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Corticothalamic connections of the superior temporal sulcus in rhesus monkeys

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Summary. The corticothalamic connections of the superior temporal sulcus (STS) were studied by means of the autoradiographic technique. The results indicate that corticothalamic connections of the STS in general reciprocate thalamocortical connections. The cortex of the upper bank of the STS–multimodal areas TPO and PGa–projects to four major thalamic targets: the pulvinar complex, the mediodorsal nucleus, the limitans-suprageniculate nucleus, as well as intralaminar nuclei. Within the pulvinar complex, the main projections of the upper bank of the STS are directed to the medial pulvinar (PM) nucleus. Rostral upper bank regions tend to project caudally and medially within the PM nucleus, caudal upper bank regions, more laterally and ventrally. The mid-portion of the upper bank tends to occupy the central sector of the PM nucleus. There are also relatively minor projections from upper bank regions to the lateral pulvinar (PL) and oral pulvinar (PO) nuclei. In contrast to the upper bank, the projections from the lower bank are directed primarily to the pulvinar complex, with only minor projections to intralaminar nuclei. The rostral portion of the lower bank projects mainly to caudal and medial regions of the PM nucleus, whereas the caudal lower bank projects predominantly to the lateral PM nucleus, and also to the PL, PO, and inferior pulvinar (PI) nuclei. The mid-portion of the lower bank projects mainly to central and lateral portions of the PM nucleus, and also to the PI and PL nuclei. The rostral depth of the STS projects mainly to the PM nucleus, with only minor connections to the PO, PI, and PL nuclei. The mid-portion of multimodal area TPO of the upper bank, areas TPO_2 and TPO_3, projects preferentially to the central sector of the PM nucleus. It is possible that this STS-thalamic connectivity has a role in behavior that is dependent upon more than one sensory modality.

Key words: Cortex – Temporal – Thalamus – Pulvinar – Multimodal – Monkey

Abbreviations: AM anterior medial nucleus; AS arcuate sulcus; AV anterior ventral nucleus; BSC brachium of the superior colliculus; Cd caudate nucleus; Cif nucleus centralis inferior; Cim nucleus centralis intermedialis; CL central lateral nucleus; CM centromedian nucleus; CM–Pf centromedian-parafascicular nucleus; Cs nucleus centralis superior; CS central sulcus; CSL nucleus centralis lateralis superior; GLd dorsal lateral geniculate nucleus; GM medial geniculate nucleus; Hb habenula; IOS inferior occipital sulcus; IPS intraparietal sulcus; LD lateral dorsal nucleus; LF lateral fissure; Li limitans nucleus; LP lateral posterior nucleus; LS lunate sulcus; MD mediodorsal nucleus; Pa paraventricular nucleus; Pcn paracentral nucleus; Pf parafascicular nucleus; PI inferior pulvinar nucleus; PL lateral pulvinar nucleus; PM medial pulvinar nucleus; PO oral pulvinar nucleus; PS principal sulcus; Pt parataenial nucleus; R reticular nucleus; Re reuniens nucleus; SG suprageniculate nucleus; STN subthalamic nucleus; STS superior temporal sulcus; THI habenulo-interpeduncular tract; VLc nucleus ventralis lateralis, pars caudalis; VLm nucleus ventralis lateralis, pars medialis; VLo nucleus ventralis lateralis, pars oralis; VLps nucleus ventralis lateralis, pars postrema; VPI ventroposteroinferior nucleus; VPLc nucleus ventralis posterior lateralis, pars caudalis; VPLo nucleus ventralis posterior lateralis, pars oralis; VPM ventroposteromedial nucleus; VPMpc ventroposteromedial nucleus, parvocellular portion; X nucleus X.

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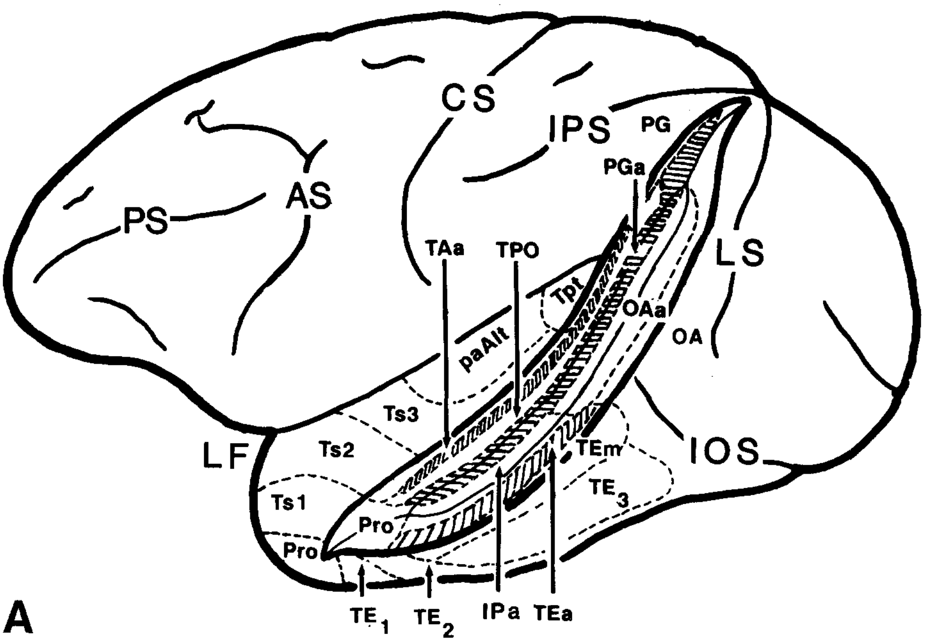
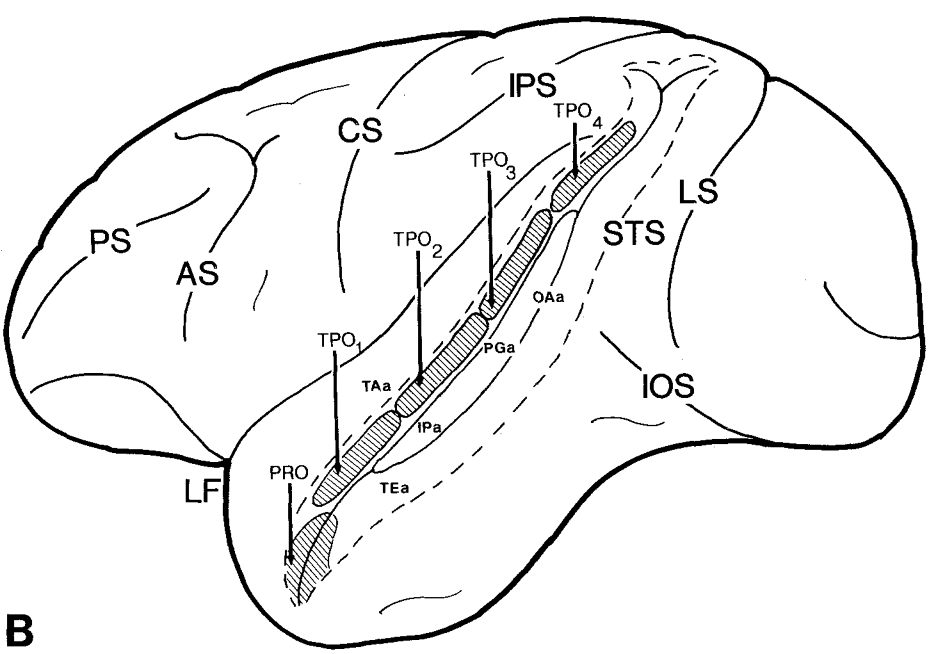
Introduction

Physiological studies have shown that there are different regions in the superior temporal sulcus (STS) that contain neurons responsive either to a single sensory modality or to more than one modality (Benevento et al. 1977; Desimone and Gross 1979; Bruce et al. 1981; Gattass and Gross 1981; Baylis et al. 1987; Hikosaka et al. 1988). The distinction between the unimodal and multimodal nature of STS regions is also evident in differential architecture and corresponding corticocortical connections (Kuypers et al. 1965; Jones and Powell 1970; Seltzer and Pandya 1978, 1989a; Zeki 1978a; Ungerleider and Mishkin 1979; Van Essen et al. 1981; Maioli et al. 1983; Maunsell and Van Essen 1983a, 1987; Standage and Benevento 1983; Van Essen and Maunsell 1983; Ungerleider et al. 1984; Kennedy and Bullier 1985; Ban 1986; Barnes and Pandya 1986; Ungerleider and Desimone 1986a, b; Shiwa 1987; Neal et al. 1988; Leichnetz 1989; Shipp and Zeki 1989a, b). Thus, areas TPO and PGa in the upper bank of the STS are considered multimodal, because they receive overlapping afferents from parasensory association areas of more than one sensory modality. The surrounding areas TAa, TEa, IPa, and OAa (MT, FST, and MST) receive input from parasensory association areas belonging to a single sensory modality, and are termed unimodal (Fig. 1A). Moreover, on the basis of architecture and cortical connections, one of the multimodal regions in the upper bank of the STS, area TPO, has been divided into four rostro-caudal subregions (Seltzer and Pandya 1989a, b) (Fig. 1B).

