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**ANATOMICAL BASES FOR AUDITORY PROJECTIONS TO SUPRASYLVIAN
VISUAL AREAS IN THE CAT CEREBRAL CORTEX**

A thesis submitted in partial fulfillment of the requirements for the degree of Master of
Science at Virginia Commonwealth University.

by

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List of Abbreviations

| | |
|--------------------|---|
| LSS | Lateral suprasylvian sulcus |
| PLLS | Posterolateral lateral suprasylvian area |
| PMLS | Posteromedial lateral suprasylvian area |
| ALLS | Anterolateral lateral suprasylvian area |
| AMLS | Anteromedial lateral suprasylvian area |
| BDA | Biotinylated dextran amine |
| AI | Primary auditory cortex |
| AII | Secondary auditory cortex |
| PAF | Posterior auditory field |
| AAF | Anterior auditory field |
| T, TEM | Temporal |
| IN | Insular |
| DZ | Dorsal zone (of AI) |
| PE | Posterior ectosylvian gyrus |
| AgNO ₃ | Silver nitrate |
| HAuCl ₄ | Hydrogen tetrachloroaurate |
| AES | Anterior ectosylvian sulcus |
| FAES | Auditory field of anterior ectosylvian sulcus |
| AEV | Visual field of anterior ectosylvian sulcus |

| | |
|------|------------------------------------|
| VAF | Ventral auditory field |
| EPSP | Excitatory post synaptic potential |
| MZ | Multisensory zone |
| SIV | Somatosensory area IV |

Abstract

ANATOMICAL BASES FOR AUDITORY PROJECTIONS TO SUPRASYLVIAN VISUAL AREAS IN THE CAT CEREBRAL CORTEX

by

Giriraj K. Sharma

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University.

Virginia Commonwealth University, 2006

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How the neural representations of different sensory modalities transition from one to another is an unexplored issue of cortical organization. The present experiments addressed this problem by examining auditory projections to the lateral suprasylvian visual area (LSS) of the cat using neuroanatomical tract tracing methods. Injections of tracer (Biotinylated Dextran Amine, BDA) were made into defined areas of the cat auditory cortex. Following transport and tissue processing, a light microscope with a digitizing stage was used to visualize and plot labeled auditory projections to the LSS. The results

showed that all auditory cortices tested demonstrated projections to a restricted portion of the LSS. While these projections were concentrated on the outer lip of the lateral bank of the LSS, some scattered auditory projections were found along the entire depth of the lateral bank. These data indicate that, at least in the LSS, projections from different sensory modalities do not form abrupt borders but exhibit areas of overlap. These overlapped projections may provide the anatomical basis for multisensory properties of neurons within transition areas between representations of different sensory modalities.

Introduction

One of the fundamental organizational features of the mammalian brain is the arrangement of sensory representations in the cerebral cortex. In every mammal, cortical representation of vision is centered on the occipital lobe, auditory in the temporal lobe, and somatosensory in the parietal lobe. These areas have been extensively studied in a wide variety of mammals, each having at least a primary thalamic-recipient area for each modality, designated as the primary sensory cortex. One question that arises, but has received little investigative attention, is what happens in the transition zones between representations of different sensory modalities? Most textbook depictions of the sensory representations show a large gap between locations of the primary sensory representations. However, these areas are not silent or inactive, but also vigorously process sensory information. In fact, as animals become more complex, the numbers of secondary or higher-level cortical areas increase. In man, for example, there are approximately 40 areas outside the primary visual cortex that also process visual information. Therefore, the sensory cortical organization of higher mammals is one where primary processing areas are generally surrounded by secondary or higher-level processing areas.

Cat auditory cortices and surrounding anatomy

The core-surround cortical arrangement is particularly evident in the representation of the auditory modality in cats, as depicted in Figure 1. The core auditory areas, termed primary auditory cortex (AI) and the anterior auditory field (AAF) are, for the most part, surrounded by other auditory representations. The secondary auditory region (AII) lies inferior to the core AI/AAF cortices, and higher-level auditory temporal (TEM) and insular (IN) reside inferior to AII. Posteriorly, multiple fields buffer the core auditory cortices from the visual areas residing in the occipital pole of the hemisphere. Superiorly, the dorsal zone of AI (DZ) and dorsal posterior ectosylvian area (dPE) are positioned between the core auditory areas (AI/AAF) and the visual representations in the banks of the lateral suprasylvian sulcus.

Lateral suprasylvian sulcus

The lateral suprasylvian sulcus contains representations of the visual modality, as documented in numerous investigations (Marshall et al., 1943; Clare and Bishop, 1954). These studies showed responsiveness to photic stimulation and electrical stimulation of the optic nerve and striate cortex, which established the presence of visually driven cells along the LSS. Further studies divided the LSS into 6 retinotopically organized regions: the posterolateral (PLLS) and posteromedial (PMLS) suprasylvian areas, anterolateral (ALLS) and anteromedial (AMLS) suprasylvian areas, and dorsal (DLS) and ventral (VLS) suprasylvian areas (Palmer et al, 1978). These regions are symmetrically organized along the LSS as three pairs, separated by the fundus.

