

Surface-view connectivity patterns of area 18 in cats

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Abstract. To determine surface-view connectivity patterns of area 18, separate injections of up to six anatomical tracers were delivered to various rostrocaudal locations of area 18 in six normal cats. Subsequently, cortex was separated from subcortical structures, manually flattened, and cut parallel to the surface. Results reveal that ipsilateral cortical connections of area 18 with three regions of cortex are topological. In areas 17 and 19, separate patches of cells labeled with different tracers progressed in a rostrocaudal sequence corresponding to the order of the injections. A similar but less precise pattern of rostrocaudal labeling occurred in more lateral visual cortex, even though several presumptive visual areas were involved. Thus, anteromedial suprasylvian cortex projected to anterior area 18 while more posterolateral suprasylvian cortex projected to posterior area 18. There was no evidence of double-labeled cells projecting to separate regions in area 18. These results are more consistent with the concept of a single suprasylvian area projecting to area 18 cortex than several.

Key words: visual cortex, extrastriate cortex, lateral suprasylvian area, fluorescent tracers, retinotopic mapping

INTRODUCTION

From the time of Brodmann's areas or "organs of the brain" (1909), there have been many efforts to identify the valid subdivisions of neocortex in numerous species, and opinions have varied considerably. Nevertheless, there has been much progress. There is also a general acceptance that each different method of subdividing cortex has its own strengths and weaknesses, and that the most reliable approach is to use multiple criteria and converging evidence from different procedures.

In cats, visual cortex has been divided using several criteria including architectonic and histochemical activity patterns (e.g., Hassler 1966, Sanides and Hoffmann 1969, Olavarria and Van Sluyters 1985), patterns of connections with other areas (Segraves and Innocenti 1985, Salin et al. 1989, Wimborne et al. 1993, Einstein 1996), the presence of partial or complete, systematic electrophysiological maps of visual space (Hubel and Wiesel 1965, 1969, Palmer et al. 1978, Tusa et al. 1978, 1979, Tusa and Palmer 1980, Grant and Shipp 1991), and distinct response properties of groups of neurons (Updyke 1986, Zumbroich et al. 1986, Sherk and Umbrellaro 1988, Sherk 1989, 1990, Payne and Siwek 1990, Toyama et al. 1990, Wieniawa-Narkiewicz et al. 1992, Wimborne and Henry 1992). These different approaches have resulted in a large body of data on cat cortical organization. Yet, there is widespread agreement on the validity of only three subdivisions of visual cortex in cats- area 17 or V1, area 18 or V2, and area 19 or V3. The functional organization of cat visual cortex beyond area 19 is still uncertain (for review, see Spear 1991). In particular, opinions vary in how the visually responsive cortex adjacent to the lateral and medial banks of the suprasylvian sulcus is subdivided into areas.

Cats exhibit one of the more complex visual systems outside of primates (Kaas 1980, 1987, 1989, Northcutt and Kaas 1995). Thus, they provide an opportunity to determine how connectivity patterns have evolved outside the primate line, and how these connectivity complexities reflect a modification of the common mammalian plan of visual cor-

tex organization. We investigated the surface-view pattern of corticocortical connections of area 18, particularly with the suprasylvian region, in normal, adult cats. Flattening cortex permitted a direct visualization of areal patterns of connections and allowed accurate comparisons of connections with cortical subdivisions determined from architectonics or histochemical stains. The results of the present study suggest that the suprasylvian region may be parcellated into fewer visual areas than commonly supposed (e.g., Tusa and Palmer 1980). This research has been reported in more abbreviated form previously (Pospichal et al. 1993).

METHODS

The corticocortical connections of visual area 18 were assessed in six normal, adult cats. Single, separate injections of wheatgerm agglutinin conjugated to horseradish peroxidase (WGA-HRP) and the fluorescent tracers Fluoro Ruby (FR), Fast Blue (FB), Diamidino Yellow (DY), rhodamine green beads (GB), and rhodamine red beads (RB) were delivered into various rostrocaudal locations within area 18. Retrogradely-transported label was subsequently related to cortical architecture.

Surgery

The day before surgery, animals received dexamethasone (2 mg/kg, IM) to prevent surgical edema. At the beginning of the experiment, each animal received initial injections of acepromazine (0.5 mg/kg b.w., SC), ketamine hydrochloride (20 mg/kg, IM) and xylazine (1 mg/kg, IM). Supplemental injections of ketamine and xylazine were administered, as needed, to maintain surgical levels of anesthesia. Each animal was placed in a stereotaxic instrument, where body temperature was maintained at 38°C. Using aseptic surgical procedures, a craniotomy was performed to expose visual cortex, and the dura was incised to permit tracer injections. Following injections, the dura was repositioned, the craniotomy was closed using dental acrylic, and the skin was sutured. Animals were

carefully monitored during recovery from anesthesia.

Post-surgically, animals received initial doses of analgesic (Butorphenol, 0.01 mg/kg, IM), penicillin (10,000-30,000 units/lb b.w., IM) and warmed lactated Ringer's (100 ml/kg, SC) to prevent dehydration; these post-surgical treatments were re-administered, as needed, during each animal's 3-6 day survival period. At the end of the experiment, animals were given a lethal dose of sodium pentobarbital. Once deeply anesthetized, as evidenced by lack of physical reflexes, they were transcardially perfused with physiological saline followed by 2% paraformaldehyde in phosphate buffer and 2% paraformaldehyde in 10% sucrose phosphate buffer. Perfused brains were removed immediately; cortex was separated from the deep structures, manually flattened, and cut parallel to the surface (5 cases) or the intact brain was cut coronally (1 case). All experimental and animal care procedures were in compliance with the principles of the Association in Vision and Ophthalmology and the National Institutes of Health Guide for the Care and Use of Laboratory Animals (NIH Publication No. 85-23, 1985).