Several studies examining the thalamic relationships of the STS have revealed that multimodal areas in the upper bank have significantly different connections as compared to unimodal areas of the lower bank (Benevento and Rezak 1976; Burton and Jones 1976; Trojanowski and Jacobson 1976; Maunsell and Van Essen 1983a; Standage and Benevento 1983; Maioli et al. 1984; Ungerleider et al. 1984; Yeterian and Pandya 1989b). A recent investigation has shown that there is differential thalamocortical connectivity from rostral versus caudal



A



B

Fig. 1. A Diagram of the lateral surface of the cerebral hemisphere of the rhesus monkey showing the architectonic areas of the superior temporal gyrus (paAlt, lateral parakoniocortex; Pro, proisocortex; Tpt, temporoparietal cortex; Ts1, Ts2, Ts3, temporalis superior cortex 1, 2, 3), the inferior temporal region (TE_1, TE_2, TE_3, rostral, middle, and caudal subdivisions of the inferior temporal region), and the superior temporal sulcus. The superior temporal sulcus is opened to expose the cortex of the upper and lower banks as well as the depth. Note that the multimodal areas (TPO and PGa) are surrounded by unimodal association regions (area TAa, auditory; area IPa and PG, somatosensory; areas TEa, TEm, OAa and OA, visual). **B** Diagram showing the rostro-caudal subdivisions of area TPO, TPO_1–TPO_4, of the upper bank of the superior temporal sulcus (Seltzer and Pandya 1989b)

subdivisions of the STS, within both the upper and the lower bank (Yeterian and Pandya 1989b). Only a few studies have addressed the corticothalamic connectivity of the superior temporal sulcus (Maunsell and Van Essen 1983a; Maioli et al. 1984; Ungerleider et al. 1984), and these have focused on the caudal portions of the sulcus, in particular the middle temporal visual area MT. A comprehensive analysis of the corticothalamic connections of the rostral and caudal regions of the STS has not been carried out.

In the present study, we have investigated the corticothalamic connections of the STS using the autoradiographic technique. We were particularly interested in discerning whether there is differential connectivity to the thalamus from multimodal versus unimodal areas of the STS. In addition, we examined the possibility that there may be systematic shifts in corticothalamic connectivity that correspond to the rostral-to-caudal architectonic progressions within the STS.

Methods

The corticothalamic connections of the superior temporal sulcus were traced in 16 rhesus monkeys *(Macaca mulatta)* using radioactively labeled amino acids. A craniotomy was performed under sodium pentobarbital anesthesia, and discrete injections (^{3}H-leucine and/or proline; volume range 0.4–1.0 µl; specific activity range, 40–80 µCi/µl) were made in different sites within the STS. In most cases involving either bank, the injections were placed in the sulcal cortex via penetration of the sulcal lip. Injections in the depths of the sulcus were made following separation of both banks to expose the target area. Following a survival time of 7–10 days, the animals were deeply anesthetized with sodium pentobarbital and perfused transcardially with isotonic saline followed by 10% formalin. The brains were removed and processed for autoradiography according to the method of Cowan et al. (1972). The exposure times ranged from 3 to 6 months.

Each hemisphere was divided coronally into two or three blocks in the stereotaxic plane. The blocks were embedded in paraffin and cut into 10-µm-thick sections in the coronal plane. Every tenth section was processed for autoradiography and stained with thionin. This stain permitted the analysis of cortical architecture, localization of the injection site, and identification of the boundaries of thalamic nuclei. The precise location of each injection site was determined by observing the cortical architecture around the labeled area, and comparing this with the architecture of the corresponding nonlabeled area in the cortex of the opposite hemisphere. The distribution of terminal label in each section as revealed under darkfield illumination was charted onto coronal tracings of the thalamus. The boundaries of the various thalamic nuclei were determined from the thionin-stained sections under brightfield illumination. The atlas of Olszewski (1952) was used as a reference for delineating thalamic boundaries and for nomenclature.

Results

The cortex of the superior temporal sulcus has been divided into several architectonic areas (Seltzer and Pandya 1978) (Fig. 1A). The rostralmost portion of the STS is designated as area Pro, or proisocortex. Caudal to the proisocortical region, the upper bank of the STS contains area TAa (auditory association area) at the rim of the sulcus, and two adjoining multimodal regions, areas TPO and PGa. Area TPO has recently been divided into four rostro-caudal regions, TPO_1 through TPO_4 (Seltzer and Pandya 1989b) (Fig. 1B). The lower bank contains unimodal visual areas TEa and TEm rostrally. Caudally, the lower bank and depths of the STS contain area OAa (or MT, FST, and MST). An additional area, IPa (mainly a somatosensory association area), is located in the rostral depth of the STS. In describing the location of injection sites, we have adhered to this classification.

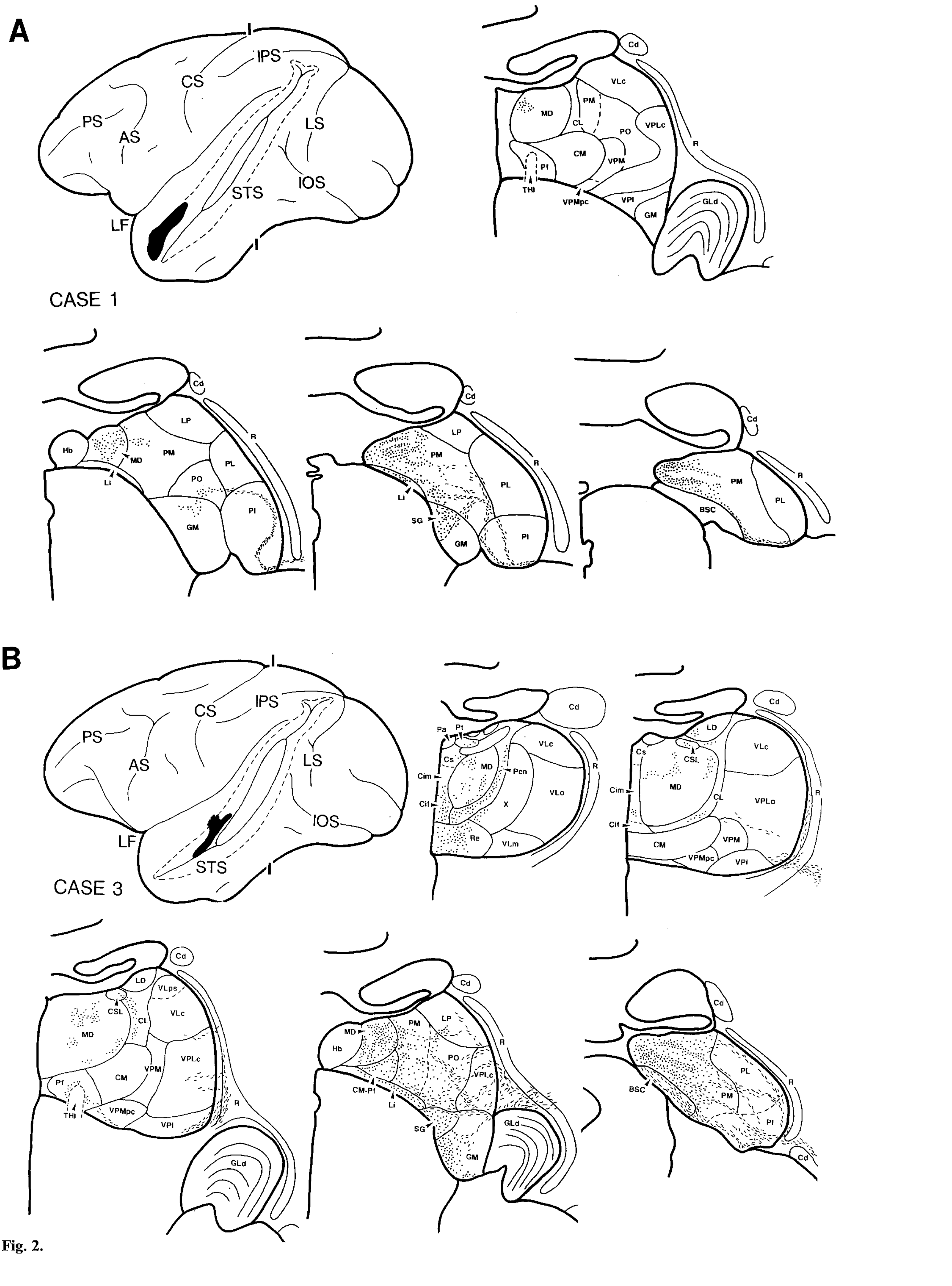
Injections of the rostral portion of the upper bank of the STS