For many years, the LSS was considered populated by modality-specific (visual) neurons. An early ‘optic flow’ model described visually-driven cells in this area with direction and orientation selectivity to light stimuli (Rauschecker et al., 1987; Sherk and Mulligan, 1993). However, recent studies have indicated that regions of the LSS accept sensory information from neighboring auditory regions. Electrophysiological experiments have indicated the presence of auditory and visual unimodal and auditory/visual bimodal cells via activation by multisensory stimuli in the PLLS, PMLS, ALLS and AMLS (Yaka et al., 2002). While the definition of LSS cells has been expanded with this finding, the transition/multisensory zones (MZ) between auditory and visual regions have not been defined.

Implications and further investigation

These observations indicate, for the cortex of higher mammals, that core sensory areas are surrounded by belts of higher-level representations of the same modality, the organization and function of many have been extensively examined. However, little is known how the higher-level, or belt representation of one sensory modality transitions into that of another modality. Is there an abrupt border that marks a distinct and obvious edge between the two different representations? On the other hand, might there be a gradual transition between the two modalities such that there is a substantial area in which representations of both modalities overlap? In the latter case, inputs from different modalities that overlap within a given area can converge onto individual neurons, thereby inducing multisensory properties (Meredith, 2004). This alternative would be very

interesting because it would provide the anatomical foundation for the recently reported multisensory properties within this area (Yaka et al., 2002). Therefore, the present study was designed to demonstrate the anatomical projection of auditory connections into the lateral suprasylvian visual area, and to assess whether the transition from visual to auditory representations forms a sharp border or exhibits overlap.

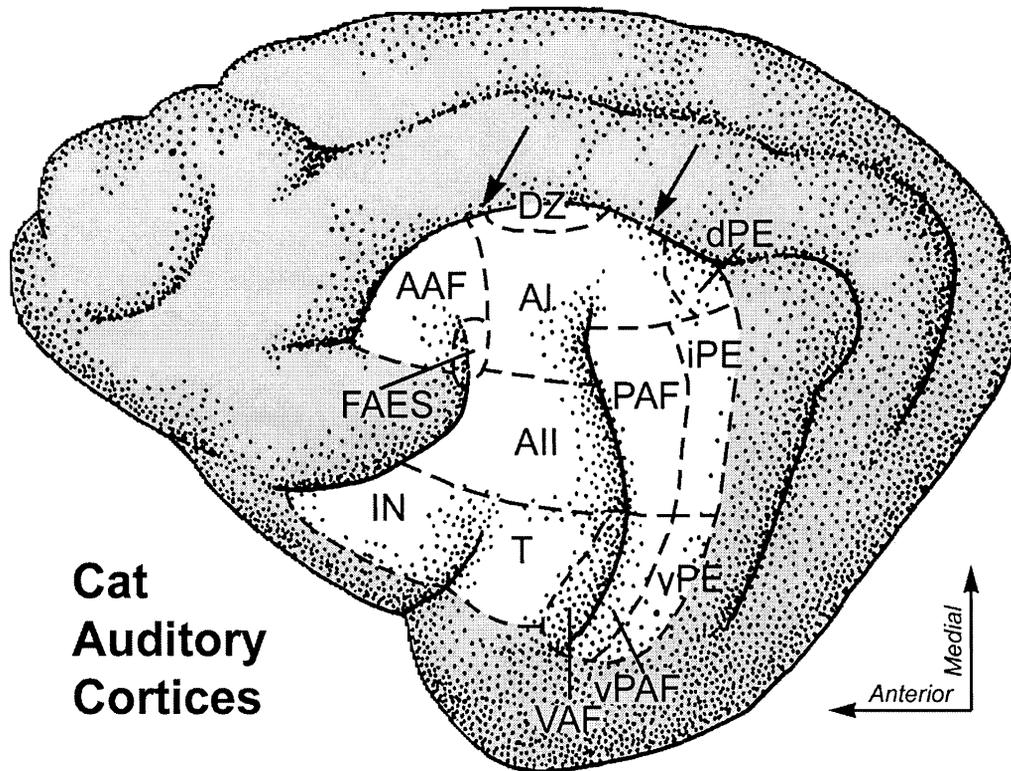


Figure 1. Lateral view of the left hemisphere of cat cerebral cortex.

Recognized regions of auditory cortex are outlined (dashed lines) and labeled; arrows point to suprasylvian sulcus where the lateral suprasylvian visual areas reside. Top is dorsal. DZ = dorsal zone of AI; AAF = anterior auditory field; fAES = anterior ectosylvian sulcus; AI = primary auditory cortex; AII = secondary auditory cortex; dPE = dorsal posterior ectosylvian gyrus; PAF = posterior auditory field; iPE = intermediate posterior ectosylvian gyrus; IN = insular region; T = temporal region; VAF = ventral auditory field; vPAF = ventral posterior auditory field; vPE = ventral posterior ectosylvian gyrus.

