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The Thalamic Relations of the Caudal Inferior Parietal Lobule and the Lateral Prefrontal Cortex in Monkeys: Divergent Cortical Projections From Cell Clusters in the Medial Pulvinar Nucleus

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ABSTRACT

The thalamic relations of the caudal inferior parietal lobule and the dorsolateral prefrontal cortex in monkeys have been investigated with both anterograde and retrograde neuroanatomical tracing techniques.

The results of these experiments indicate that the medial pulvinar nucleus (Pul.m.) is the principal thalamic relay to the gyral surface of the caudal inferior parietal lobule (area 7a). Within the Pul.m. there are two or three disklike aggregates of neurons which project to area 7a; these disklike neuronal aggregates are oriented from dorsomedial to ventrolateral and extend over most of the rostrocaudal extent of the nucleus. Within these disks there are rodlike clusters of neurons which are elongated in the rostrocaudal dimension of the thalamus, and which project in a topographically ordered manner to area 7a. Thus, the more rostrally located neurons within the Pul.m. disks project to more rostral parts of area 7a and, conversely, the more caudally located neurons project to the caudal part of this cortical field. Similarly, the medial part of each disk projects to the *lateral* part of area 7a while the laterally placed neurons project to the *medial* part of the cortical field. In addition to its input from the Pul.m., area 7a is also reciprocally connected with the magnocellular division of the nucleus ventralis anterior, with the nuclei which abut upon the medullary capsule of the laterodorsal nucleus, and with the suprageniculate nucleus and the nucleus limitans.

The cortex on the lateral bank of the intraparietal sulcus (the so-called lateral intraparietal area, LIP) projects principally to the lateral pulvinar nucleus (Pul.l) of the thalamus rather than to Pul.m. Area LIP has been found to project to the pregeniculate nucleus, the zona incerta, the anterior pretectal nucleus, and the superior colliculus. Area 7a projects to none of these structures, but it does project to the posterior pretectal nucleus. The thalamic relations of the neighboring cortical regions, such as the prelunate gyrus and area 7b, are also distinct from those of area 7a. It thus seems that the prelunate gyrus is primarily interconnected with the Pul.l., and area 7b with the oral pulvinar nucleus. Taken together these different subcortical relationships provide further evidence for the view that the caudal inferior parietal lobule is not a homogeneous cortical area, but is composed of a number of subsidiary fields.

The projection from the Pul.m. to the lateral prefrontal cortex arises from disklike aggregates of neurons, similar in their orientation to the neuronal disks that project to area 7a. These two populations of Pul.m.

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neurons occupy partially overlapping zones so that after large dye injections into both the parietal and frontal lobes there are label-free spaces between the disklike neuronal aggregates. However, although they overlap, it is evident from double labeling experiments with distinct retrogradely transported fluorescent dyes that the two populations of cortically projecting neurons are essentially separate.

Key words: posterior parietal cortex, inferior parietal lobule, lateral prefrontal cortex

In recent years the physiological properties of individual neurons in the associational cortex of the inferior parietal lobule have been subject to extensive analysis in behaving monkeys. As a result there is now a substantial body of evidence indicating that visually responsive neurons in the caudal inferior parietal lobule play a central role in the integration of spatial orientation and attention (Hyvärinen and Poranen, '74; Mountcastle et al., '75; Lynch et al., '77; Mountcastle, '81; Motter and Mountcastle, '81; Mountcastle et al., '81; Andersen and Mountcastle, '83; Bushnell and Goldberg, '81). Both spatial orientation and selective visual attention are known to be significantly compromised following lesions that involve the inferior parietal lobule in human patients (Critchley, '53) and in macaque monkeys (Ettlinger and Kalsbeck, '62; Ungerleider and Brody, '77; LaMotte and Acuña, '78). However, it is evident that these complex neural functions are not unique to the inferior parietal lobule since similar deficits have also been reported after lesions involving the prefrontal cortex (Critchley, '53; Heilman and Valenstein, '72), the cortex lining the superior temporal sulcus, the cingulate cortex, and the medial pulvinar nucleus of the thalamus (Critchley, '53; Chalupa et al., '76; Chalupa, '77; Ungerleider and Christensen, '77, '79; Keys and Robinson, '79; Ogren et al., '84). Moreover, recent single-unit studies have begun to reveal similarities in the discharge properties of neurons in certain of these other regions with those in the inferior parietal lobule (Bizzi, '68; Bizzi and Schiller, '70; Mohler et al., '73; Mountcastle et al., '75; Wurtz and Mohler, '76a; Lynch et al., '77; Suzuki and Azuma, '77; Pigarev et al., '79; Mikami et al., '82; Goldberg and Bushnell, '81; Petersen et al., '82; Acuña et al., '83).

To further our understanding of the neural mechanisms that control spatial orientation and attention, it is important to define more precisely the distribution of the various afferent and efferent connections of the inferior parietal lobule and especially its interrelationship with the pulvinar complex of the thalamus, which has been known for almost 50 years to be the principal subcortical relay to the inferior parietal lobule (Le Gros Clark and Northfield, '37). Retrograde cell degeneration studies had suggested that the cortical relations of the pulvinar complex were rather diffuse and included not only the parietal cortex but also extensive areas of the occipital and temporal lobes (Le Gros Clark and Northfield, '37; Walker, '38; Chow, '50). However, more recent studies have established that each of the various subdivisions of the pulvinar complex has rather circumscribed connections with particular cortical fields (Campos-Ortega and Hayhow, '72; Trojanowski and Jacobson, '74, '75, '76; Bos and Benevento, '75; Benevento and Rezak, '76; Mesulam et al., '77; Baleydier and Mauguière, '77, '85; Stanton et al., '77; Divac et al., '77; Kasdon and Jacobson, '78; Pearson et al., '78; Rezak and Benevento, '79; Standage and Benevento, '83; Ungerleider et al., '84; Mufson and Mesulam, '84; Weber and Yin, '84). Nevertheless, the exact distribution of the thalamocortical relay cells which project to the inferior parietal lobule remains unclear. Since there is increasing evidence that the area is subdivided, with respect to both function and connections (Seltzer and Pandya, '80; Pandya and Seltzer, '82; Andersen et al., '85), it is important to define more precisely the organization of its thalamic input and to determine to what extent one of the principal nuclei involved, the medial nucleus of the pulvinar complex—Pul.m., is interconnected with other cortical fields.

Detailed anatomical and physiological studies of several principal thalamic relay nuclei in rodents, cats, and monkeys have demonstrated the existence of distinct subsidiary units within cytoarchitectonically uniform nuclei (see Jones '84 for review). This has been most thoroughly studied in the ventrobasal complex of monkeys, where systematically arranged, rostrocaudally elongated, rodlike aggregations of medial lemniscal axonal arborizations (Jones, '83) and of thalamocortical relay neurons projecting to punctate loci within the somatic sensory cortex (Jones et al., '79; Jones and Friedman, '82) have been correlated with the rostrocaudally elongated foci of neuronal activity seen in this nucleus following localized and modality specific somatic sensory stimuli (Poggio and Mountcastle, '63; Jones et al., '82; Juliano et al., '83). Distinct rodlike aggregations of afferent terminations and of relay neurons projecting to cortical foci have also been demonstrated in the ventrolateral complex of the monkey (Jones et al., '78; Thach and Jones, '79; Asanuma et al., '83a), and in the medial geniculate nucleus of the cat (Andersen et al., '80a,b; Middlebrooks and Zook, '83), suggesting that the transmission of ascending information through these other thalamic nuclei also takes place through similar systematically organized modules. There is some evidence for a similar topographic and focal organization in the inferior division of the pulvinar nucleus (on the basis of the corticothalamic projections which it receives from the visual cortex—Campos-Ortega and Hayhow, '72) and it is therefore of some interest to determine whether a comparable organization exists in the connections between the pulvinar and the inferior parietal lobule.

With these issues in mind, we have reexamined the thalamocortical and corticothalamic relations of the inferior parietal lobule in monkeys using the recently introduced method for tracing afferent pathways based on the retrograde transport of fluorescent dyes and the anterograde transport of ^{3}H-labeled proteins, respectively. In particular we have attempted: (1) to define the organization within the pulvinar complex of the cells that project to the visually re-

sponsive, caudal inferior parietal lobule; (2) to explore differences in the thalamic relationships of the caudal inferior parietal lobule from those of other subdivisions of the inferior parietal lobule; and (3) to examine the relationship of the cells within the medial nucleus of the pulvinar which project to the inferior parietal lobule with those that project to the prefrontal cortex. A preliminary report of some of these findings has been presented earlier (Asanuma et al., '82).

MATERIALS AND METHODS

This study is based on 20 experiments carried out on ten cynomolgus monkeys. All the experimental procedures were carried out with the animals under Ketamine and Nembutal anesthesia, and with full aseptic precautions. In ten of the experiments the autoradiographic technique for tracing connections was used. In five experiments, the retrograde transport of the fluorescent dyes fast blue (FB) or true blue (TB)—which selectively label cytoplasmic components—was used. In the remaining five experiments, the retrogradely transported fluorescent marker nuclear yellow (NY) was used.

Autoradiographic experiments

For the autoradiographic experiments equal parts of ^{3}H-proline (L(2-, 3-, or 5- ^{3}H-proline), specific activity 17 or 13 Ci per mmol) and ^{3}H-leucine (L(4- or 5- ^{3}H-leucine), specific activity 47 Ci per mmol) which had been evaporated to dryness and then reconstituted in normal saline to yield a final activity of 100 μCi/μl, were injected into the appropriate cortical region. Either single or multiple injections of 0.4–0.5 μl of the isotope mixture were made over periods of 15–30 minutes through a 1.0-μl Hamilton syringe. After survival periods of 2–7 days, the animals were perfused through the heart with saline followed by 10% formalin in 0.1 M phosphate buffer. After a further period of fixation in the same solution, the brains were removed, photographed, and blocked. Three brains were dehydrated and embedded in Paraplast. From these, serial sections 25 μm in thickness were cut and every tenth section was mounted, defatted, hydrated, and coated with Kodak NTB-2 emulsion as described by Cowan et al. ('72). After exposure at 4°C for 4–12 weeks, the autoradiographs were developed in Kodak D19, fixed, and stained through the emulsion with 0.5% thionin at low pH. The remaining seven brains were equilibrated in a 20% sucrose solution prior to sectioning at 30 μm on a freezing microtome. Again a one-in-ten series of sections from each brain was mounted on gelatinized slides and processed for autoradiography in the manner outlined above.

Projection drawings of the relevant sections containing the injection sites and the thalamic nuclei to which the label had been transported were made using a Beseler projection apparatus. The detailed analysis of the cytoarchitecture was done on a Wild dissecting microscope equipped with a camera lucida, and the terminal labeling was plotted under a compound microscope. The effective injection site was considered to be the entire zone in which there was a dense accumulation of silver grains over neuronal cell bodies; local concentrations of silver grains overlying the neuropil in the regions to which the label had been transported were interpreted as terminal labeling.

Retrograde labeling experiments

The afferents to the inferior parietal lobule were investigated using certain of the fluorescent markers introduced by Kuypers and his colleagues (Van der Kooy and Kuypers, '79; Bentivoglio et al., '80). This approach enabled us to compare directly the nature and distribution of the thalamic inputs either to two locations within the inferior parietal lobule or to the inferior parietal lobule and the frontal lobe, in single animals. For these experiments single or multiple injections of 0.5 μl of a 5% aqueous solution of FB or TB, or a 2% solution of NY, were made into the appropriate cortical region over a period of 15–30 minutes, again using a 1-μl Hamilton syringe. After survival times of 2 weeks in the case of the FB and TB injections, and 2–3 days for those with injections of NY, the animals were perfused and their brains prepared for frozen sectioning in the manner described earlier for the autoradiographic experiments.

Again, projection drawings through the injection sites and the thalamus were made with the projection apparatus using an ultraviolet filter. The locations of the injection sites and of the retrogradely labeled neurons were plotted onto these drawings using a Leitz Dialux 20 fluorescence microscope equipped with a mercury ultraviolet light source and filter system "A". Photographs of these sections were also made with a Nikon photomicrographic camera. Most of these brains were also used for the autoradiographic experiments described previously; the analysis of the dye labeling was done prior to the autoradiographic procedure and thionin counterstaining.

Olszewski's ('52) atlas was used for the delineation of the various thalamic nuclei except for the posterior complex, which was subdivided according to the criteria proposed by Burton and Jones ('76). The localization of the injection sites on the gyral surface of the inferior parietal lobule was based in part on the cytoarchitectonic subdivision of areas 7a (PG) and 7b (PF) made by Vogt and Vogt ('19) and by Von Bonin and Bailey ('47) (see Fig. 1A,B). Area 7a, as we delineate it, is limited to the gyral surface of the caudal inferior parietal lobule, as is illustrated in Figure 1C; it does not include the medial superior temporal area, area MST, recently identified by Maunsell and Van Essen ('83), on the dorsal bank of the superior temporal sulcus. A further zone within the caudal aspect of the lateral bank of the intraparietal sulcus, corresponding to the caudal half of area POa of Seltzer and Pandya ('80), has also been identified. Although it corresponds, in part, to area POa of Seltzer and Pandya ('80), it is clearly distinct, both anatomically and physiologically, from the anterior half of area POa (Andersen et al., '85; Siegel et al., '85). To avoid confusion, therefore, we shall refer to this field as the lateral intraparietal area (LIP).

