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Lack of projections from medial geniculate body to suprasylvian cortex in cat: a study with horseradish peroxidase

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Abstract. Because both electrophysiological and behavioral methods have implicated the suprasylvian cortex of cat in audition, its afferents were studied using retrograde transport of horseradish peroxidase. The bulk-filling method was used to maximize the likelihood that virtually all afferents to the area would be labeled. Despite the vivid retrograde labeling of many thalamic cells with this procedure, no direct auditory projections to the suprasylvian cortex could be found in the thalamus (i.e. in medial geniculate body or in the dorsolateral part of the posterior nucleus). Furthermore, very few cells were labeled in the primary auditory cortex of the nearby ectosylvian gyrus. The source of afferents to the suprasylvian cortex originate mostly from the pulvinar-lateral posterior complex and to a lesser extent from ventral lateral and ventral anterior nuclei of the thalamus.

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Key words: suprasylvian cortex, auditory thalamus, pulvinar, lateral posterior, medial geniculate

INTRODUCTION

Electrophysiological maps of auditory cortex in the cat often indicate a target of the ascending auditory system in the anterior suprasylvian cortex (e.g. Woolsey 1961, Toldi and Fehér 1984). Neuro-behavioural experiments also suggest suprasylvian cortex plays a role in auditory localization. For example, bilateral removal of the parietal suprasylvian cortex in dogs results in an impairment on a short-term memory task with auditory location stimuli (Stasiak et al. 1992).

The present study was undertaken to examine the anatomical basis of these electrophysiological and behavioral observations. Specifically, sites of origin of projections to the suprasylvian cortex were labeled using the widely inclusive retrograde labeling method of Hicks and D'Amato (1977). Special attention was paid to the possible labeling of known auditory forebrain structures including auditory thalamic nuclei and the juxtaposed auditory cortex located just ventral to the suprasylvian cortex.

METHODS

Although conventional horseradish peroxidase (HRP) method was used here, we were aware of a previous study of cortical area 5 which did not demonstrate afferents originating from unarguably auditory tissue (Avendao et al. 1988). The possibility exists that auditory afferents to suprasylvian cortex were not demonstrated because the injections were too small, specific and confined to result in obvious labeling of auditory tissue. This failure would be exacerbated if the auditory projections were sparse or terminated in widely scattered areas (i.e. "sustaining" projections via axon collaterals; Rose and Woolsey 1949).

To eliminate this possibility, we adopted Hicks and D'Amatos (1977) bulk-filling method to maximize retrograde labeling. This method relies on the maximal retrograde transport of HRP if it is applied directly to freshly cut axons. This method, in fact, makes use of a what is otherwise a known drawback to the HRP method, that the retrograde transport of HRP is affected by damage to axons with resulting false positives (i.e. label in structures which may not project to the area in question). In this study, we welcomed the false positives (i.e. retrogradely labeled cells in nuclei which may not project to the suprasylvian cortex) since the goal is to find nuclei (i.e. the medial geniculate body) which do not have retrogradely cells. While the intensity of HRP labeling may be affected by various factors (i.e. survival time, concentration of HRP, etc.) we rely on the general acceptance of this method and the use of standardized procedures. The efficacy of this method has been shown in a study of other systems, in which this method has labeled literally tens of thousands of neurons over long distances, from spinal cord to cerebral cortex (e.g. Nudo and Masterton 1988).

For the present application, the cortex of the suprasylvian gyrus was first ablated by means of a surgical aspirator. Unadulterated flakes of raw HRP were then placed directly on the freshly exposed white matter. The object of this technique of HRP application was to ensure that no axon which projected to the suprasylvian cortex would escape exposure to the HRP. The success of this bulk-filling was verified at histology by the vivid retrograde labeling of many of thalamic neurons.

Four adult female cats were used. After halothane premedication, the animals were anesthetized with pentothal and an aseptic surgical techique was used. The scalp was incised and retracted. A large unilateral opening on the right side was then made in the bone overlying the suprasylvian region. The dura was opened and the suprasylvian gyrus exposed. The cortex was then gently removed by aspiration. HRP was then applied to the surface of the white matter, either in dry form or in concentrated solution. After arresting slight bleeding with electrocautery, the wound was covered with gelfoam and the the muscles and scalp sutured. Following surgery the animals were treated with Amoxycillin.

After a 2-day survival, the cats were perfused with saline followed by 1% paraformaldehyde and 1.25% glutaraldehyde. The brains were then extracted, frozen and sectioned at 300 μm from caudal to rostral. Tetramethyl benzidine procedures were followed for visualizing the HRP-labeled cells (Mesulam 1978).

RESULTS

The sites of HRP application in the four cases are illustrated in Figs. 1-4. The application varied from a small rostral area (case 96-2 in Fig. 1) to an extensive lateral area (case 95-24 in Fig. 4). Some degree of undercutting of the surrounding, unablated, grey matter occurred in all of the cases. An example of the degree of undercutting and of HRP application is illustrated in Figs. 2 and 5 (case 95-58).