Materials and Methods

All procedures were performed in compliance with the Guide for Care and Use of Laboratory Animals (NIH publication 86-23) and approved by the Institutional Animal Care and Use Committee at Virginia Commonwealth University. This investigation used archived materials from previously conducted procedures performed in the following manner.

Surgery and tracer injections

Cats (n = 17) were anesthetized with sodium pentobarbital (45 mg/kg) and their heads were immobilized in a stereotaxic frame. A craniotomy and durectomy were performed under aseptic surgical conditions to expose the auditory cortices. A 5 μ l Hamilton syringe containing the neuroanatomical tracer biotinylated dextran amine (BDA; 10,000 mol.wt; lysine fixable; 10% in 0.1M phosphate buffer) was supported by a modified electrode carrier and positioned by cortical landmarks. Once the desired cortical site was selected, the syringe needle (31 gauge) was inserted to a depth of 1.0-3.0 mm into the cortex. After a 5 minute delay to allow the tissue to equilibrate, the tracer was pressure injected at a rate of 15-20 nl/min. When the full volume (350-1200 nl) was injected, approximately 10 minutes elapsed before withdrawing the needle. For large cortical areas, such as AI and PAF, this process was repeated 2-5 times to label as wide an area as

possible without significantly encroaching on other areas or the subadjacent white matter. Once the tracer injections were complete, the cortex was covered with gelfoam and dental acrylic for protection, the scalp sutured closed and the animal was treated with standard post-operative protocol.

Histological processing

Following a 10-14 day survival period, the cats were euthanized by sodium pentobarbital overdose (120 mg/kg pentobarbital) and intracardial perfusion with heparinized saline, followed by fixative (4.0% formaldehyde, 0.1% glutaraldehyde). The cranium was exposed and the brain was stereotaxically blocked and cryoprotected (25% sucrose in 0.1 M phosphate buffer at 4°C). A freezing microtome was used to serially cut coronal sections at 50 µm thickness. Series were saved at 200-250 µm intervals, and processed for BDA visualization using the Veenman *et al.* protocol. Sections were intensified with silver nitrate (1.42% AgNO₃ at 56°C) and gold chloride (0.2% HAuCl₄ at 25°C). Reacted sections were mounted serially on chrome-alum treated slides, dehydrated, counterstained and coverslipped.

Data analysis

To assess the extent and locations of BDA-labeled regions, the tissue was viewed using low power light microscopy. Selected regions of labeled neuronal processes were visualized using a light microscope (Nikon Eclipse E600) and were plotted using a PC-driven digitizing stage piloted by NeuroLucida software (MicroBrightfield, Inc., Williston,

VT, USA). Each tissue section was traced showing its tissue outline, grey matter/white matter border, upon which the locations of labeled neurons and/or boutons and axon terminals were plotted. The injection site was defined as the region at the end of the injection needle track with the most dense region of labeled neuronal cell bodies, axon terminals and dendrites. BDA-labeled neurons appeared densely black along the soma, although some neurons presented a red-brown hue. BDA-labeled axon terminals appeared as distinct black swellings at the end of thin axon stalks, or as symmetrical varicosities along the length of the axon. A ticker feature on NeuroLucida kept count of the number of labeled axon terminals as they were manually marked. Plotted tissue sections from each case were digitally transferred to a graphics program and serially superimposed (Adobe Photoshop; Adobe Systems, Inc., San Jose, CA, USA) for final visualization and graphic display.

Results

To examine the neural connections of auditory cortices to the banks of the lateral suprasylvian sulcus of the cat, cases were selected in which tracer injections were made in the auditory cortical areas listed in Table 1. Most of the selected cases were characterized by large volume injections and/or involved multiple locations within the chosen area in order to facilitate detection of the projection. In most of these cases, the injection site spanned the full thickness of the cortex.

From the injection site, axonal transport carried the tracer to terminal endings, which were consistently found in the upper half of the lateral bank of the lateral suprasylvian sulcus. In fact, for every auditory cortical site injection and in nearly every case listed in Table 2, terminal label was found within this same lateral suprasylvian region. Representative examples of labeled axon terminals within the lateral suprasylvian cortex, taken through a light microscope, are shown in Figure 2. Note that both terminal endings, as well as endings in passage, were observed. In each case, the incidence of labeled terminals became progressively fewer with depth along the lateral bank of the suprasylvian sulcus, were rarely observed in the fundus, and were completely absent from the medial bank. In contrast, terminal labeling around the lip of the sulcus was consistently quite dense and continued out onto the gyrus (corresponding to one of 3 known auditory areas).

From the 17 cases of auditory cortical injections, 3 were selected for more detailed analysis: one case each from the anterior, middle, and posterior regions of auditory cortex. Accordingly, Figure 3 shows the results from injection of the AAF, Figure 4 shows the data from injection of the AI, and Figure 5 summarizes the effects of injection of the PAF. As noted qualitatively, above, these three different areas each accessed the same portion of the upper, lateral bank of the suprasylvian sulcus, while virtually avoiding the remainder of the region (lower lateral bank, fundus, and entire medial bank). In addition, projections from each of these regions were substantially denser and deeper in the anterior aspects of the lateral suprasylvian sulcal cortex than in its posterior part. In fact, near the point where the lateral suprasylvian sulcus bends to become the posterior suprasylvian sulcus, the auditory projection ceased completely.

