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# Thalamic Connections of Three Representations of the Body Surface in Somatosensory Cortex of Gray Squirrels

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ABSTRACT

The anatomical tracer, wheat germ agglutinin, was used to determine the connections of electrophysiologically identified locations in three architectonically distinct representations of the body surface in the somatosensory cortex of gray squirrels. Injections in the first somatosensory area, S-I, revealed reciprocal connections with the ventroposterior nucleus (VP), a portion of the thalamus just dorsomedial to VP, the posterior medial nucleus, Pom, and sometimes the ventroposterior inferior nucleus (VPI). As expected, injections in the representation of the face in S-I resulted in label in ventroposterior medial (VPM), the medial subnucleus of VP, whereas injections in the representation of the body labeled ventroposterior lateral (VPL), the lateral subnucleus of VP. Furthermore, there was evidence from connections that the caudal face and head are represented dorsolaterally in VPM, and the forelimb is represented centrally and medially in VPL. The results also support the conclusion that a representation paralleling that in VP exists in Pom, so that the ventrolateral part of Pom represents the face and the dorsomedial part of Pom is devoted to the body. Because connections with VPI were not consistently revealed, the possibility exists that only some parts or functional modules of S-I are interconnected with VPI.

Two separate small representations of the body surface adjoin the caudoventral border of S-I. Both resemble the second somatosensory area, S-II, enough to be identified as S-II in the absence of evidence for the other. We term the more dorsal of the two fields S-II because it was previously defined as S-II in squirrels (Nelson et al., '79), and because it more closely resembles the S-II identified in most other mammals. We refer to the other field as the parietal ventral area, PV (Krubitzer et al., '86). Injections in S-II revealed reciprocal connections with VP, Pom, and a thalamic region lateral and caudal to Pom and dorsal to VP, the posterior lateral nucleus, Pol. Whereas major interconnections between S-II and VPI have been reported for cats, raccoons, and monkeys, no such interconnections were found for S-II in squirrels. The parietal ventral area, PV, was found to have prominent reciprocal interconnections with VP, VPI, and the internal (magnocellular) division of the medial geniculate complex (MGi). The pattern of connections conforms to the established somatotopic organization of VP and suggests a crude parallel somatotopic organization in VPI. Less prominent interconnections were with Pol. Sparse, fine label in part of the ventral (principal) nucleus of the medial geniculate complex (MGv) suggests the existence of some input from PV.

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The connections demonstrated in the present study help characterize three somatosensory areas in squirrels. Such information is essential for identifying homologous areas of cortex across species, and several possibilities are outlined in the Discussion. In addition to VP, the results suggest the presence of two somatic nuclei, the medial and lateral nucleus of the Po group; and evidence is provided for the existence of VPI in rodents. Furthermore, consistent with many recent reports, we found that each cortical area has interconnections with more than one thalamic nuclei, and each thalamic nucleus has interconnections with more than one cortical field. Finally, in keeping with the responsiveness of neurons in PV to both somatic and auditory stimuli (Krubitzer et al., '86), PV was found to have interconnections with both somatic and auditory thalamic nuclei.

**Key words: ventroposterior nucleus, parietal cortex**

*The thalamus in higher mammals becomes such a complicated structure that it is well-nigh impossible to unravel its complexities by direct anatomical methods. It is essential, in order to define the fundamental elements of its composition, to study it in the more simple form in which it is found in small generalized mammalian types* (Le Gros Clark, 1932).

Many mammals have two or more representations of the body surface in the parietal cortex. A first or primary representation, S-I, has been identified with a high degree of certainty in a wide range of mammals (see Kaas, '83) including squirrels (Sur et al., '78). S-I is characterized by: 1) a systematic representation of cutaneous receptors proceeding from the medial cortex devoted to the tail and hindlimb to the lateral cortex devoted to the tongue and face, 2) densely packed layer IV granule cells and dense myelination, and 3) prominent interconnections with the major cutaneous relay nucleus of the thalamus, the ventroposterior nucleus (VP). Other thalamic connections of S-I are less certain, probably species-variable (see Jones, '85), and may relate to distinct subdivisions of the S-I region in some mammals.

In rats and many other rodents, the S-I region is clearly divisible architectonically into the granular cortex, containing the "map" of the body surface, and the dysgranular cortex, which is unresponsive to low-threshold cutaneous stimulation in anesthetized animals (e.g., see Welker, '76; Killackey, '83; Chapin and Lin, '84). In rats, the major thalamic connections of granular S-I are with VP, whereas a thalamic zone just dorsal to VP, generally considered part of the posterior thalamic group (Po), has connections with the dysgranular (unresponsive) zones (Akers and Killackey, '78; Killackey, '83). In squirrels, a large dysgranular zone of almost 1 mm in diameter within S-I (Kaas et al., '72) has been distinguished as the "unresponsive zone," UZ (Sur et al., '78). This unresponsive zone has dense thalamic connections with part of the thalamus just dorsal to VP and less prominent connections with VP (Gould, '81). One goal of the present study was to further determine what parts of the somatosensory thalamus are interconnected with S-I in squirrels. In particular, we were interested in finding out if the thalamic region dorsal to VP, in addition to VP, projects to granular as well as dysgranular parts of S-I. A related goal was to use connection patterns to reveal features of the somatotopic organization of VP of squirrels. Since the somatotopic organization of S-I has been determined in detail in squirrels, whereas the somatotopic organization of VP has not, connection patterns of different locations in S-I could provide missing information. In addition, connections of the face and body representations of S-I, respectively, could help identify the major subnuclei of VP, ventroposterior medial (VPM), and ventroposterior lateral (VPL), which are not always clear in rodents and have not been previously distinguished in squirrels. Finally, connections of known body parts in S-I could help reveal the somatotopic organization of thalamic nuclei other than VP that interconnect with S-I.

Other issues concern the thalamic connections of cortical fields defined as the second somatosensory area, S-II, and the parietal ventral area, PV, of squirrels (Krubitzer et al., '86). The second somatic area, S-II, was first defined electrophysiologically in cats as a small representation of the body surface adjoining the caudal border of the representation of the face in S-I (Adrian, '40; Woolsey, '43). Subsequently, an S-II has been defined in a similar relative position in a large number of mammalian species (see for review, Nelson et al., '79; Sur et al., '81), but there have been marked differences in the reported somatotopic organization and connections of S-II across, and sometimes within, species by various investigators. Thus, S-II has been reported as "upright" in organization with the feet pointing ventrally toward the rhinal fissure by some investigators (e.g., Haight, '72; Burton et al., '82 for cats; Johnson et al., '74 for sheep; Herron, '78 for raccoons, and Sur et al., '81 for tree shrews) or "inverted" in organization with feet pointing dorsally by other investigators (Woolsey and Fairman, '46 for pigs and sheep; Woolsey, '58 for cats; Pinto-Hamay, '56 for dogs). In rodents, S-II has been reported as upright for squirrels (Nelson et al., '79), capybaras and guinea pigs (Campos and Welker, '76), agoutis (Pimentel-Souza et al., '80), and mice (Carvell and Simmons, '86), and inverted for porcupines (Lende and Woolsey, '56) and rats (Welker, '71). Major thalamic connections of S-II have long been considered to be with VP (for review, see Jones, '85), but recently evidence has been presented in raccoons (Herron, '83), cats (Herron and Dykes, '81), and monkeys (Manzoni et al., '84; Friedman and Murray, '86; Krubitzer and Kaas, '86; however, see Burton, '84) that the major thalamic connections of S-II are with VPI.

Recently we discovered a third representation of the body surface in squirrels (Krubitzer et al., '86) in cortex that is caudal to lateral S-I and ventral to the region identified as S-II in squirrels (Nelson et al., '79). We termed the field the parietal ventral area (PV), because of its relative cortical

location, but without a previously defined S-II, we probably would have assumed the field to be S-II. Since the feet in PV point dorsally, PV resembles S-II of some reports, whereas the more dorsal S-II of squirrels has the "upright" organization more commonly reported for S-II. Thus, it occurred to us that the two similarly located representations of about the same size, PV and S-II, if they both exist in other mammals, could have been confused in different studies with each field identified as S-II. The possibility of confounding S-II and PV also exists in studies of connections. Both S-II and PV of squirrels are densely interconnected with S-I (Krubitzer et al., '86), a feature commonly reported for S-II. However, only PV had notable connections with the motor cortex, which are sometimes reported for S-II (see Krubitzer et al., '86). Because of this uncertainty over the homology of S-II across species, we felt that it was extremely important to characterize further S-II and PV in squirrels by describing thalamic connections.