Tracer injections and histology

Using traditional gyral and sulcal landmarks and Horsley-Clarke co-ordinates as guides, multiple tracers were injected in discrete regions throughout area 18. In two animals, limited electrophysiological recordings helped confirm injection placement in area 18. Typically, 3-6 tracers were used in each case. The locations of these tracers were varied between-cases, to ensure that differential transport of tracer types did not confound the findings. Additionally, injection locations were replicated in different animals; thus, most anatomical findings represent data from at least two animals. Injections were made using glass micropipettes coupled to Hamilton syringes as follows: 2% WGA-HRP in saline, 0.5-0.8 μ l; 10% FR in saline, 0.2-0.4 μ l; 3% FB in distilled water, 0.6-1.0 μ l; GB and RB, 5 μ l; DY, 2% in phosphate buffer, 1 μ l, or in pellet form (Griffin et al. 1979).

After appropriate survival times and removal of brains, cortex was frozen and cut on a sliding microtome at 40-50 μ m. In both flattened and coronal preparations, series of sections were mounted for fluorescent microscopy and an adjacent series was reacted with tetramethylbenzidine (TMB: Mesulam 1978) to visualize WGA-HRP label. The remaining alternate series were stained for myelin (Gallyas 1979) and/or reacted for cytochrome oxidase (Wong-Riley 1979) to identify cortical areas in flattened sections, or stained with cresyl violet to visualize the cellular lamination of the cortex in sections cut coronally. In each case, the LGN was cut coronally on a freezing microtome at 50 μ m, and label transport was assessed to assist confirming the topographic location of cortical injection sites.

Data analysis

Fluorescent label and tissue borders were illustrated using a fluorescent microscope electronically coupled to an X-Y plotter, using the BIOQUANT computer program (R and M Biometrics, Nashville, TN). A microscope with a drawing tube was used to produce detailed drawings of WGA-HRP label in individual brain sections at high magnification. Reconstructions of variations in architecture allowed the identification of areal borders. Local landmarks in tissue that crossed the depth of cortex, such as blood vessels and sulci, were used to align drawings of adjacent sections, so that label transport and architectonic borders could be consolidated into a single figure.

RESULTS

The surface-view connectivity patterns of area 18 are presented from six normal cats, and were revealed by injecting WGA-HRP and up to five fluorescent tracers in separate locations along the rostrocaudal extent of area 18. Our general findings include: (1) for connections of area 18 with areas 17 and 19, separate labeled patches of individual tracers progressed in a rostrocaudal sequence that corresponded to the order in which the different tra-

cers were injected; (2) a similar pattern of rostrocaudal labeling occurred with visual cortex of the suprasylvian sulcal region; (3) rostral area 18 connections arose from the medial suprasylvian cortical region only, whereas more caudal area 18 received input from both medial and lateral suprasylvian sulcal regions; (4) connections of the portion of area 18 representing central vision tended to be relatively expansive and, although topological, more overlapping than connections of area 18 devoted to paracentral and peripheral vision. The patchy, highly topological connectivity patterns with areas 17 and 19 were consistent with a generally-accepted scheme of corticocortical connectivity, but the single, global pattern of connections with more lateral cortical visual regions was unexpected. Detailed results are described below.

Demarcation of cortical area 18

Placement of injections and verification of injection sites were initially determined using traditional, topographical features visible on the cortical surface. Specifically, area 18 injections were made on the medial bank of the lateral sulcus, and injection positions were further determined using the Horsley-Clarke coordinate maps of Tusa et al. (1979). In some cases, limited electrophysiological mapping was used to confirm injection placement in area 18. Subsequent processing of flattened cortex for CO and myelin allowed confirmation of the locations of injections in area 18. In favorable preparations discrete CO blobs were apparent in area 17 but not area 18. In area 18, CO-dark regions appeared larger with less distinct borders. Boundaries between areas 17, 18 and 19 were also apparent in myelin preparations, with the adjacent myelin-light areas 17 and 19 and the myelin-dense area 18 forming sharp borders.

Area 18 connectivity patterns

In all six cases, the patterns of retrogradely-labeled cells in areas 17, 19, and cortex along the suprasylvian sulcus were patchy and topologically

matched to injection sites. Following separate area 18 injections of WGA-HRP and FB in case 93-8 (Fig. 1A), patches of cells in area 17 were seen immediately medial to the respective injection sites, and the rostrocaudal positions of these patches reflected the placement of the associated injections. This arrangement of area 17 inputs to area 18, as revealed by the locations of patches of retrogradely-labeled cells in area 17, was also apparent following separate FR, FB and WGA-HRP area 18 injections in case 92-81 (Fig. 1B). In case 93-99, six different tracers were applied in distinct locations along the rostrocaudal extent of area 18 (Fig. 2). Five of these tracers were placed parallel to midline at 2 mm intervals, and the sixth was placed quite laterally (ML 16) in cortex representing upper visual space. The pattern of labeled cells in area 17 was closely aligned with the placement of the six tracer injections in area 18. A similar alignment of patches of labeled cells with associated area 18 injections was evident in area 19 (see Figs. 1A,B and 2). Thus, patches of neurons in areas 17 and 19 were shown to converge onto discrete regions of area 18 in a reliable and orderly fashion.