A total of 17 sections through the suprasylvian sulcus were examined and the distribution of terminal labeling plotted. Even though the labeled auditory terminals in many of these sections extended from the upper lateral bank, across the lip of the sulcus onto the neighboring gyrus, only that portion of the projection within the banks of the sulcus were plotted and analyzed in these cases. A total of 241,550 labeled boutons were plotted on 17 sections from 3 animals. In each case, terminal labeling was found within the upper lateral bank of the suprasylvian sulcus. When the labeling in Figures 3-5 is compared, several patterns became apparent. Injection of the AAF produced a terminal labeling pattern that was the most sparse of all the regions tested and favored the superficial layers of the cortex in a 80:20 ratio (supra- vs. infragranular) throughout the

lateral bank of the suprasylvian sulcus (Figure 6A). In contrast, injection of AI yielded terminal labeling throughout the full thickness of the upper lateral bank with a strong supragranular laminar preference; 89:11 supra:infragranular ratio (Figure 6B). Similarly, the PAF injection produced dense terminal labeling in the upper lateral bank of the suprasylvian sulcus also with a supragranular laminar preference; 76:24 supra:infragranular ratio (Figure 6C). Figure 6 shows the distribution of labeling between supragranular and infragranular layers of the LSS for all 3 injection sites. As indicated, the number of auditory boutons decreased with anterior-posterior position along the sulcus. In each case, this reduction in auditory boutons was continuous and gradual.

Table 1 : Auditory Areas that project to LSS

| Case# | Injection site | Injection Volume | Label in LSS? |
|--------------|-----------------------|-------------------------|----------------------|
| BDA7 | FAESm | 550nl | Yes |
| BDA8 | FAESd | 550nl | Yes |
| BDA10 | FAESm | 700nl | Yes |
| BDA44 | FAESm | 700nl | No |
| BDA47 | FAESm | 750nl | No |
| BDA19 | AI | 8 x 200nl = 1600nl | Yes |
| BDA31 | AI | 8 x 1.15nl = 1200nl | Yes |
| BDA32 | AII | 8 x 1.1nl = 1100nl | Yes |
| BDA34 | PAF | 8 x 1.2nl = 1600nl | Yes |
| BDA36 | sAAF | 3 x 400 = 1100nl | Yes |
| BDA49 | sAAF | 1000nl | Yes |
| BDA50 | sAAF | 500nl | Yes |
| BDA58 | sAAF | 800nl | Yes |
| BDA59 | sAAF | 800nl | Yes |
| BDA33 | gAAF | 7 x 1.1nl = 1000nl | Yes |
| BDA54 | gAAF | 800nl | Yes |
| BDA55 | gAAF | 800nl | No |

LSS = lateral suprasylvial sulcus; BDA = biotinylated dextran amine; FAES = auditory field of anterior ectosylvian sulcus; AI = primary auditory cortex; AII = secondary auditory cortex; PAF = posterior auditory field; AAF = anterior auditory field.