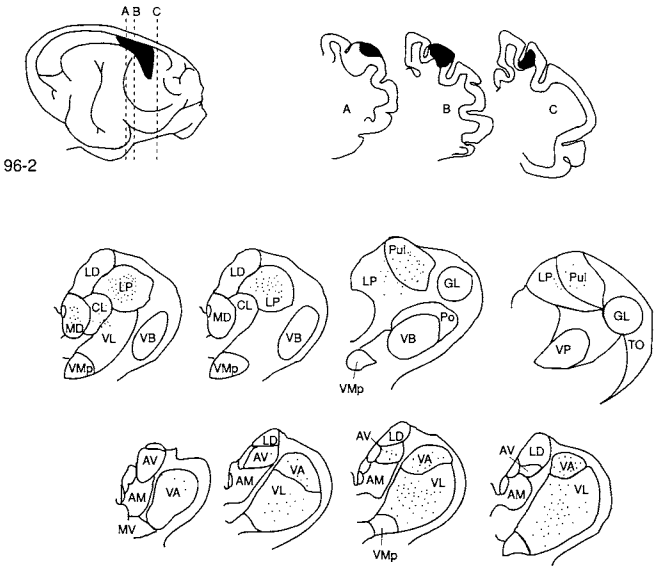

Fig. 1. Case 96-2. Schematic of the placement of HRP paint (gray area) and location of labeled thalamic cells in the smallest and most rostral paint of suprasylvian cortex. This case had the greatest percentage of labeled cells in VL (comprising 33.8% of its total of labeled thalamic nuclei). In this and following three figures the top left shows the extent of HRP paint in each case. The top right in this and following three figures shows three sections (A, B and C) from the levels indicated on the lateral view. Each black dot within the thalamus represents a single labeled neuron on a standardized view of the thalamus. None of the cases had labeled cells in the medial geniculate body (MG: see Table I). All cases had labeled cells in LP and Pul (ranging from 36.5%-93.8% of the total number of thalamic cells labeled). Abbreviations in this and following figures: AM, anteromedial nucleus; AV, anteroventral nucleus; CM, center median nucleus; CL, central lateral nucleus; GL, dorsal lateral geniculate body; LD, lateral dorsal nucleus; LP, lateral posterior nucleus or complex; MG, medial geniculate body, MGmc, magnocellular nucleus of MG, MGd, dorsal nucleus of MG; MGv, ventral nucleus of MG; MD, mediodorsal nucleus; OR, optic radiation; Po, posterior complex or nucleus; Pul, pulvinar nucleus; VP, ventral posterior nucleus; TO, optic tract; VA, ventral anterior nucleus; VGL, ventral lateral geniculate body; VMp, principal ventral medial nucleus; VL, ventral lateral complex.

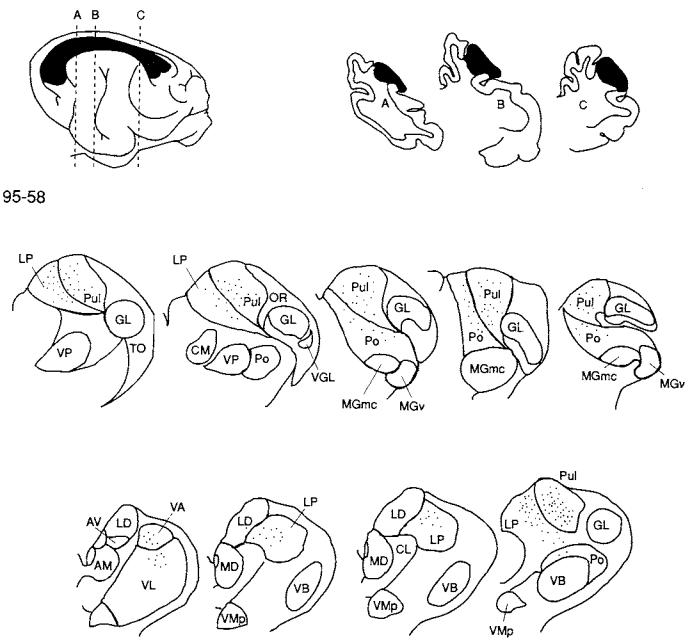

Fig. 2. This is the only case (95-58) in which labeled cells in Po (13.7%, see Table I) were found. In this case most retrogradely labeled thalamic cells were found in LP and Pul (63.6%, see Table I).

Retrogradely labeled cells in thalamus

The HRP procedure resulted in the opaque labeling of hundreds of thalamic cells in each case. However, the chief result, common to all four cases, is that not one labeled cell was found in the medial geniculate body (MG; Table I, Figs. 1-4 and 6). In only one case (95-58) were cells found in the posterior nucleus (Po; Table I, Fig. 2).

In each of the four cases, most of the retrogradely labeled cells in the thalamus were found in the pulvinar (Pul) or lateral posterior (LP) nucleus. Pul-LP complex had the greatest number and the highest percentage of labeled cells (an avereage of 71.0% of all labeled thalamic cells; Table I, Figs. 1-4 and 7).

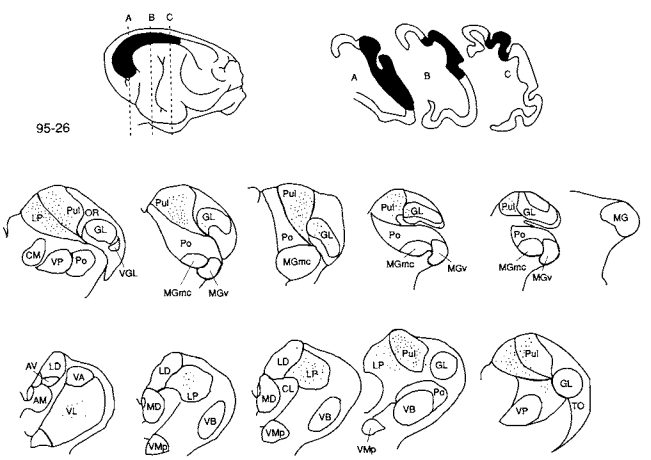

Fig. 3. This is the case (95-26) with the most undercutting, resulting in some labeled cells in GL (13.6%, see Table I). Again, most retrogradely labeled thalamic cells were found in LP and Pul (75.1%, see Table I).