RESULTS

Cytoarchitecture

Four distinct nuclei can be recognized in the pulvinar complex of monkeys (Olszewski, '52; Fig. 2), these are the oral pulvinar nucleus (Pul.o.), the medial pulvinar nucleus (Pul.m.), the lateral pulvinar nucleus (Pul.l.), and the inferior pulvinar nucleus (Pul.i.). Together with the lateroposterior nucleus (LP) these nuclei constitute the lateral group of nuclei as defined by Le Gros Clark ('36); the whole complex occupies a large, winglike mass in the caudolateral part of the dorsal thalamus. Each of the nuclei is composed principally of multipolar, medium-sized, and medium-staining neurons, but with some small, lightly staining neurons interspersed. Although the entire region appears to be relatively homogeneous, there are subtle differences in cellu-

lar packing density and in the staining characteristics of the neurons present which allow for distinctions to be made among the constituent nuclei.

Centrally placed among the nuclei of the lateral group is the Pul.m. Its neurons are evenly dispersed, with a low packing density. The Pul.m. occupies a rostrally directed wedge-shaped mass whose base reaches to the caudal end of the dorsal thalamus. Rostromedially, the Pul.m. abuts upon the caudalmost, densocellular division of the mediodorsal nucleus (MDdc) and the central lateral nucleus (CL) of the intralaminar complex. The Pul.m. and MDdc can be readily distinguished from one another on the basis of their neuronal packing densities: The MDdc is more cellular, and its cells tend to be grouped in distinct clusters. The cells of the CL are slightly larger than those of the Pul.m., and are, again, more densely packed and more often clustered. Caudomedially, the Pul.m. adjoins the lateral habenular nucleus (HI), while ventrolaterally and dorsolaterally it is bounded by the Pul.l. and LP, respectively. The neurons of the Pul.l. are smaller, more darkly staining, and more compactly arranged than those in the Pul.m. In addition, the prominent fiber bundles that run mediolaterally through the Pul.l. give it a strikingly banded appearance even in Nissl preparations. The homogeneously distributed neurons of the LP are similar in size and staining characteristics to those of Pul.m.; however, because they are more densely packed the LP appears decidedly more cellular than the Pul.m.

Abbreviations

APN	anterior pretectal nucleus
CG	central gray
CM	centre médian nucleus
CL	central lateral nucleus
GM	medial geniculate nucleus
GL	lateral geniculate nucleus
HI	lateral habenular nucleus
LD	laterodorsal nucleus
LIP	lateral intraparietal area
LP	lateroposterior nucleus
mc	medial geniculate nucleus, magnocellular division
mf	mediodorsal nucleus, multiformis division
MD	mediodorsal nucleus
MT	middle temporal area
NOT	nucleus of the optic tract
OPN	olivary pretectal nucleus
Pa	post auditory area
PF	parafascicular nucleus
Po	posterior nucleus
PPN	posterior pretectal nucleus
Preg.	pregeniculate nucleus
Pul.i	inferior nucleus of the pulvinar complex
Pul.l.	lateral nucleus of the pulvinar complex
Pul.m.	medial nucleus of the pulvinar complex
Pul.o.	oral nucleus of the pulvinar complex
R	thalamic reticular nucleus
Ri	retroinsular area
SII	second somatosensory area
SG/Li	suprageniculate and limitans nuclei
SGI	stratum griseum intermedium of the superior colliculus
SGP	stratum griseum profundum of the superior colliculus
SGS	stratum griseum superficiale of the superior colliculus
Sub.Th.	subthalamic nucleus
TP	posterior temporal lobe
VLc	ventral lateral nucleus, pars caudalis
VLps	ventral lateral nucleus, pars postrema
VMb	basal ventromedial nucleus
VPI	ventral posterior inferior nucleus
VPLc	ventral posterolateral nucleus, pars caudalis
VPLo	ventral posterolateral nucleus, pars oralis
VPM	ventral posteromedial nucleus, pars medialis
ZI	zona incerta

(1, 2, 3a, 3b, 5, 6, 7a, 7b, 8a, 19, 45, 46—various areas of the cerebral cortex)

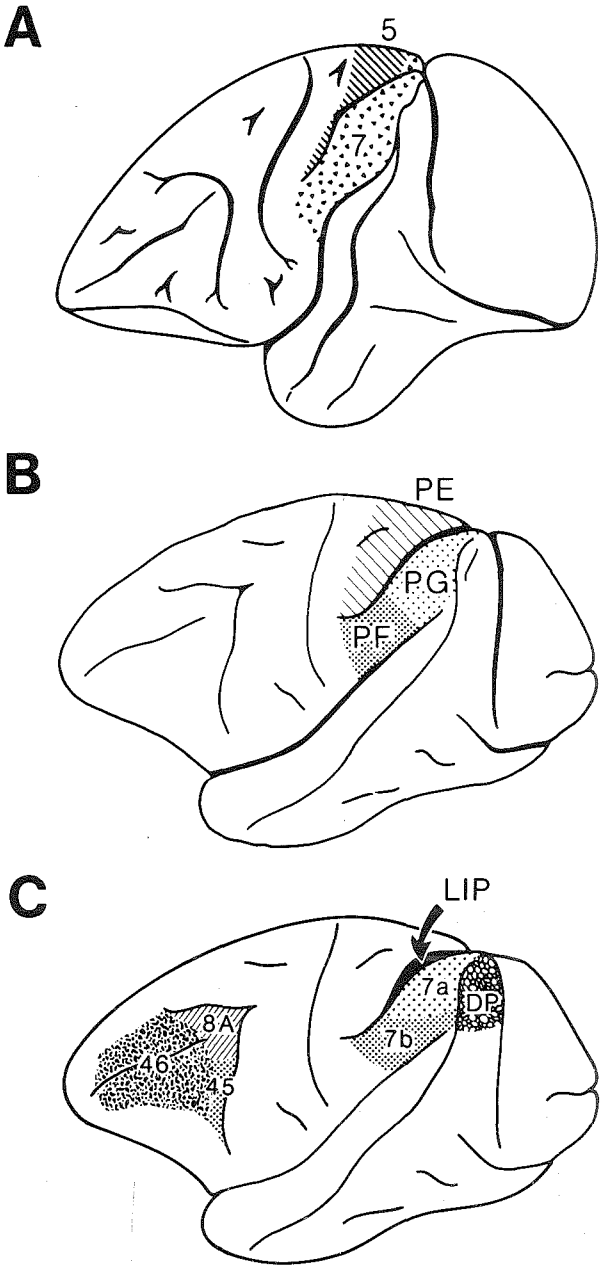

Fig. 1. Schematic diagrams to show some of the cytoarchitectonic parcellations made by (A) Brodmann ('05) in cercopithecus monkeys, and by (B) Von Bonin and Bailey ('47) in macaque monkeys. (C) illustrates the approximate locations of the major cortical areas involved in the present study.

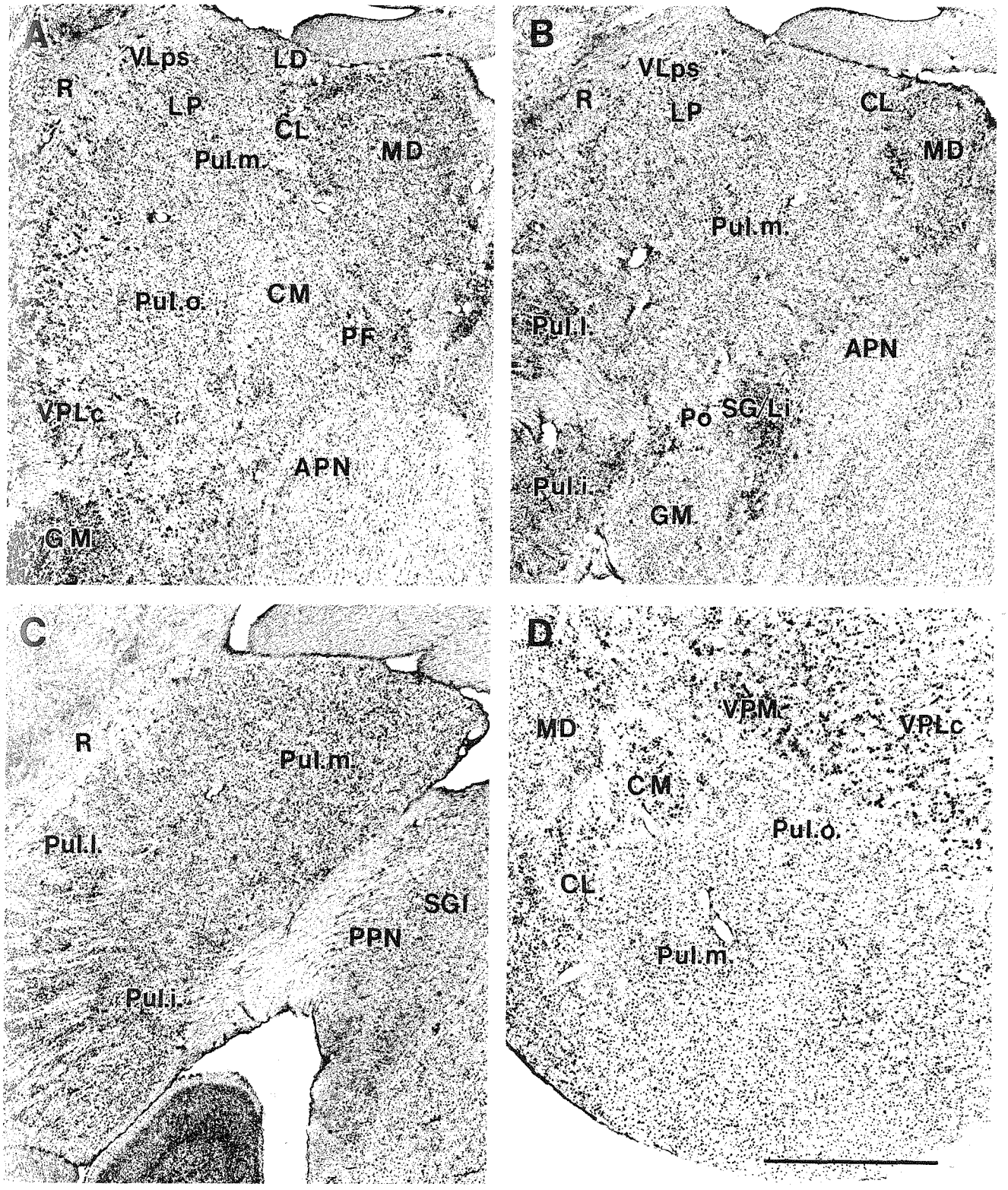

Fig. 2. A–C. Nissl-stained, frontal sections through the caudal thalamus from a *Macaca fascicularis* brain, to illustrate the topographic relationships of the nuclei of the lateral complex and the surrounding structures. D. A horizontal section through the caudal thalamus in a different brain to show the distinction between Pul.o. and Pul.m. Scale bar = 2 mm for all four photomicrographs.

At caudal levels, the suprageniculate and limitans nuclei (SG/Li), the posterior nucleus (Po), the corticotectal tract, the Pul.i., and the brachium of the superior colliculus adjoin the Pul.m. The spindle-shaped neurons of the SG/Li are more darkly staining and more compactly arranged than those in the Pul.m. In contrast, the Po is formed of small- to medium-sized pale-staining neurons which are loosely and irregularly dispersed among the fibers of the corticotectal tract. The Pul.i., which is largely separated from the Pul.m. by the corticotectal tract, is formed for the most part of medium-sized, densely packed neurons among which there are interspersed a few large, darkly staining cells.

Rostrally, the apex of the wedge-shaped Pul.m. overlies the caudal portion of the Pul.o. and since both consist of moderately staining, medium-sized cells, it is difficult to distinguish the two nuclei in frontal sections. However, the overall packing density of the cells in the Pul.o. is lower than in Pul.m. and on the whole the cells tend to be more irregularly dispersed. In horizontal sections, the boundary between the two nuclei is easier to define (Fig. 2D).

Autoradiographic studies

Area 7a. In eight of the autoradiographic experiments the injections of ^{3}H-amino acids involved area 7a (see Fig. 3A for a typical isotope injection of this type). In one of these cases area LIP was also partly labeled. In two of the experiments, the injection had spread into area 7b; in one area 5 was involved; and in another the prelunate gyrus was partially affected.

Figure 4 illustrates the findings in a typical experiment in which multiple injections of ^{3}H-amino acids were made into area 7a. In this case, there was some spread of the injected label into areas 5 and 7b, but area LIP was not affected. Following injections of this type in area 7a, anterogradely transported label is observed in a number of thalamic nuclei. Within the lateral group, the Pul.m., Pul.o., and LP all show evidence of transported label, but this labeling is densest in Pul.m. In frontal sections through this nucleus, two or three disklike labeled zones (300 μm $\times$ 2 mm) are consistently seen. These "disks" are separated by label-free regions and are oriented from dorsomedial to ventrolateral within Pul.m. extending throughout much of its rostrocaudal extent. Figure 5A and B (taken from a different case in which the injection was restricted to area 7a) are dark- and brightfield photomicrographs, respectively, of these disklike aggregates of label in Pul.m. In the brightfield illustration one can detect no distinct cytoarchitectonic correlate of these labeled regions. Among the intralaminar nuclei, only the nucleus centralis lateralis (CL) contains label, but additional labeled zones are seen in the pars caudalis and the pars postrema of the ventral lateral nucleus (VLc and VLps), in the magnocellular division of the ventroanterior nucleus (VAmc), and in the laterodorsal nucleus (LD). Labeling in the CL, VLc, VLps, LP, and LD tends to be concentrated around the margins of the fibrous lamella that surrounds the laterodorsal nucleus (see Fig. 5C,D).