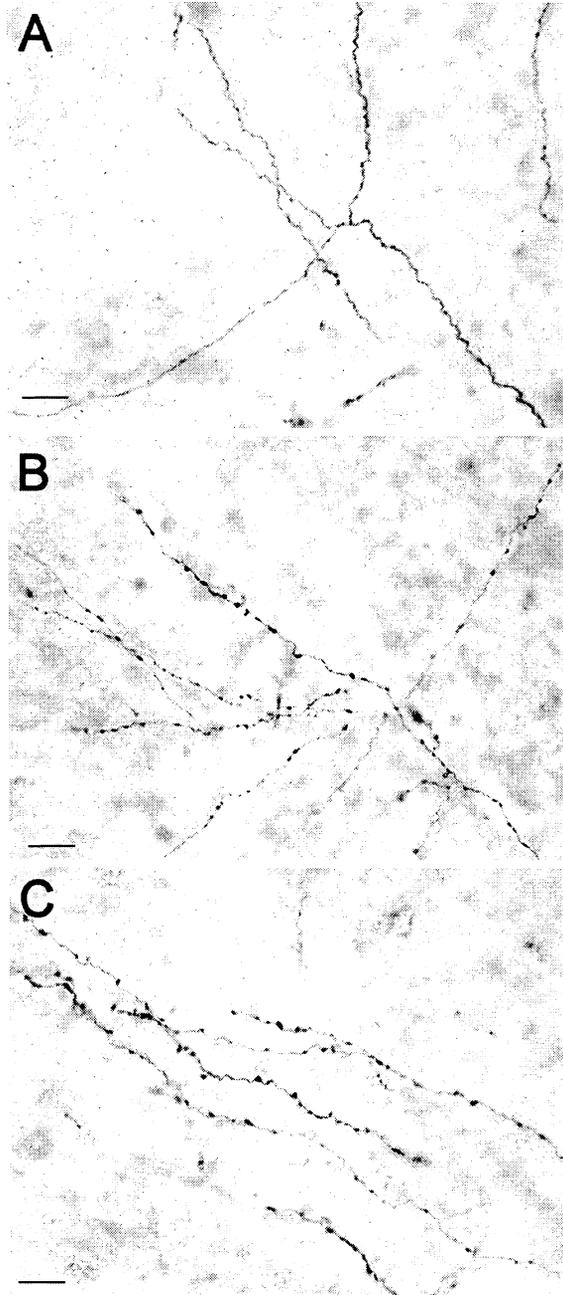


Figure 2. Micrographs of auditory projections to visual LSS

Injections of BDA into sAAF (A), AI (B) and PAF (C) result in labeled axons and terminals (arrows) in the banks of the lateral suprasylvian sulcus. Micrograph scale=100 μm (x100/oil).

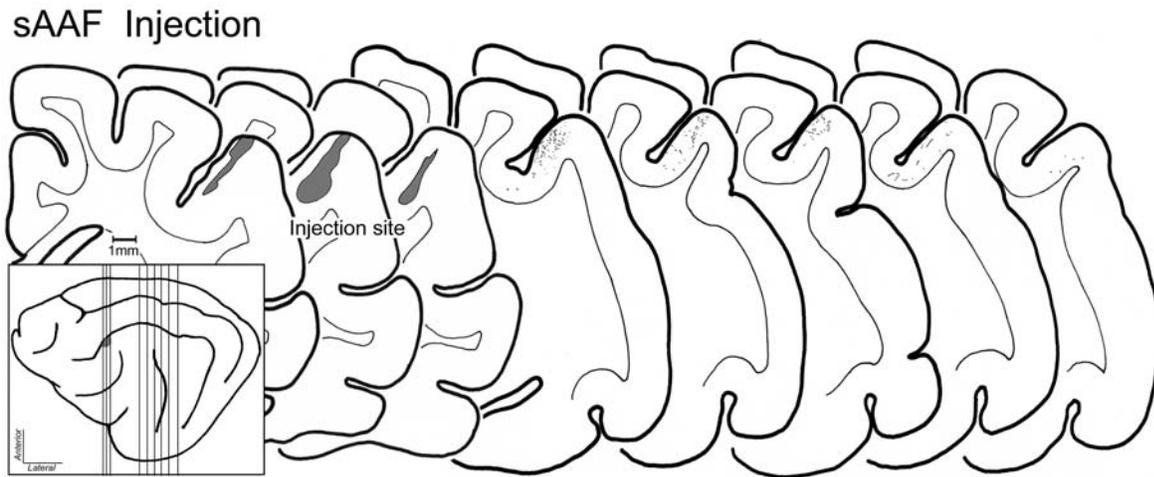


Figure 3. Orthograde projections from sAAF to LSS

Injections of tracer result in labeled axons and terminals in the lateral bank of the LSS. Coronal sections are arranged from the left, anterior to posterior. Grey regions indicate location and extent of injection; each black dot represents a single bouton or axon terminal. Inset on left indicates the cortical level from which each coronal section originates. Note: Labeling was very light, generally visible in the dorsal region of the lateral bank, with a diminution in number towards the fundus. Scale bar = 1mm.



Figure 4. Orthograde projections from AI to LSS

Injections of tracer result in labeled axons and terminals in the lateral bank of the LSS. Coronal sections are arranged from the left, anterior to posterior. Grey regions indicate location and extent of injection; each black dot represents a single bouton or axon terminal. Inset on left indicates the cortical level from which each coronal section originates. Note: Labeling was very dense at the lip of the sulcus and reduced substantially in number toward the fundus region. Scale bar = 1mm.