Although the patches of retrogradely-labeled cells in cortex along the suprasylvian sulcus were somewhat more overlapping than in areas 17 or 19, the distributions were centered in topological sequence. Thus, the pattern of labeled neurons in areas 17, 19 and the suprasylvian region following three separate injections (WGA-HRP, FB, FR) in area 18 in case 92-81 (Fig. 1B) reflected the rostrocaudal position of the three injection sites. The FR injection labeled the most rostral patches of cells in areas 17, 19 and suprasylvian cortex, reflecting the rostral-most position of this injection site (at approximately AP +8); the WGA-HRP injection site and labeled patches of cells were most caudal (injection site at AP -10), and the FB injection (AP + 2) and associated labeled cells were intermediate in position. This global topography of connections of areas 17, 19 and suprasylvian cortex was evident in all animals, but is perhaps best demonstrated in case 93-99 (Fig. 2), wherein rostral-most FR-labeled patches of cells in all three regions with connections

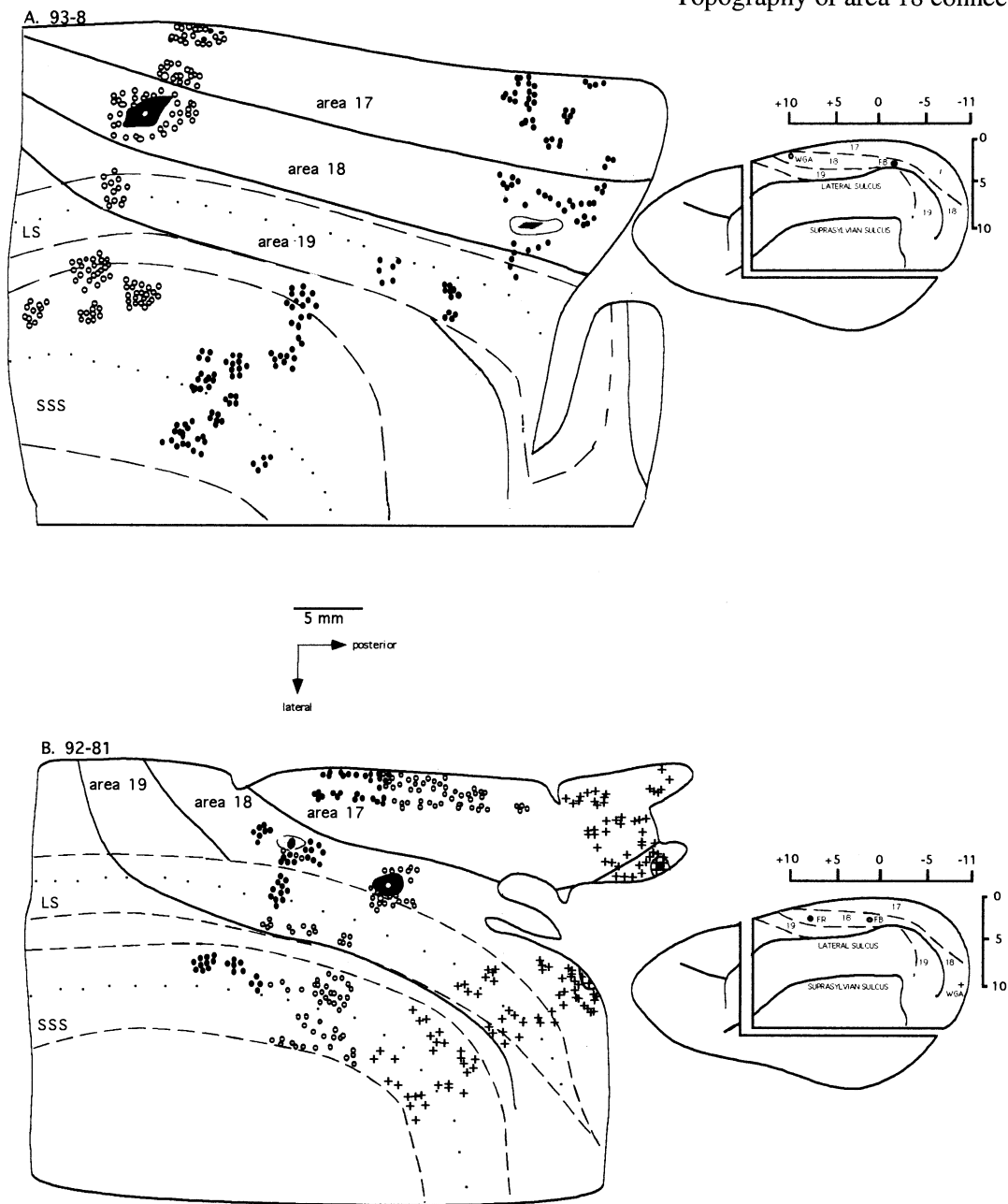


Fig. 1. Reconstructions of the distribution of labeled neurons in flattened cortex after tracer injections in area 18. A, connection topography in cat 93-8 following 2 area 18 injections and B, connection topography in cat 92-81 following 3 area 18 injections. To the right in each panel is a dorsolateral schematic of a cat brain, with relevant landmarks and injection sites indicated. The posterior brain blocks reflect the approximate regions of caudal cortex depicted in the flattened views. On the left in each panel is the flattened cortex for each case, with relevant landmarks, injection sites, and corresponding surface-view patterns of retrogradely-labeled cells. The contours of the lateral and suprasylvian sulci are indicated by dashed lines and the sulcal depths by dotted lines. Unlike the dorsolateral drawings, the flattened pieces are not schematized, but are composite reconstructions of each case. In both cases, patchy, topological distributions of label are located in area 17, area 19, and along both banks of the suprasylvian sulcus. Label from rostral injections is restricted to the medial bank but more caudal injections result in label along both banks. Approximate Horsley-Clarke and elevation/azimuth locations (estimates based on the mapping studies of Tusa et al. 1979) for panel A: WGA, AP +15/ML2, visual space -30/5; FB, AP -2/ML 4, visual space -4/5; for panel B: FR AP +8/ ML 3, visual space -10/5; FB AP +1/ ML 3, visual space -5/5; WGA AP -9/ ML 10, visual space +15/10. Structures: LS, lateral sulcus; SSS, suprasylvian sulcus; 17, 18, 19, areas 17, 18, 19, respectively.

