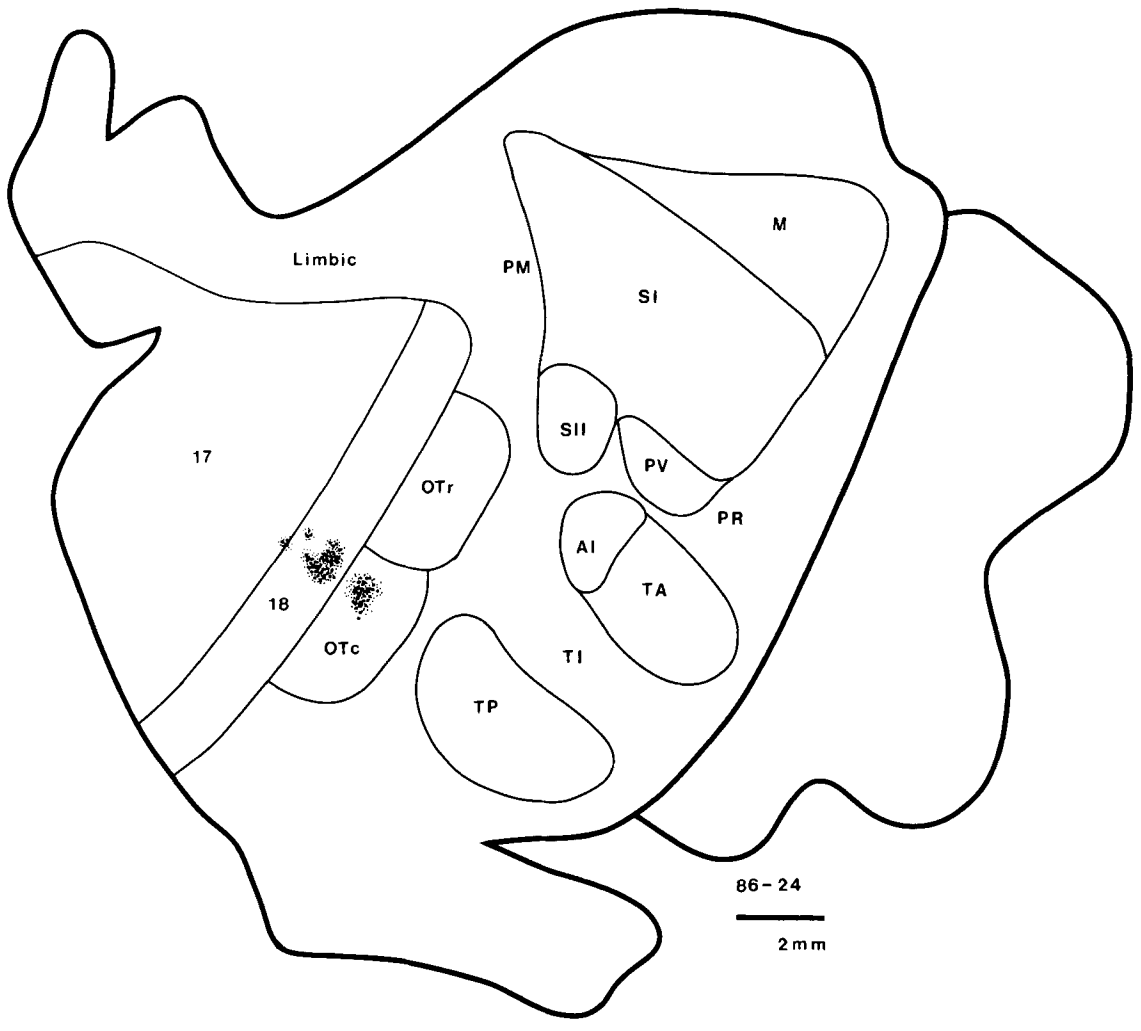


Fig. 17. The distribution of cortical label after an injection of WGA-HRP into area 18 of the opposite hemisphere (see Fig. 14). Conventions as in Figure 4.