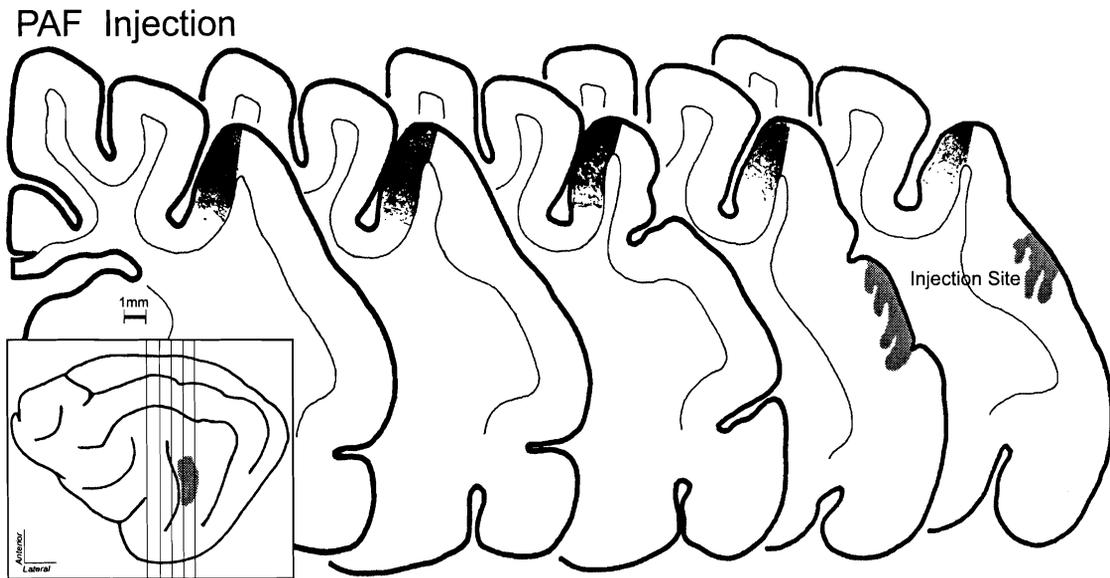


Figure 5. Orthograde projections from PAF to LSS

Injections of tracer result in labeled axons and terminals in the lateral bank of the LSS. Coronal sections are arranged from the left, anterior to posterior. Grey regions indicate extent and location of injection; each black dot represents a single bouton or axon terminal. Inset on left indicates the cortical level from which each coronal section originates. Note: Labeling was very dense at the lip of the sulcus which reduced dramatically toward fundus region. Scale bar = 1mm.

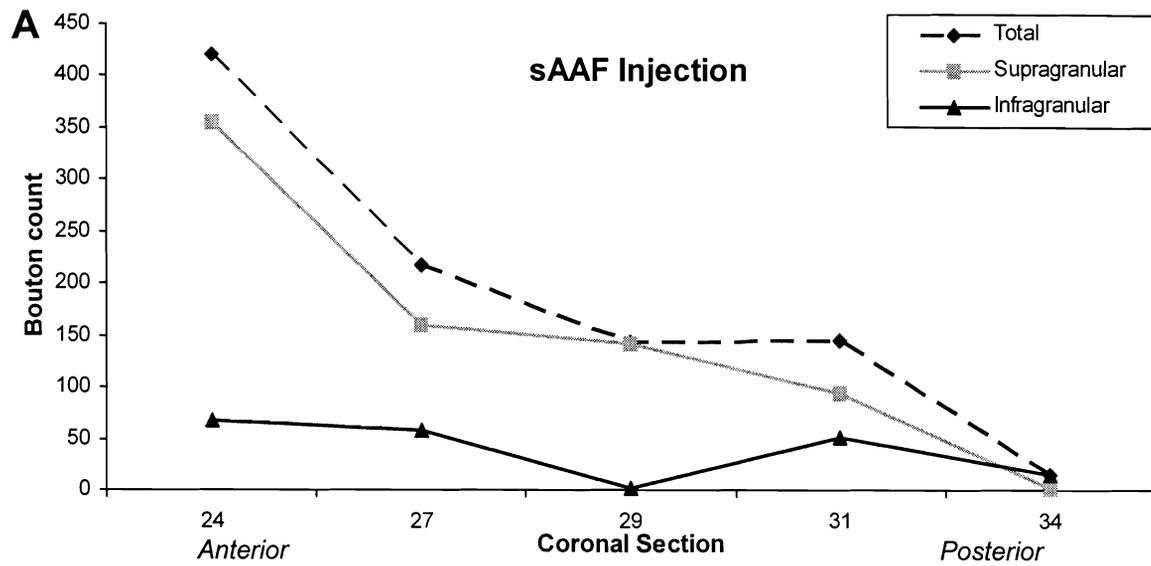


Figure 6A.