In two cases, isotope injections were placed in the rostral part of the upper bank of the STS. In case 1, the injection involved area Pro and the rostral part of area TPO, area TPO_1, as well as a portion of the adjoining superior temporal gyrus (STG), areas TS_1 and TS_2 (Fig. 2A). In case 2 (not illustrated), the injection involved mainly the STG (portions of areas TS_1 and TS_2) and the adjoining portions of areas TAa and TPO_1 within the STS. The resulting thalamic label in both of these cases was similar. Thus, grains were noted in the mediodorsal (MD), the intralaminar, the limitans-suprageniculate (Li-SG), and the pulvinar nuclei. In the MD nucleus, label occurred in the caudal one-half, and was located predominantly medially in discrete clusters. The intralaminar label was noted in the central lateral superior (CSL) nucleus anteriorly (not shown). Within the Li-SG nucleus, label was observed caudally in both components. The heaviest and most extensive labeling in the thalamus occurred in the caudal two-thirds of the medial pulvinar (PM) nucleus, in its medial one-half, and extended up to the caudal pole (Fig. 7A). The dense label in the PM nucleus was distributed in bands in a medio-lateral orientation against a background of lighter labeling. Only relatively minor amounts of label were seen in the oral pulvinar (PO) nucleus.

Injections of the middle region of the upper bank of the STS

In two cases, isotope injections were placed in the cortex of the STS immediately caudal to the injection sites in cases 1 and 2. In case 3 (Fig. 2B), the injection involved

Fig. 2. A Diagrammatic representation of the lateral surface of the cerebral hemisphere showing an isotope injection site (dark area) in the rostral portion of the upper bank of the STS (case 1, upper left). Also shown are four representative rostral-to-caudal sections through the thalamus depicting the distribution of terminal label in various nuclei (dots). Dashed lines represent labeled fibers. **B** Diagrammatic representation of the cerebral hemisphere showing an isotope injection site in the rostral mid-portion of the upper bank of the STS (case 3, upper left). Also shown are four representative rostral-to-caudal sections depicting the distribution of terminal label in various thalamic nuclei. In this and subsequent figures, the vertical marks on the hemispheric surface indicate the line of cut in the coronal plane for the thalamic sections


A
CS
IPS
PS
AS
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STS
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CASE 1
Cd
VLc
PM
MD
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Pf
THI
VPMpc
VPI
GM
GLd
LP
Hb
Li
PL
PI
SG
BSC
B
CASE 3
Pa
Pt
Cs
Cim
Cif
Pcn
X
VLo
Re
VLm
LD
CSL
VPLo
VLps
CM-Pf

Fig. 2.

the caudal part of area TPO_1 and the rostral part of area TPO_2, as well as adjoining portions of area TAa laterally and area PGa medially. There was some spread of isotope into the laterally adjoining cortex of the STG, and into the depth of the lower bank of the Sylvian fissure adjacent to the ventral insular cortex. In case 4 (not illustrated), the injection was restricted to the same areas of the STS as case 3, and also involved adjoining area TS_2 of the STG, but did not involve the cortex within the Sylvian fissure.

In case 3 (Fig. 2B), the main distribution of terminal label was to the MD, intralaminar, and midline nuclei, the GM complex, the Li-SG nucleus, and pulvinar nuclei. Some additional label was seen in the lateral posterior (LP) and lateral dorsal (LD) nuclei (Figs. 2B and 7B). In the MD nucleus, terminal label was observed mainly in the parvocellular portion, occurring in clusters throughout the rostro-caudal extent of the nucleus. The intralaminar and midline labeling in this case was quite extensive, involving the parataenial, central inferior (Cif), reuniens (Re), paracentral (Pcn), CSL, central lateral (CL), centromedian-parafascicular (CM–Pf), centralis densocellularis (Cdc–not shown), and centralis latocellularis (not shown) nuclei. The terminal label observed in the midline nuclei in this case can be attributed to the involvement of the cortex in the depth of the Sylvian fissure, since no such terminations were seen in cases that did not involve this region. In the GM complex, labeling was observed primarily in the magnocellular division. Both the Li and the SG nuclei contained substantial amounts of terminal label. The label in the pulvinar was located mainly in the PM nucleus, somewhat more lateral than in cases 1 and 2, and extending up to the caudal pole (Fig. 7B). As in cases 1 and 2, dense labeling occurred in horizontal bands within the pulvinar. Additionally, some label was noted in the PO, LP, and PL (not shown) nuclei.

In case 4, the terminal labeling was less extensive, and was found mainly in the caudal one-half of the thalamus, in the MD and Li nuclei, the GM complex, and the PM nucleus. As in case 3, the label in the PM nucleus occurred in horizontal bands, and was located in central and ventral portions. The label in the pulvinar again extended up to the caudal pole. In the GM complex, the label was confined to the caudal one-half of the nucleus.

In another three cases isotope injections were placed more caudally within the middle portion of the upper bank of the STS. In case 5, the injection involved only area TPO_2 (Fig. 3A). In case 6, the isotope injection involved the entire extent of area TPO_3 as well as part of adjoining area TAa (Fig. 3B). In this case, there was also an extension of the injection dorsally into the lower bank of the Sylvian fissure, involving part of the primary auditory cortex, area KA, and the cortex adjoining this region medially. The injection in case 7 (not illustrated) involved area TPO_3 only minimally, but extended into area TAa and the adjoining STG (areas TS_3 and paAlt).

In case 5, with a relatively limited injection in the STS, terminal label was observed in the MD, GM, and pulvinar nuclei (Fig. 3A). Label was distributed in discrete patches in these nuclei. In the pulvinar, terminal label was observed in the PO and PM nuclei, primarily in central and ventral locations.

The terminal label in case 6 was found in the MD, intralaminar and midline, the GM, the Li-SG, the pulvinar and the LP nuclei (Fig. 3B). The label in the MD nucleus occurred mainly in the dorsal portion, throughout the rostro-caudal extent of the nucleus. Within the intralaminar nuclei, label was found mainly in the Pcn, CL and CSL (not shown) nuclei. In the Pcn nucleus, label tended to occur ventromedially and laterally, whereas in the CL nucleus, label was found dorsally and laterally. Additionally, label was noted in midline nuclei, Re, Cdc (not shown), and Cif (not shown). As in case 3, labeling of the midline nuclei may have resulted from involvement of the cortex in the depth of the Sylvian fissure. Heavy labeling occurred in the Li-SG nucleus, and also within the GM complex, in the parvocellular as well as magnocellular divisions. In the pulvinar, label was observed in the PO as well as the PM nucleus. In the PO nucleus, the accumulation of terminal label was mainly ventral in location, whereas in the PM nucleus the label tended to be in central, ventral, and lateral locations, in the rostral two-thirds of the nucleus, avoiding the caudalmost portion. The heavy labeling in the GM complex in this case may have resulted from the involvement of area KA in the injection site. In contrast to cases 5 and 6, case 7 also showed a few restricted patches of label in the PL nucleus.

Injections of the caudal portion of the upper bank of the STS

In four cases, isotope injections were placed in the caudalmost portion of the upper bank of the STS. In case 8, the injection was confined to the rostral portion of area TPO_4 and the caudal segment of area TPO_3, with slight involvement of area Tpt (Fig. 4A). In case 9 the injection was located mainly in the caudal portion of area TPO_4, and also encroached slightly upon the adjacent inferior parietal cortex, area PG (Fig. 4B). In cases 10 and 11 (not illustrated), although the injections involved area TPO_4, there was relatively greater spread of isotope into ventral area PG and adjoining area Tpt.