As might be expected, smaller injections result in more restricted labeling. Figure 6 is an example of an experiment with a single, small ^{3}H-amino acid injection centered in, and confined to, the rostral part of area 7a. Within the thalamus of this brain, labeling is seen only in the Pul.m. and CL. Compared to the cases with the larger injections, the labeling in Pul.m. is less dense and is restricted to the rostral portion of the nucleus. And, interestingly, instead of

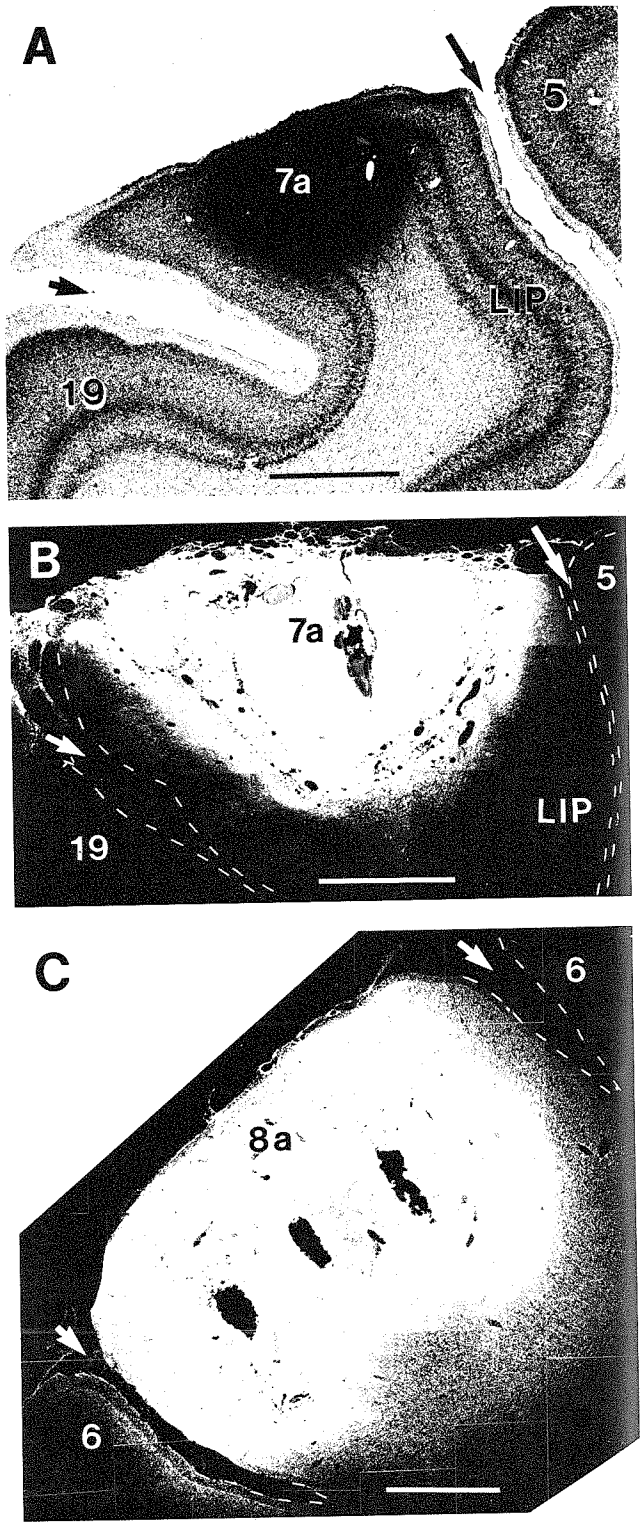

Fig. 3. Low-power photomicrographs of typical injection sites in cases in which (A) a mixture of tritiated amino acids was injected into area 7a; (B) fast blue was injected into area 7a; and (C) nuclear yellow was injected into areas 8a, 45, and 46 of the lateral prefrontal cortex. The long and short arrows in A and B mark the intraparietal and superior temporal sulci, respectively; the arrows in C indicate the arcuate sulcus. Frontal sections. All scale bars = 2 mm.

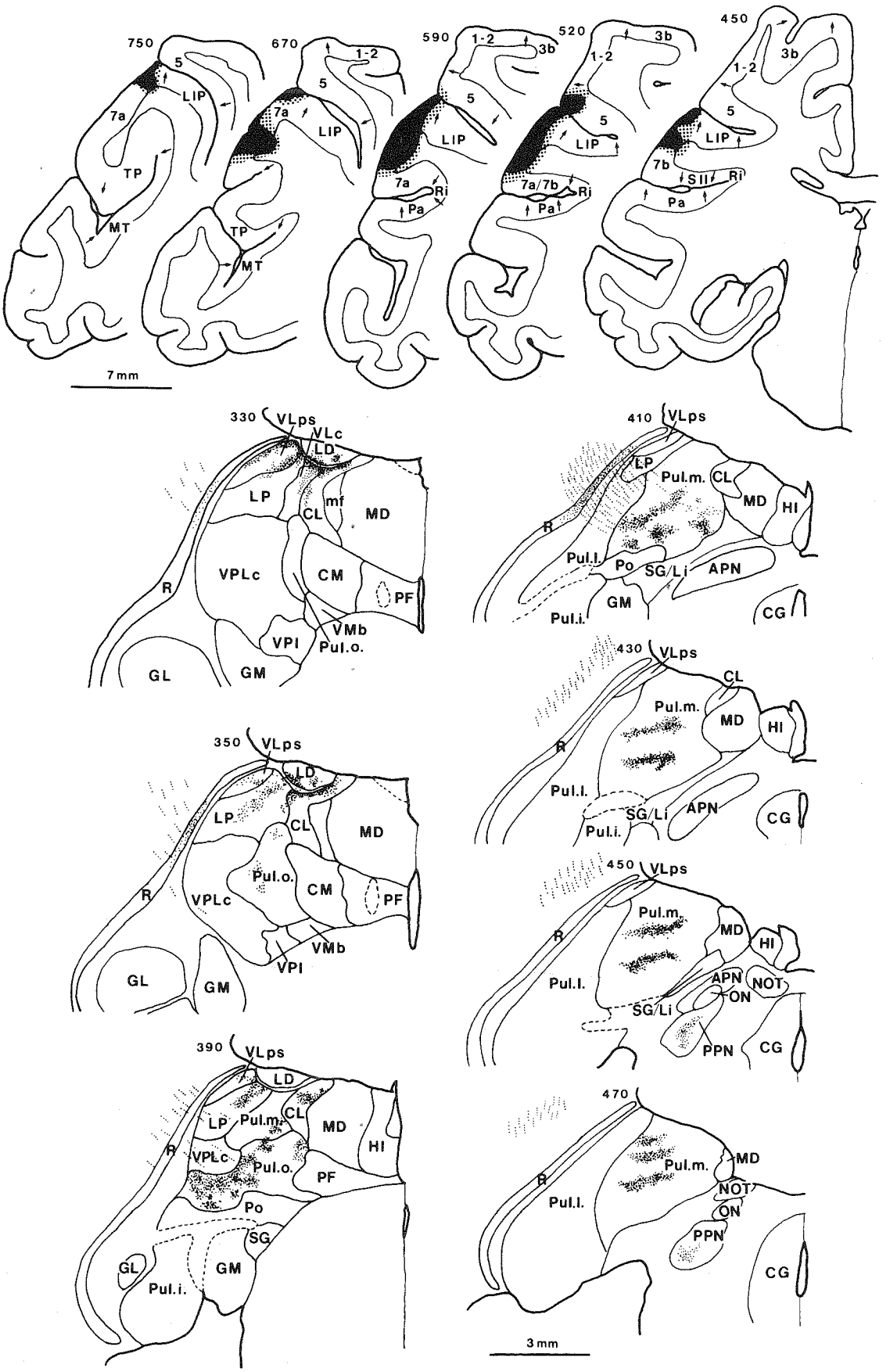

Fig. 4. Line drawings of serially arranged frontal sections through the cortex and thalamus in an experiment with multiple injections of tritiated amino acids in the exposed gyral surface of the posterior parietal cortex. The injection primarily involved area 7a, but areas 7b and 5 were also affected. Similar distinctive labeling patterns were seen in the Pul.m. in each case with large injections of this type. In this and subsequent line drawings, the numbers refer to the position of the section in the series with the rostralmost section toward the right in the cortical drawings, and in the top left in the thalamic drawings.

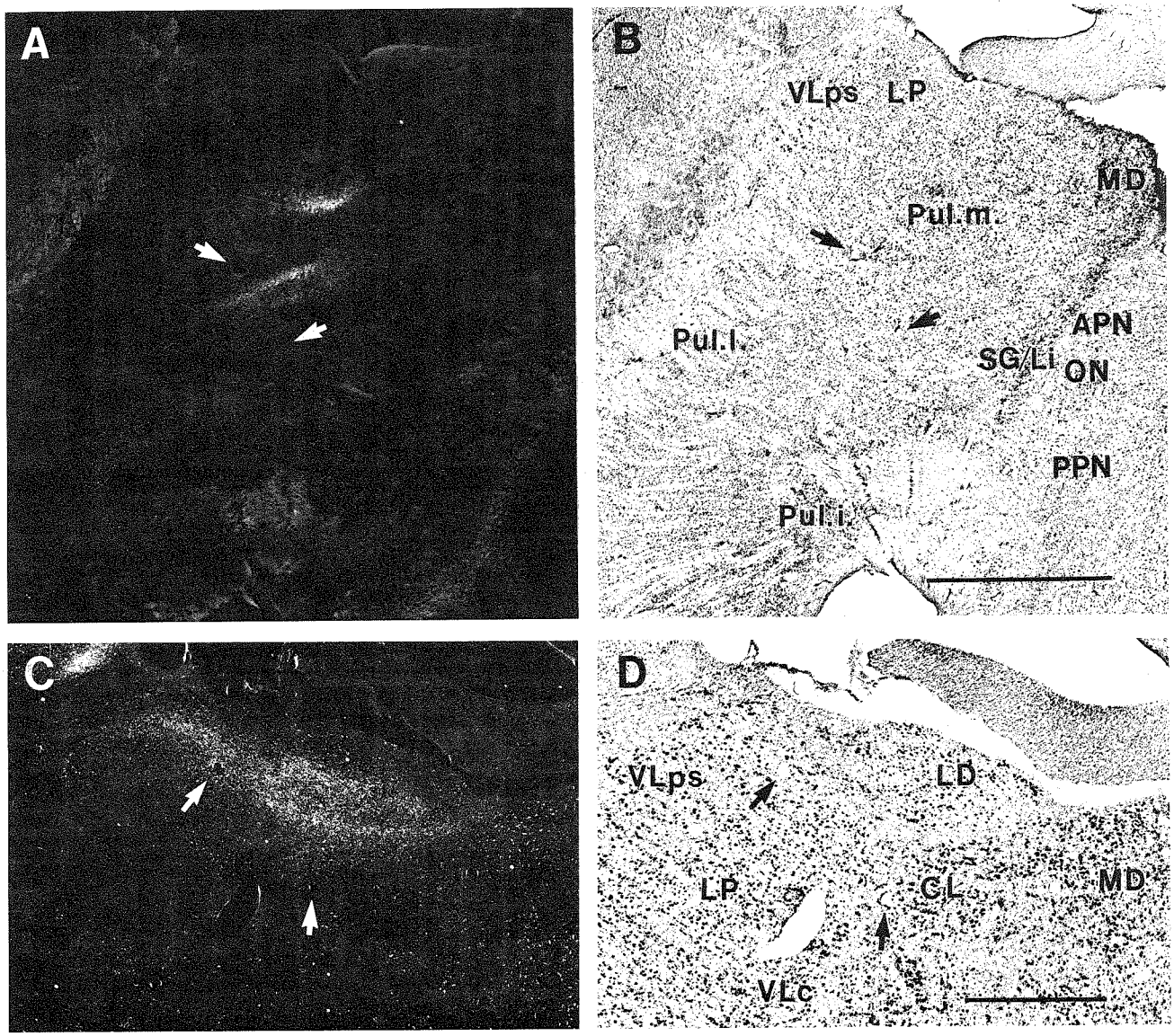

Fig. 5. Darkfield (A,C) and brightfield (B,D) photomicrographs of the disklike aggregations of the transported label in Pul.m. (A,B) and the concentration of labeling around the margins of the medullary lamina surrounding the laterodorsal nucleus, in CL, VLc, VLps, and LD (C,D) following a tritiated amino acid injection in area 7a. Frontal sections. In this and the subsequent figures of this type, the arrows point to the same identified blood vessels in the corresponding bright- and darkfield photomicrographs. Bar = 2 mm in B; 1 mm in D.

the dense disklike aggregations of label, the silver grains are clustered within punctate foci which, when examined in sequential sections, appear to be cross sections of rostrocaudally elongated rodlike aggregations of label. In occasional sections (see for example Fig. 6, section 380), these clusters of silver grains are connected to form elliptical patterns that are reminiscent of the labeling patterns seen after larger injections.

Lateral intraparietal area. Injections centered in the lateral intraparietal area (area LIP) result in a quite different pattern of distribution of the transported label within the thalamus (Fig. 7). While each of the nuclei that is labeled following injections in area 7a shows evidence of above-background densities of silver grains in these cases, there is, in addition, dense label within the Pul.l. and in the SG/Li. Within the Pul.m., the label is concentrated laterally, but is again clustered, with each cluster appearing to form the lateralmost extension of one of the disklike aggregations of label seen following area 7a injections. A thin sheet of dense terminal labeling is evident along the dorsolateral edge of the Pul.l. and extends throughout much of the rostrocaudal extent of the nucleus. In other parts of the Pul.l., the label is more clustered. The Pul.l. labeling is seen not only when the injection involves the caudal part of LIP, but also when the injection was directed toward the rostralmost portion of area LIP, close to the 7a/7b border (Fig. 8).