## METHODS

Interconnections between the parietal cortex and the thalamus were studied in ten gray squirrels (*Sciurus carolinensis*). The primary somatosensory area (S-I), the second somatosensory area (S-II), and the parietal ventral area (PV) were mapped using multiunit recording methods. After boundaries of these fields were determined, injections of anatomical tracers were confined to these regions so that interconnections of these areas with the thalamus could be readily determined. Labeled cell bodies and axon terminals were assigned to architectonically defined nuclei in the thalamus. Cortical connections and basic procedures have been reported previously (Krubitzer et al., '86).

Each squirrel was initially anesthetized with ketamine hydrochloride (100 mg/k,IM), which was supplemented with acepromazine maleate, (4.3 mg/k,IM). In addition, local anesthetic (2% xylocaine hydrochloride) was injected subdermally where the scalp was to be cut and at pressure points where ear bars were to be inserted. Surgical levels of anesthesia were maintained throughout the experiment with additional doses of ketamine and acepromazine as needed. After the animal was deeply anesthetized, the scalp was cut and a portion of the skull was removed. The dura was then retracted so that most or all of the somatosensory cortex was exposed.

Microelectrodes were used to record from the cortex to determine patterns of somatotopic organization (see Krubitzer et al., '86). After the particular area of interest (S-I, S-II, or PV) was physiologically defined, boundaries were lesioned and a 0.5% solution of wheat germ agglutinin conjugated with horseradish peroxidase was injected at a physiologically defined location. In one case, tritiated WGA, rather than WGA-HRP, was used. The amount of tracer injected ranged from 0.05 to 0.1 $\mu$l. Typically the tracer was injected over a period of 20 minutes. When the injection was complete, the cortex was covered with an acrylite cap and the animal was recovered. Two days after surgery, the animal was deeply anesthetized and perfused transcardially with 0.9% saline followed by 1.5% glutaraldehyde and 1% paraformaldehyde in phosphate buffer (pH 7.4). The brain was then removed from the skull, and the cortex was separated from the brainstem and flattened between glass slides. Both the flattened cortex and the brainstem were soaked in 30% sugar phosphate buffer for approximately 24 hours. The flattened cortex was frozen and cut parallel to the surface. Alternate sections of cortex were reacted for HRP using tetramethylbenzidine (TMB) (Mesulam, '78) or stained for myelin using the Gallyas ('79) silver procedure. Thus, cortical architecture, physiological maps, and patterns of connections could be related. The brainstem was cut coronally and one of every three sections through the thalamus was reacted for HRP. In the case where tritiated WGA-HRP was injected, one in three sections were processed for autoradiography (Cowan et al., '72). The remaining sections were stained with cresyl violet or reacted for cytochrome oxidase, CO (Wong-Riley, '79).

Enlarged drawings were made of the TMB sections reacted to show labeled cell bodies and axon terminals and prominent blood vessels. Projections of adjacent thalamic sections stained with cresyl violet or reacted for CO were superimposed upon these drawings by matching prominent blood vessels, tissue artifacts, and boundaries so that labeled regions could be related to thalamic architecture.

One unoperated squirrel was used to examine thalamic architecture. The thalamus was cut coronally and one in three sections was stained with cresyl violet; remaining sections were stained using the Gallyas ('79) silver procedure. Myeloarchitectonic boundaries were related to cytoarchitectonic boundaries in this case and to thalamic borders revealed in other cases with cytochrome oxidase.

## RESULTS

The present report describes the thalamic connections of three electrophysiologically and architectonically defined subdivisions of the somatosensory cortex in gray squirrels, S-I, S-II, and a newly defined field, parietal ventral (PV). Because the gray squirrel is not a common laboratory animal and the somatosensory thalamus has not been delineated in detail before, we first illustrate and define the architectonic subdivisions of the thalamus, including a ventroposterior inferior nucleus not commonly recognized in rodents, and two somatosensory nuclei located dorsomedial and dorsolateral to VP, Pom and Pol, respectively. Next we describe the interconnections of thalamic nuclei with cortical fields.

### Thalamic architecture

The major subdivisions of the thalamus and especially the visual nuclei, the dorsal lateral geniculate nucleus, and the pulvinar complex, have been described for the gray squirrel previously (Kaas et al., '72). The present description concentrates on thalamic structures associated with subdivisions of somatosensory cortex. The major somatosensory nucleus is the ventroposterior nucleus (VP), which is traditionally divided into a ventroposterior medial "nucleus" or subnucleus (VPM) representing the face and head, and a ventroposterior lateral "nucleus" or subnucleus (VPL) representing the body. Dorsal to VP, we recognize two apparent nuclei in the general region of the posterior complex (Po) of rodents and other mammals (see Jones, '85). We refer to these nuclei as Pom, residing dorsal and medial to VP, and Pol, which is found more laterally and caudally to VP. Ventral to VP, we distinguish a ventroposterior inferior nucleus (VPI), although there are questions about the existence of VPI in mammals other than primates (Jones, '85; see Discussion). Finally, we describe auditory nuclei of the medial geniculate complex because one of the subdivisions of the somatosensory cortex, PV, also responds to auditory stimuli and has connections with part of the medial geniculate complex. These and other thalamic subdivisions are shown in a series of frontal brain sections stained for cells

*Abbreviations*

Thalamic nuclei:

| | |
|---|---|
| AD | anterior dorsal nucleus |
| AM | anterior medial nucleus |
| AV | anterior ventral nucleus |
| CL | central lateral nucleus |
| CM | centre median nucleus |
| EML | external medullary lamina |
| F | fasciculus |
| Hb | habenula |
| LD | lateral dorsal nucleus |
| LSd | lateral geniculate dorsal nucleus |
| LGv | lateral geniculate ventral nucleus |
| MGd | medial geniculate dorsal nucleus |
| MGi | medial geniculate internal nucleus |
| MGv | medial geniculate ventral nucleus |
| MD | mediodorsal nucleus |
| OT | optic tract |
| Pc | paracentral nucleus |
| Pf | parafascicular nucleus |
| Pol | posterior lateral nucleus |
| Pom | posterior medial nucleus |
| PT | pretectum |
| Pul | pulvinar |
| SG | supragenicnlate nucleus |
| SC | superior colliculus |
| RT | reticular nucleus |
| VL | ventral lateral nucleus |
| VM | ventral medial nucleus |
| VPI | ventral posterior inferior nucleus |
| VPL | ventral posterior lateral nucleus |
| VPM | ventral posterior medial nucleus |
| ZI | zona incerta |

Cortical areas:

| | |
|---|---|
| AI | primary auditory area |
| M | primary motor area |
| PM | parietal medial field |
| PR | parietal rhinal area |
| PV | parietal ventral area |
| SI | primary somatosensory area |
| S-II | second somatosensory area |
| TA | temporal anterior field |
| TP | temporal posterior field |
| UZ | unresponsive zone |
| 17 | area 17 or first visual field |