The terminal label in case 8 was observed in the MD, intralaminar, Li-SG, and pulvinar nuclei (Fig. 4A). Similar to previous cases, the label in the MD nucleus was located dorsally in discrete patches in the caudal one-half of the nucleus. Intralaminar label was confined to the Pcn and CL nuclei. Only limited labeling occurred in the SG and in the Li (not shown) nuclei. In the pulvinar, label was located mainly in the ventral portions of the PM (Fig. 7C) and PO nuclei, with relatively little label in the PL nucleus. The label in the PM nucleus was primarily in the rostral portion.

In case 9, the overall pattern of terminal label was similar to that of case 8, with labeling in the MD, intralaminar, and pulvinar nuclei (Fig. 4B). Additionally, both the LP and the LD nuclei showed some evidence of terminal labeling. The terminal label in the MD nucleus was considerably less than in case 8, and involved mainly

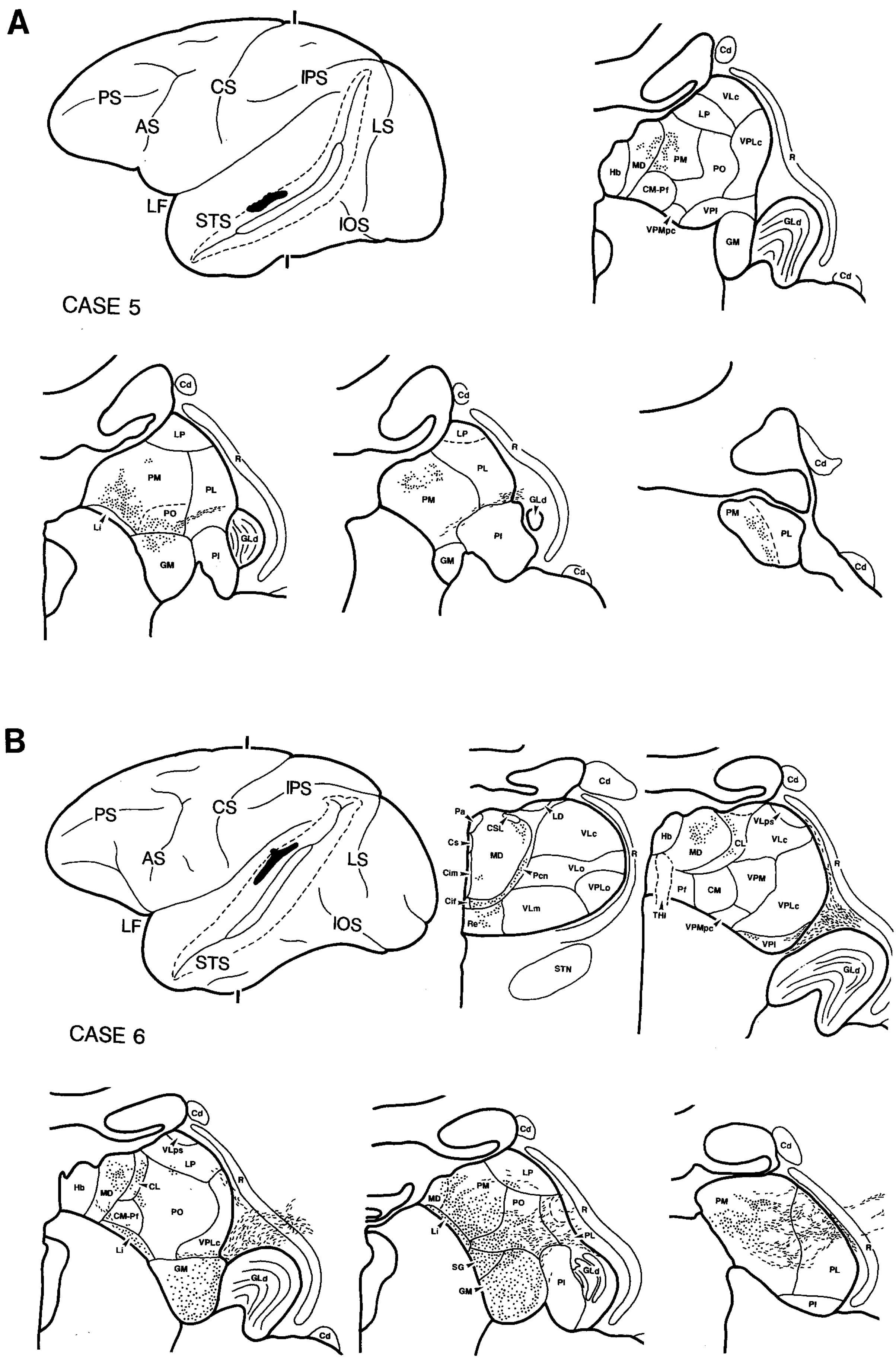

Fig. 3A, B. Diagrammatic representation of isotope injection sites in the rostral mid-portion of the upper bank of the STS (**A**, case 5; **B**, case 6), as well as representative thalamic sections for each case showing the distribution of terminal label

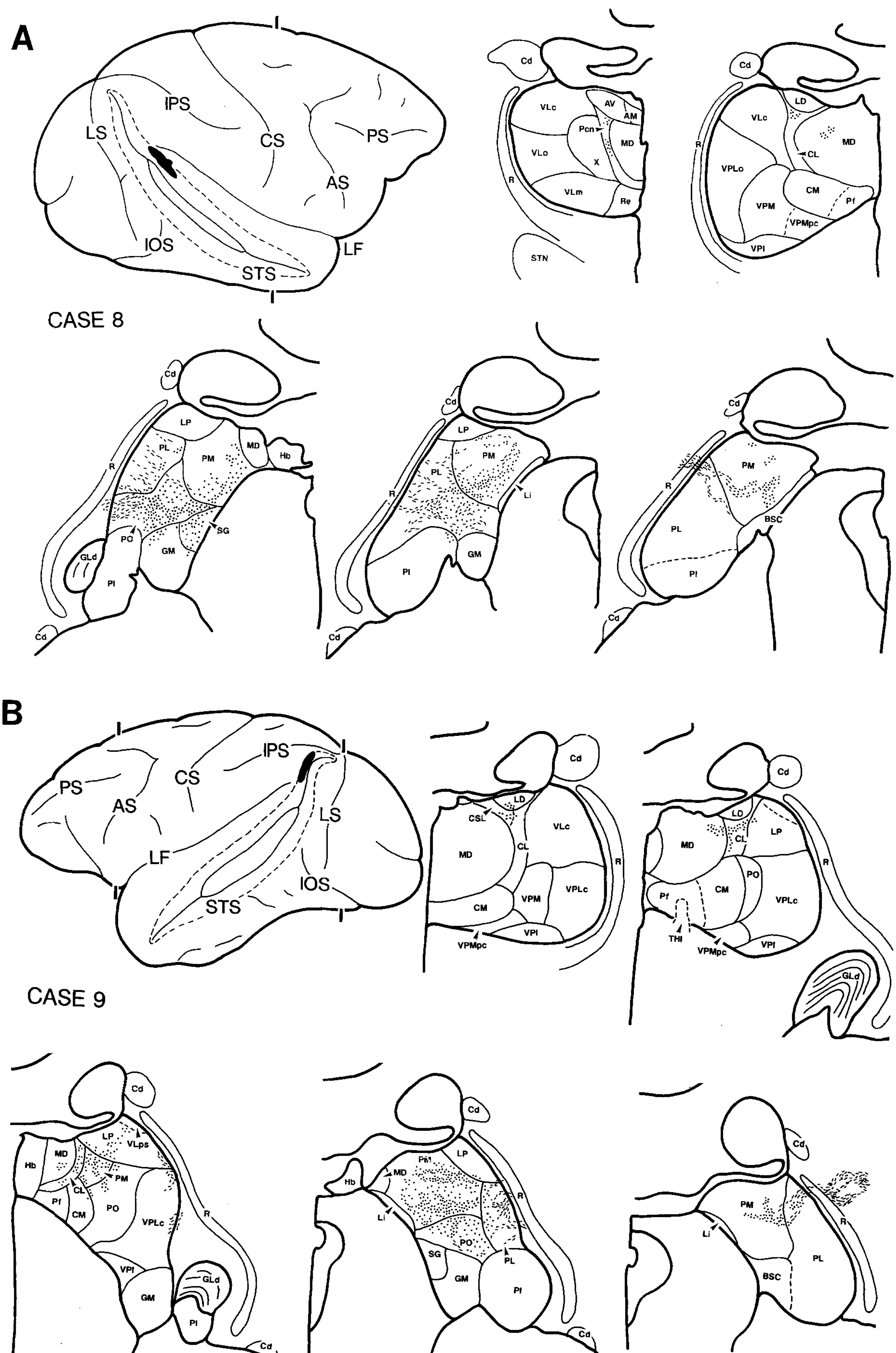

Fig. 4A, B. Diagrams showing isotope injection sites in the caudal mid-portion of the upper bank of the STS (**A**, case 8; **B**, case 9), as well as representative thalamic sections for each case depicting the distribution of terminal label