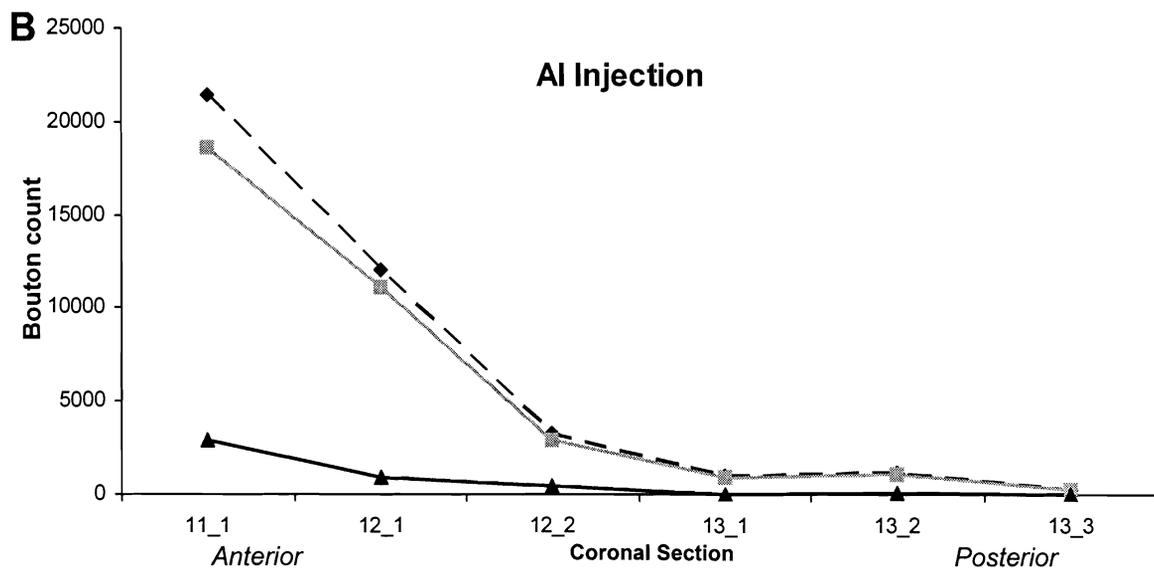


Figure 6B.

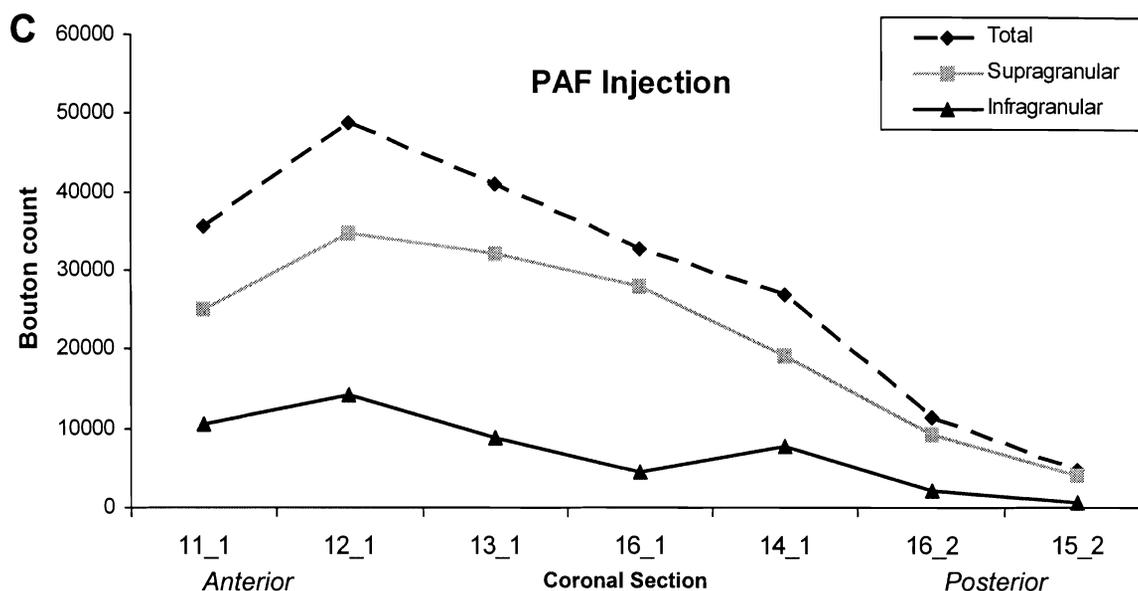


Figure 6C.

Figure 6. Laminar distribution of labeled boutons within the LSS.

The laminar distribution of labeled boutons within the LSS are shown following injections to auditory sAAF (A), AI (B) and PAF (C). The number of labeled boutons within the LSS is plotted in each graph (dashed lines), as well as the subset of boutons found in the supragranular (grey lines) or infragranular layers (black lines). In each case, the number of boutons was greatest in the most anterior sections (at left) and gradually reduced toward the more posterior sections (right). In addition, in each case, the number of boutons found in the supragranular layers far exceeded that found in infragranular locations. These observations suggest that auditory projections to the LSS represent a feedback-type projection.

Discussion

Although the LSS is widely regarded as a visual area of the cat cortex, these results show that auditory projections also target the upper portions of the lateral bank. Furthermore, these auditory projections are quite dense in their termination zone and they arise from multiple cortical loci that also represent the auditory modality. Ultimately, these findings indicate that not only does the auditory modality occupy the upper portion of the lateral bank of the LSS, but suggests that substantial portions of this region may be a site of multisensory (visual and auditory) convergence.

The present results show that only a specific portion of the banks of the lateral suprasylvian sulcus are targeted by auditory inputs. This auditory-recipient region is confined exclusively to the lateral bank, with the densest accumulation of auditory boutons located in the upper aspects of this bank toward the crest or lip of the sulcus. Furthermore, as indicated in Figure 6, the number of auditory boutons decreased with anterior-posterior position along the sulcus, with the most boutons found anterior in the region and the fewest posterior. In each case, this reduction in auditory boutons was continuous and gradual. These observations are consistent with the gradual, overwhelming presence of visual representations as the occipital pole of the cortex is approached.