It would appear then that area LIP projects primarily to

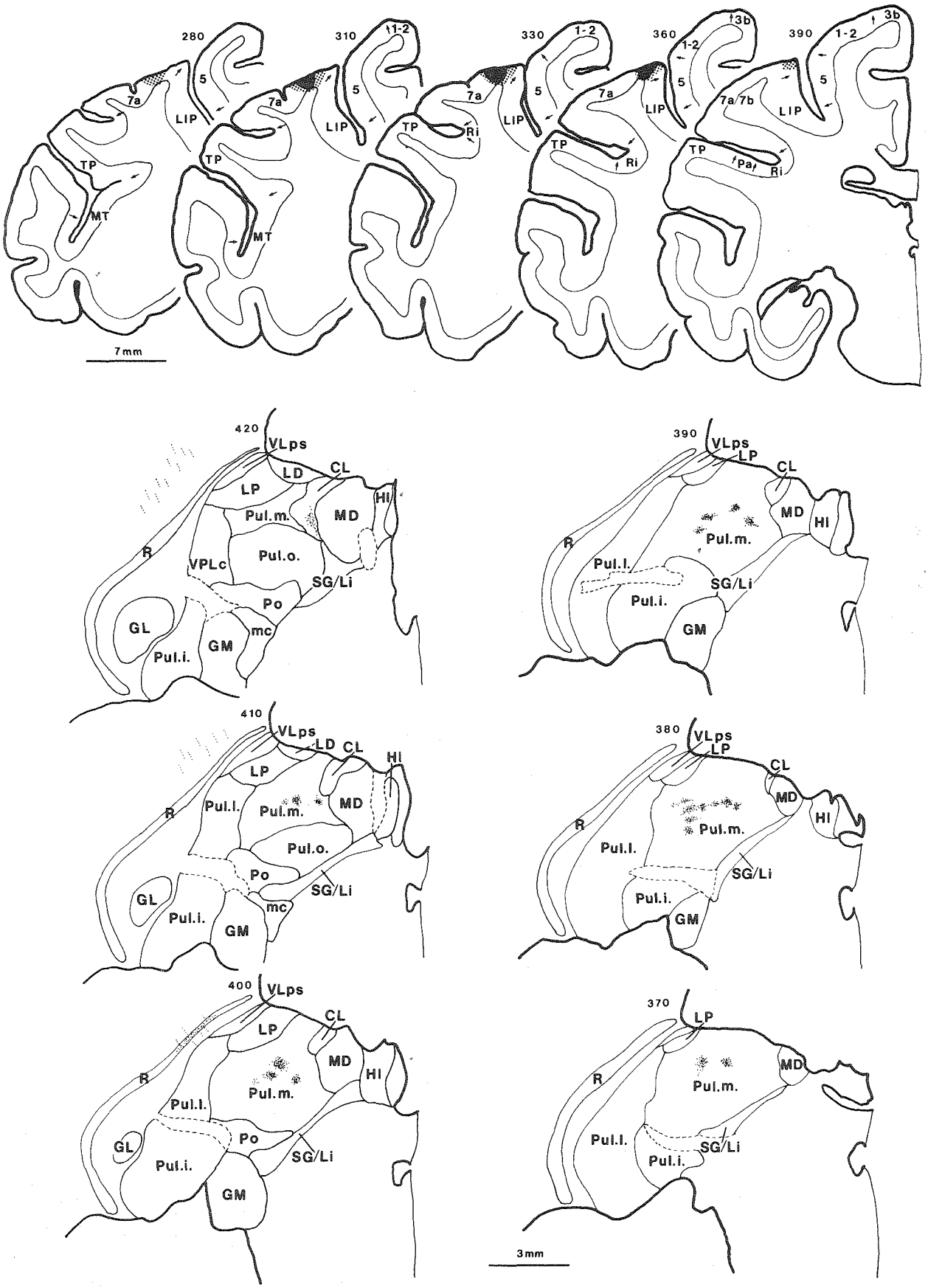

Fig. 6. Line drawings of the cortex and thalamus following a restricted injection of tritiated amino acids centered in the rostral part of area 7a. The autoradiographic labeling in this case is aggregated in punctate, rostrocaudally elongated, foci which are occasionally connected in disklike patterns.

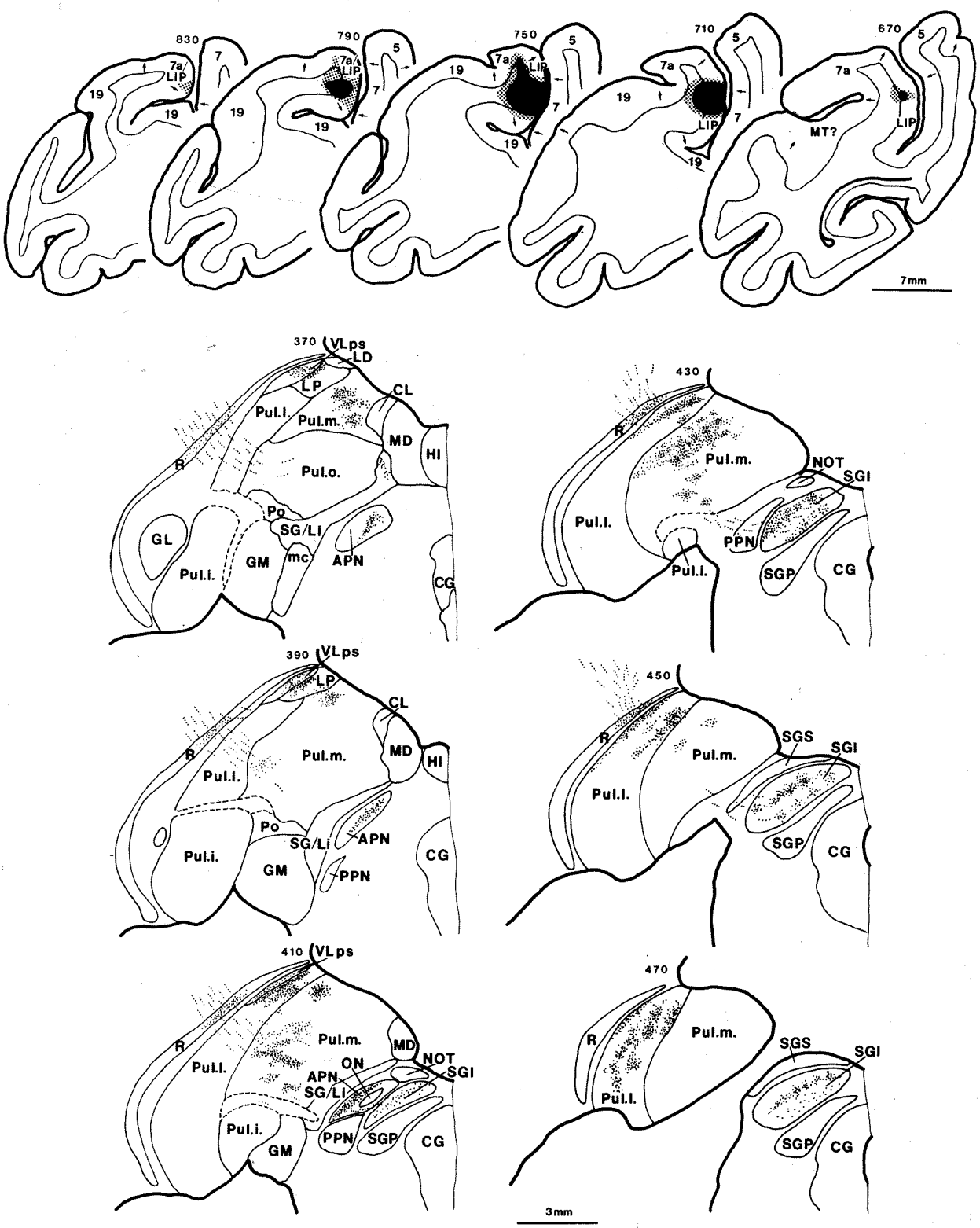

Fig. 7. Line drawings of the cortex and thalamus following a tritiated amino acid injection in the caudal part of area LIP, to show the dense labeling in Pul.l. and in Pul.m. In this case the labeling in Pul.m is located further laterally than after injections in area 7a (cf. Figs. 1, 6).

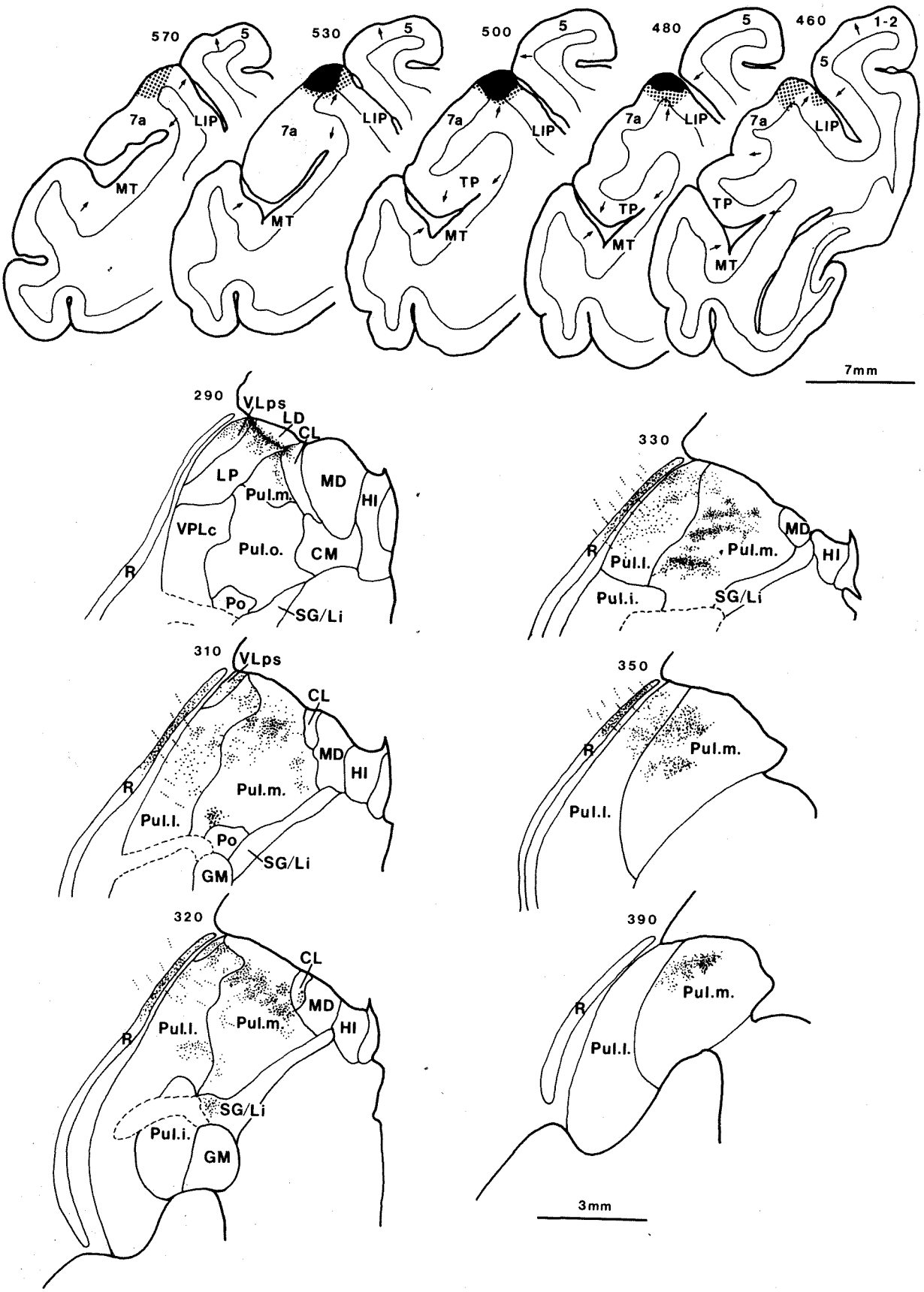

Fig. 8. Line drawings of the cortex and thalamus following a tritiated amino acid injection at the border between the rostral part of area 7a and area LIP. Though the injection was primarily in area 7a, some of the isotope had spread to involve LIP. Note that in addition to the characteristic thalamic labeling seen after area 7a injections, there is also light labeling in Pul.l.