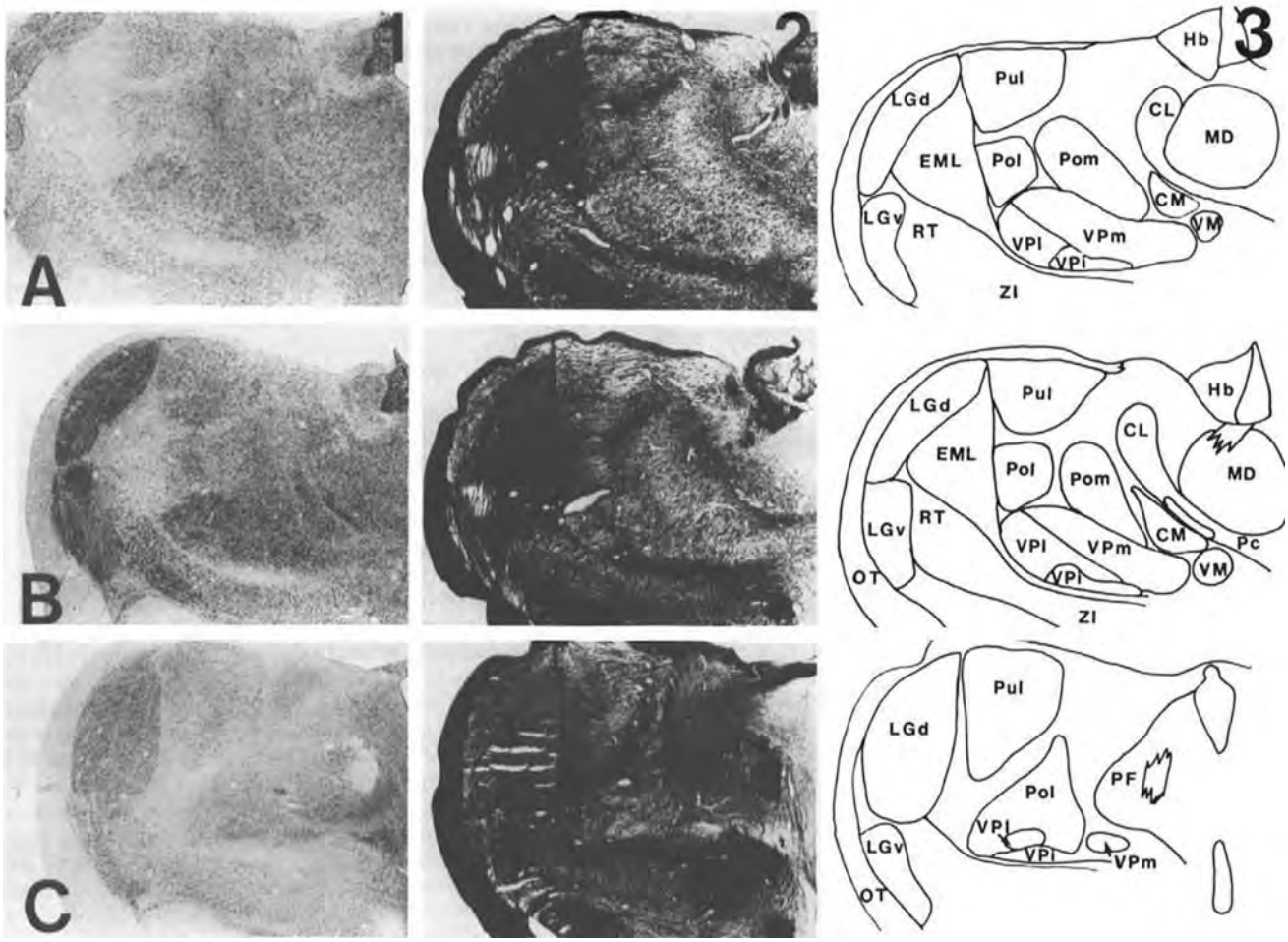



Fig. 1. Light-field photomicrographs of a rostrocaudal series (A through G) of thalamic sections stained for Nissl substance (column 1) or myelin (column 2), and boundaries of thalamic nucleus (column 3) obtained by correlating adjacent Nissl- and fiber-stained sections. Dorsal, top; medial, right. See Abbreviations list.

or fibers in Figure 1. In addition, the three-dimensional spatial relationships of the somatosensory and auditory nuclei are illustrated from medial and ventral perspectives in Figure 2. Characteristics of these nuclei in cytochrome oxidase preparations are indicated in Figure 3; see also Figure 5.

### The ventroposterior nucleus (VP): the ventroposterior medial (VPM) and ventroposterior lateral (VPL) subnuclei

The ventroposterior nucleus is easily recognized by its characteristic large, densely staining, and tightly packed neurons (Fig. 1A,B). The nucleus is also highly reactive for cytochrome oxidase (CO) in comparison to surrounding structures (Fig. 3B). VP is partly encapsulated with myelinated fibers, so that VP can be distinguished as a relatively myelin-poor region outlined by myelinated fibers and transversed somewhat by bands of myelinated fibers (Fig. 1A,B). VP is clearly subdivided into lateral (VPL) and medial (VPM) subnuclei by a cell-poor obliquely orientated band (Fig. 3A) that also reflects low CO activity (Fig. 3B) and stains darkly for myelin (Fig. 1A,B). VPM is larger, comprising approximately 55% of the volume of VP. VPM also has somewhat larger, more densely stained cells and slightly greater CO activity than VPL (Fig. 3). In some mammals, a fiber band is apparent that divides VPL into lateral and medial regions devoted to the hindpaw and forepaw, respectively (for review see Kaas et al., '84), but there is only a suggestion of these subdivisions in squirrels. Thus, a faint, oblique band of slightly fewer cells and somewhat reduced CO activity that is parallel to the band (arcuate lamina) separating VPL and VPM is sometimes apparent in VPL (Fig. 3). VP is bounded rostrally by VL, dorsally by nuclei Pom and Pol ventrally by VPI, laterally by the external medullary lamina (EML), medially by VM and CM, and caudally by the medial geniculate complex. The posterior pole of VP is adjacent to the ventral division of the medial geniculate complex (MGv) so that the boundary between the two is sometimes difficult to determine (Figs. 1C,D, 2).

***VPI.*** The ventroposterior inferior nucleus is a small, thin nucleus about one-tenth the size of VP. VPI consists of

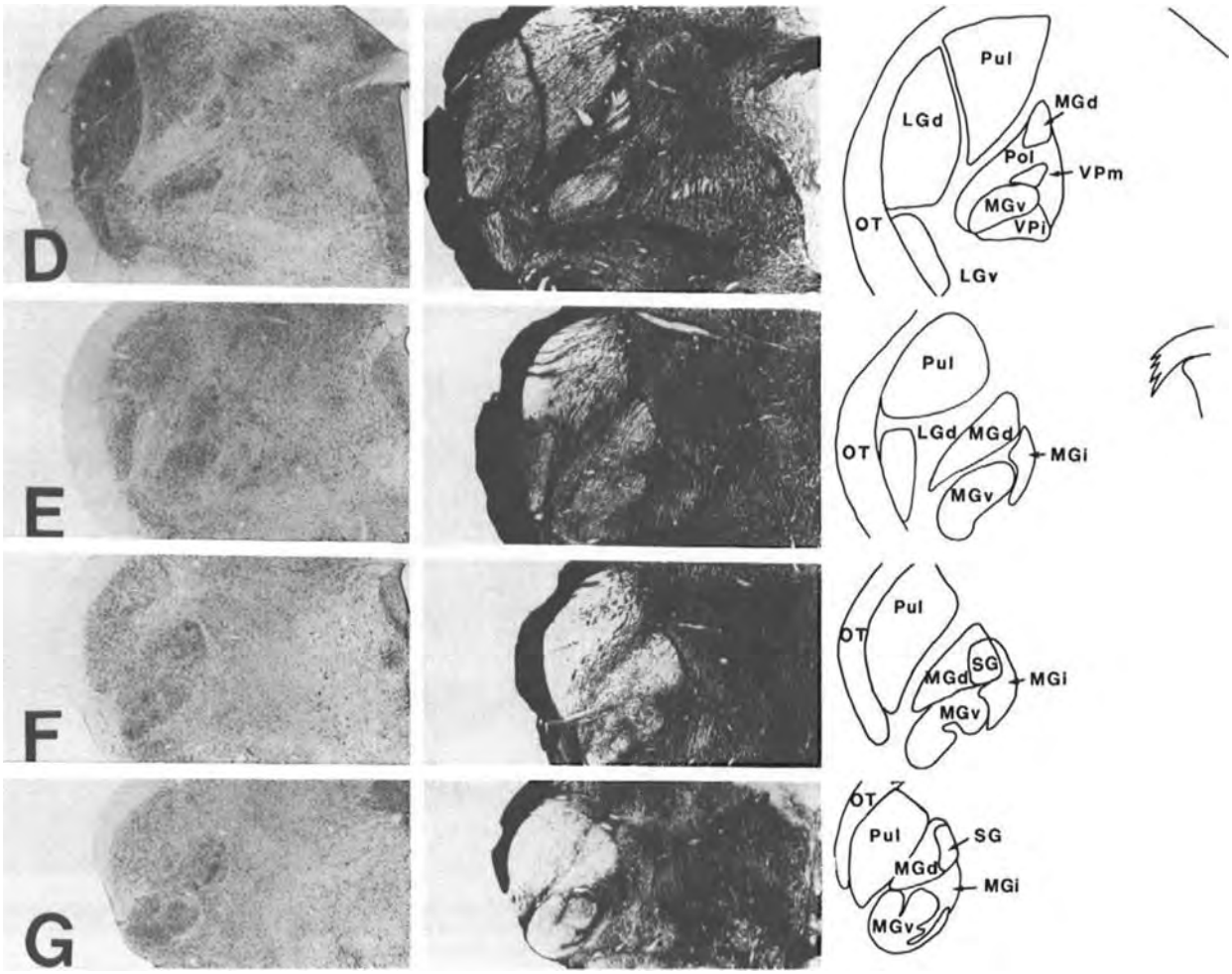
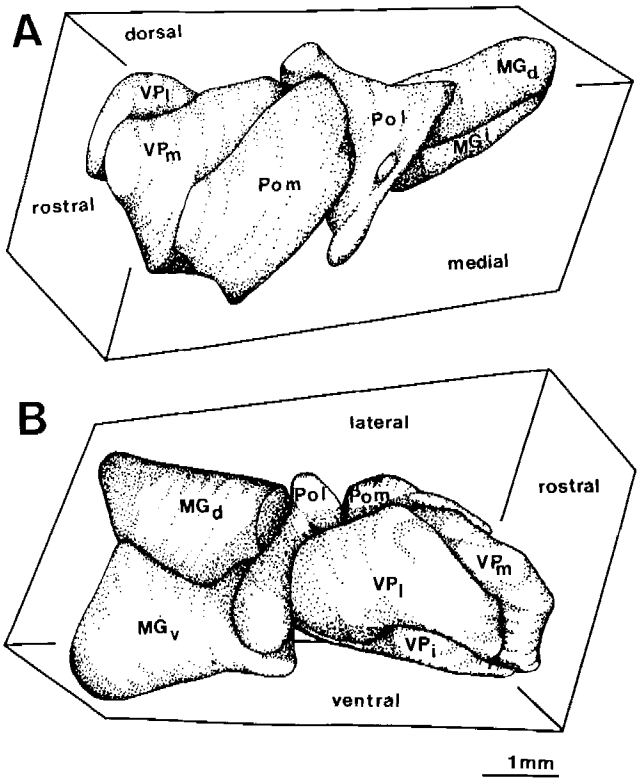