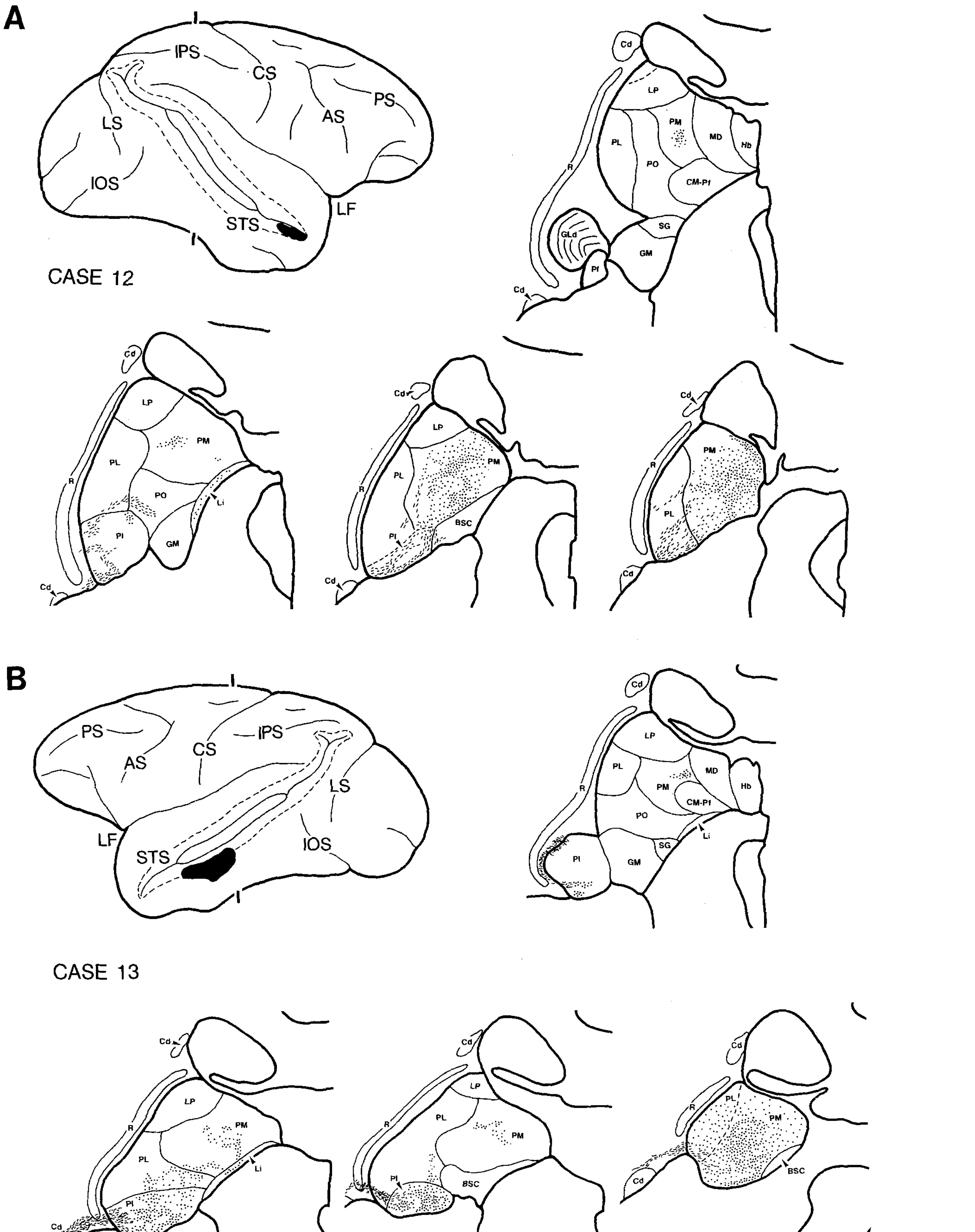

Fig. 5. A Diagrams showing an isotope injection site in the rostral portion of the lower bank of the STS (case 12), as well as representative thalamic sections depicting the distribution of terminal label. **B** Diagrams showing an isotope injection site in the rostral mid-portion of the lower bank of the STS (case 13), as well as representative thalamic sections depicting the distribution of terminal label

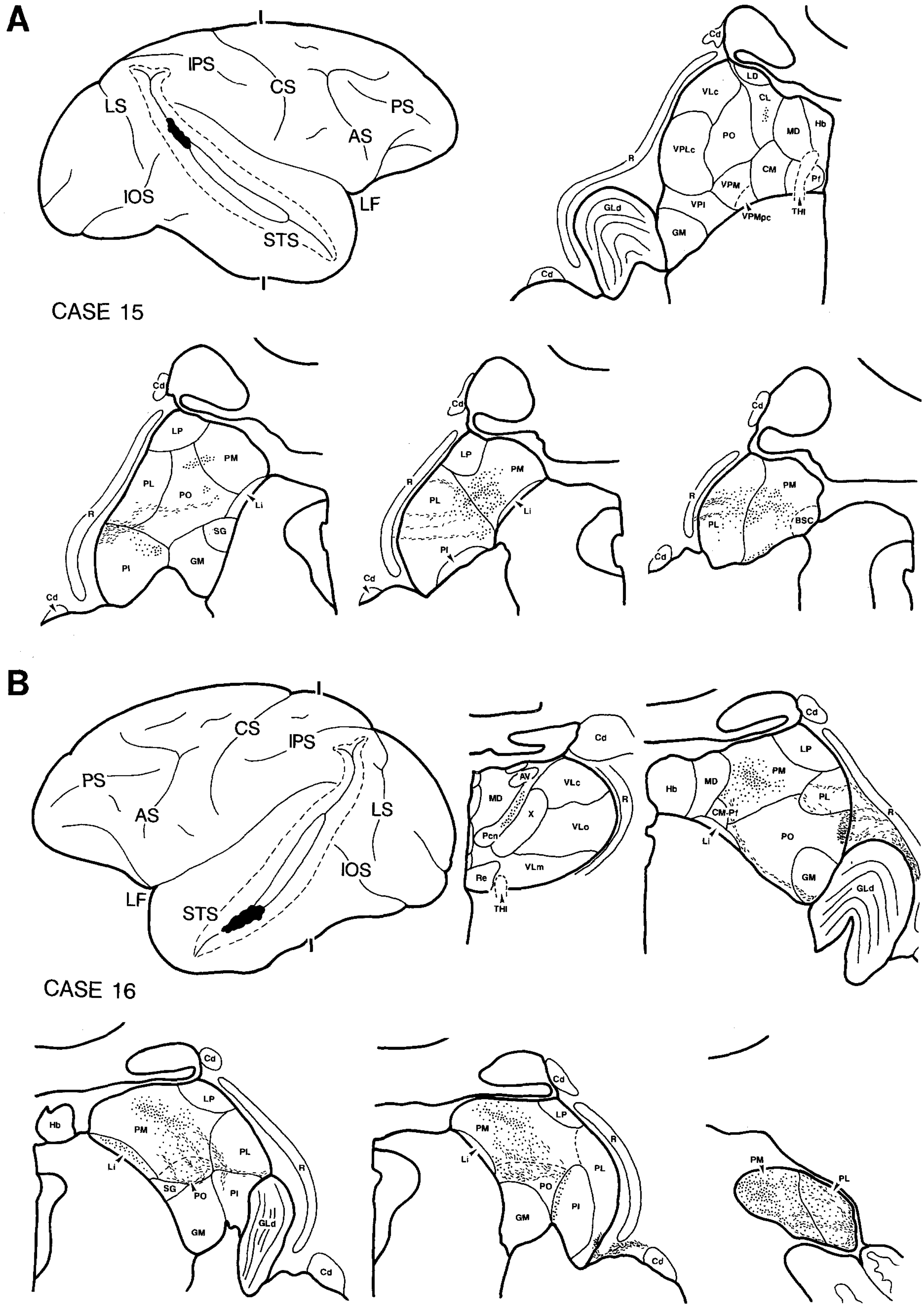

Fig. 6. **A** Diagrams showing an isotope injection site in the caudal portion (area OAa or MT) of the lower bank of the STS (case 15), as well as representative thalamic sections depicting the distribution of terminal label. **B** Diagrams showing an isotope injection site in the rostral depth of the STS (case 16), as well as representative thalamic sections depicting the distribution of terminal label

the lateral portion. The label in the intralaminar nuclei was located primarily in the CL (dorsal portion) and CSL nuclei, with only minor label in the CM and Pf (not shown) nuclei caudally and in the Pcn nucleus (not shown). The heaviest terminal label was observed in the PM nucleus (Fig. 7D), centrally to laterally, throughout most of its rostro-caudal extent. Additional label was seen primarily in a dorsal location in the PO nucleus, and in the medial portion of the PL nucleus.