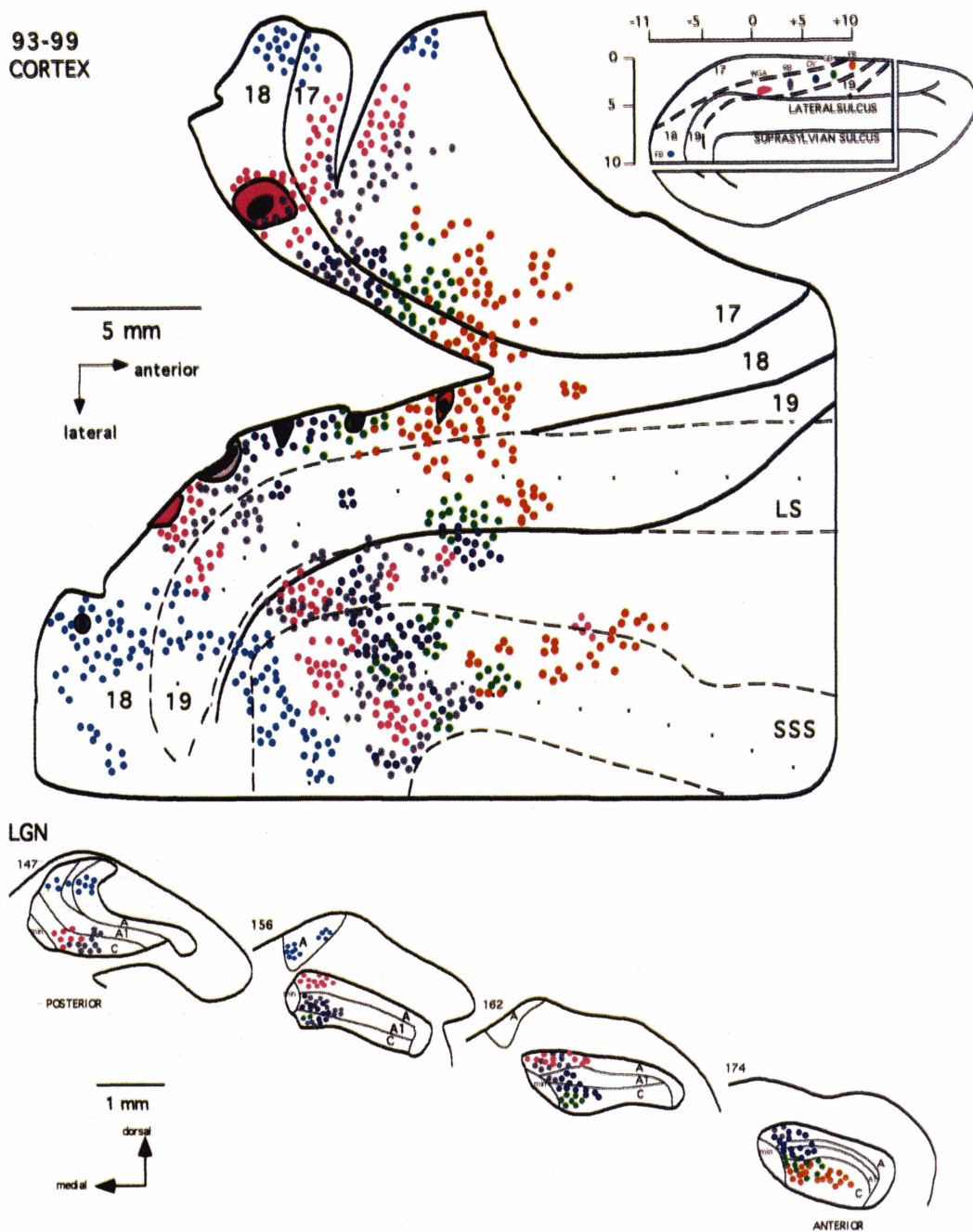


Fig. 2. The distribution of labeled neurons after single injections of 6 anatomical tracers in separate locations in area 18 of cat 93-99. Cortex: For connections of area 18 with area 17, area 19, and the suprasylvian region, groups of patches of neurons labeled by individual tracers progress in a rostrocaudal sequence that corresponds to the order in which different tracers were injected into area 18. There is also some scatter in the distribution of patches and some overlap of patches related to different tracers. The rostral-most area 18 injection (FR) results in labeled cells mainly in the medial bank of the suprasylvian sulcus. For more caudal injections, labeled neurons are seen along both banks. Injections in adjoining points in area 18 result in overlapping, although still topological, distributions of labeled cells in all three regions to which area 18 is connected. Horsley-Clarke and elevation/azimuth values: FR AP +10/ML 3, visual space -15/5; GB AP +8/ML 4, visual space -10/10; DY AP +6/ML 3, visual space -8/5; RB AP +4/ML 3, visual space -6/5; WGA AP +2/ML 3, visual space -4/5; FB AP -8/ML 16, visual space +20/5. LGN: Retrograde labeling of LGN neurons following 6 tracer injections into area 18 in cat 93-99. The patterns of labeled cells confirm both the restriction of injections to area 18 as well as the visuotopic placement of the injections. See text for details. Other conventions as in Fig. 1.

to area 18 were associated with the rostral-most FR injection, caudal-most FB-labeled patches of cells reflected the caudal-most position of the FB injection, and other patches of labeled cells were aligned with their associated tracers. Thus, for connections of area 17, area 19, and the suprasylvian region, groups of patches of neurons progressed in a rostrocaudal sequence that corresponded to the order of tracer injections in area 18 (see also Fig. 1A).