Figure 1 continued




small, lightly staining neurons that are scattered among ascending somatosensory fibers entering VP (Figs. 3A, 4A). In tissue reacted for CO, VPI is lighter than VP and denser than the ventral fiber bands (Fig. 3B). In brain sections stained for myelin, VPI appears much darker than VP (Figs. 1C, 4B). VPI forms the ventral border of the ventral posterior complex and extends caudally to the region of the medial geniculate complex (Figs. 1D, 4).

## Pol and Pom

Nuclei Pol and Pom form the dorsal border of VP (Fig. 2). They differ from VP by consisting of more scattered and less densely stained cells, and by being less reactive for CO (Fig. 3). Pol and Pom are distinguished from each other largely by a cell-poor region between them (Fig. 1A,B). Fibers also separate the two nuclei from the more dorsal pulvinar complex. At anterior levels, Pom is bounded by the ventral lateral nucleus (VL) on all sides except ventrally where Pom abuts VPM. At intermediate levels, Pom is medial to Pol, dorsal to VPM, and lateral to the central lateral nucleus (CL) and the centre median nucleus (CM). Posteriorly, the medial neighbors of Pom are the parafascicular nucleus (PF) and CM; the caudal pole of Pom is

Fig. 2. Three-dimensional views of auditory and somatosensory thalamic nuclei from medial (A) and lateral (B) perspectives. Pol drapes over the rostral portion of the medial geniculate complex and the caudal portion of the ventrobasal complex. Parts of the nuclei in each complex insert into the large, irregularly shaped Pol. See Abbreviations list.

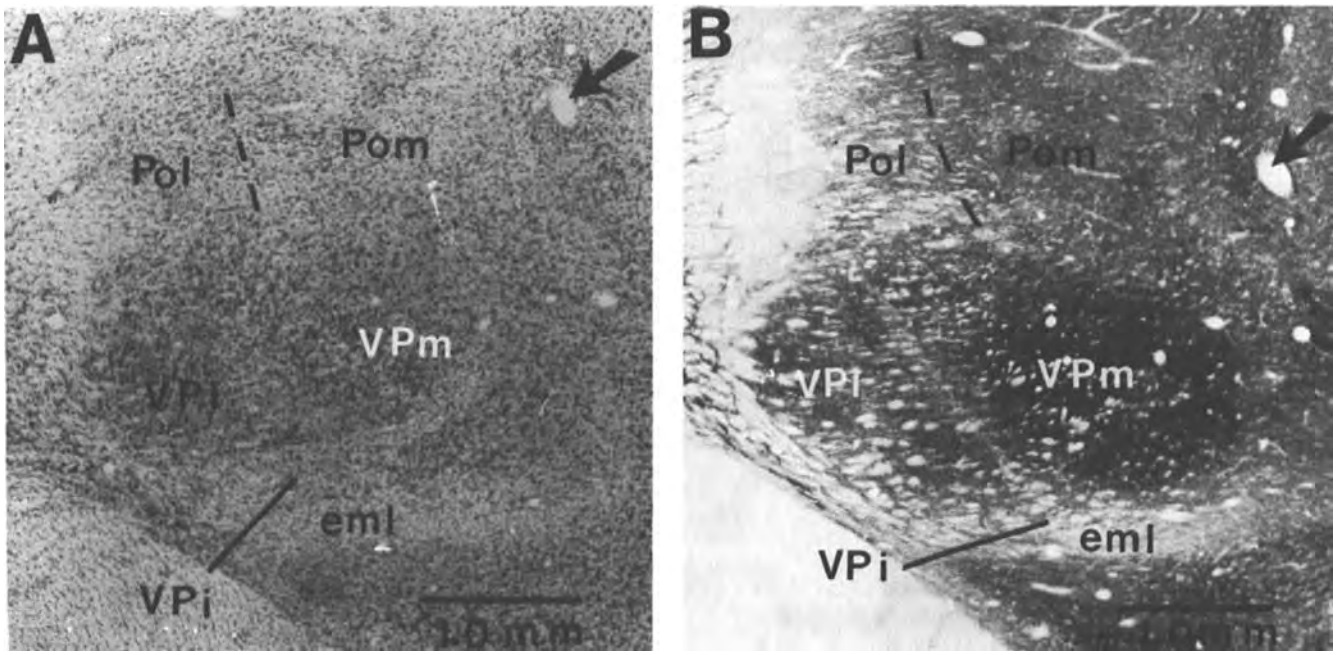



Fig. 3. Light-field photomicrographs taken at intermediate levels of the ventral posterior nucleus of the thalamus. **A.** Section of the thalamus that has been stained for Nissl substance. **B.** Adjacent thalamic section reacted for cytochrome oxidase. In A, note the large, darkly staining neurons in VPl and VPM relative to the surround. Also note the smaller, less tightly packed and lightly staining neurons in VPi. Pol and Pom are dorsal to the ventral posterior nucleus. In the adjacent section (B) reacted for cytochrome oxidase, VPL and VPM are darkly stained, whereas VPi is more lightly stained. Dorsal to VP, Pol and Pom are moderately stained with Pom slightly darker than Pol. Note the cell-poor zone in A and the lightly stained zone in B that separates the medial (VPM) and lateral (VPL) subnuclei of the ventral posterior nucleus. The large arrows point to the same blood vessel in both A and B. Dorsal is to the top and medial is right. See Abbreviations list.

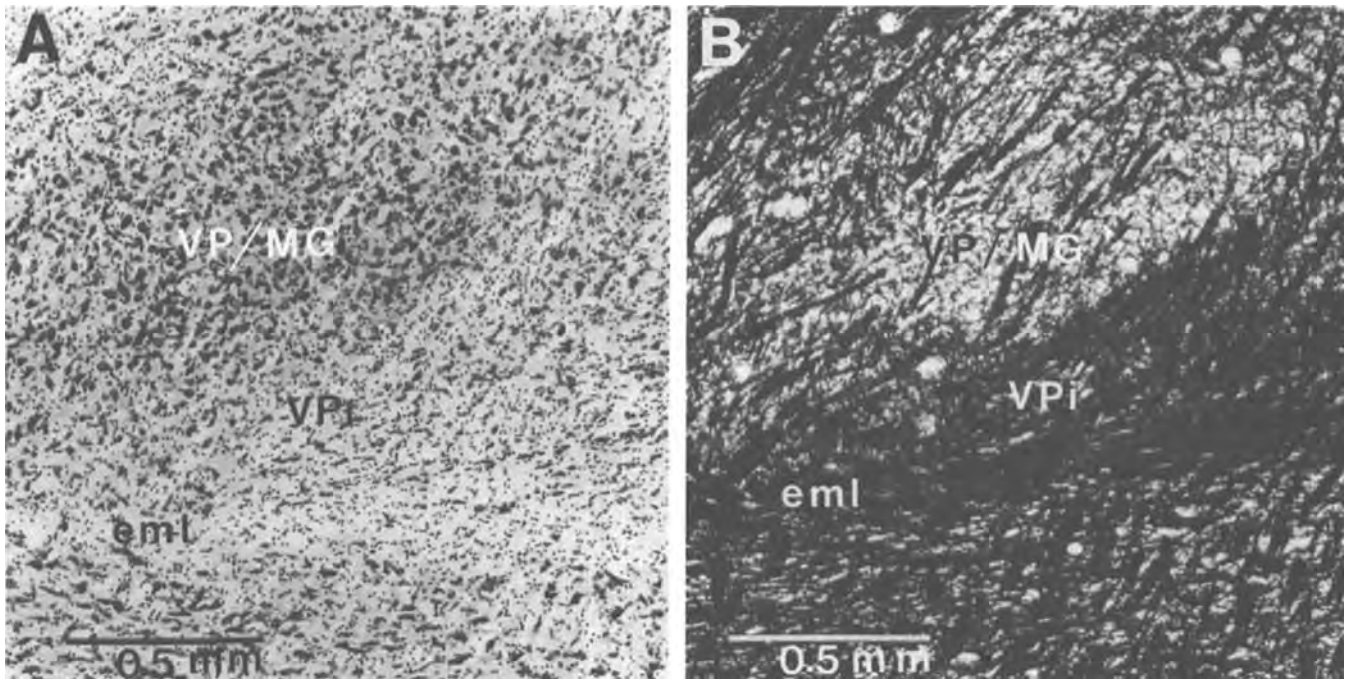



Fig. 4. Light-field photomicrographs of Nissl (A) and fiber (B) preparations taken at the junction of the medial geniculate complex and the ventroposterior complex. A. Section that has been stained for Nissl. B. Adjacent section stained for myelin. In A, the small, lightly staining, horizontally elongated soma of neurons comprising VPI are distinct from the larger, more darkly staining, and densely packed neurons at the VP/MG junction. In B, the densely myelinated VPI nucleus is quite distinct from the lightly stained VP and MG. Dorsal is to the top and medial is right. See Abbreviations list.