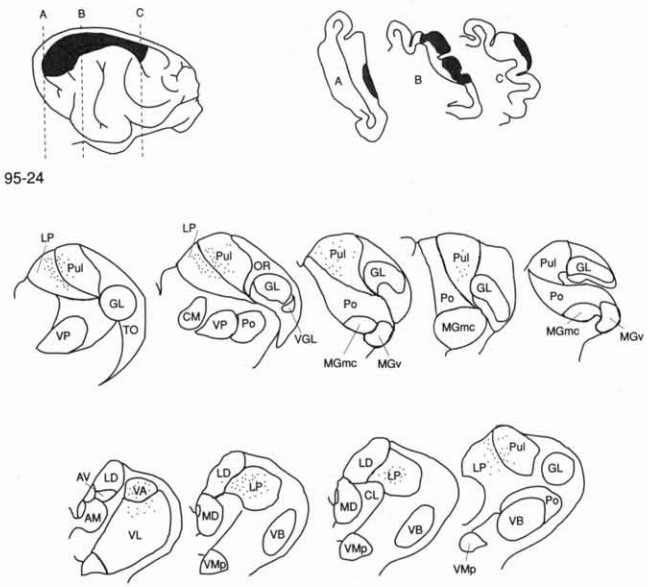

Fig. 4. Case with the largest paint (95-24). The paint extends ventrally into the sylvian gyrus but includes the little undercutting. Again, the greatest majority of retrogradely labeled thalamic cells were found in LP and Pul (91.3%, see Table I).

In 3 of the 4 cases a number of retrogradely labeled cells were also found in the ventral anterior (VA) nucleus. These labeled cells averaged about 2.6% of the total of labeled thalamic cells (Table I, Figs. 1,2,4 and 8). Most cells in VA were found in case 95-24 (6.1%; Table I, Fig. 4). The one case with no retrogradely labeled cells in VA (95-26; Fig. 3) was distinctive by its more caudal application of HRP and the lack of undercutting except at the most caudal levels.

All of the cases had labeled cells in VL (Figs. 1-4), with most in case 96-2 (36.5%, Fig. 1). The overall percentage of total labeled cells for VL was greater than that for VA (5.8% VL vs. 2.6% VA; see Table I). Also in case 96-2 (Fig. 1), labeled cells were found in reticular nucleus (6 cells (2.3%), not shown), anteroventral nucleus (AV; 18 cells (2.5%)) and medialis dorsalis (MD; 36 cells (13.7%)).

Fewer numbers of retrogradely labeled cells were found scattered among several other thalamic nuclei (combined together as "Other" in Table I). The locations of the few retrogradely labeled cells in case 95-26 (Fig. 3) included: lateral geniculate (GL) nucleus (122 cells (13.6%)), lateral dorsal (LD) nucleus (17 cells (1.9%)), central lateral (CL) nucleus (11 cells (1.2%)), area pretectalis (48 cells (5.3%)), and in cell clusters straddling the stria terminalis (19 cells (2.1%)).

Finally, in case 95-58 (Fig. 2) some labeled cells were found in the posterior (Po) nuclear group (55 cells (13.7%)) but not in the auditory region of Po near the medial geniculate (MG) body (cf. Imig and Morel 1985)

Retrogradely labeled cells in auditory cortex

Few clearly labeled neurons were found in the adjacent auditory cortex of the ectosylvian gyrus. Some of

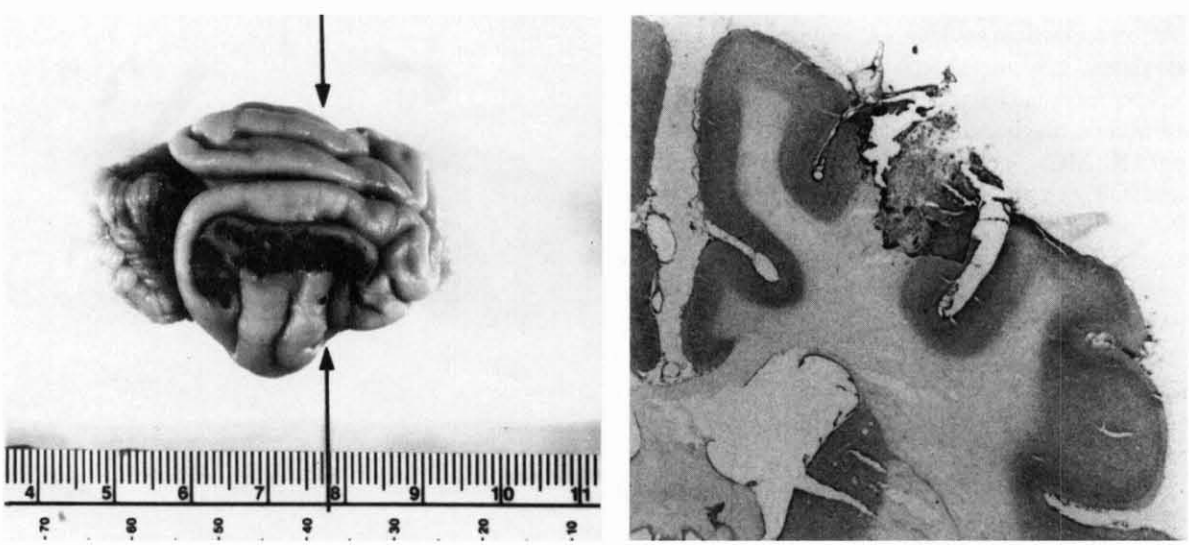

Fig. 5. The paint of HRP in case 95-58. Left is dorsolateral view of right hemisphere of the gross brain. Right is a section through the brain at the level indicated by arrows (coordinate was AP 15.0: approximately at level B in Fig. 2). The undercutting of white matter (illustrated in section on right) probably accounts for variation in the location of labeled cells found in this and other cases.