Injections of the rostral portion of the lower bank of the STS

In case 12, the isotope injection was placed in the rostral-most portion of the lower bank of the STS, and involved sulcal area Pro as well as rostral portions of areas TEa and TEm (Fig. 5A). The main bulk of terminal label in this case was in the caudal portion of the PM nucleus (Fig. 8A), and occurred in clusters in dorsomedial, central, and ventral locations, extending to the caudal pole. Only occasional label was noted in the inferior pulvinar (PI) and the Li nuclei.

Injections of the middle portion of the lower bank of the STS

In cases 13 and 14 isotope injections were placed in the mid-portion of the lower bank of the STS. In both cases, injections involved areas TEa and TEm and the adjoining portions of areas TE_1 and TE_2. The injection in case 13 (Fig. 5B) was rostral compared to that in case 14 (not illustrated). In both cases, terminal labeling was similar, and confined mainly to the pulvinar. In case 13, label was found in central and ventral portions of the PM nucleus, extending up to the caudal pole, and in the PI nucleus

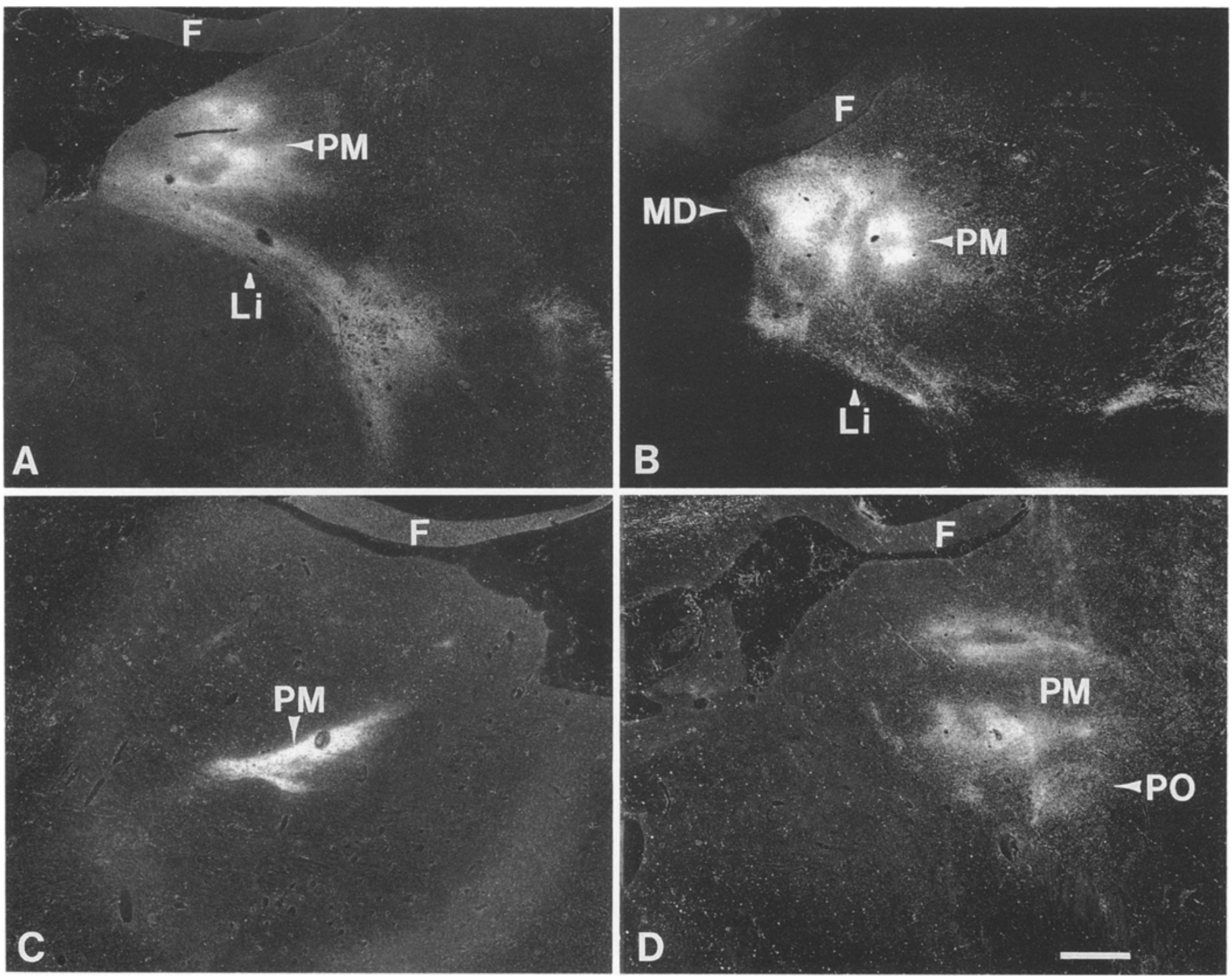

Fig. 7A–D. Darkfield photomicrographs of coronal sections showing evidence of terminal label in the thalamus. **A** Shows label over the medial portion of the PM nucleus and over the Li nucleus after an isotope injection in the rostral portion of the upper bank of the STS (case 1). **B** Shows label over the PM, MD, and Li nuclei following an injection in the rostral mid-portion of the upper bank of the STS (case 3). **C** Shows label over the ventral portion of the PM nucleus after an injection in the caudal mid-portion of the upper bank of the STS (case 8). **D** Shows label over the lateral PM and the PO nuclei following an injection in the caudal portion of the upper bank of the STS (case 9). Bar indicates 1 mm