bounded by Pol. Pol is approximately equal in size to Pom but occupies a more posterior portion of the thalamus. At its anterior pole, Pol abuts Pom (Fig. 2B), and at anterior levels, Pol is bounded by Pom medially, VPM ventromedially, VPL ventrolaterally, and the EML laterally (Fig. 2A,B). At posterior levels, Pol is bounded by the pulvinar dorsolaterally, CM medially, and by MGi ventrally. The posterior border of Pol is formed by the three major divisions of the medial geniculate complex (Fig. 1D).

## The medial geniculate complex

The medial geniculate complex is commonly divided into a ventral or principal nucleus, a dorsal nucleus, and an internal or magnocellular nucleus. These three divisions are described below.

***MGv.*** The ventral or principal division of the medial geniculate complex is a large spherical nucleus that is lobulated at intermediate levels (Figs. 1G, 5A,B). MGv comprises about 55% of the total volume of the complex. In sections stained for Nissl substance, MGv is clearly discernible as a nucleus with darkly staining, densely packed neurons of moderate size (Fig. 5A). MGv stains lightly for myelin, whereas in tissue reacted for cytochrome oxidase MGv is very dark (Fig. 5B,C).

***MGd.*** The dorsal nucleus (MGd) occupies about 30% of the total area of the medial geniculate complex and is the second largest nucleus in this nuclear group. MGd is characterized by moderately staining neurons that are quite small and loosely packed laterally and more tightly packed medially. The medial part of MGd may include the suprageniculate nucleus described by others (see Jones, '85). MGd stains lightly for myelin (Fig. 5B). In tissue reacted for CO, MGd appears somewhat darker than MGi but much lighter than MGv (Fig. 5C). MGd forms a wedge between the pulvinar and MGi and MGv (Figs. 1F,G). At its anterior pole, MGd is inserted into Pol, whereas at intermediate levels it adjoins the pulvinar dorsolaterally, the anterior pretectum (PT) medially, MGi ventromedially, and MGv ventrolaterally.

***MGi.*** The internal, or magnocellular, division is located largely medial to but partially between the dorsal and ventral divisions of the medial geniculate complex. Throughout most levels, MGi is lateral to the pretectum. The rostral pole of MGi is adjacent to the ventral posterior nucleus and is embedded in Pol (Fig. 2A). MGi is a small crescent-shaped nucleus comprising 15–20% of the total volume of the complex. Neurons in this division are large, sparsely packed, and are very dark in tissue stained for Nissl substance (Fig. 5a). MGi is densely myelinated (Fig. 5B). In tissue reacted for cytochrome oxidase, MGi is less dense than surrounding nuclei (Fig. 5C).

## Connections

Thalamic connections were determined after cortical areas S-I, S-II, and PV were mapped with microelectrodes, boundaries were marked with microlesions, and electrophysiologically defined regions of the cortex were injected with the anatomical tracer WGA-HRP or tritiated WGA. Brain sec-

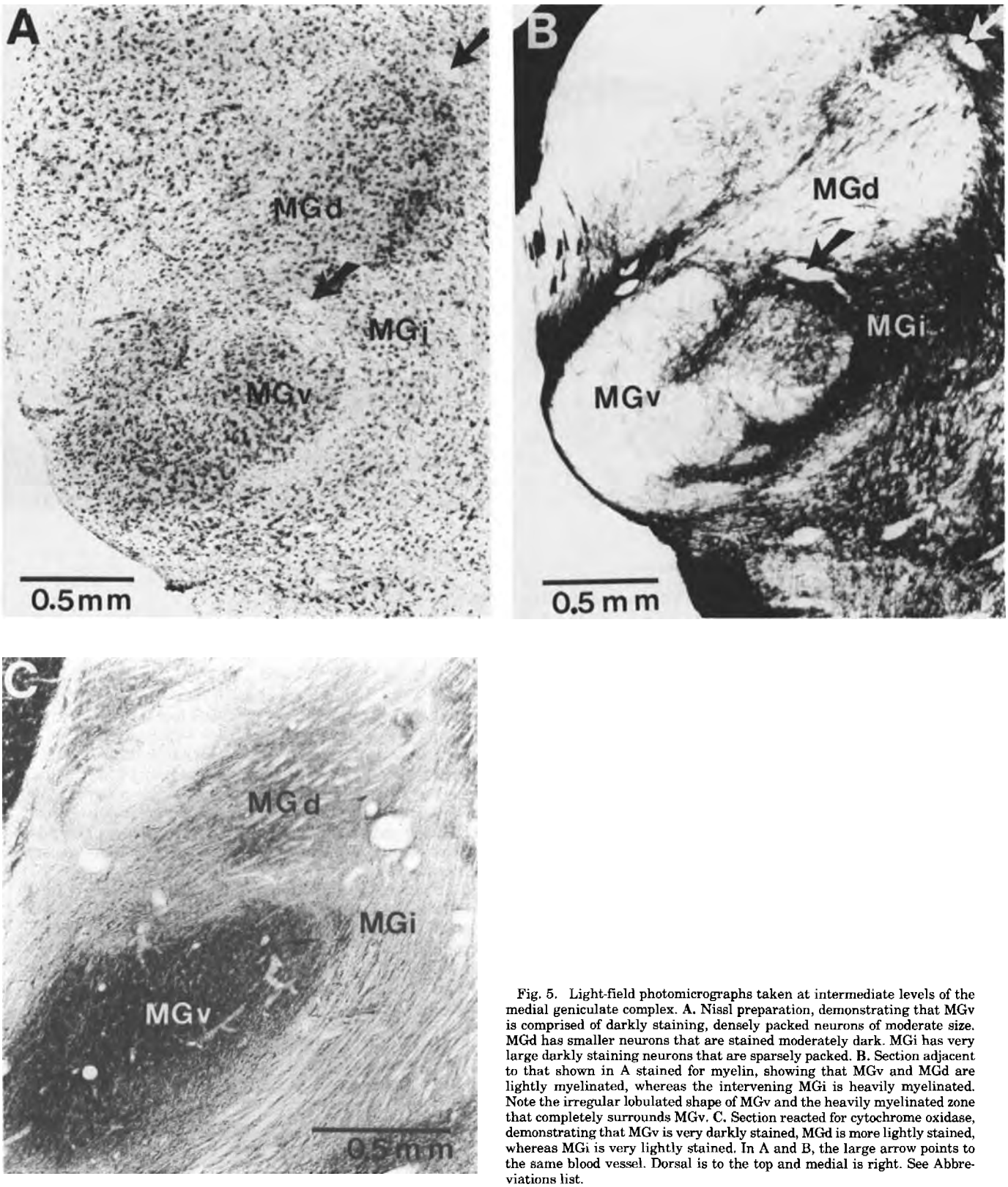



Fig. 5. Light-field photomicrographs taken at intermediate levels of the medial geniculate complex. **A.** Nissl preparation, demonstrating that MGv is comprised of darkly staining, densely packed neurons of moderate size. MGd has smaller neurons that are stained moderately dark. MGi has very large darkly staining neurons that are sparsely packed. **B.** Section adjacent to that shown in A stained for myelin, showing that MGv and MGd are lightly myelinated, whereas the intervening MGi is heavily myelinated. Note the irregular lobulated shape of MGv and the heavily myelinated zone that completely surrounds MGv. **C.** Section reacted for cytochrome oxidase, demonstrating that MGv is very darkly stained, MGd is more lightly stained, whereas MGi is very lightly stained. In A and B, the large arrow points to the same blood vessel. Dorsal is to the top and medial is right. See Abbreviations list.