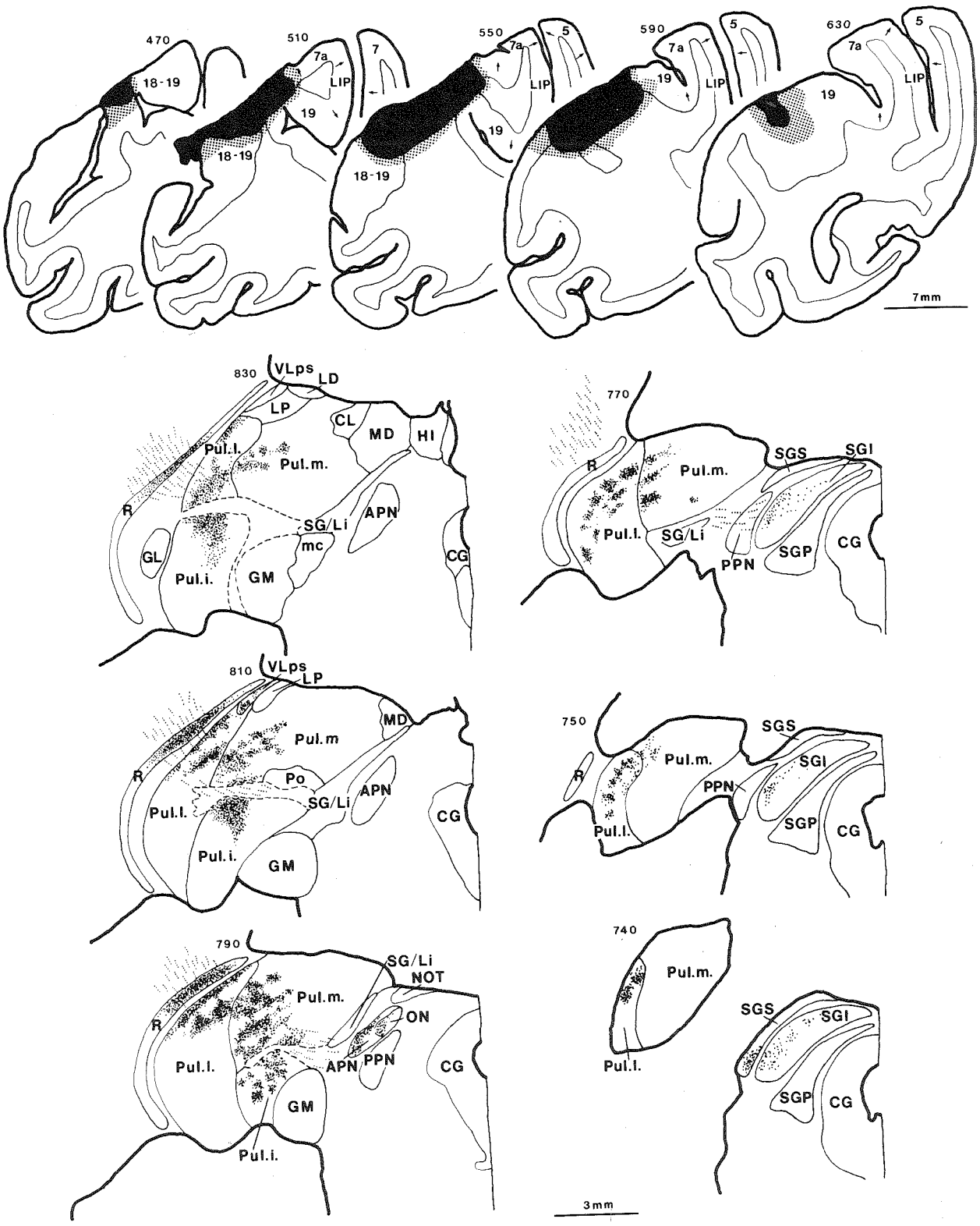

Fig. 9. Line drawings of frontal sections of the cortex and thalamus following multiple injections of tritiated amino acids in the dorsal prelunate gyrus. Dense terminal labeling occurs in Pul.l., in the lateral part of Pul.m., and in Pul.i.

the Pul.l. and in this respect is quite different from area 7a. Unfortunately, since our area LIP injections had spread into area 7a, we cannot be sure whether the labeling seen in the Pul.m. is due to involvement of area 7a, or if LIP also projects to the nucleus. However, we can say that labeling in the Pul.l. only occurs in those cases in which the injections involved the lateral bank of the intraparietal sulcus.

Dorsal prelunate gyrus. Figures 9 and 10C,D show the results of an experiment in which large multiple injections of ^{3}H-amino acids were made into the dorsal aspect of the prelunate gyrus. The injections were centered in the dorsal prelunate area (DP) in the dorsal part of the prelunate gyrus, but continued ventrally to include area V4. They were placed posteriorly in the sulcus to avoid leakage to the inferior parietal lobule, but there may have been some diffusion of the tracer to areas V3 and V3a. Neither area 7 nor area MT was involved.

In this experiment, the bulk of the labeling in the thalamus is concentrated in the Pul.l. and Pul.m., but the Pul.i is also implicated. Within the Pul.l., there is a thin sheet of dense label along the dorsolateral margin of the nucleus, which in its configuration resembles the labeling seen after area LIP injections. More densely clustered labeling is seen at the lateral edge of the Pul.m., in the caudal part of Pul.l., and throughout Pul.i. The only other thalamic nucleus in which labeling is above background is in the CL (not illustrated); the other nuclei bordering the medullary lamina

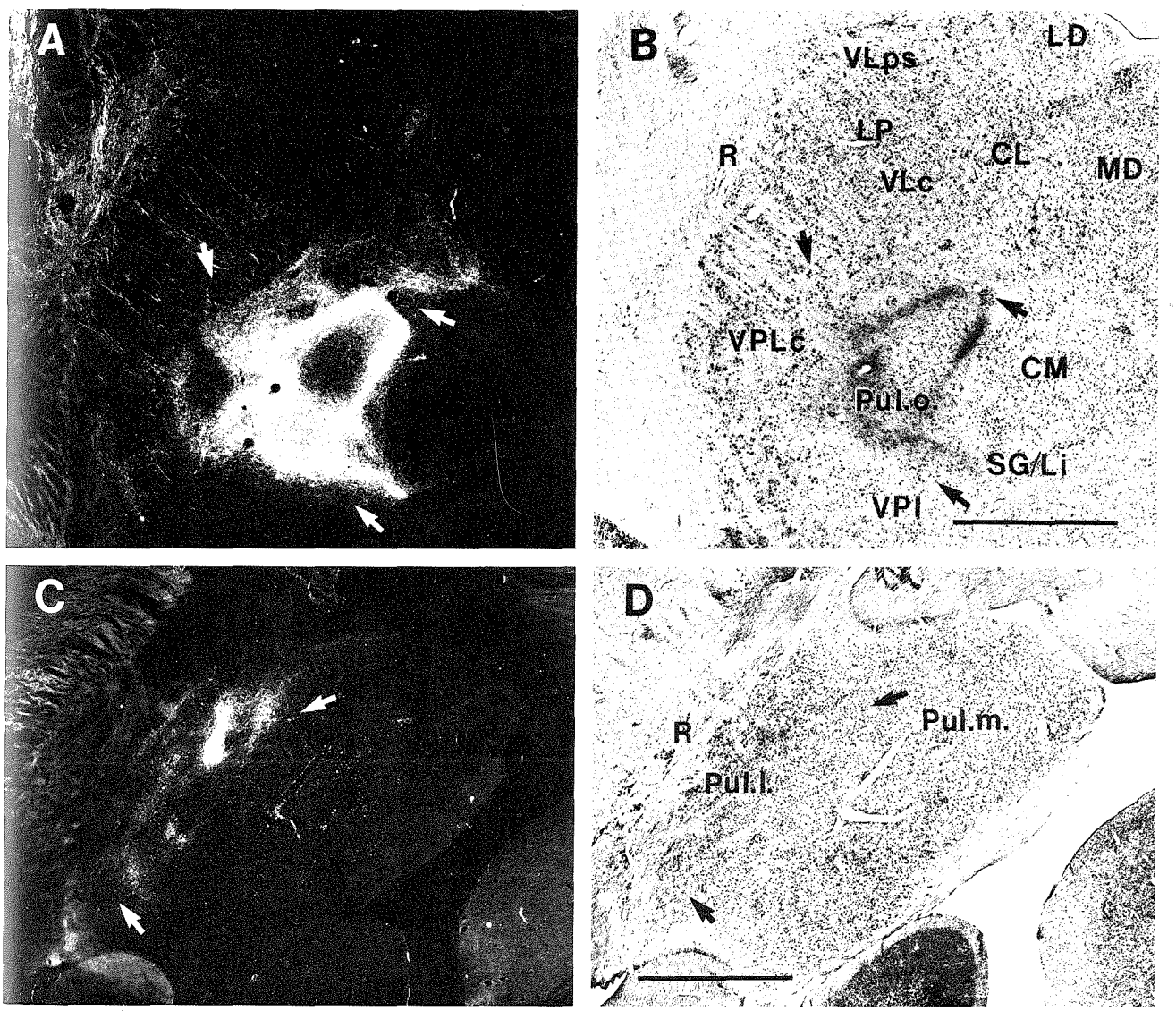

Fig. 10. Darkfield (A,C) and brightfield (B,D) photomicrographs to show the terminal labeling patterns in Pul.o. (A,B) and in Pul.l. (C,D). In A and B, the ^{3}H-amino acid injection was into area 7b; in the case shown in C and D, multiple injections of ^{3}H-amino acids were made in the dorsal prelunate gyrus. Frontal sections. Scale bars = 2 mm.

surrounding the laterodorsal nucleus (i.e., VLc, VLps, LP and LD) are completely free of transported label.

Area 7b. In order to compare the thalamic projection of area 7a with that of area 7b, a large injection of ^{3}H-amino acids was made into area 7b (Fig. 11). The injected label had spread into the second somatosensory area along the dorsal bank of the lateral sulcus, and, unfortunately, there was also some slight involvement of area 7a. The insular cortex and the cortex on the ventral bank of the lateral sulcus were not affected.

Most of the transported label within the thalamus in this case is found at more rostral levels than that seen after area 7a injections. Within the lateral group of nuclei, dense labeling is largely restricted to the Pul.o. in those regions of the nucleus which contain irregularly scattered medium-to-small neurons. It is specifically excluded from the centromédian nucleus (CM) with its more uniformly dispersed, spindle-shaped neurons, and from the clustered medium and large neurons of the ventrobasal complex (VPLc and VPM—Fig. 10A,B). As with the labeling in the Pul.m. in the other experiments, the transported label in the Pul.o. is patchy in its distribution. Elsewhere in the lateral group there is some labeling of the LP and the Pul.m. It seems probable that the latter is due to the spread of the injection into area 7a. Label is also found in the CL, the paracentral nucleus (Pc), the nucleus centralis medialis (CeM), the VLc, the VLps, and the nucleus ventralis posterior inferior (VPI). The label in VPI is probably due to the involvement of the second somatosensory area (Friedman et al., '83).

Ventral thalamus, pretectum, and colliculi. In addition to the projections to the dorsal thalamus several other corticofugal systems were labeled in all these experiments with ^{3}H-amino acid injections. The most striking differential projections labeled were those to the ventral thalamus and midbrain. Following injections in the dorsal prelunate gyrus or in area LIP, irregular patches of terminal labeling are seen in the reticular nucleus, the pregeniculate nucleus (Preg.; Fig. 12A,B) and in the zona incerta (ZI; Fig. 12C,D). After area 7a and area 7b injections, the only labeling seen in the ventral thalamus is in the reticular nucleus.

Labeling is found in the ipsilateral pretectum in most of these experiments; however, its distribution varies depending on the site of the injection. Thus, whereas injections in area 7a give light terminal labeling in the posterior pretectal nucleus (PPN), injections that involve the dorsal prelunate gyrus and LIP always result in denser labeling concentrated in the anterior pretectal nucleus (APN) (Fig. 12E,F; see also Figs. 4, 14). Additional labeling in the olivary pretectal nucleus (ON) is seen only after the dorsal prelunate gyrus injections. Only after the injection centered in area 7b is there *no* labeling in the pretectum.

Injections into area LIP also result in sparse labeling in the stratum griseum intermedium (SGI) of the ipsilateral superior colliculus (Fig. 7). Although this labeling extends throughout the SGI it is less dense than that seen after injections into the dorsal prelunate gyrus; the latter injections also result in labeling of the deep part of the stratum griseum superficiale (SGS) (Fig. 9). In both cases there is additional light labeling in the corresponding regions of the contralateral superior colliculus. No comparable projection to the superior colliculus is evident following injections restricted to area 7a, but following area 7b injections labeling is seen ipsilaterally in the medial part of the stratum griseum profundum of the colliculus (Fig. 11) and in the intercollicular region.

Fluorescent dye studies

Ten experiments were done to determine the distribution of the thalamocortical relay neurons that project to area 7a and to the lateral prefrontal cortex.

Area 7a. In six experiments the dye injections were aimed at elucidating the thalamic projection to area 7a. In four of these FB was injected; in one of the remaining two cases TB was used, while in the other we used NY. Figure 3B illustrates a typical dye injection from this group of experiments. In none of the cases did the dye injection involve the prelunate gyrus or the dorsal bank of the lateral sulcus. Two of the injections involved the posterolateral portion of area 7a buried within the dorsal bank of the superior temporal sulcus; both injections may have incidentally involved part of the medial superior temporal area (MST) (Maunsell and Van Essen, '83).

In each of these brains retrogradely labeled neurons were found in Pul.m., always aggregated within disklike zones which extend over a considerable rostrocaudal distance. Figures 13A and B illustrate two such disklike aggregations of labeled neurons following an injection of FB into area 7a. Other retrogradely labeled neurons are seen in the SG/Li, in the VAmc, and in the nuclei surrounding the medullary lamina which encapsulates the laterodorsal nucleus, namely, CL, VLc, VLps, LP, and LD.

In Figure 14 the overall distribution of retrograde labeling in the thalamus following a fluorescent dye injection into area 7a (in this case, of NY) is shown by the open triangles. The injection in this case was large and directed toward the medial part of area 7a; with the exception of part of the dorsal bank of the superior temporal sulcus the dye does not seem to have spread to involve the adjoining cortical fields. Again, within the Pul.m., there are two rostrocaudally elongated disklike aggregations of labeled neurons, and scattered labeled cells in the SG/Li complex, in VLps, and in the nuclei surrounding the medullary capsule of LD. In this brain, a second injection (of ^{3}H-amino acids) had been made further laterally in area 7a; interestingly the autoradiographic labeling in the Pul.m. is located further ventrally than the NY-labeled cells. This suggests that in addition to the rostrocaudal topography discussed above, there is a dorsoventral topography within Pul.m. such that the medial part of area 7a is interconnected with cells in the dorsal part of the Pul.m. while lateral regions of 7a are connected to more ventral parts of the Pul.m. This topographical arrangement is found consistently in all our experiments with injections into area 7a.

Lateral prefrontal cortex. In four experiments we examined the projection from the thalamus to the lateral prefrontal cortex. In each case large, multiple injections of NY were made rostral to the arcuate sulcus to involve areas 8a, 45, and 46 of Walker ('40). Figure 3c, which is from a frontal section through area 8a, illustrates a typical large injection of this type. In no brain did the injection spread caudally into area 6, or deeply into the underlying caudate nucleus. With the exception of some bilateral labeling in two of the midline thalamic nuclei (CeM and the nucleus centralis densocellularis [Cdc]) the labeling in the thalamus in these brains was confined to the side of the injection. A typical example is shown in Figure 15.