TABLE I

The number and percentage of labeled cells (number per nucleus/total labeled thalamic cells) in each of the four cases shown in Fig. 1-4. The two top rows are auditory thalamus (MG and PO). The lower rows are thalamic nuclei with a significant number of labeled neurons. The row labeled Other includes labeled cells found in scattered regions (e.g., medialis dorsalis, reticular nucleus, pretectalis); case 95-24 was the only case in which no undercutting occurred and also had no labeled cells in these regions. Thus, it is presumably undercutting which accounts for the labeled cells in the Other category. The bottom row is a total of all labeled cells found in the thalamus of each of the cats. The percentages do not come to exactly 100% due to rounding off of decimals. The second to last column is the total number of labeled cells found in each thalamic nucleus across all four cases. The last column is the percentage of label in each thalamic nucleus divided by the total of labeled cells in thalamic nuclei in all four cases

	96-2		95-58		95-26		95-24		Total 4 cats	
Structure	Number	%	Number	%	Number	%	Number	%	Number	%
Auditory thalamus										
MG	0	0	0	0	0	0	0	0	0	0
Po	0	0	55	13.7	0	0	0	0	55	2.8
Other thalamic nuclei										
Pul-LP	96	36.5	255	63.6	675	75.1	377	91.3	1403	71.0
VA	18	6.8	7	1.7	0	0	25	6.1	50	2.6
VL	89	33.8	8	2.0	7	0.8	11	2.7	115	5.8
GL	0	0	0	0	122	13.6	0	0	122	6.2
AV	18	6.8	0	0	0	0	0	0	18	0.9
Other	42	16.0	76	19.0	95	10.5	0	0	213	10.8
Thalamic total	263	99.9	401	100.0	899	100.0	413	100.1	1976	100.0

those that appeared to be labeled did not conform to the usual form of the cells in the juxtaposed cortical layer. Instead, the ectosylvian labeling appeared as only a few cells near to the cortical surface (see Figs. 9 and 10).

DISCUSSION

Drawback of the HRP technique

In the present study we have relied on the HRP technique since the presence or absence of label with its use has been a traditionally accepted method for illustrating major pathways in the central nervous system. While some anatomical methods may be more sensitive than HRP technique in visualing connections not previously identified (e.g. Winer and Larue 1987), the paints of HRP made in the present study are useful in illustrating the presence or absence of major projections. While, negative results from this or any technique can never be conclusive, they are useful as a comparison within a section of brain tissue. For example, in the present study, the lack of label in MG is in strong contrast to the heavy label in other thalamic areas. We conclude that the absence of labeled cells in MG reflects the absence of a major projection and not simply the inadequacies of the method.

Thalamocortical input to suprasylvian cortex

PULVINAR-LATERAL POSTERIOR (PUL-LP) COMPLEX

The present results show that thalamic input to suprasylvian cortex arises mostly, almost exlcusively, from the Pul-LP complex and not from the auditory thalamic nuclei. These results are consistent with the anatomical findings of others. The reciprocal connections between the Pul-LP complex and the suprasylvian (SS) cortex has been revealed by a plethora of anatomical data (e.g. Graybiel 1972, Robertson and Rinvik 1973, Robertson