central connections. We hypothesize that neurons along the 17/18 border project densely to the opposite 17/18 border and sparsely via collaterals to central locations in the opposite area 17. Thus, central injections label neurons and local recurrent collaterals along the opposite 17/18 border, but injections near the 17/18 border fail to adequately label sparsely distributed, fine axons terminating more centrally within the opposite area 17. Of course this suggests that other sparse connections may not be revealed by present methods, and that in squirrels and other mammals, current procedures underestimate the full extent of connections. Previous studies using degeneration methods or multiple injections of horseradish peroxidase in squirrels also revealed callosal connections in area 17 only near the lateral border (Gould, '84). The alternative possibility, that our central injections in area 17 resulted in large effective injection sites that included the 17/18 border, seems unlikely in view of the extensive evidence that the transport zone includes only the center core of a WGA-HRP injection site (see Shook et al., '84; Cusick and Kaas, '88b). In rats, Miller and Vogt ('84) also concluded from localized injections that all parts of area 17 project callosally to the lateral border zone of area 17.

The present results also indicate that callosal connections are unevenly distributed. Larger HRP-WGA injections in area 17 (e.g., Figs. 6, 7) result in several patches of label along the 17/18 border of the opposite hemisphere and in patches in area 18. Studies of the total callosal pattern in squirrels (Gould, '84) and rats (Cusick and Lund, '81; Miller and Vogt, '84) demonstrate a periodicity in the density of terminations along the 17/18 border that may be related to the patchy distribution we found after restricted injections. Callosal connections were even more obviously distributed in patches in area 18 (see Fig. 7), after area 18 injections (Figs. 10, 11). Uneven distributions of callosal projections characterize area 18 of many mammals (see Cusick and Kaas, '86, for review). Such patterns of uneven connections have commonly been considered evidence of functional heterogeneity and modular organization (see Kaas, '89), but presently there is no understanding of how cell classes are