As might be expected on the basis of previous reports (Akert, '64; Kievit and Kuypers, '77), there is a prominent wedge-shaped zone, densely filled with retrogradely labeled neurons within the pars parvicellularis and the pars mul-

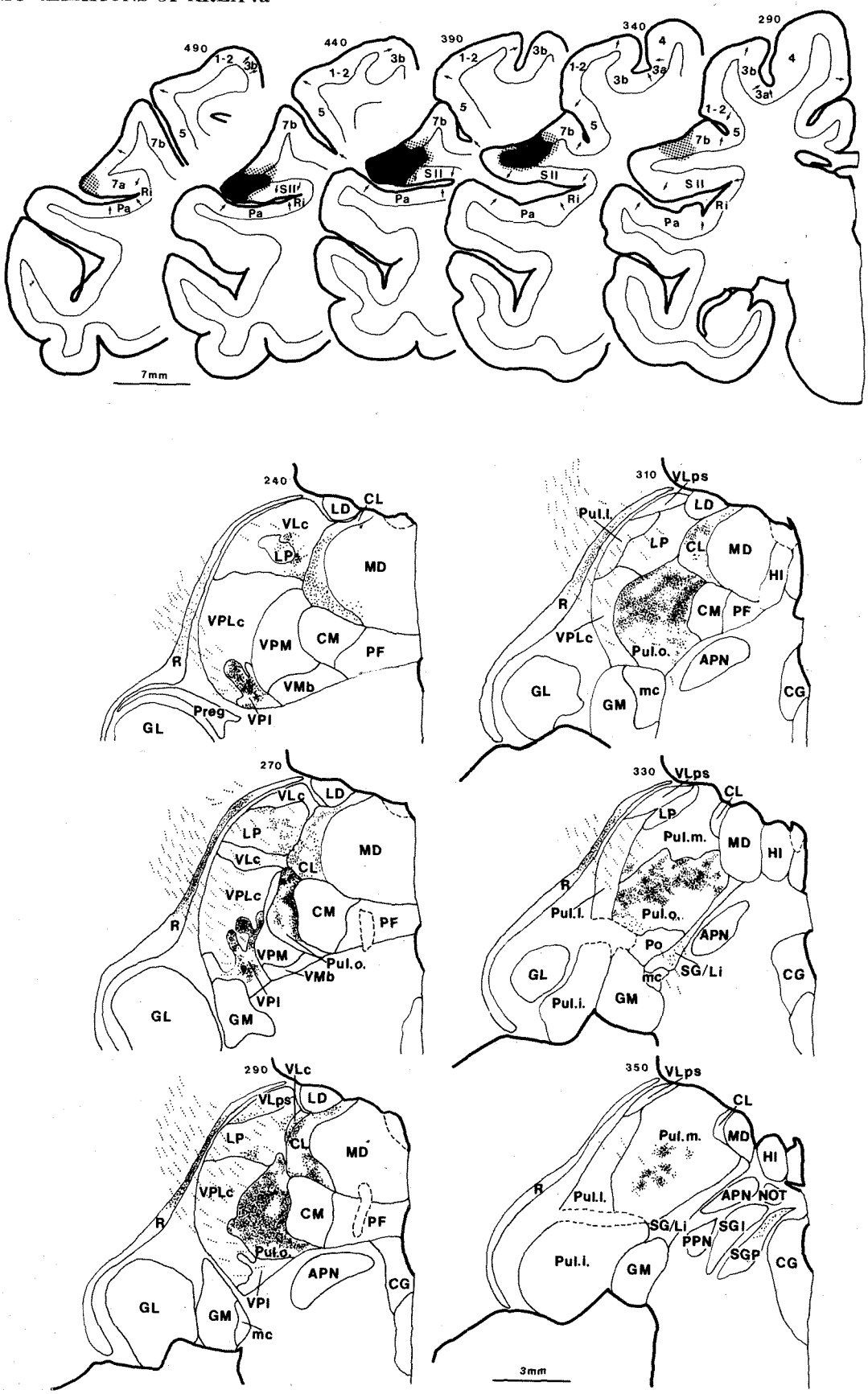

Fig. 11. Line drawings of frontal sections through the cortex and thalamus following a ^{3}H-amino acid injection into the rostral part of the posterior parietal lobule. The injection involved areas 7b, SII, and the rostralmost portion of area 7a. The bulk of the thalamic labeling occurs in Pul.o., although some labeling is also seen in VPl and in Pul.m.

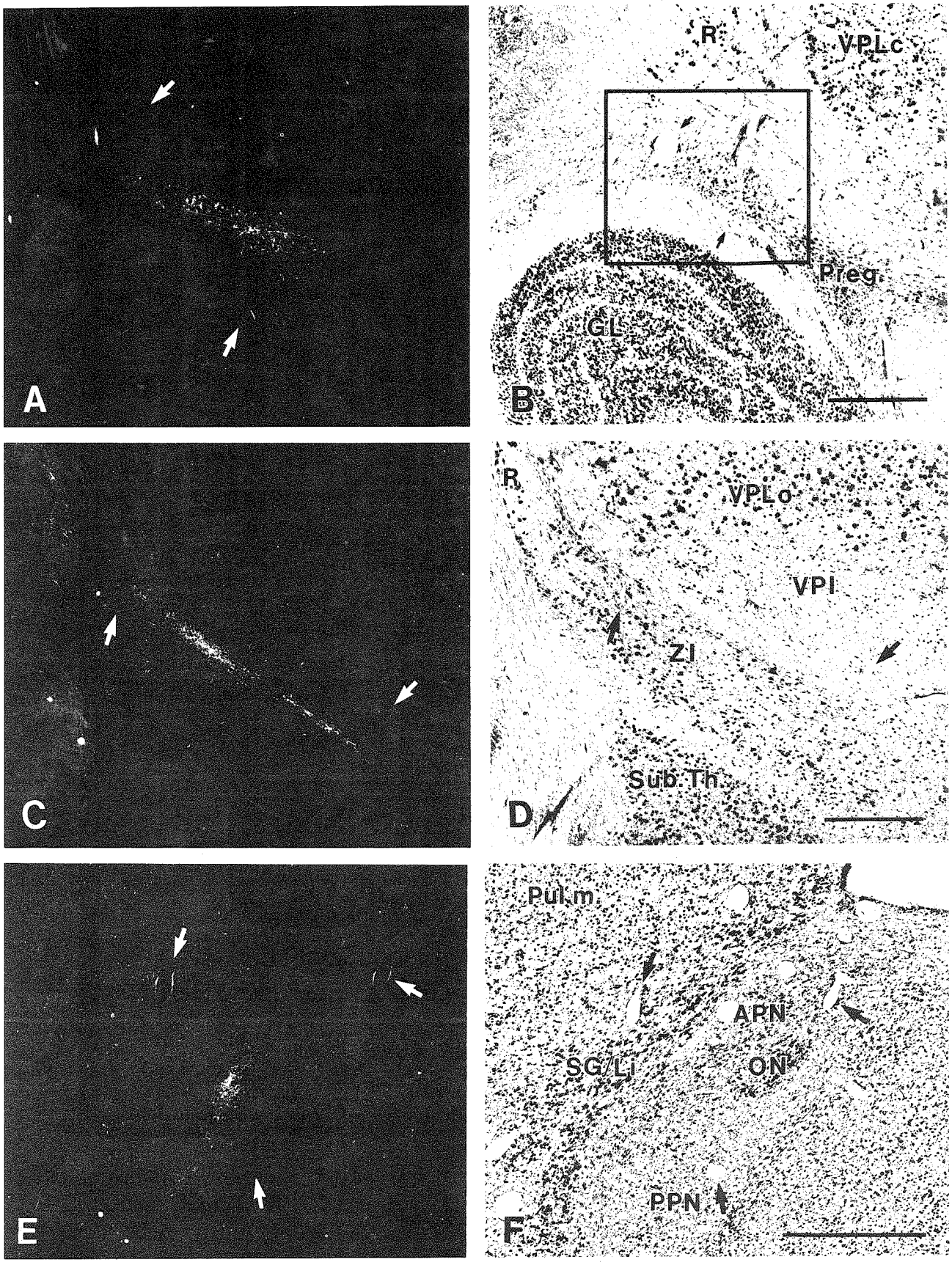

Fig. 12. Darkfield (A,C,E) and brightfield (B,D,F) photomicrographs of some ventral thalamic and pretectal projections following ^{3}H-amino acid injections in LIP and in the dorsal prelunate gyrus. A–D. Terminal labeling in the pregeniculate nucleus (A,B) and in the zona incerta (C,D), following an injection in LIP. The location of the darkfield photomicrograph in A is indicated by the inset square in B. E,F. Labeling in the anterior pretectal and olivary pretectal nuclei following the dorsal prelunate gyrus injections. Frontal sections. All scale bars = 1 mm.

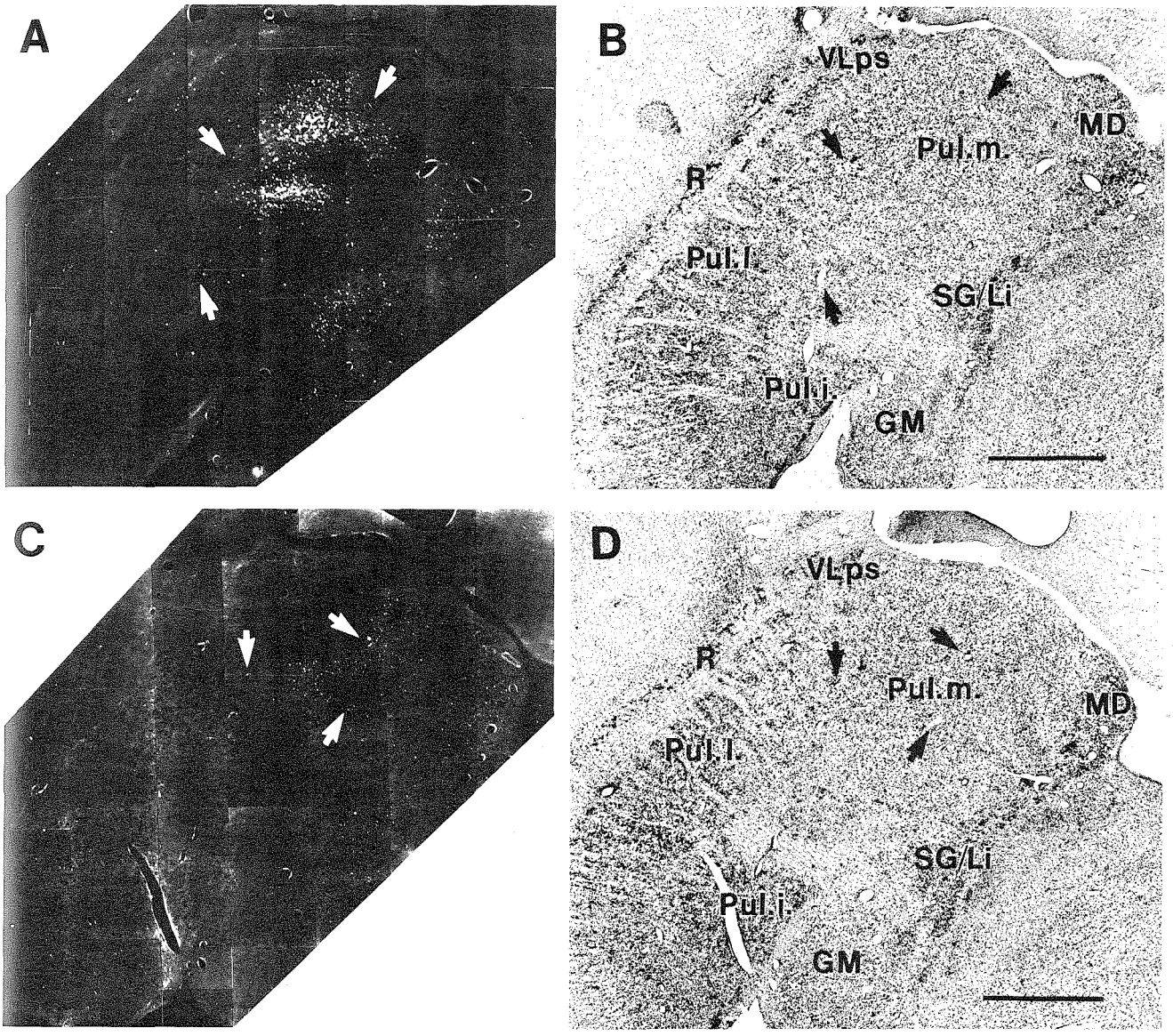

Fig. 13. Fluorescence photomontages (A,C) and brightfield photomicrographs (B,D) of labeling in the medial pulvinar nucleus (Pul.m.). In A and B, multiple injections of FB were made into area 7a. In C and D, multiple injections of NY were made into the lateral prefrontal cortex. Frontal sections. Scale bars = 2 mm.

tiformis of the mediodorsal nucleus (MD), and there are scattered retrogradely labeled cells in the Pc, SG/Li, VAmc, and the nuclei surrounding the LD. Further caudally, there is another dense focus of retrogradely labeled neurons in the Pul.m. Unlike the dense, though evenly dispersed labeling in the MD, the labeled neurons in the Pul.m. are aggregated into characteristic disklike aggregates that have the same dorsomedial-to-ventrolateral orientation as was seen following injections into area 7a. One such disklike aggregation of NY-labeled neurons is illustrated in the photomontage of Figure 13C. A comparison of Figures 13A and B with C and D suggests that the cells which project to the lateral prefrontal cortex probably extend further medially than do those which project to area 7a. Also, after prefrontal injections, one disk is always much more prominent than the others, whereas after area 7a injections the labeling seems to be more equally distributed between the disks.