Although connections of area 18 with areas 17, 19 and suprasylvian cortex were topological, in many instances there was an overlapping of patches of labeled cells and, qualitatively, this overlap seemed related to at least three factors. One influence on the overlapping of patches of cells from different tracers was the relative distance between injection sites. For example, in case 92-81, there was a slight overlapping of populations of FR- and FB-labeled neurons in all three projection regions: these injection sites were located in cortex representing lower vision and were separated by approximately 7° of visual space (Fig. 1B). In contrast, there was no overlap of either of these populations with those which were labeled following the WGA-HRP injection, which was many millimeters caudal and lateral to the other two injection sites, in a region of cortex representing upper visual space. Similarly, in case 93-99 (Fig. 2) neighboring injections in area 18 (within about 10° or less of visual space) resulted in overlapping, although still topological, distributions of labeled cells in all three regions to which area 18 was connected. The most notable exception to a strict topology was WGA-HRP transport to a few cells in the rostral-most portion of the medial suprasylvian bank (see below).

Another factor that seemed to be associated with an overlapping of patches of cells labeled with different tracers was the relative location of injection sites in cortex representing central versus paracentral or peripheral vision. The qualitative impression was that injections in cortex nearest central vision resulted in the most widespread patches of cells and that this rostrocaudal expansiveness of patches of labeled neurons resulted in a greater overlap with patches of other cells. This can be appreciated by

comparing the rostrocaudal extents of labeled cells for different injection sites within-cases. Thus, in case 93-8, the more centrally positioned FB injection labeled more expansive patches of cells than did the WGA-HRP injection, placed in cortex representing peripheral visual space (Fig. 1A; see also Fig. 1B). Similarly, in case 93-99 (Fig. 2), the WGA-HRP injection site in area 18 was nearest the area centralis representation, and this injection resulted in greater expanses of labeled cells.

Finally, there appeared to be a greater overlap of populations of cells in suprasylvian cortex than in areas 17 or 19. For example, in case 93-99 patches of RB- and WGA-HRP-labeled cells were non-overlapping with FR-labeled cells in areas 17 and 19, but a small patch of WGA-HRP overlapped a patch of FR-labeled cells in the medial suprasylvian bank, and FR cells overlapped slightly with RB-labeled cells in the lateral suprasylvian bank (Fig. 2).

In addition to suprasylvian inputs to area 18 being topographic and patchy, the inputs of the medial and lateral banks of the suprasylvian sulcus differed. The medial bank along the suprasylvian sulcus had connections to all regions of area 18 evaluated in this study, but the lateral suprasylvian bank lacked connections with rostral-most area 18. For example, the FB injection in case 93-8 (Fig. 1A) in lower central vision (AP -2), labeled cells extending to both the medial and lateral banks of the suprasylvian sulcus, whereas the WGA-HRP injection in more peripheral lower visual field cortex (AP + 15), resulted in labeled cells only along the medial suprasylvian bank. Similarly in case 93-99 (Fig. 2), the rostral-most area 18 injection (FR; AP + 10) resulted in labeled cells only along the medial suprasylvian bank. More caudal injections labeled neurons along both medial and lateral suprasylvian banks. Finally, in case 92-81, the FB and WGA-HRP injections into central and upper vision regions of area 18 labeled patches of cells in both suprasylvian banks, but the FR injection labeled only medial bank neurons (Fig. 1B).

Since the WGA-HRP serves as both a retrograde and anterograde tracer, patterns of labeled terminals were also observed. Labeled terminals coincided

with patches of WGA-labeled neurons such that terminals appeared within and throughout the patches of cells but also often extended slightly beyond cell patches to surround patches of cells in a diffuse halo (data not shown).

LGN connectivity patterns

Retrograde transport of label to the dorsal lateral geniculate nucleus (LGN) provided further information about the retinotopic placement of injections in area 18, as well as some information about the amount of convergent input to area 18 from the LGN. The pattern of LGN label after injection of six different anatomical tracers in area 18 (case 93-99, Fig. 2) reflected the well-documented retinotopic organization of the LGN (e.g., Sanderson 1971, Kaas et al. 1972). Thus the most anterior FR injection in area 18 labeled cells in the most anterior aspects of the LGN but were no longer present at more posterior levels, and progressively more caudal injections labeled cells in progressively posterior locations in the LGN. The mediolateral patterns of labeled neurons in the LGN reflected differences in the placement of injections across the width of area 18.

DISCUSSION

Although this is the first published report of using as many as six distinguishable tracers in individual animals to reveal surface-view topography in manually flattened cat visual cortex, the general approach of using one or more anatomical tracers to reveal patterns of corticocortical connectivity in coronal, manually-flattened, or computationally-flattened sections of cat visual cortex has been in widespread use for some time (e.g., Kawamura and Naito 1980, Montero 1981, Symonds and Rosenquist 1984, Henry et al. 1991, Salin et al. 1992, Sherk and Mulligan 1993, Price et al. 1994). The anatomical results from the current and previous studies are in close agreement. The present results indicate that area 18 in cats has patchy, topological connections with three other visual areas: area 17, area 19, and

a large band of cortex along the suprasylvian sulcus (Fig. 3). Anterograde transport following limited WGA-HRP injections suggest these connections are reciprocal. The zone of suprasylvian projections to area 18 is limited to the medial bank of the suprasylvian gyrus rostrally (for projections to parts of area 18 representing paracentral lower fields, -15° and beyond), but includes both banks more caudally. Because of the caudolateral limits of our upper field injections, the full extent of the connection zone in lateral posterior suprasylvian cortex is uncertain. However, the two injection sites in area 18 representing upper vision do not appear to label as many neurons in the suprasylvian cortex, suggesting a reduced representation of the upper visual quadrant. Injections in the part of area 18 representing central vision label the largest regions of suprasylvian cortex.