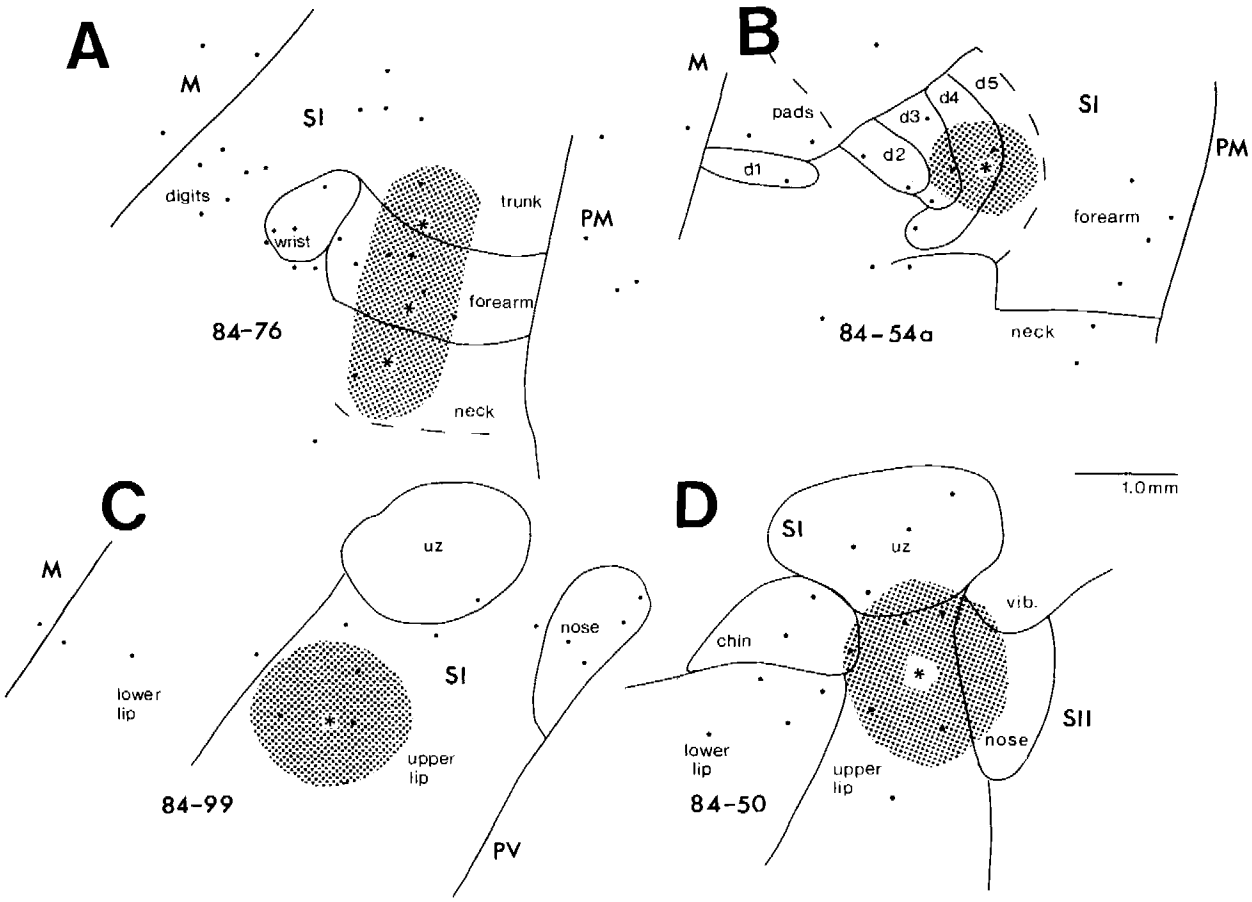



Fig. 6. The locations of the injection sites (stipple) relative to physiologically identified representations of body parts in S-I of four cases. Injections were placed in the forearm, trunk, and neck representations (A), in the digit representation (B), and in the upper lip representations (C, D). Dots mark electrode penetrations; asterisks mark where the injection pipette punctured cortex; solid lines indicate estimated boundaries between body part representations. Dorsal is to the top and caudal is right. See Abbreviations list.

tions were later examined to relate physiological borders with architectonic boundaries, and labeled cell bodies and axon terminals in the thalamus were plotted and related to thalamic architecture.

***The first somatosensory area, S-I.*** Connections of the first somatosensory area were determined after injections were placed in different parts of the body surface representation in five gray squirrels. All injections were restricted so that none spread beyond the physiological or myeloarchitectonic boundaries of S-I. Three injections were made in the face representation 84-50, 84-99, and 84-57 (not shown), whereas two were restricted to the limb and trunk representations (84-54a, 84-76). Injection sites are shown relative to cortical fields in illustrations of individual cases for four of these squirrels (see Figs. 7-10; also see Krubitzer et al., '86). In addition, the dense label of the injection site is related to local maps of the body surface in S-I for four of these five cases in Figure 6.

Injections in the face representation in S-I resulted in both anterograde and retrograde label in the medial division of the ventral posterior nucleus, the ventral portion of Pom, and in one case (84-50), the rostromedial portion of VPI. Injections in the hand (84-54a) and shoulder-trunk (84-76) representations in S-I revealed transported tracer in the lateral division of the ventral posterior nucleus, the dorsal portion of Pom, and in the middle portion of the ventral posterior inferior nucleus.

Because different body part representations were injected in S-I, the transported tracer revealed aspects of the somatotopic organization of the thalamic nuclei. Three cases provide information about thalamic representations of the face. In case 84-99, the injection was restricted to the upper lip representation in S-I (Fig. 6c). As expected, dense interconnections were observed between the cortex and VPM (Fig. 7). The location of the label indicates that the upper lip is represented somewhat centrally in VPM, occupying much of the dorsoventral dimension of the nucleus. Label was not found at the rostral and caudal poles of VPM. A separate patch of both anterograde and retrograde label was also found in the adjoining ventral portion of Pom, suggesting that Pom also contains a second representation of the upper lip. Similar results were obtained in another case (84-50; Figs. 6D, 8) where an injection into the representation of the upper lip was placed somewhat more me-