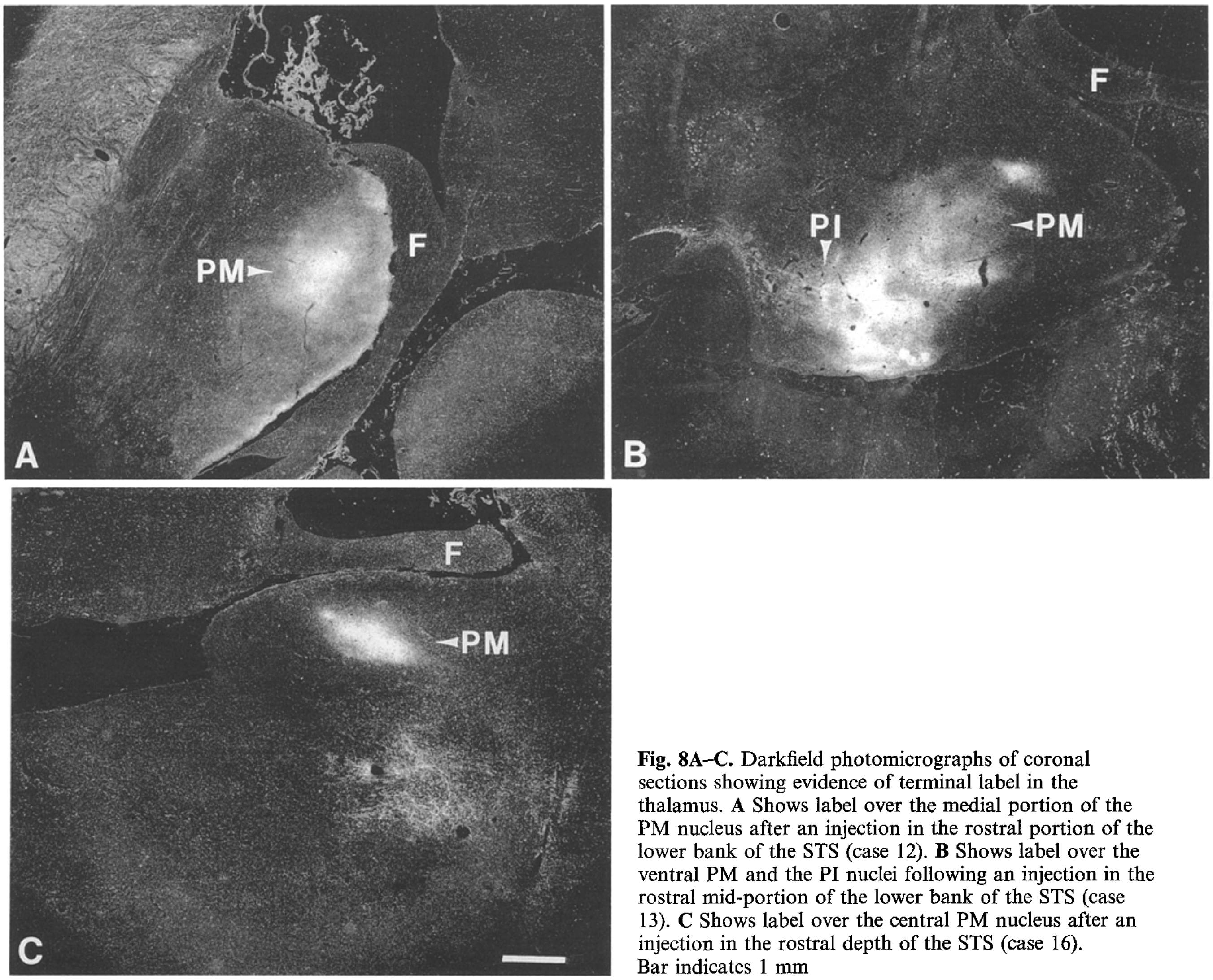

Fig. 8A–C. Darkfield photomicrographs of coronal sections showing evidence of terminal label in the thalamus. **A** Shows label over the medial portion of the PM nucleus after an injection in the rostral portion of the lower bank of the STS (case 12). **B** Shows label over the ventral PM and the PI nuclei following an injection in the rostral mid-portion of the lower bank of the STS (case 13). **C** Shows label over the central PM nucleus after an injection in the rostral depth of the STS (case 16). Bar indicates 1 mm

throughout its caudal two-thirds (Fig. 8B). A small amount of label was noted in the PL nucleus ventrally. Occasional patches of label were observed in the Li nucleus.

Injections of the caudal portion of the lower bank of the STS

In case 15, the injection involved the caudal portion of the lower bank, and extended into the depth involving primarily area OAa or MT. In this case terminal label was found in the PM, PI, PO, and the PL nuclei (Fig. 6A). In the PM nucleus, terminal label was confined mainly to central and lateral sectors, whereas in the PL nucleus, the label was dorsal and medial. Occasional restricted label was seen also in the CL nucleus in this case.

Injections of the rostral depth of the STS

In case 16, an injection was placed in the rostral depth of the STS, and involved mainly area IPa, although there was some extension into adjoining area TEa (Fig. 6B). In this case, the main bulk of terminal label was in the PM nucleus, located primarily in central to dorsal sectors (Fig. 8C), extending to the caudal pole of the pulvinar. Caudally within the PM nucleus, label occupied a medial location. Some label was noted also in the Pcn, Li, and PI nuclei.

Discussion

The results of the present study indicate that there are differences as well as similarities in the corticothalamic projections of the upper and lower banks of the STS. The cortex of the upper bank, which contains the multimodal areas TPO and PGa, appears to project to four major thalamic targets: the pulvinar complex, the mediodorsal nucleus, the intralaminar nuclei, and the limitans-suprageniculate nucleus. In contrast, the cortex of the lower bank has projections mainly to the pulvinar complex.

The main bulk of projections from the upper bank of the STS is to the PM nucleus. There is a differential medio-lateral distribution of corticothalamic connections as one proceeds from rostral to caudal regions of the upper bank. Thus, the rostral portion of the upper bank, containing areas Pro and TPO_1, projects mainly to the medial portion of the PM nucleus. In contrast, the caudal portion of the upper bank, containing caudal area TPO_3 and area TPO_4, is related predominantly to central and lateral portions of the PM nucleus. The mid-portion of the upper bank, containing area TPO_2 and rostral area TPO_3, has pulvinar connections intermediate to those of more rostral and more caudal regions, that is, primarily central in location within the PM nucleus. There is also a rostro-caudal organization evident in the connections of the upper bank to the PM nucleus. The distribution of projections from the rostral upper bank tends to be more caudal, extending up to the caudal pole of the PM nucleus, whereas that of the caudal upper bank tends to be more rostral, extending to the rostralmost portion of the nucleus. In addition to connections from the upper bank to the PM nucleus, there are projections to the PO and the PL nuclei. Projections to the PO nucleus are primarily from the middle and caudal regions of the upper bank, whereas those to the PL nucleus arise mainly from the caudal portion of the upper bank.

In comparison to the projections to the pulvinar, the connections from the upper bank of the STS to the MD nucleus, to intralaminar nuclei, and to the Li-SG nucleus do not seem to have as distinct a topographic organization. Thus, rostral, middle, and caudal regions of the upper bank are related to the MD nucleus, with a tendency for rostral regions to project more medially, and caudal regions, more laterally. The main connections to the intralaminar nuclei from the upper bank of the STS are directed to the Pcn, CSL, and CL nuclei. Whereas the projections to the Pcn and CL nuclei arise from middle and caudal regions of the upper bank, those to the CSL nucleus originate from the rostral sector as well. Projections are directed to the Li-SG nucleus from all sectors of the upper bank, albeit to varying degrees (see Table 1).

The corticothalamic connectivity of the lower bank, in contrast to that of the upper bank, is quite restricted. The main projections of the lower bank are to the pulvinar complex, with only minor connections to the Li and intralaminar (CL) nuclei. The rostral portion of the lower bank (area Pro and rostral area TEa) is related mainly to caudal and medial regions of the PM nucleus, up to the caudal pole. The middle sector of the lower bank (middle area TEa and area TEm) has substantial connections with central and lateral portions of the PM nucleus as well as with the PI nucleus. In addition, this sector has projections to the PL nucleus. The caudal portion of the lower bank (caudal area TEa, and area OAa or MT) projects predominantly to the lateral PM nucleus and also to the PL, PO, and PI nuclei (see Table 1). These connections to the pulvinar complex are in agreement with earlier reports (Maunsell and Van Essen 1983a; Standage and Benevento 1983; Ungerleider et al. 1984). Thus, it seems that the rostral portion of the lower bank projects more medially within the PM nucleus, whereas the caudal portion projects more laterally.

The cortex of the rostral depth of the STS, area IPa, like that of the rostral upper and lower banks, has a

Table 1. Summary of the corticothalamic connections of the cortex of the upper and lower banks of the superior temporal sulcus

	Upper bank of the STS		
	Pro, TPO_1	TPO_2, rostral TPO_3	Caudal TPO_3, TPO_4
Pulvinar	Caudal and medial PM PO	Central PM PO	Rostral and lateral PM PO, PL
Mediodorsal	Medial MD		Lateral MD
Intralaminar	CSL		CSL, CL, Pcn, Li-SG
Limitans-suprageniculate	Li-SG		Li-SG

	Lower bank of the STS		
	Pro, rostral TEa	Middle TEa, TEm	Caudal TEa, OAa
Pulvinar	Caudal and medial PM PI	Central and lateral PM PI, PL	Lateral PM PI, PL, PO
Intralaminar	–	–	CL
Limitans-suprageniculate	Li	Li	–

substantial projection to the PM nucleus, extending up to the caudal pole. This region has only minor connections to the PO, PI, and PL nuclei, as well as to the Li and Pcn nuclei. Unlike the rostral upper bank, area IPa has no projections to the GM complex or to the SG nucleus.

There seem to be similarities as well as differences in corticothalamic connections between multimodal area TPO of the upper bank, and the surrounding unimodal cortices of the STG as well as those of the lower bank and the inferior temporal region (ITR). The STG is connected mainly with the magnocellular and parvocellular divisions of the GM complex, and with the PM and PL nuclei of the pulvinar complex (Trojanowski and Jacobson 1975; Pandya et al. 1986). In contrast, multimodal area TPO of the STS projects heavily to the central portion of the PM nucleus and to the Li-SG nucleus. The unimodal visual areas of the lower bank of the STS and of the ITR differ from area TPO in terms of corticothalamic connectivity. Thus, the middle and caudal portions of the ITR and of the lower bank project heavily to the PI and PL nuclei, with minor projections to the PM nucleus. The rostral ITR and lower bank are related strongly to the medial portion of the PM nucleus, and also have projections to the PI nucleus.