Double-dye injections. In order to compare the distribution of neurons in the Pul.m. that project to area 7a and the lateral prefrontal cortex directly, in one monkey large multiple injections of FB were made into area 7a, and several equally large injections of NY were made into the lateral prefrontal cortex on the same side. Figure 16 summarizes in a schematic way the distribution of the Pul.m. neurons containing the two markers. It is evident from these data that the disklike aggregations of FB- or NY-labeled neurons partially overlap; the greatest degree of overlap in-

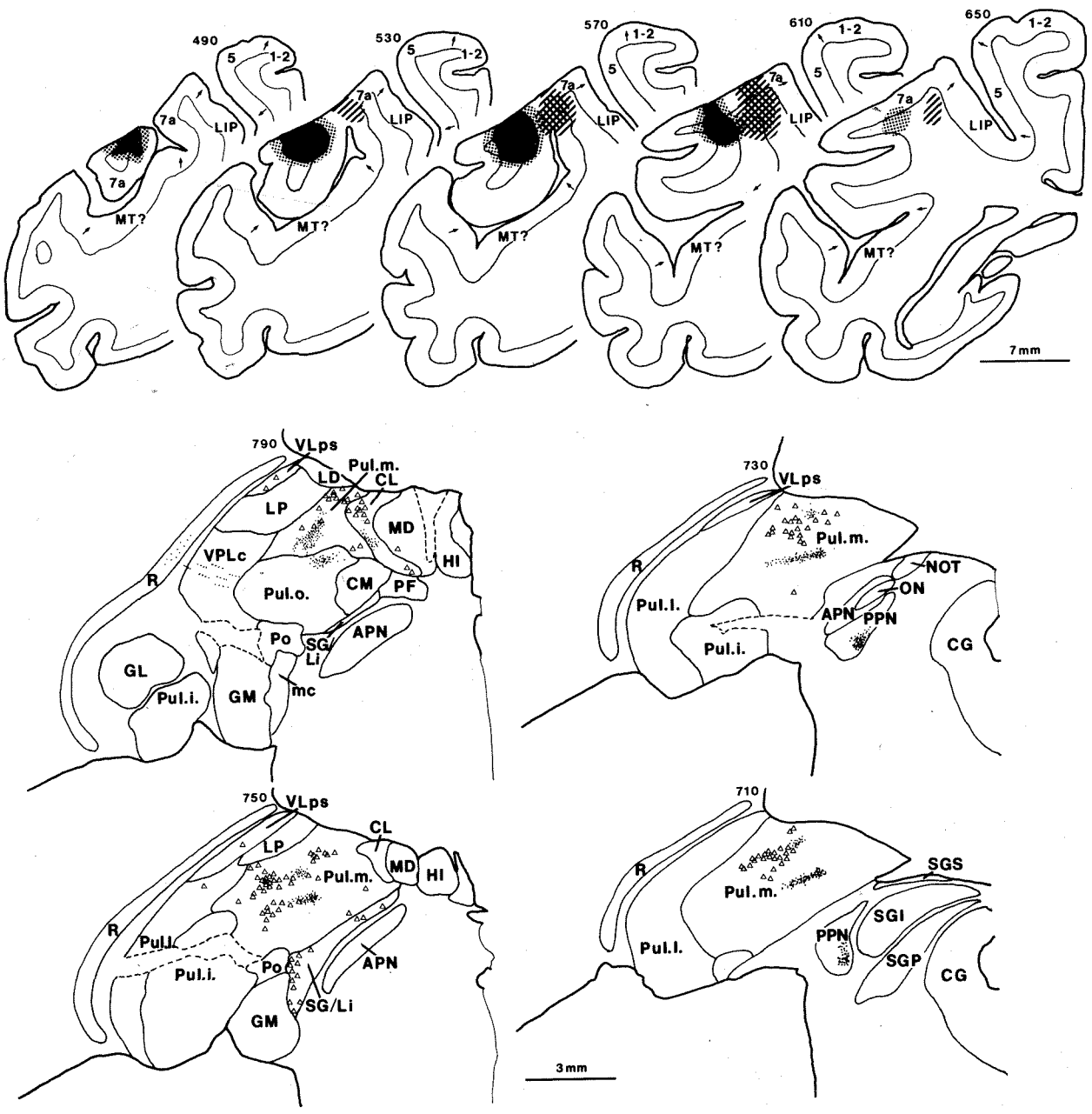

Fig. 14. Line drawings of frontal sections through the cortex and thalamus following a ^{3}H-amino acid injection laterally in area 7a (solid black) and an injection of NY medially in area 7a (crosshatching). The autoradiographic labeling in the thalamus is represented by dots, the NY labeling by open triangles.

volves the ventrolateral portion of the major disk that projects to the prefrontal cortex and to the dorsomedial part of one of the disks that project to area 7a. Furthermore, the NY-labeled disks tend to extend further medially than those labeled with FB; similarly, the FB-labeled cells tend to be concentrated more laterally. Despite this mediolateral difference there is a substantial zone of overlap in the middle of the Pul.m. in which there is a complete intermingling of FB-labeled cells with cells labeled with NY. Upon careful inspection at higher magnifications, it is clear that only a small proportion (probably not more than 0.1%) of the labeled neurons in the zone of overlap is doubly labeled (Fig. 17).

DISCUSSION

The early pioneering physiological studies of the inferior parietal lobule by Mountcastle and his colleagues (Mountcastle et al., '75; Lynch et al., '77) have stimulated a number of antomical studies aimed at elucidating the connections of the region (Mesulam et al., '77; Baleydier and Maugière,

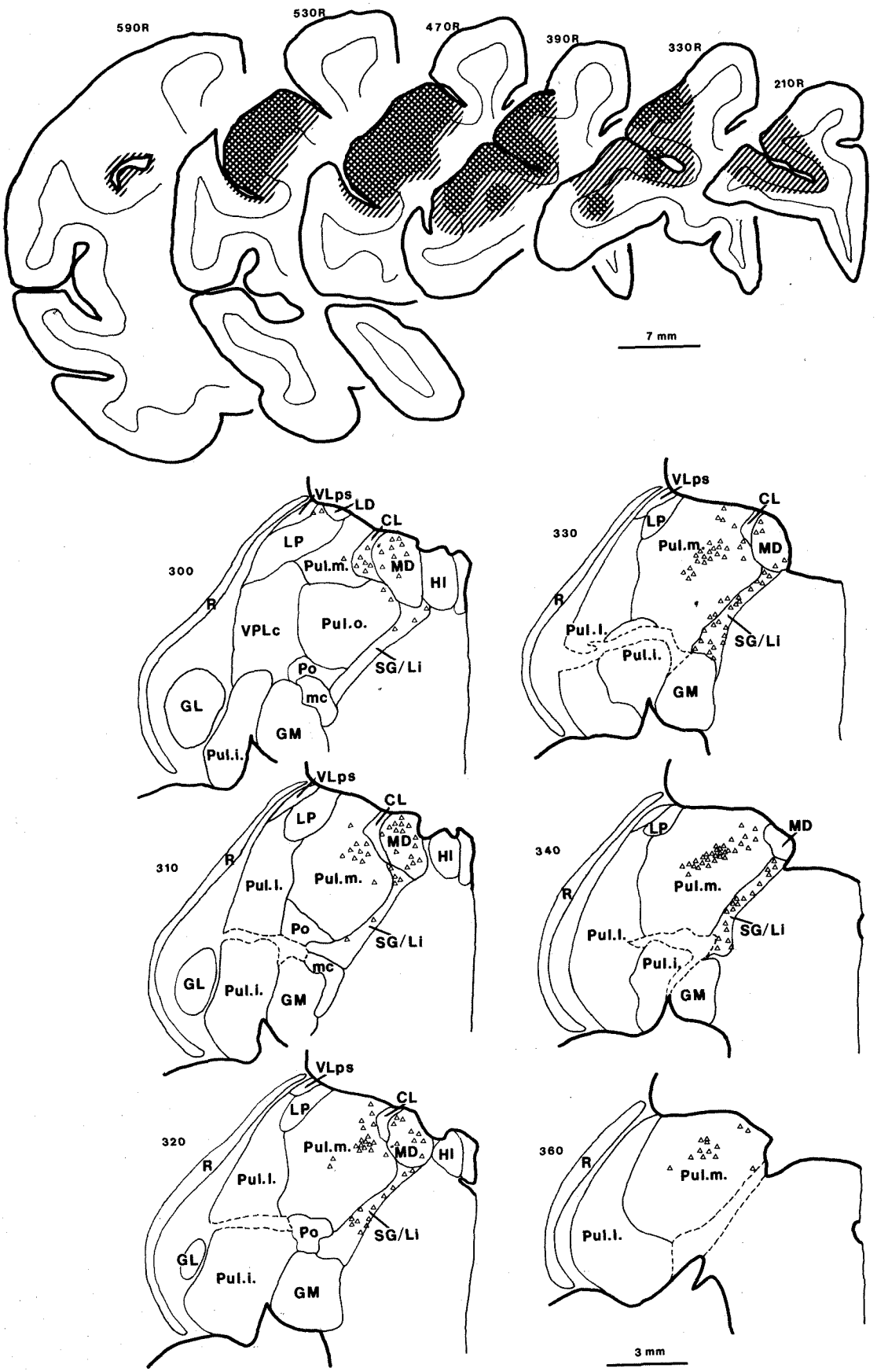

Fig. 15. Line drawings of frontal sections through the cortex and thalamus following large multiple injections of NY into areas 8a, 45, and 46 of the lateral prefrontal cortex. The effective extent of the NY injection is indicated by crosshatching and the distribution of retrogradely labeled neurons in the thalamus by open triangles.

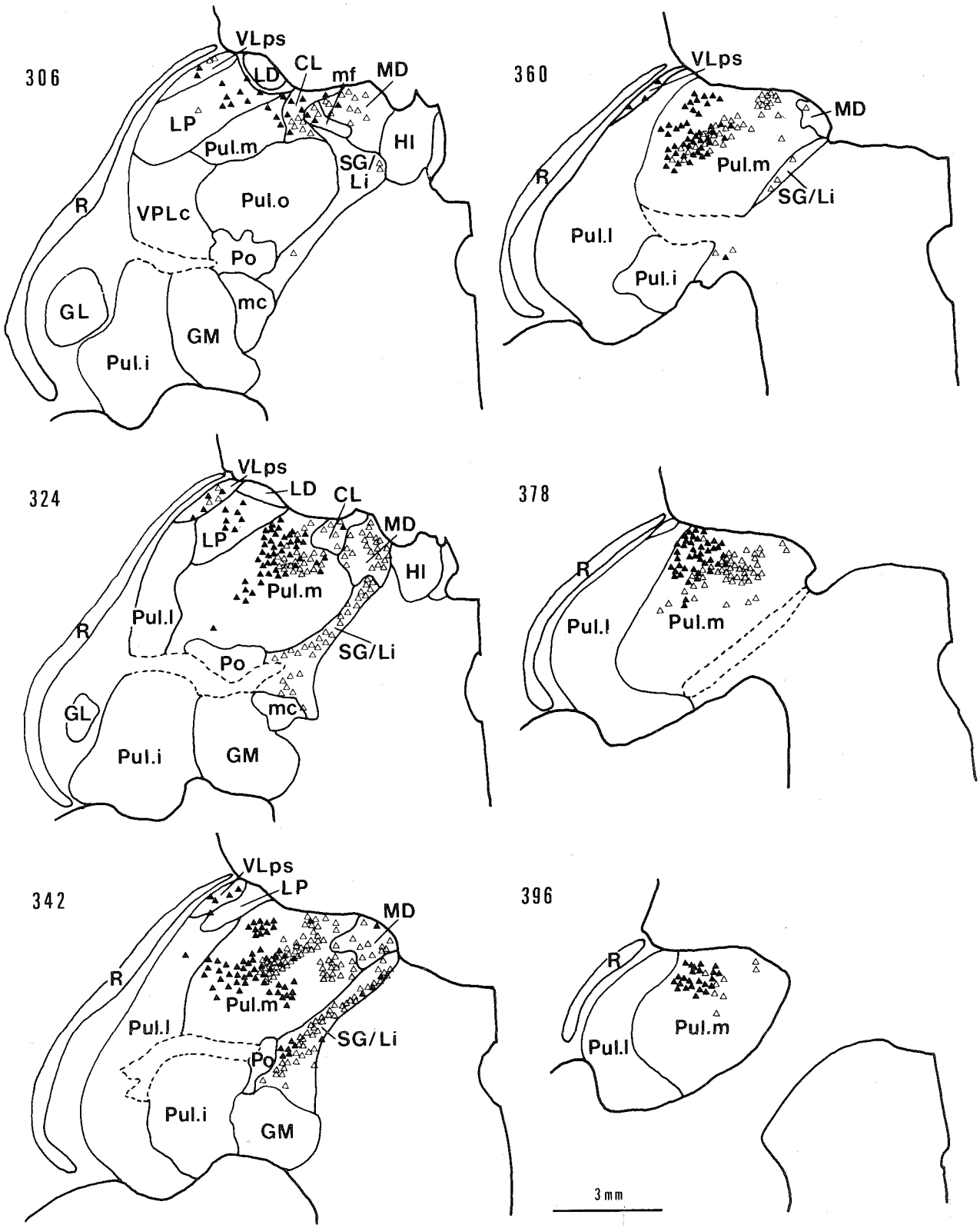

Fig. 16. Line drawings of frontal sections through the thalamus following multiple injections of FB into area 7a and large multiple injections of NY into the lateral prefrontal cortex in the same hemisphere. The solid triangles mark the distribution of FB-labeled cells; the open triangles represent NY-labeled cells.