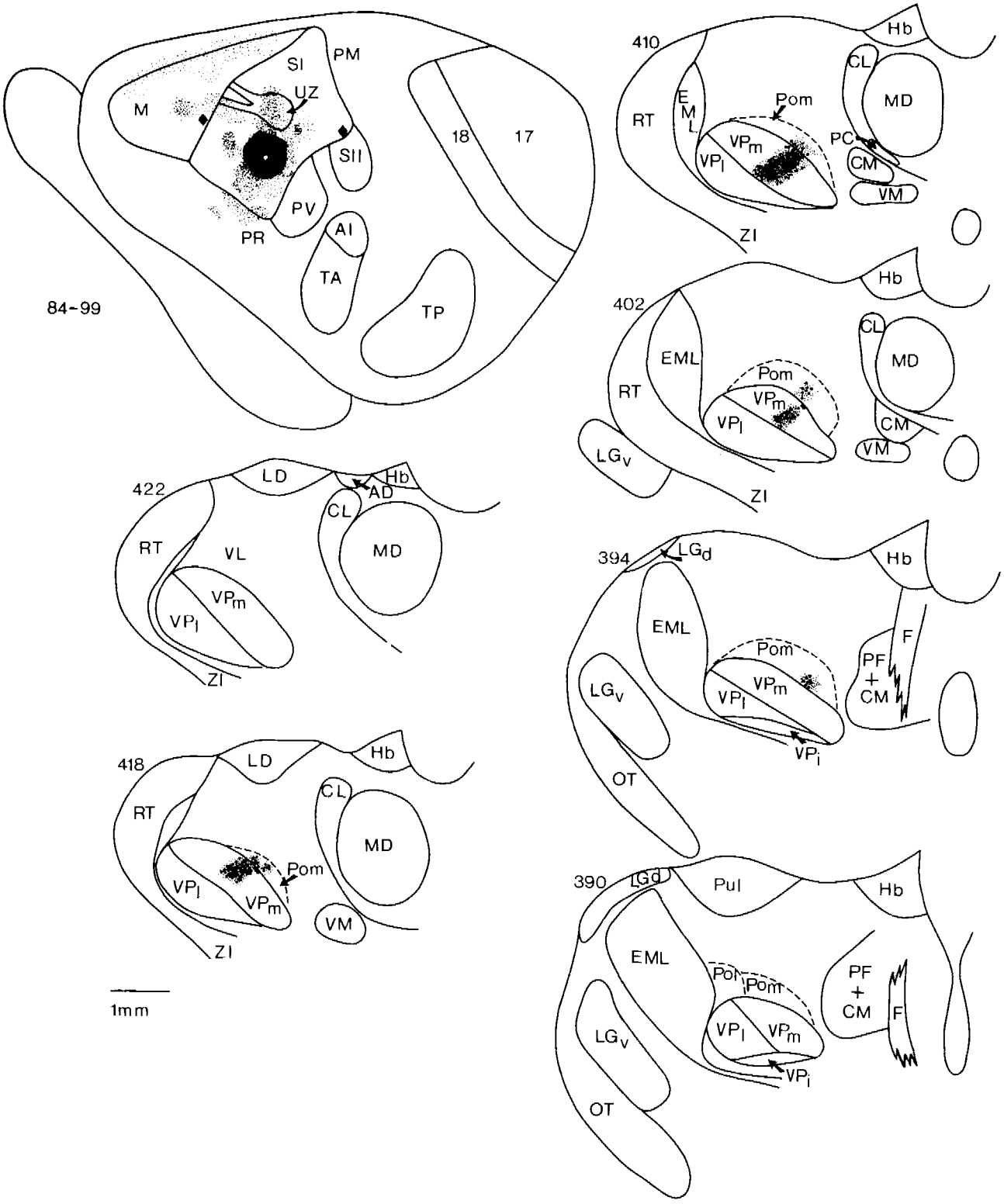



Fig. 7. Thalamic label in a numbered rostrocaudal series of coronal sections after an injection in the representation of the upper lip in S-I (upper left). Dense label is concentrated in VPm and more moderate amounts of label are found in the dorsal portion of Pom. Solid lines denote architectonic boundaries. Diamonds mark lesions at physiological boundaries. In the thalamic sections, dorsal is up and medial is right. Thalamic sections in this and the following cases were cut at 40 $\mu$m and numbered caudorostrally. Consecutive changes in thalamic number = 40 $\mu$m and nonconsecutive change = the numerical change times 40. Large dots illustrate retrograde label and small dots denote presumptive anterograde label subdivisions of cortex are from the reports of Kaas et al., '72; Krubitzer et al., '86; and Merzenich et al., '76. See Abbreviations list.

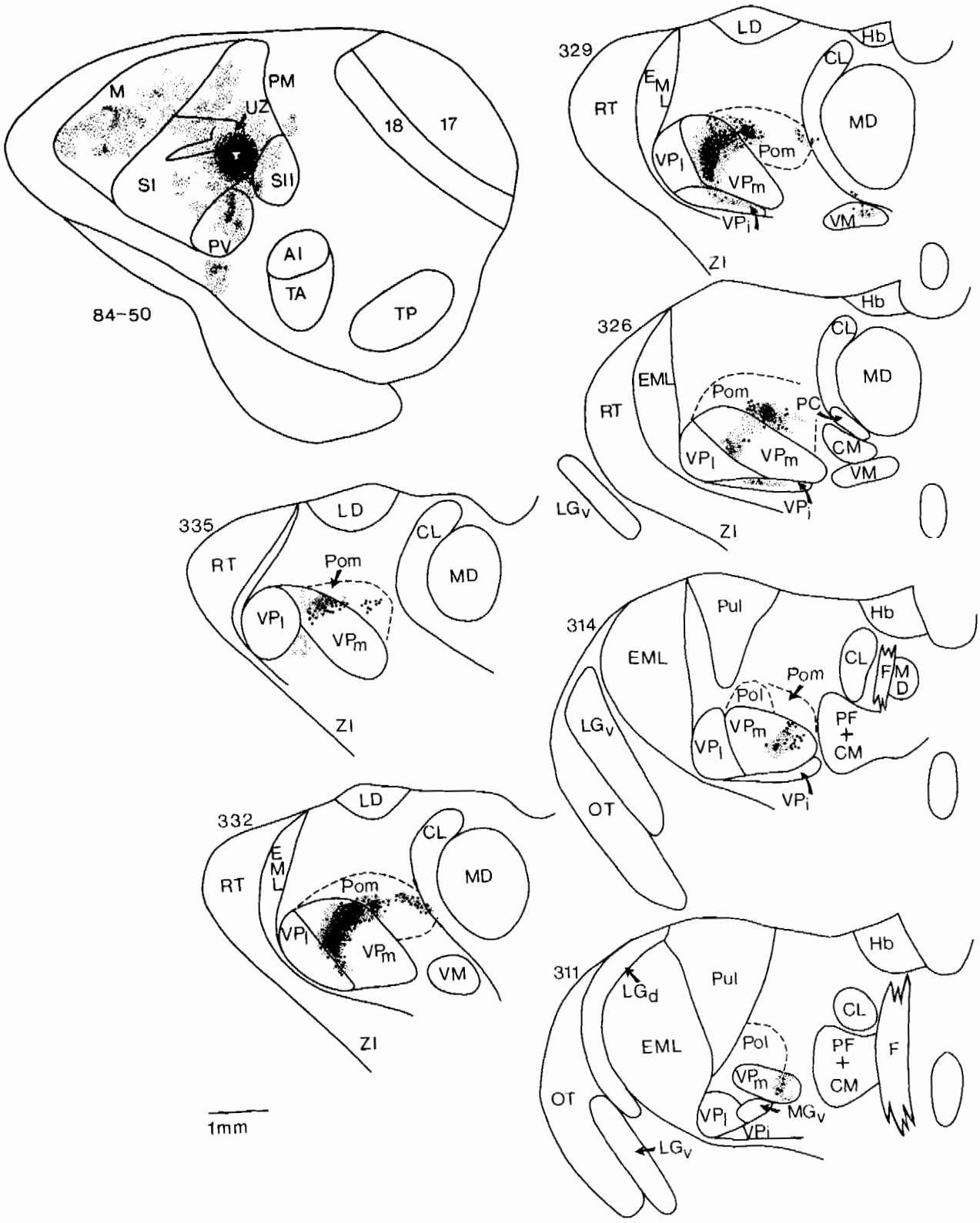



Fig. 8. Thalamic label after an injection in the representation of the upper lip in S-I. Portions of the representations of the nose and vibrissae as well as the dysgranular UZ were also involved in the injection site (compare with Fig. 6). Label found in VPm in this case is slightly more lateral than the label found in VPm after a restricted upper lip representation injection (Fig. 7) suggesting that the caudal face is represented more laterally than the rostral face in VPm. Other conventions as in Figure 7. See Abbreviations list.