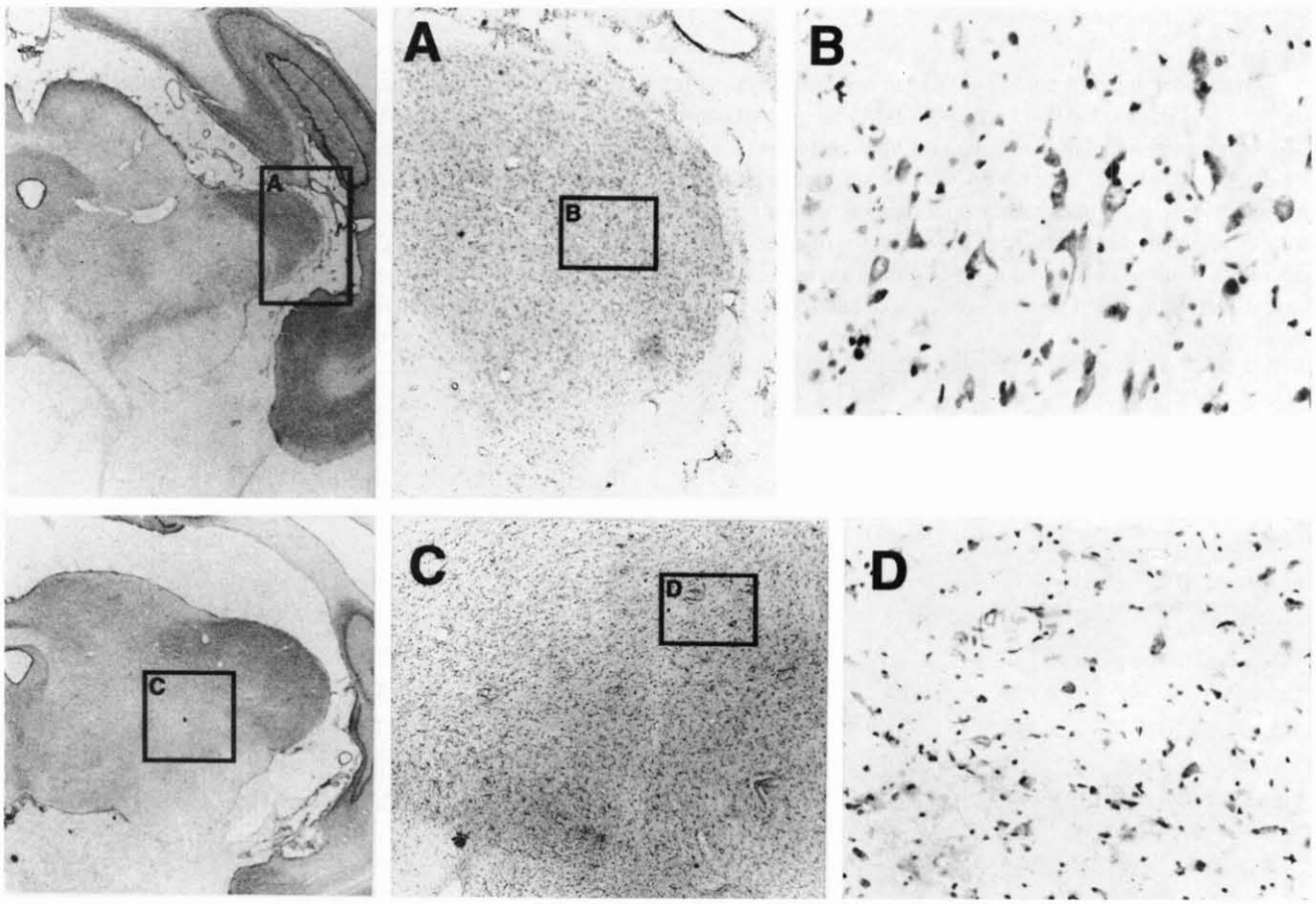

Fig. 6. Two auditory nuclei: medial geniculate body (MG: top) and posterior complex (Po: bottom). Left is low power photomicrograph indicating where higher magnification photographs were taken (Top row: A and then still higher magnification in B. Bottom row: C and then still higher magnification in D). This and all subsequent photomicrographs are from the case with the smallest paint of HRP (case 96-2). No labeled cells were found in MG in this or any other case. Labeled cells were found in Po in one (95-58) of the four cases (probably due to undercutting of fibers (see Fig. 2)).

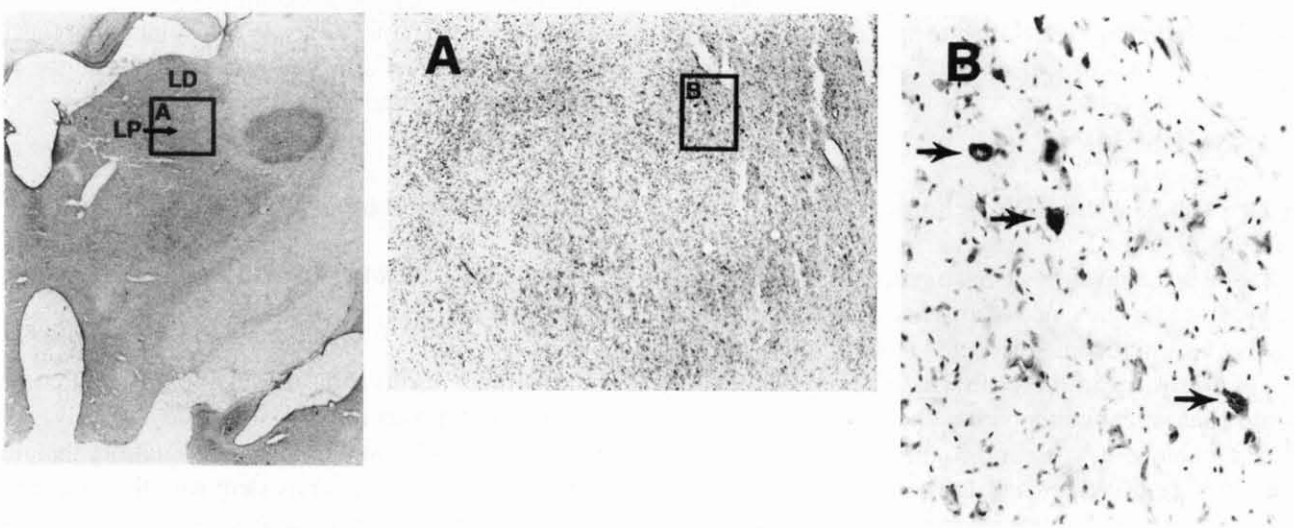

Fig. 7. Labeled cells were found in pulvinar-lateral posterior complex in all four cases ranging from 36.5% to 91.3% (from the case with the smallest paint (96-2) to that with the largest paint (95-24)). Left is low power photomicrograph indicating where higher magnification photographs were taken (A and then still higher magnification in B). Arrows in B indicate labeled cells.