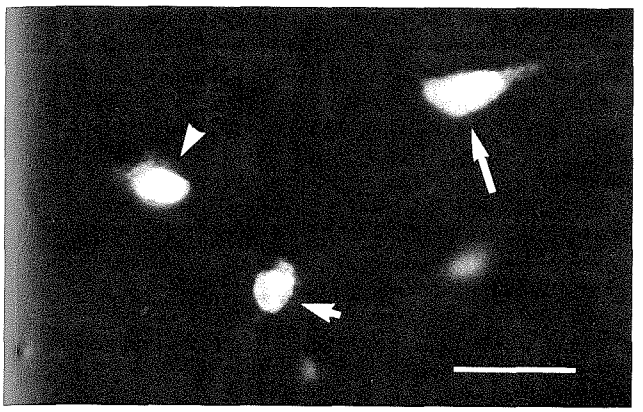

Fig. 17. A high-power fluorescence photomicrograph of labeled neurons in Pul.m. from the experiment illustrated in Figure 15. The long arrow points to a neuron that is labeled only with FB. The short arrow points to a neuron that is labeled only with NY. The arrowhead points to a neuron that was doubly labeled, with both FB and NY. The presence of the brilliant yellow-stained nucleus against the bright blue cytoplasm is easy to detect in the fluorescence microscope, but difficult to reproduce photographically in black and white. Doubly labeled neurons amount to only about 0.1% of the total population of labeled cells. Scale bar = 25 μm.

'77; Divac et al., '77; Stanton et al., '77; Kasdon and Jacobson, '78; Pearson et al., '78; Weber and Yin, '84). As a result of these studies it has become clear that while a number of the thalamic nuclei project to the lobule, its principal relationship is with the Pul.m. and the Pul.o., and that the former is especially closely related to its caudal part while its rostral part is preferentially related to the Pul.o. Our observations have confirmed these points and have served to establish that the Pul.m. is, in fact, the only nucleus within the pulvinar complex that is interconnected with the gyral surface of the caudal inferior parietal lobule (area 7a) and, furthermore, that its interconnections with area 7a are focally organized and topographically ordered. This is true only of the gyral portion of area 7a; it does not apply to the lateral bank of the intraparietal sulcus (which we have termed area LIP). Area LIP, together with the dorsal prelunate gyrus and area 7b, is primarily related to other components of the pulvinar complex. At the same time it is clear that the relationship of Pul.m. to area 7a is not an exclusive one: cells within the nucleus which have a similar focal organization (that partially overlaps that of the projection to area 7a) project to the lateral prefrontal cortex.

Seltzer and Pandya ('80) were the first to suggest, on the basis of cytoarchitectonic features and corticocortical connectivity, that the cortex which occupies the lateral bank of the intraparietal sulcus constitutes a functional zone distinct from area 7a on the exposed gyral surface. They termed this separate zone area POa. Our findings on the subcortical connections of the two areas lends support to their view. Within the pulvinar complex, area 7a is exclusively connected (in a reciprocal fashion) with Pul.m., whereas what we have termed area LIP is preferentially connected with Pul.l. Furthermore, while area LIP projects to the pregeniculate nucleus, the zona incerta, the anterior pretectal nucleus, and the superior colliculus, area 7a has no direct connection with these structures but does project to the posterior pretectal nucleus. Our observations indicating that area LIP is the principal source of the projection from the inferior parietal lobule to the superior colliculus confirm a recent report by Lynch et al. ('85).

Our findings on the cortex of the dorsal prelunate gyrus are less clear-cut (in large part because in the critical experiment the ^{3}H-amino acid injection was relatively large and encroached upon some of the neighboring cortical fields). But the major observation, namely that the dorsal prelunate gyrus projects heavily to the lateral and inferior nuclei of the pulvinar complex, is not in question. Whether or not there are smaller zones within the prelunate gyrus that project differentially to the lateral and inferior pulvinar nuclei, remains to be determined. But it is worth noting here that the autoradiographic labeling seen along the dorsolateral margin of the lateral pulvinar nucleus in our case with an injection into the dorsal prelunate gyrus is quite similar, both in its configuration and location, to that seen after ^{3}H-amino acid injections in area LIP (cf. Figs. 7, 8). The fact that the other subcortical projections of the dorsal prelunate gyrus and area LIP to the pregeniculate nucleus, the zona incerta, the anterior pretectal nucleus, and the superior colliculus are shared in common, together with the finding that the two areas are richly interconnected through reciprocal corticocortical projections, strongly suggests that they are functionally related in some important way.

Each of our fluorescent dye injections into area 7a resulted in the labeling of disklike aggregations of thalamocortical relay neurons in the medial pulvinar nucleus which in their size and distribution closely parallel the zones of termination of the corticothalamic projections revealed by our autoradiographic experiments. Collectively these findings confirm and extend the previous observations of Mesulam et al. ('77) and of Pearson et al. ('78) using the horseradish peroxidase method and those of Weber and Yin ('84) who also used the autoradiographic method. By using smaller injections of the various tracers than these earlier authors, we have been able to demonstrate that the rodlike clusters of cells and corticothalamic terminals in the Pul.m. are topographically organized such that rostral sectors of the disks project rostrally within area 7a while the caudal sectors project further caudally; in addition, medial sectors of the disks project further laterally upon area 7a than do the more laterally placed sectors.

The densely aggregated neurons within the Pul.m. which project to area 7a and/or to the lateral prefrontal cortex appear to be distinct from the more diffusely organized neurons detected within the CL and MD. Although a few scattered neurons have been reported throughout the pulvinar complex of monkeys following injections of retrograde tracers into the putamen (Parent et al., '83), it is unlikely that the retrograde labeling we see in the Pul.m. following our cortical injections is due to collaterals of striatally projecting neurons; the neurons within the pulvinar complex which project to area 7a and/or to the lateral prefrontal cortex are always localized to the Pul.m. and instead of being loosely scattered throughout this nucleus they make up a substantial population of neurons within distinct disklike zones. It should also be noted that following tritiated amino acid injections in the Pul.m., terminal labeling within these cortical areas is densest in deep layer III and superficial layer IV (Bos and Benevento, '75; Trojanowski and Jacobson, '76; Baleydier and Mauguière, '85), while the cortical collaterals of striatally projecting neurons have been reported to terminate in layers I and VI and to avoid the middle layers (see Jones, '84, for review).

It is evident from the consistent occurrence, in even our largest dye-labeling experiments, of label-free zones between the aggregates of Pul.m. neurons that project to area 7a and to the lateral prefrontal cortex, that the intrinsic organization of this nucleus is extremely complex, and it is not at all clear what the cortical relationships of these "label-free-zones" may be. It is known from the earlier retrograde cell degeneration studies of Walker ('35) and Siqueira ('71) that the integrity of the entire Pul.m. is dependent on the neocortex. However, our observations indicate that the cells in the label-free zones do not project to (or, for that matter, receive afferents from) the cortical fields that surround area 7a, such as area LIP, the dorsal prelunate gyrus, or area 7b. Furthermore, it is evident from our double-dye injection experiments that although the Pul.m. projections to area 7a and to the lateral prefrontal cortex both arise in disklike neuronal aggregates which partially overlap, there are large portions of the nucleus that are unlabeled by either dye. Conceivably these unlabeled areas are the source of the projections from the medial pulvinar to the superior parietal lobule (Chow, '50; Walker, '38), the medial surface of the parietal lobe (Chow, '50), the amygdala (Burton and Jones, '76), the cingulate gyrus (Gower and Mesulam, '78; Yeterian, '83; Baleydier and Mauguière, '85), the orbital cortex (Bos and Benevento, '75; Trojanowski and Jacobson, '76; Yeterian, '83), the retrosplenial area (Yeterian, '83; Baleydier and Mauguière, '85), the parahippocampal gyrus (Yeterian, '83; Baleydier and Mauguière, '85), and the temporal lobe (Le Gros Clark and Northfield, '37; Walker, '38; Chow, '50; Whitlock and Nauta, '56; Locke, '60; Siqueira, '65, '71; Jones and Burton, '76; Trojanowski and Jacobson, '75, '76; Yeterian, '83). Clearly what is now needed is a systematic study of the cells of origin of the projection from Pul.m. to these other forebrain areas, using multiple dye-labeling procedures, to define more precisely their relation to the cells that project to the inferior parietal lobule and the lateral prefrontal cortex.

The finding of focal aggregations of cells and axon terminals within the Pul.m. is, of course, not unique. There are many reports in the literature of similar rostrocaudally elongated rodlike arrangements of projecting neurons and afferent fibers in other thalamic nuclei (e.g., Cajal, '11; Campos-Ortega and Hayhow, '72; Jones et al., '78, '82; Andersen et al., '80a,b; Jones and Friedman, '82; Asanuma et al., '83b; Jones, '83; see Jones, '84, for review). In the ventrobasal complex of monkeys where this arrangement has been studied most intensively, it is evident that the neurons in each aggregation have similar place and modality characteristics (Poggio and Mountcastle, '63; Jones et al., '82; Juliano et al., '83). These clusters have been suggested to provide a structural basis for maintaining the segregation of somatic sensory information en route from the periphery to the somatic sensory cortex (Mountcastle, '67; Jones et al., '82). Systematically organized elongated foci of afferent terminations and of thalamic neurons projecting to focal zones within the cortex, highly suggestive of a modular organization in the relay of ascending information, have also been demonstrated in the ventral lateral nucleus of monkeys (Jones et al., '78; Thach and Jones, '79; Asanuma et al., '83b) and in the medial geniculate nucleus of cats (Andersen et al., '80a,b). In the Pul.m. there are multiple disklike aggregations of neurons which project to area 7a. This is apparent even when rather small injections of tracers are made into area 7a (see Fig. 6). This arrangement suggests that there is some form of modularity in the thalamic input to area 7a, but at present the functional significance of these intriguing anatomical units is not at all evident. It seems fairly certain that they are not responsible for the "visual inputs" to area 7a since the major visual centers of the brain (including the visual cortex, the superficial layers of the superior colliculus, and the retinorecipient layers of the pretectum) project mainly to the lateral and/or the inferior pulvinar nuclei (Campos-Ortega and Hayhow, '72; Benevento and Fallon, '75; Ogren and Hendrickson, '76, '79; Benevento et al., '77; Harting et al., '80; Ungerleider et al., '83; Benevento and Standage, '83). The major subcortical input to the medial pulvinar nucleus, on the other hand, appears to arise in the deep layers of the superior colliculus (Benevento and Fallon, '75; Benevento et al., '77; Harting et al., '80; Benevento and Standage, '83), where visually driven responses are infrequent (Mohler and Wurtz, '76; Wurtz and Mohler, '76). Thus it seems more likely that the "visual" inputs to area 7a are derived directly from other cortical areas (see Andersen et al., '85).

We can only speculate at this time about the possible significance of the cellular aggregates in Pul.m. If, by analogy with other more intensively studied thalamic nuclei we assume that the neurons within each aggregate relay similar information, then in large part the same information must be transmitted, in parallel, to both area 7a and the lateral prefrontal cortex. In this connection it is worth noting that the activity of visually responsive neurons in both area 7a and the frontal eye fields can be facilitated under certain (admittedly different) behavioral conditions (Mountcastle, '81; Mountcastle et al., '81; Goldberg and Bushnell, '81; Bushnell et al., '81). And, furthermore, it appears from recent physiological studies of this thalamic region in behaving monkeys that there is some correspondence in the behavioral conditions required to elicit enhanced visual responses in area 7a and the frontal eye fields, and in the activity of individual pulvinar neurons (Petersen et al., '82; Acuña et al., '83). However, it is entirely possible that the information relayed from the Pul.m. to area 7a and to the lateral prefrontal cortex is, for the most part, quite different. Although the aggregations of the relevant thalamocortical neurons overlap quite extensively, they really consist of two separate populations. Indeed, our double-labeling experiments make it clear that only a very small proportion of the Pul.m. neurons have collateral projections to both cortical regions.

The consistent finding of retrogradely labeled cells in the suprageniculate and limitans nuclei after dye injections into the parietal and prefrontal cortex indicates that in addition to their dense input to the granular insular cortex (Burton and Jones, '76), these nuclei may have rather widespread cortical projections. Since the granular insular cortex was not involved in any of our dye injection experiments, it seems likely that these additional cortical projections are either rather sparse and diffuse, or are formed of fine-calibered collaterals which are not readily labeled by ^{3}H-amino acid injections into the nuclei (Burton and Jones, '76).

Small amounts of both the anterograde and retrograde labels that we have used were observed in the VLc, VLps, LP, LD, and CL after both parietal and prefrontal injections. This observation, taken together with certain other features shared by these nuclei in our experiments, suggests that collectively they may constitute a common system of cortical afferents. Among the relevant features that may be mentioned are: (1) the finding that dispersed label was consistently present in these nuclei after each of our

area 7a and prefrontal cortex injections; (2) the fact that there is no obvious topography discernible in their cortical relations; and (3) the repeated observation that the transported label was never localized to one or another nucleus, but instead seemed always to be rather widely scattered throughout the entire group of nuclei. This is perhaps somewhat surprising given that these various nuclei do not commonly share all of their other extrinsic inputs. For example, it is known that whereas the cerebellothalamic afferents terminate in the VLc, VLps, and CL, the spinothalamic inputs are restricted to the CL, and the limbic afferents (in the fornix) terminate in the LD (Valenstein and Nauta, '59; Mehler et al., '60; Kalil, '81; Boivie, '79; Stanton, '80; Asanuma et al., '83a). Only the inputs to these nuclei from the superficial and deep layers of the superior colliculus, and since saccade-related responses have recently been recorded from this thalamic region (Petersen et al., '82), it is possible that this is one of the sources of ing that cells responsive to eye movement and eye position have recently been found in the rostral intralaminar nuclei (including those elements which surround the LD—Schlag-Rey and Schlag, '84; Schlag and Schlag-Rey, '84). Whether these cells are responsible in part for the eye position and eye-movement-related activity found in area 7a (Mountcastle, '81; Shibutani et al., '84; Essick et al., '84) has yet to be explored. But what is clear is that the Pul.m. receives its major ascending input from the deep layers of the superior colliculus, and since saccade-related responses have recently been recorded from this thalamic region (Petersen et al., '82), it is possible that this is one of the sources of oculomotor information to the inferior parietal lobule and the lateral prefrontal cortex.

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