In a previous study (Yeterian and Pandya 1989b), it was observed that the central portion of the PM nucleus provides a major source of input to multimodal area TPO. The present observations indicate that all sectors of area TPO project to the PM nucleus. However, a comparison of the corticothalamic connections of the TPO subregions suggests that the middle portion of the upper bank, areas TPO_2 and TPO_3, projects preferentially to the central sector of the PM nucleus. In contrast, the rostral subdivision, area TPO_1, tends to project to more caudal and medial regions of the PM nucleus, whereas the caudal subdivision of the upper bank, area TPO_4, is related mainly to rostral and lateral portions of the PM nucleus. Moreover, just as at the cortical level the multimodal region of the STS is surrounded by unimodal association areas (Seltzer and Pandya 1978), at the thalamic level the central portion of the PM nucleus is surrounded by zones projected upon by unimodal cortical regions (Trojanowski and Jacobson 1975; Yeterian and Pandya 1985; Pandya et al. 1986; Rosene and Pandya, unpublished observations).

The unimodal association areas of the STG (auditory) and ITR (visual) surrounding the multimodal regions of the STS have been shown to have progressive architectonic features, with emphasis on infragranular layers at the temporal polar region, and on supragranular layers more distally (Pandya and Yeterian 1985). These architectonic progressions are paralleled by specific patterns of corticocortical and subcortical connectivity (Pandya and Sanides 1973; Galaburda and Pandya 1983; Rosene and Pandya 1983, and unpublished observations; Pandya et al. 1986). Similarly, multimodal area TPO of the upper bank of the STS has been shown to contain subareas (TPO_1–TPO_4) with progressive architectonic features (Seltzer and Pandya 1989b). Each of these areas has distinctive corticocortical connectivity (Seltzer and Pandya 1989a). The present data indicate that these subregions of area TPO have differential corticothalamic connections as well. Therefore, as has been shown for surrounding unimodal regions (Weber and Yin 1984; Pandya and Yeterian 1985; Pandya et al. 1986), it seems that systematic shifts in corticothalamic connectivity are consistent with the concept of progressive differentiation at the cortical level (Sanides 1969, 1972; Pandya and Yeterian 1985).

The present observations, together with those of other investigations (Maunsell and Van Essen 1983a; Standage and Benevento 1983; Maioli et al. 1984; Ungerleider et al. 1984; Benevento and Rezak 1976; Burton and Jones 1976; Trojanowski and Jacobson 1976; Yeterian and Pandya 1989b), indicate that the STS has a major anatomical relationship with the pulvinar. It is not unreasonable to assume that this connectivity has a role in complex perceptual processes. In this regard, it is of interest to compare the functions of the cortex of the STS with those of the pulvinar. Physiological and behavioral studies have indicated that there are functionally distinct zones within the cortex of the STS. The cortex of the upper bank, in particular area TPO, contains neurons that have large receptive fields and that are responsive to multimodal as well as unimodal stimuli (Benevento et al. 1977; Desimone and Gross 1979; Bruce et al. 1981; Baylis et al. 1987; Hikosaka et al. 1988). Moreover, certain neurons in this region respond preferentially to facial features and facial motion (Bruce et al. 1981; Perrett et al. 1982, 1984, 1985a, b, 1987; Desimone et al. 1984; Rolls 1984; Baylis et al. 1985, 1987; Rolls et al. 1985, 1987, 1989; Rolls and Baylis 1986; Hasselmo et al. 1989a, b). The results of lesion behavior studies have implicated neurons of the upper bank of the STS in functions such as multimodal attention (Heilman et al. 1971) and intermodal associations (Petrides and Iversen 1978). Caudally within the STS, area OAa (areas MT, MST, and FST) contains neurons that have large receptive fields, and that are sensitive to stimulus dimensions such as speed, direction and orientation, and are thought to have an important role in the perception of visual motion and in visual tracking (Zeki 1978b, c; Gattass and Gross 1981; Maunsell and Van Essen 1983b, c, 1987; Albright 1984, 1989; Albright et al. 1984; Perrett et al. 1985a; Desimone and Ungerleider 1986; Saito et al. 1986, 1989; Tanaka et al. 1986, 1989; Albright and Desimone 1987; Komatsu and Wurtz 1988a, b; Erickson and Dow 1989; Erickson et al. 1989; Komatsu and Wurtz 1989; Logothetis and Schall 1989; Newsome et al. 1989; Raiguel et al. 1989; Rodman and Albright 1989; Tanaka and Saito 1989). The results of lesion behavior studies complement the physiological observations. Thus, ablations involving area OAa, in particular areas MT or MST located in this region, produce deficits in visual pursuit movements (Newsome et al. 1985; Dürsteler et al. 1987; Dürsteler and Wurtz 1988; Newsome and Paré 1988; Newsome and Wurtz 1988). Other behavioral studies have implicated this region in visual attentional and exploratory processes (Wilson et al. 1977; Luh et al. 1986). The neurons of the rostral and middle portions of the lower bank (areas TEa and TEm) are predominantly unimodal (visual), and are responsive to stationary stimuli (Desimone and Gross 1979; Baylis et al. 1987). A limited number of neurons in the rostral portion of the lower bank, in particular in area TEa and also in area IPa, have been shown to be involved in the perception of faces (Bruce et al. 1981; Perrett et al. 1982; Desimone et al. 1984; Rolls and Baylis 1986; Baylis et al. 1987; Hasselmo et al. 1989a, b).

Although physiological and behavioral studies have implicated the pulvinar in complex functions, its specific contributions remain to be determined (Jones 1985; Bender 1988). Neurons in the pulvinar have been shown to have large visual receptive fields and to be responsive to moving visual stimui (Mathers and Rapisardi 1973). In addition, certain neurons in the pulvinar have been shown to have multimodal response properties (Gattass et al. 1978b; Magariños-Ascone et al. 1988). The inferior and lateral pulvinar nuclei are retinotopically organized (Gattass et al. 1978a; Bender 1981), and contain neurons that are sensitive to various features of stimulus movement (Mathers and Rapisardi 1973; Gattass et al. 1979; Benevento and Miller 1981; Bender 1982; Robinson and Petersen 1985). Moreover, neurons in both nuclei are involved in saccadic eye movements (Petersen et al. 1985, 1987; Robinson et al. 1986). The results of lesion behavior studies concur with physiological observations to some extent. A role for the PI (and PL) nucleus has been shown in visual pattern discrimination (Chalupa et al. 1976, 1977; Nagel-Leiby et al. 1984). The involvement of the pulvinar in functions such as visuospatial attention and visual scanning has been suggested, but remains controversial (Ungerleider and Christensen 1977, 1979; Leiby et al. 1982; Bender and Butter 1987; Bender 1988). Finally, a role for the pulvinar in intentional and decisional processes relating to motor programming also has been proposed (Acuña et al. 1983, 1986; Yirmiya and Hocherman 1987; Cudeiro et al. 1989).

There appear to be certain commonalities between the known functions of specific regions of the STS and those of the pulvinar nuclei. Thus, area TPO of the upper bank, which contains multimodal as well as unimodal neurons (e.g., Bruce et al. 1981; Baylis et al. 1987), is connected mainly with the PM nucleus, which also has neurons with both types of response properties (Gattass et al. 1978b). Area OAa in the caudal portion of the STS contains neurons that have been shown to be involved in visual motion processing (e.g., Desimone and Ungerleider 1986), and is connected with the PI, PL, and the PM nuclei. The neurons of the PI and the PL nuclei have been shown to be responsive to visual stimulus movement, and are sensitive to direction (Mathers and Rapisardi 1973; Gattass et al. 1979; Benevento and Miller 1981; Bender 1982; Robinson and Petersen 1985). Areas TEa and TEm of the lower bank of the STS contain neurons which, unlike those of the upper bank, respond to simple as well as complex stimuli (e.g., Baylis et al. 1987). These areas are related preferentially to the PI and the PL nuclei, and to a lesser extent to the PM nucleus, except for their rostralmost portion which has substantial projections to the PM nucleus. Behavioral studies of the PI and the PL nuclei have suggested their role in visual pattern discrimination (Chalupa et al. 1976; Nagel-Leiby et al. 1984). Therefore, the corticothalamic connectivity between the STS and the pulvinar may provide a substrate whereby these regions contribute to similar processes, such as multimodal function and visual motion perception.

In conclusion, a comparison of the present data with those of a study of thalamocortical connections using a retrograde tracer (Yeterian and Pandya 1989b) indicates that the corticothalamic connections of the upper bank of the STS appear to reciprocate the thalamic input to this region. These corticothalamic connections are quite substantial, and may have a significant role in the modulation of thalamocortical influences in a manner similar to feedback connections at the cortical level (Rockland and Pandya 1981; Maunsell and Van Essen 1983a; Pandya and Yeterian 1985).

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