Our finding that connections of area 18 with areas 17 and 19 are patchy and reciprocal has been described many times previously. For example, injections of DY or FB into area 17 reveal patchy inputs from both areas 18 and 19 (Bullier et al. 1984, Salin et al. 1989). Single WGA-HRP injections in area 18, resulting in both anterograde and retrograde transport, reveal reciprocal, patchy connections with areas 17 and 19 (Symonds and Rosenquist 1984). Similarly, studies wherein combinations of the retrograde tracers FB, RB, DY or WGA-HRP were applied in area 18 have demonstrated patchy convergence of inputs to this area from areas 17 and 19 (Bullier et al. 1984, Ferrer et al. 1988, Henry et al. 1991, Salin et al. 1992, Price et al. 1994). Thus, our finding of patchy, reciprocal connections of area 18 with areas 17 and 19 is consistent with the results of many previous studies.

The relatively fewer previous descriptions of the connections of area 18 with the visually responsive cortex along the suprasylvian sulcus have demonstrated reciprocal and patchy connectivity patterns, as in the present report. Patterns of anterogradely-labeled terminals following injections of tritiated amino acids, or of terminals and cells following HRP injections, into discrete points throughout the rostrocaudal extent of area 18 revealed patchy, re-

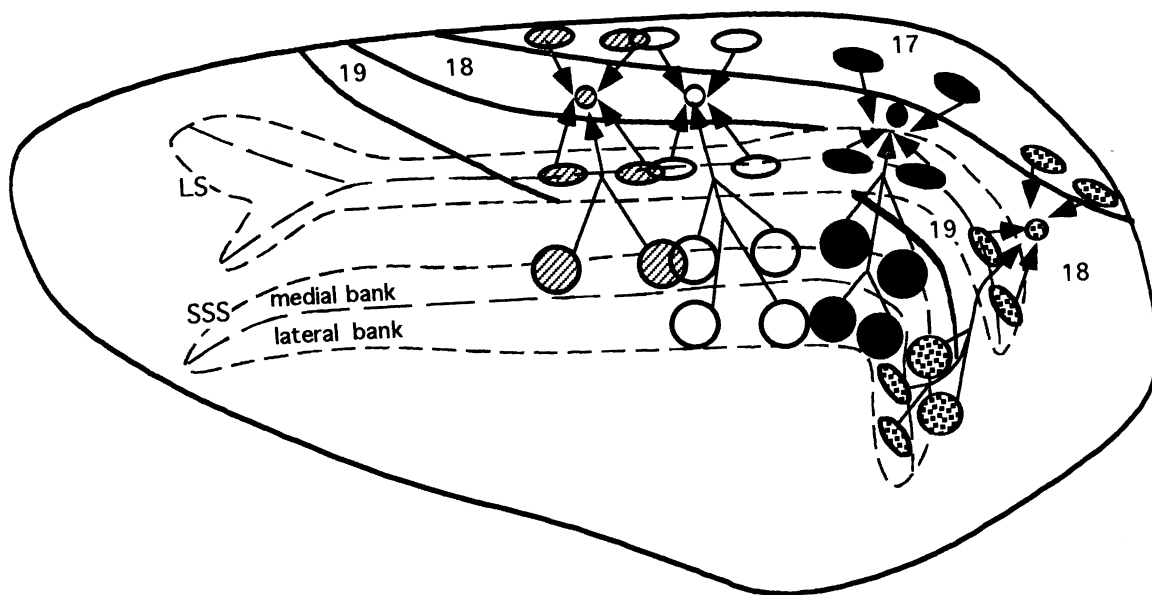


Fig. 3. A dorsolateral schematic representation of visual cortex organization in cats, based on the topology of area 18 connections in the present report. Area 17, 18 and 19 borders are depicted with solid lines. Small-dashed lines define the contours of the medial and lateral banks of the suprasylvian sulcus (SSS) and a large-dashed line indicates the fundus; the lateral sulcus (LS) is similarly depicted. This summary diagram illustrates several findings: (1) connections of area 18 with area 17, area 19, and the suprasylvian region are patchy and topological; (2) rostral area 18 has connections with medial, but not lateral, suprasylvian cortex and more caudal area 18 receives inputs from both suprasylvian banks; and (3) nearby regions of area 18 receive input from overlapping populations of neurons. Other conventions as in Fig. 1.

ciprocal connections with widespread regions of suprasylvian cortex (Montero 1981, Symonds and Rosenquist 1984, Sherk 1986a). FB or DY injections into area 18 have also revealed similar patches of labeled neurons within suprasylvian cortex (Bullier et al. 1984). The patchy nature of the clusters of labeled neurons and terminals in both the present and other reports reflects convergence of inputs and divergence of outputs, as discussed elsewhere (Salin et al. 1989, Henry et al. 1991).

The topography of area 17 and 19 inputs to area 18 revealed in the present experiments using multiple tracers (see Fig. 3) are consistent with findings following single injections in area 18. By placing these injections in electrophysiologically identified locations in area 18 and then subsequently mapping parts of areas 17 and 19 as well, divergent and convergent connections among areas 17, 18, and 19 have been shown to link visuotopically-matched regions (e.g., Montero 1981, Sherk 1986a, Salin et al. 1992, Price et al. 1994).

Our data demonstrate that, as with area 17 and 19 inputs, the inputs from the suprasylvian region to area 18 also form a single topological pattern that is in parallel with those in areas 17, 18 and 19. Other anatomical studies provide additional support of an interpretation for a unified, topographical cortical area along the suprasylvian cortex. Montero (1981) noted that single injections of tritiated amino acids into area 17 resulted in the anterograde labeling of terminals in areas 18, 19 and suprasylvian cortex which, although divergent, were topographically matched to the placement of the injection. Thus, rostral area 17 was shown to have connections with the most rostral portions of the suprasylvian sulcus, area 17 near the area centralis representation had connections across the genu of the suprasylvian sulcus, and caudal-most area 17 inputs were connected with caudolateral portions of the suprasylvian cortex. In one cat, Montero (1981) injected two different, distinguishable tracers into two separate loci in area 17 and showed that the patterns of labeled ter-

minals in areas 18, 19, and suprasylvian cortex maintained the topological relationship reflected by injection positions. Following HRP injections into suprasylvian cortex (Kawamura and Naito 1980), the locations of patches of retrogradely-labeled cells in areas 17, 18 and 19 varied in rostrocaudal location in parallel to the placement of individual suprasylvian injections. In other studies where two or more retrograde tracers were used in single cases, patches of labeled cells in suprasylvian cortex were aligned to the placement of the respective injection sites area 18 (e.g., Montero 1981, Ferrer et al. 1988, Salin et al. 1992).