The present results also show that the auditory portion of the LS receives inputs from multiple auditory cortical regions. Analysis of labeling from injections into 6 different auditory cortical regions (AI, AII, gAAF, sAAF, FAES, and PAF) indicate that each sent projections to the upper lateral bank of the LS. In addition, these qualitative judgments were supported by the data plotted from cases in which the sAAF, AI and PAF regions were injected. Although the density of labeling varied between these cases, each revealed approximately the same distribution of terminal labeling within the lateral bank of the LS.

For the three cases that were quantitatively analyzed by plotting the locations of labeled auditory boutons in the LS, the resulting laminar distribution was remarkably similar. Each area favored projections which terminated within the supragranular layers by a large ratio. When the proportion of boutons in supra- vs. infragranular layers was determined for each different projection, the supra:infragranular ratio was 80:20 for projections from sAAF, 89:11 for AI, and 76:24 for PAF. Projections which show preference for supragranular terminations are regarded as “feedback” projections, which usually indicates that information is being relayed from a higher hierarchical level to a lower one (Felleman and Van Essen, 1991). However, in this case the strongest preference for supragranular terminations was that which originated in the primary auditory area, AI, which is regarded as the lowest or entry level for auditory information in cortex. It does not seem likely that the proportion of boutons in this case was miscounted, since it consistently favored the supragranular layers by a large proportion. Even if it was, the alternative form of connection which might fit this pattern is one of a “lateral” projection, which does not

alleviate the hierarchical problem either. The function of feedback projections is to regulate lower-level activity through higher-level processing. In this way, only activity in response to certain types of stimuli at lower levels is permitted access to higher level processing.

The present experiments did not examine the distribution of visual inputs to the LS. This has been done in numerous other studies (Marshall et al., 1943; Clare and Bishop, 1954; Rauschecker et al., 1987; Sherk and Mulligan, 1993). These studies showed that visual responses, and even precise maps of visual space, are present along both the medial and lateral banks of the LS. Some studies document not only the presence of visual responses here, but also the presence of auditory activity along the upper aspects of the lateral bank of the LS (Palmer et al., 1978). A more recent study confirmed these observations as well as the presence of multisensory neurons, which are neurons that are responsive to both visual and to auditory stimuli when presented independently (Yaka et al., 2002). Therefore, it is quite likely that the points along the bank of the LS sulcus where visual and auditory inputs overlap represent the areas in which multisensory convergence occurs, thereby producing neurons that are responsive to both sensory modalities. In fact, recent experiments have shown that the area of the lateral bank of the LS in which auditory boutons are present also represents the site at which multisensory, auditory-visual neurons have been identified and recorded (Allman and Meredith, IMRF abstract, 2006).

Several studies have focused on evaluating the borders between modality-specific domains in cortex. The functional architecture and convergence patterns underlying multisensory processing were surveyed by Meredith (2002), and two basic forms were

described. An excitatory-excitatory convergence was identified as the convergence of two excitatory inputs, resulting in multisensory enhancement. In addition, an excitatory-inhibitory convergence resulting from the convergence of excitatory and inhibitory inputs from different modalities was also reported, resulting in modulation as inhibition and disinhibition (Meredith, 2002). A later study by Meredith (2004) went into further analysis of the distribution of these different types of multisensory neurons and specifically examined the transition between auditory FAES and visual AEV in the anterior ectosylvian sulcus of the cat. Of these forms, the excitatory-excitatory type was most often encountered at borders between representations of different sensory modalities, while excitatory-inhibitory convergence was characterized by occurring well inside the borders of otherwise unimodal sensory representations (Meredith, 2004). Wallace et al. (2004) performed a similar analysis via electrophysiological recordings of the transition zones between unimodal sensory cortical regions. The cerebral cortex of the rat was used to show that the borders between visual, auditory and somatosensory domains contain multisensory neurons which are responsive to sensory stimuli from both neighboring zones. These neurons were also capable of integrating their cross-modal sensory cues and produced enhanced or depressed responses when multisensory stimuli were presented (Wallace et al., 2004). Other studies on the rat auditory-somatosensory cortical region (parietotemporal cortex) confirm the presence of a multisensory zone (MZ) of transition between the different representations using electrophysiological recordings and retrograde labeling (Brett-Green et al., 2003). In this study, extracellular recordings indicated a parietotemporal MZ where responses to combined auditory/somatosensory inputs had a

shorter latency period and larger response magnitude. Intracellular recordings confirmed the presence of a MZ and multisensory cells therein exhibited excitatory postsynaptic potentials (EPSPs) to unisensory stimulation from different sensory modalities as well as to multisensory stimulation (Brett-Green et al., 2003). Given the multisensory properties observed, these physiological studies collectively are consistent with the presence of anatomical overlap of inputs in areas of transition between representations of different sensory modalities.

Conclusions

Combined with observations from other studies, the present results indicate that the lateral bank of the lateral suprasylvian sulcus is a region that receives converging inputs not only from visual cortical regions, but from multiple auditory cortical locations as well. Therefore, it is likely that the area presently described in this location as the PLLS visual area actually exhibits multisensory properties whereby auditory inputs influence neuronal responses to visual stimulation.

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