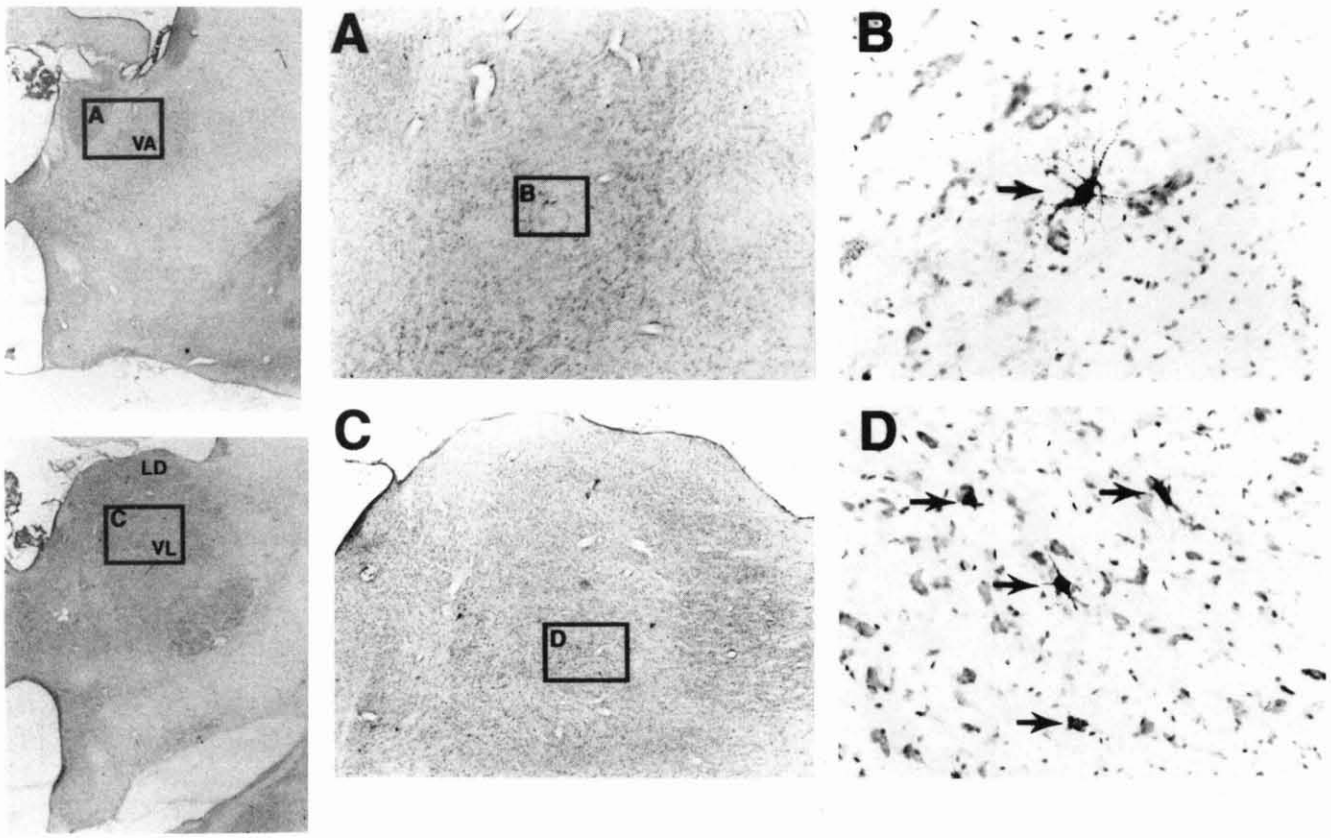

Fig. 8. Labeled cells were found in ventral anterior nucleus (VA: top) and ventral lateral nucleus (VL: bottom). Left is low power photomicrograph indicating where higher magnification photographs were taken (Top row: A and still higher magnification in B. Bottom row: C and then still higher magnification in D). Labeled cells were found in VA in three of the four cases ranging from 0-6.1% of the total number of labeled thalamic cells. Labeled thalamic cells were found in VL in all cases ranging from 0.8%-33.8% of the total number of labeled thalamic cells. Most of the labeled cells in VL (33.8%) were in the case with the smallest, and most rostral paint of HRP (case 96-2). Arrows in B and D indicate labeled cells.

1977, Berson and Graybiel 1978, Robertson and Cunningham 1981, Tekian and Afifi 1981, Rodrigo--Angulo and Reinozo-Suárez 1995).

Importantly, the Pul-LP complex has a cortical auditory input from secondary (AII) auditory cortex (Rodrigo--Angulo and Reinoso-Suárez 1995) and projects to the posterior ectosylvian (Ep) auditory cortex (Tekian and Afifi 1981). The subcortical afferents to the Pul-LP complex has been observed to include the deeper layers of the superior colliculus (Rodrigo-Angulo and Reinoso-Suárez 1982). Studies of the superior colliculus implicate its role in multisensory integration (see Stein et al. 1994 for discussion). The deep superior colliculus is not exclusively auditory so that projection to the medial part of the posterior group could be somatic and visual as well as auditory (Gordon 1973, Drager and Hubel 1975, Stein et al. 1976, King 1993, King and Carlile 1995). Electrophysiological investigations support this view with evidence that auditory as well as multisensory inputs reach the Pul-LP complex (Kreindler et al. 1968, Huang and Lindsley 1973, Khachaturian et al. 1975). Hence, the Pul-LP complex may act as a polysensory data processor (see for discussion Crighel and Kreindler 1974, Siquiera and Frank 1974, Jones 1985).

VENTRAL THALAMUS

In the present investigation a small input to the SS cortex from the ventral anterior (VA) nucleus and ventral lateral (VL) nucleus was found. These results are consistent with anatomical findings of others (e.g. Mizuno et al. 1975). It has been known from electrophysiological study, that VA and VL may play some role in auditory processing (Hinman and Buchwald 1983).