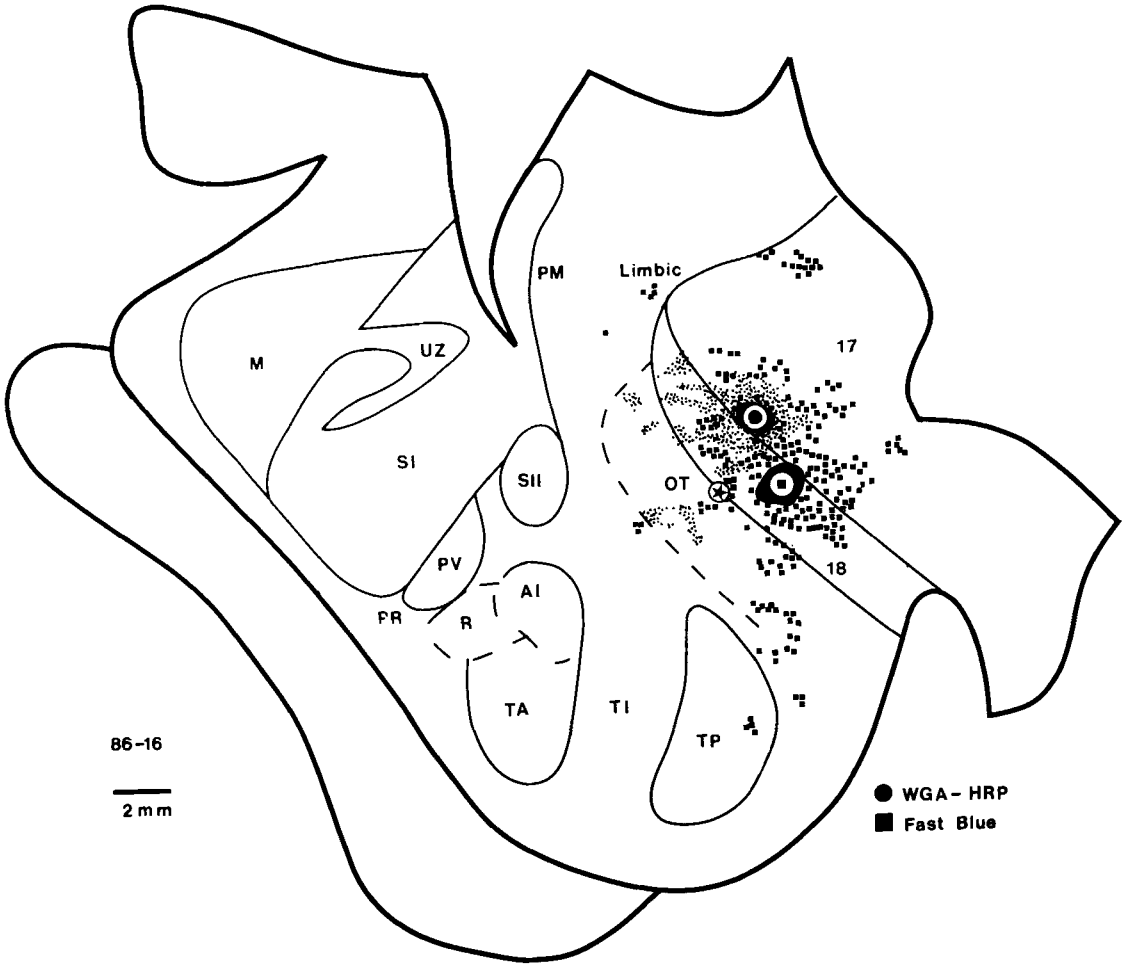


Fig. 18. Distributions of label after injections of WGA-HRP (dots) into area 17 and fast blue (squares) into area 18. Conventions as in Figure 4.

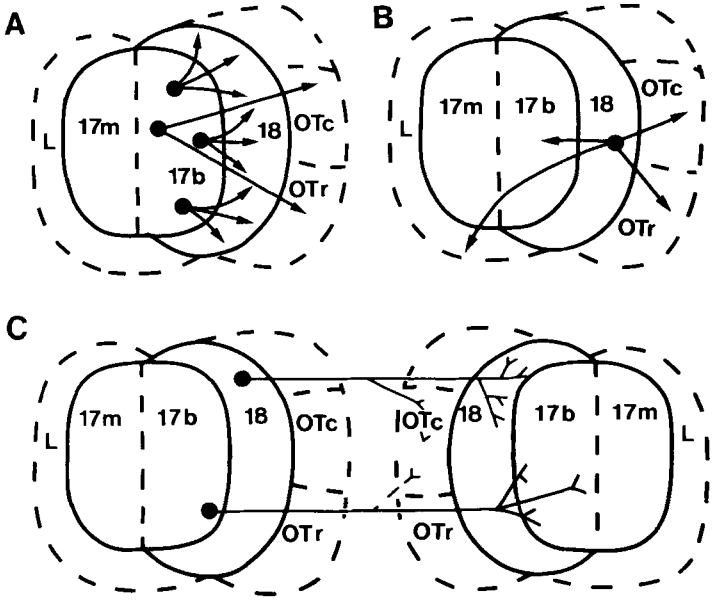


Fig. 19. Ipsilateral cortical connections of area 17 (A) and area 18 (B), and callosal connections of areas 17 and 18 (C) in squirrels. **A:** Projections of area 17 to area 18 are widespread but reflect a topographic the binocular (17b) rather than the monocular (17m) portion of area 17. **B:** Area 18 projections include those to limbic (L) cortex. **C:** Central areas of area 17 project densely to the 17/18 border zone. Dashed lines

distributed in areas 17 and 18 of squirrels.

A final finding is that both areas 17 and 18 have callosal connections with caudal OT cortex. This result is consistent with the common finding that a cortical area in a processing hierarchy has the most dense connections with the matched area of the other hemisphere but also may have callosal connections with the areas just above and just below it in the hierarchy (see Cusick and Kaas, '86). Similar findings of callosal connection with visual areas higher in the processing hierarchy have been reported for areas 17 and 18 in cats (e.g., Segraves and Rosenquist, '82) and for area 18 in monkeys (e.g., Tigges et al., '79; Kennedy et al., '86; Cusick and Kaas, '88a).

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