The topography of projections of area 17 or area 18 to suprasylvian cortex described in the present and other reports have also been shown to be visuotopically-matched using electrophysiological mapping of both injection sites and regions of anatomical projections (e.g., Sherk 1986a, Bullier 1988, Sherk and Ombrellaro 1988, Grant and Shipp 1991, Shipp and Grant 1991, Sherk and Mulligan 1993). In these studies, lower visual space representations and connections are found in rostral regions of areas 17, 18, and suprasylvian cortex. Connections and representations of the area 17 or 18 area centralis regions cross the genu of the suprasylvian sulcus, and upper visual space representations and connections reside in posterolateral locations of suprasylvian cortex and areas 17 and 18.

Our interpretation of these results is that a portion of cortex along the suprasylvian sulcus that includes most or all of the medial bank, the caudal pole of the lateral suprasylvian sulcus, and parts of both banks along the posterior suprasylvian sulcus contains a single, global representation of the visual hemifield and thus constitutes a single visual area. The visually responsive region along the suprasylvian cortex (see lower Fig. 3) has traditionally, albeit tentatively, been portrayed as containing as many as 13 separate visual areas (summarized in Tusa et al. 1981, reviewed in Rosenquist 1985, Spear 1991). The present results may be more compatible with a scheme in which some of these suprasylvian cortical areas are modules of a single visual

area (see Kaas 1990), in agreement with recent proposals of Sherk (1986ab, 1990) and Shipp and Grant (Shipp and Grant 1991, Grant and Shipp 1991), as well as earlier proposals (e.g., Hubel and Wiesel 1969, Heath and Jones 1971).

A global representation of visual space in suprasylvian cortex has been reported using electrophysiological mapping techniques alone. The most exhaustive electrophysiological mappings published for this cortical region were performed by Palmer et al. (1978) and Tusa and Palmer (1980). The areas along the banks of the suprasylvian sulcus were tentatively identified in pairs, based on mirror-symmetric representations of portions of visual space (Palmer et al. 1978). Receptive fields were large with a good deal of scatter, and multiple representations of single points in space were observed throughout these areas. The anterior-most areas comprised all of the medial bank (AMLS) and the deep portion of the lateral bank (ALLS) of the middle suprasylvian sulcus. AMLS and ALLS together represented up to 60° of azimuth and horizontal visual space from $+20^\circ$ to -50° elevation. PMLS and PLLS represented slightly higher elevations (to -35°) and, as maps progressed posteriorly came to represent only the horizontal meridian, with receptive field sizes decreasing. DLS and VLS represented the area centralis and points within 10° of the horizontal meridian. Two characteristics of these latter two areas were, first, that the representation of horizontal space was not systematic and, second, multiple representations of single points in visual space were scattered throughout DLS and VLS. Tusa and Palmer (1980) later showed that areas 21a, 21b, 20a, and 20b represented upper visual space only, with eccentricities up to 90° in area 21b. If the finding of mirror-reversals of receptive field progressions in the suprasylvian fundus is overlooked, the visuotopic organization along the middle and posterior suprasylvian sulci is one in which the lowest portions of visual space are represented most rostrally, central visual space is represented at the genu of the suprasylvian sulcus, and upper visual space is represented posterolaterally. Many reports on the visuotopic organization

of more restricted regions of suprasylvian cortex largely support the global visuotopy of the maps of Palmer et al. (1978) and Tusa and Palmer (1980) (e.g., Hubel and Wiesel 1969, Spear and Baumann 1975, Updyke 1986, Zumbroich et al. 1986, Shipp and Grant 1991, Sherk and Mulligan 1993).

Thus, the present anatomical connectivity report and the reports of others using a wide range of approaches suggest that, in addition to the representations of visual space in areas 17, 18, and 19, an expanse of cortex along the suprasylvian sulcus may house a single representation of visual space. The results are also consistent with the concept of two parallel representations of the visual hemifield. The additional finding of the present report that not all cortex along the suprasylvian sulcus may comprise the projection zone region to area 18 has long had experimental support. The visually responsive cortex along the suprasylvian sulcus, first identified by Marshall and colleagues (1943) based on evoke-potentials, was later reduced to a portion of cortex along the medial suprasylvian bank that extended to the caudal pole of the medial and lateral banks of the sulcus and included a few millimeters of the posterior suprasylvian sulcus based on striate cortex stimulation (Clare and Bishop 1954) and architectonic patterns (Otsuka and Hassler 1962, Sanides and Hoffmann 1969). Degeneration studies showed this region (often called Clare-Bishop or Lateral Suprasylvian "LS") to have strong connections with the LGN and striate cortex (Garey and Powell 1967, Glickstein et al. 1967, Hubel and Wiesel 1967, Kaas et al. 1968, Wilson 1968, Heath and Jones 1971, Spear and Baumann 1979) and the earliest electrophysiological recordings of this region demonstrated a clear, crude topographic representation of part of contralateral visual space (Hubel and Wiesel 1969). This portion of the suprasylvian region appears to closely correspond to the area 18 projection zone of the present report.