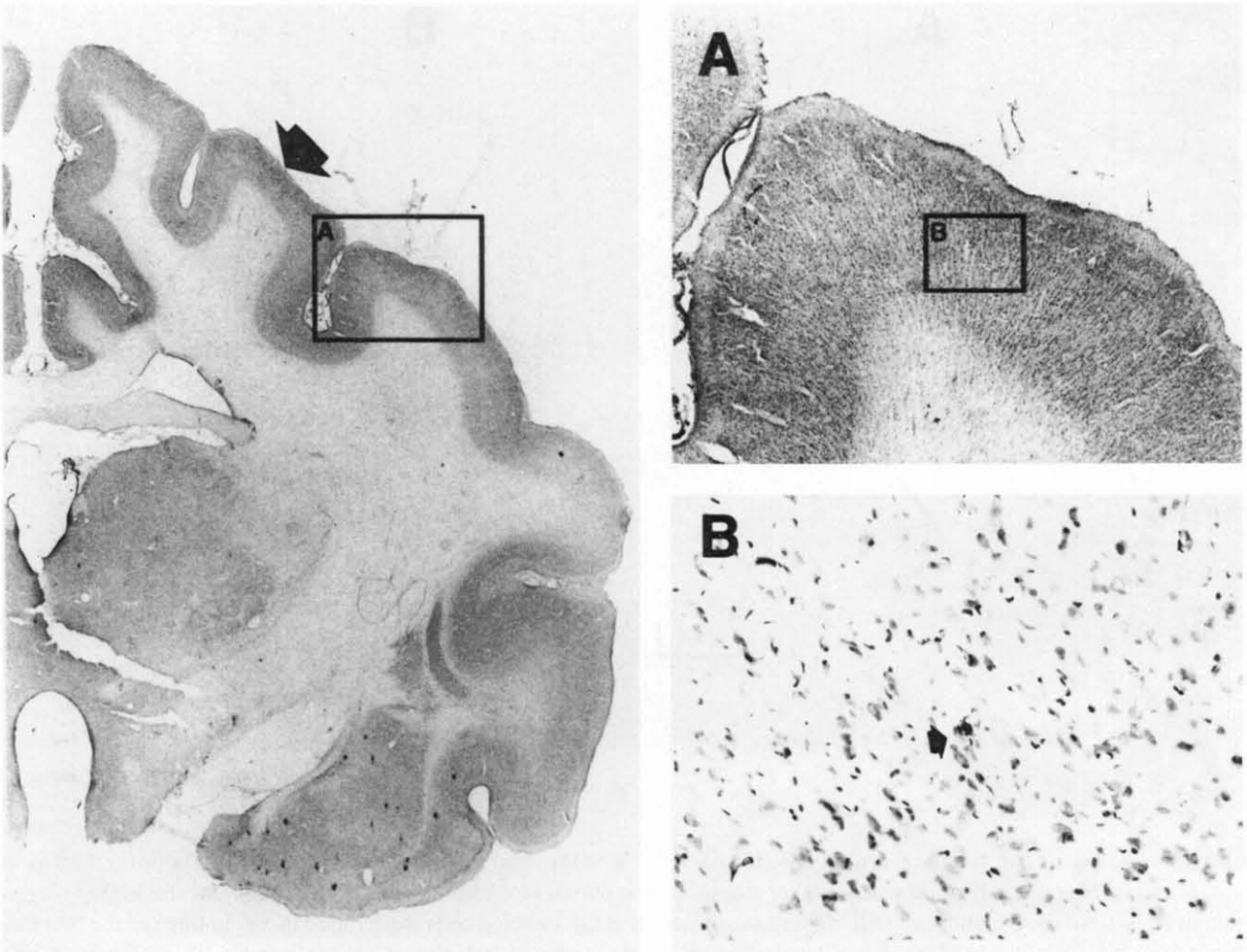

Fig. 9. Poor labeling in auditory cortex resulting from HRP paint in the suprasylvian gyrus. Auditory cortex was examined adjacent to the labeled suprasylvian gyrus to determine the presence of cortico-cortical connections. It was thought that perhaps these could account for the auditory physiology of these cells (see text). In this and Fig. 10: left is low power photomicrograph indicating where higher magnification photographs were taken (A and then still higher magnification in B). Arrow in B indicates a labeled cell.

MEDIAL GENICULATE (MG) BODY

In the present investigation no labeled cells were found in MG body. This result is consistent with the studies of HRP injections in auditory areas AI and AII, which resulted in many retrogradely labeled cells in all divisions of MG (Winer et al. 1977, Winer and Larue 1987). However, the present result is inconsistent with the suggestion that direct auditory input from the MG reaches the anterior suprasylvian gyrus (ASG) of a cat (Rojik et al. 1984). It has been shown that axons from the medial division of MG in cat reach large areas of neocortex outside the primary auditory fields (possibly including ASG; Rojik et al. 1984). However, the results of the present investigation are consistent with other studies of the projections of MG showing that the ventral division of MG projects only to AI (e.g. Winer et al. 1977). Although the magnocellular division of MG has been found to project the most widely (e.g. Winer et al. 1977), still, in the present experiment, no retrogradely labeled cells were found within it.

Corticocortical input to suprasylvian cortex

Cortical input to suprasylvian cortex arises from most adjacent cortical regions: the anterior, medial and posterior parts of this cortex are connected with each other (e.g. Kawamura 1973, Avendao et al. 1988; see also for

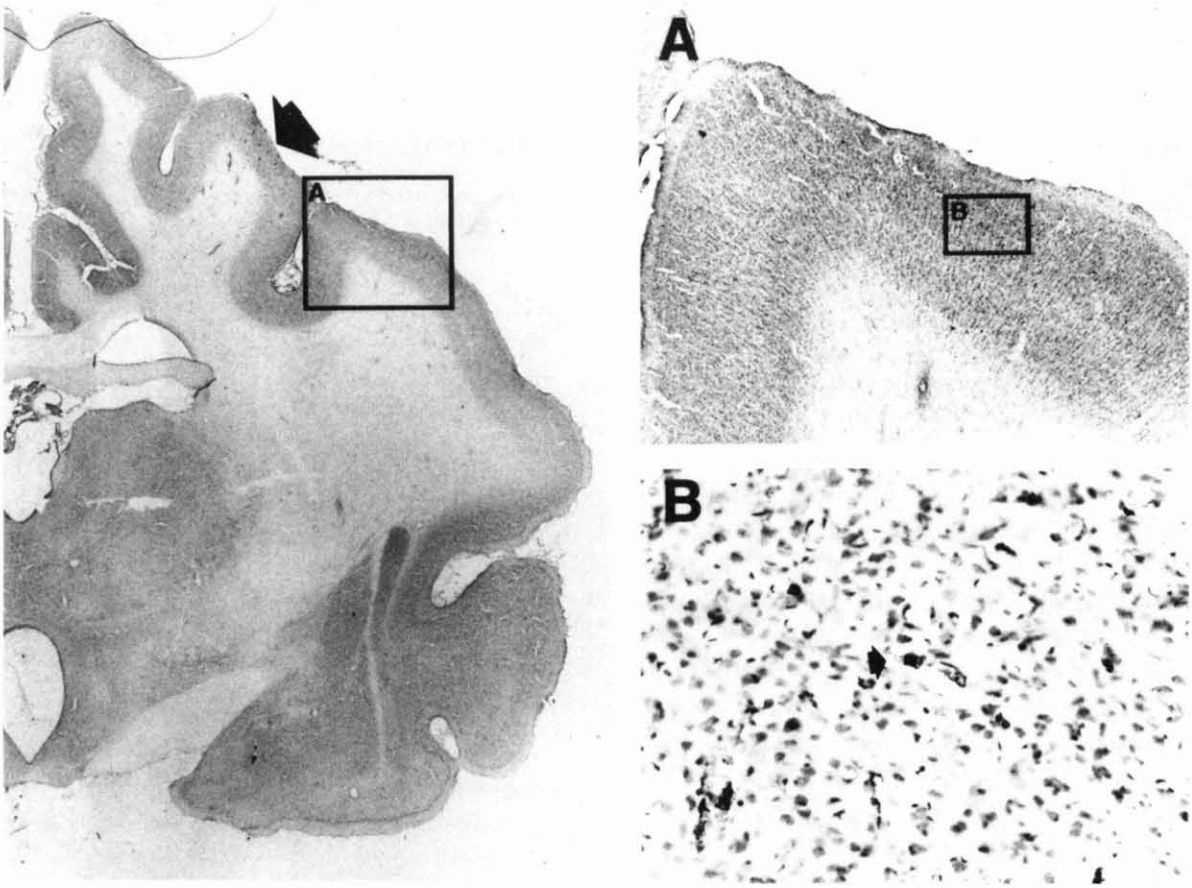

Fig. 10. Poor labeling in auditory cortex resulting from HRP paint in the suprasylvian gyrus. A slightly more rostral section to that in Fig. 9. A few poorly labeled cells were found in the cortex (photomicrographs on the right). These cells were in layers II and III of cortex. Since all of the cortical cells were poorly labeled, their contribution to the auditory responsiveness of the region is considered doubtful. A comparison of the labeling in auditory cortex (Figs. 9 and 10) with that found in thalamic nuclei (Figs. 6-8) indicates a minor role if any of cortico-cortical connections.

reviews, Heath and Jones 1971, Scannel et al. 1995). However, cortical input to suprasylvian cortex from the auditory cortex of the ectosylvian gyrus appears to be sparse at best. Although a few investigations have reported auditory cortex projections to suprasylvian cortex using retrograde methods (i.e. Diamond et al. 1968, Kawamura 1973, Avendao et al. 1988), orthograde autoradiographic methods applied to ectosylvian auditory cortex have failed to confirm such a projection (Imig and Reale 1980).

THE RELATIONSHIP OF PRESENT RESULTS TO CORTICAL SUBDIVISIONS AS DEFINED BY CONNECTIONS

The key to understanding the significance of the cortex and especially of the cytoarchitectonic subdivisions of the cortex lies in the study of the afferent projections to cortex and the efferent projections from the cortex. This has been the first principle of the study of the cortex since the days of Elliot Smith (1910). The first study of cortical architectonic patterns as the relate to projections of the auditory thalamus was first done by Rose and Woolsey (1949, see also Rose 1949). The auditory pathway taken as a whole is divided into functionally distinct pathways. For example, in what can be called the primary or lemniscal path, auditory impulses are relayed by the central nucleus of the inferior colliculus to the ventral division of MG (e.g. Woollard and Harpman 1940, Moore and Goldberg 1963, van Noort 1969). Other pathways have also been suggested (e.g. Morest 1965, Niimi et al. 1970, Harting et al. 1973, Glendenning et al. 1975, Casseday et al. 1976).

THE RELATIONSHIP OF PRESENT RESULTS TO CORTICAL SUBDIVISIONS AS DEFINED BY ELECTROPHYSIOLOGY

Apart from anatomical observations, electrophysiological investigations seem to indicate that in cats the suprasylvian cortex is responsive to auditory stimulation (e.g. Thompson et al. 1963, 1969, Phillips et al. 1972, Robertson and Thompson 1973, Wester et al. 1974, Robertson et al. 1975, Irvine and Huebner 1979, Toldi et al. 1981, Shipley and Fisher 1988, Dickerson and Buchwald 1992). In addition, the suprasylvian cortex is purported to be a region of multimodal convergence from auditory, visual and somatic modalities in cats (see refs. Heath and Jones 1971, Irvine and Phillips 1982, Rosenquist 1985, Scannel et al. 1995 for discussion).

Furthermore, the properties of acoustically responsive neurons in the anterior part of the suprasylvian gyrus (ASG) show similarities to those of primary auditory cortex (AI); e.g. short latency of the responses to pure tones of different frequencies (Toldi and Féher 1984). The properties of responses of the ASG cells seem to suggest direct sensory projection from the thalamic relay nuclei as supported by finding afferents to the anterior suprasylvian cortex from the MG (Rojik et al. 1984). Nevertheless, we could not confirm this projection despite our specific attention.

Behavioral studies on dogs

The results of behavioral experiments on dogs show, that after bilateral suprasylvian gyrus cortex lesions, there is an impairment of the performance in both a short-term memory task (Stasiak et al. 1992) and a simple differentiation task (Stasiak et al., unpublished data) on auditory localization. Because there is a similarity between the effects following bilateral ablation of auditory cortex (Stasiak et al. 1992, 1993) and suprasylvian cortex (Stasiak et al. 1992), it may be concluded that the effects of the bilateral suprasylvian removal consist in loss of the perception of auditory locus. It should be added, that there is a clear contradiction between the pattern of an impairment after suprasylvian cortex lesion and after ablation of another association area, i.e. proreal prefrontal cortex. Namely, bilateral proreal removal results in a completely unaffected the performance of a simple differentiation task and a deficit in solving the short-term memory task, involving auditory localization (Stasiak and Ławicka 1990).

Due to partial discrepancy of the data collected so far, there is a need for further extensive studies concerning the nature of the suprasylvian cortex in Carnivora.

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