That this expanse of suprasylvian cortex has different patterns of cortical and subcortical connectivities from the remainder of the suprasylvian sulcus was first suggested by early degeneration studies (Wilson and Cragg 1967, Graybiel 1970, Heath and

Jones 1971). Area 17 projections were to the medial suprasylvian bank, the caudal pole of the lateral bank, and an expanse of cortex along the posterior suprasylvian bank, but did not include other portions of the lateral bank (Heath and Jones 1971). More recent studies, using neuroanatomical tracers alone or in combination with electrophysiological mappings, have supported and extended the distinction between medial and lateral suprasylvian cortical banks. The region originally defined by Heath and Jones as LS (1971) has strong connections with primary retinorecipient areas such as areas 17, 18, 19, LGN C layers, MIN, the geniculate wing (GW), and the lateral region of the lateral pulvinar (LPI) (Rosenquist et al. 1974, Symonds et al. 1981, Symonds and Rosenquist 1984, Sherk 1986a, Grant and Shipp 1991, Miceli et al. 1991). In contrast, the remaining lateral bank cortex has strong connections with area 19, but far weaker connections with areas 17 and 18, LGN, MIN or GW. The lateral suprasylvian bank, unlike the medial bank, has connections with many cortical "association" areas (Symonds et al. 1981, Symonds and Rosenquist 1984, Bowman and Olson 1988b, Grant and Shipp 1991). The main source of thalamic input is from LP nuclei (Maciewicz 1974, Graybiel and Berson 1981, Symonds et al. 1981, Symonds and Rosenquist 1984, Bullier 1986, Dreher 1986, Sherk 1986b, Bowman and Olson 1988ab, Grant and Shipp 1991). Superior colliculus (SC) connections of the two banks of the suprasylvian sulcus also differ, with neurons from superficial SC layers sending axons to the medial "LS" bank and neurons from deeper SC layers terminating in the lateral bank (Grant and Shipp 1991). Additionally, both suprasylvian regions have very strong within-bank connections and only sparse connections with each other (in particular see Symonds et al. 1981, Symonds and Rosenquist 1984, Grant and Shipp 1991). Taken together, most connectivity reports support a general separation of the medial suprasylvian bank (including the caudal pole of the lateral bank and at least some cortex along the posterior suprasylvian sulcus) and the lateral bank. Additionally, within this medial bank-caudal pole-posterior suprasyl-

vian expanse, receptive field properties for neurons are reported to be similar (e.g., Camarda and Rizzolatti 1976, Guedes et al. 1983, Sawa et al. 1992, reviewed in Spear 1991). The present results do not clearly indicate such a separation, but they do not rule out the possibility of separate, parallel representations.

A wide range of findings suggest that cortex along the suprasylvian sulcus consists of fewer cortical areas than traditionally ascribed to it, and that the area 18 connection region identified in the present report may comprise a single visual area. However, there are findings that suggest a more complicated organization to the suprasylvian cortex. For example, virtually every proposed LS area (based on Palmer et al. 1978) appears to have corticocortical connections with areas 20a, 20b, or both (Symonds and Rosenquist 1984). Additionally, the 20a-20b region is reported to receive converging input from throughout the entire mediolateral extent of the pulvinar-LP complex (Symonds et al. 1981). Such unique connectivity patterns may mark the 20a-20b complex as a cortical area separate from the medial or lateral bank regions.

Of all the visual areas along the suprasylvian cortex, area 21a appears to have the most distinct receptive field characteristics (see Spear 1991). As with other suprasylvian neuronal populations, cells in area 21a are orientation selective but, in contrast to other areas, these neurons have relatively small receptive fields and all (*versus* the 70-80 % reported for other suprasylvian regions) are binocular (Wimborne and Henry 1992). Also distinguishing this population of neurons from others, area 21a cells respond to very slow, *versus* fast, movement (Michalski et al. 1993, 1994) and have very few neurons that are active in oculomotor responses (Vanni-Mercer and Magnin 1982). Thus, using receptive field characteristics alone, area 21a seems most likely to represent a single, separate visual area. This conclusion would not be reached, however, based upon its limited representation of only upper visual space and its topographic connections with areas 17, 18 and 19.

To summarize, there are ample reasons to distinguish most of the lateral bank of the suprasylvian

sulcus from a strip of cortex along the medial bank that includes the caudal pole of the lateral bank and extends at least several millimeters lateral along the posterior bank (i.e., the suprasylvian-area 18 projection zone of the present report). Most anatomical and electrophysiological mapping data support the inclusion of at least the posterior portions of AMLS as well as area 21a of Palmer et al. (1978) in this medial band, as does the topographic pattern of connections of this complete medial band with area 18. Area 21a is the one region in the suprasylvian visual cortex that prefers slow movement to fast and appears to have little significant oculomotor function. However, the majority of anatomical reports, including the present one, reveal connectivity patterns and/or receptive field representations consistent with its inclusion as a module of the medial suprasylvian bank region.

Ideally, visual space representations, receptive field properties, cortical and subcortical patterns of connectivity, and architectonic patterns all converge to reflect the same divisions of cortical areas. In reality, despite a large body of research, there is widespread agreement on the validity of only areas 17, 18 and 19, but the functional organization of cat visual cortex beyond area 19 has remained unresolved (for review see Spear 1991). Data are often limited or ambiguous for this expanse of cortex without simple retinotopic maps and locating or isolating cortical fields in the banks of the lateral suprasylvian sulcus can be technically difficult. Finally, continued differing views on the number and nature of visual areas in cat cortex raises the issue of what constitutes a visual area. If cortical areas are functionally homogeneous, a simple, point-to-point pattern of connections to and from that area would be expected. In contrast to this expectation, most connection patterns of extrastriate regions occur in patches, and separate patches could be interpreted as connections of separate visual areas (see Kaas et al. 1989, Malach 1989). However, even a single, small injection of anatomical tracer into area 17 results in several, separate patches of label in nearby locations in area 18 (e.g., Montero 1981, Sherk and Umbrellaro 1988, Salin et al. 1989), a region that re-

searchers generally agree is a distinct cortical area. Thus, the patchiness of connections between visual areas may indicate that much or all of cat visual cortex is comprised of areas organized into distinct modules.

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