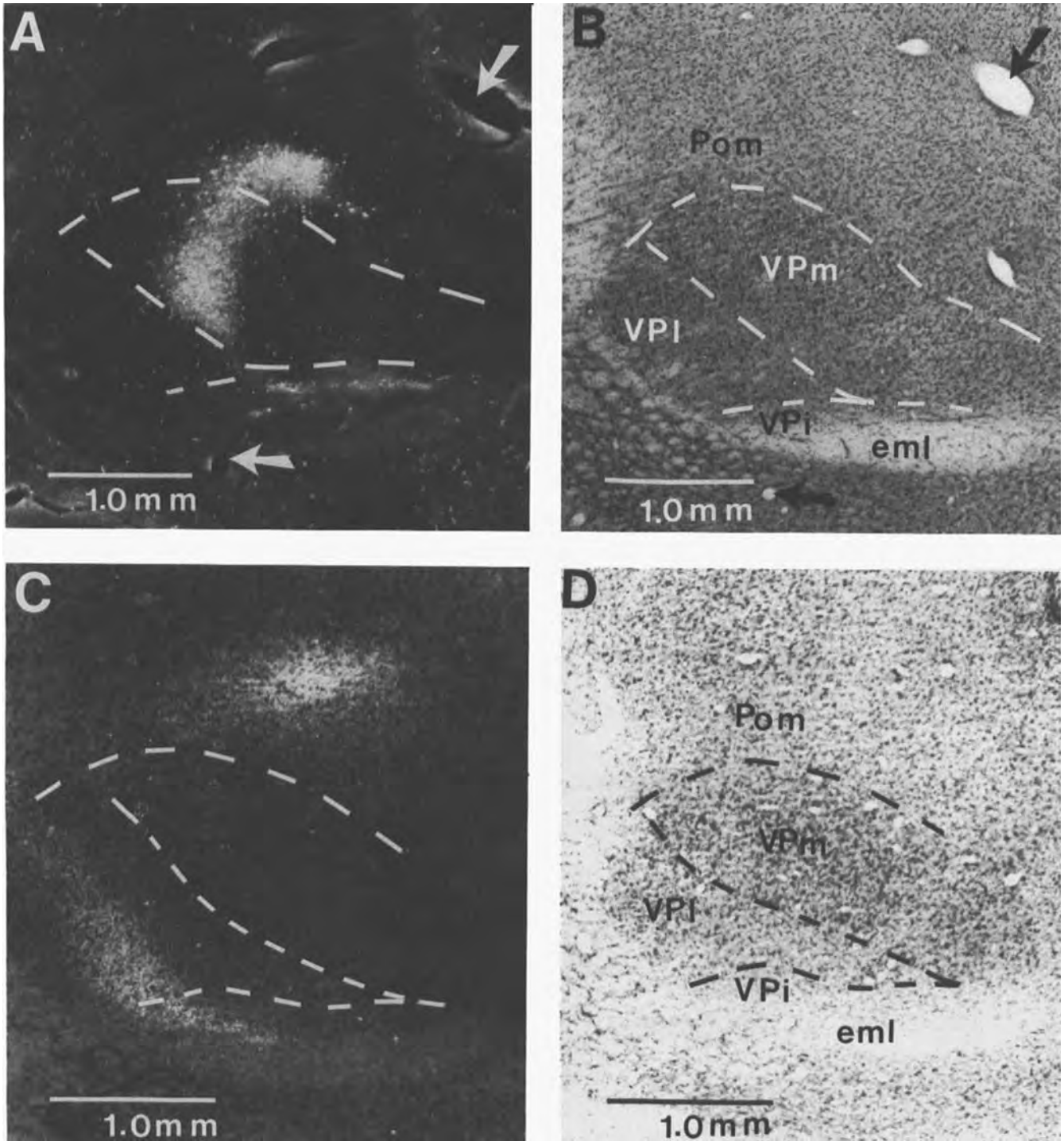



Fig. 9. Dark-field (A, C) photomicrographs of transported tracer in the thalamus after injections in S-I, and adjacent thalamic sections (B, D) stained for Nissl substance. A. Anterograde and retrograde label in VPm, Pom and VPi after an injection of WGA-HRP in the representation of the face in S-I. C. Anterograde and retrograde label in VPL, Pom and VPi after an injection in the forepaw digit representation in S-I. D. Section in C viewed under light-field illumination. Coronal sections. Dorsal is to the top and medial is right. See Abbreviations list.

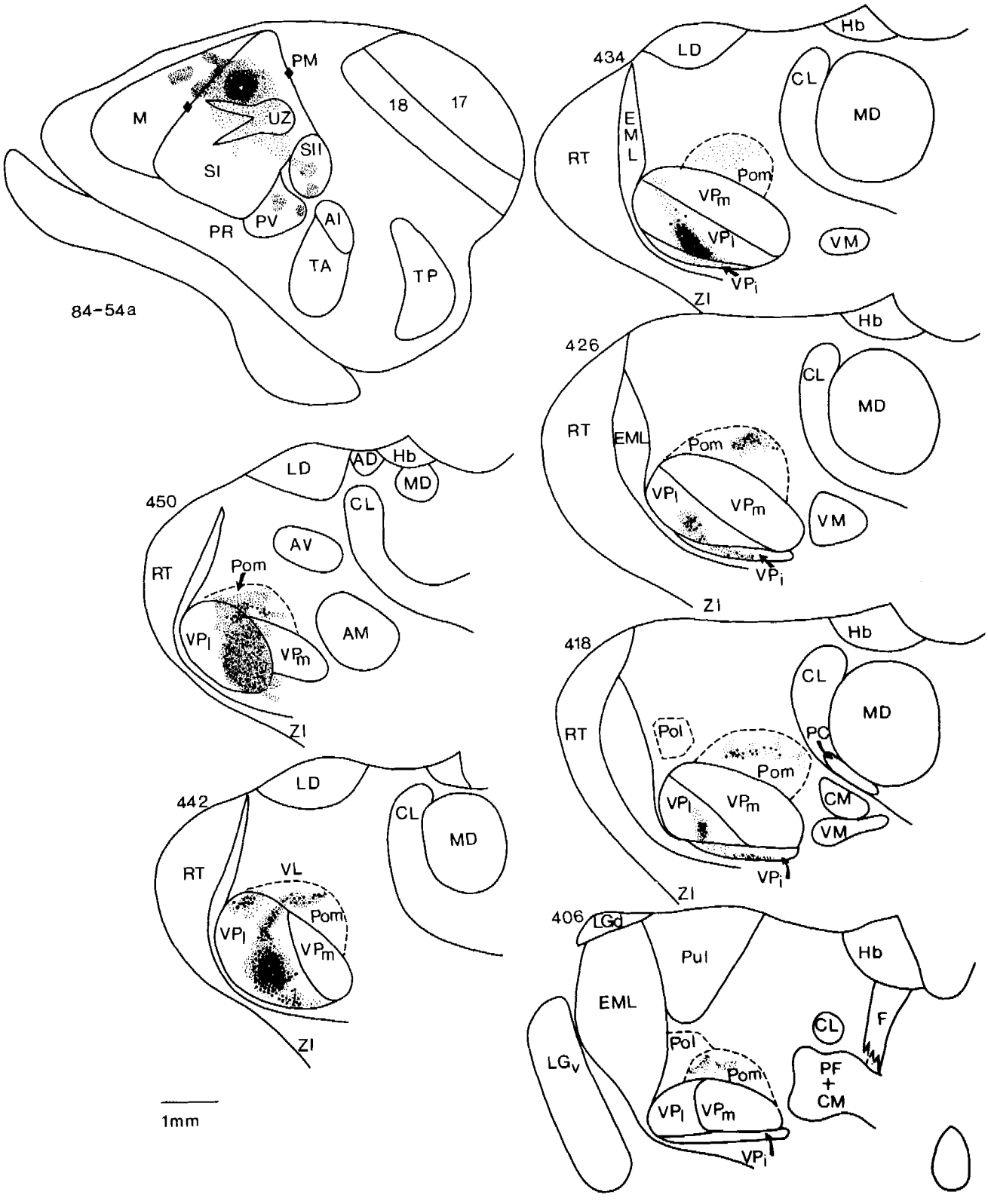



Fig. 10. Thalamic label after an injection of tritiated WGA in the representation of the digits of the forepaw in S-I. Rostrally, label is found medially in VPL, whereas at intermediate and caudal levels of the nucleus, the transported tracer resides ventrally. Label is also apparent in Pom, but the label occupies a more dorsal position than label found in Pom after a face injection. Compare with Figures 7, 8. Other conventions as in Figure 7. See Abbreviations list.

dially in S-I so that the injection site included more of the dysgranular, unresponsive zone (see Krubitzer, '86) and probably involved some of the representations of the nose and vibrissae. As in case 84-99 (Fig. 7), cells and terminations were labeled in the middle portion of VPM in case 84-50 (Fig. 8), but the label was slightly more lateral than in case 84-99. Thus, more caudal portions of the upper lip and adjoining vibrissae appear to be represented more laterally in VPM. In addition to the restricted band of label in VPM, another focus of label was in the adjoining portion of Pom (Figs. 5, 8, 9a). The patch of both anterogradely and retrogradely transported tracer in the ventral midportion of Pom was in a more lateral position and extended more dorsally than in case 84-99 (compare Fig. 7 with Fig. 8). Interconnections were demonstrated with the middle portion of rostral VPI (Fig. 9a), as well as with VM and CL (Fig. 8). Finally, case 84-57 (not shown) had an injection centered in the vibrissae representation of S-I that spread into a portion of the lateral face representation. Transported tracer crossed VPM dorsoventrally and extended from the anterior to the posterior pole of the subnucleus. This zone of label was located even farther laterally in VPM than that seen in case 84-50. A separate distinct patch of label, adjacent to that found in VPM, was also apparent in Pom. Like the previously described cases, the label was ventral in Pom and extended from the anterior to the posterior pole. However, the label in Pom was situated more laterally than the label found in the other two cases of injections in the face representation in S-I.

Taken together, results from these three cases support the conclusion that the face and head are represented in VPM of squirrels, and that the upper caudal face is represented lateral to the rostral face. In addition, a second parallel representation of the face clearly exists in the adjoining portion of Pom. Finally, interconnections with VPI, found only in case 84-50, may relate to the large involvement of the injection site with the UZ, or the possible extension of the injection site to caudal borders of S-I.

Results from two cases provide information on how the trunk and forelimb are represented in the thalamus. In case 84-54a, an injection of tritiated WGA-HRP was placed in the representation of the forepaw digits in S-I; the injection may have spread slightly into the wrist representation as well (Fig. 6b). Labeled cell bodies and axon terminals were found in the medial half of VPL. The transported tracer crossed the ventrodorsal dimension of the rostral portion of VPL (Fig. 10); more caudally, the label was in a ventral position only. Both anterograde and retrograde label were also located in Pom in a region more dorsal than that described for injections in the face representation in S-I (Fig. 9c). The label extended from the rostral to the caudal pole of Pom. A mediolateral strip of anterograde and retrograde label was also found in the middle ventral portion of VPI at intermediate levels.

In another case (84-76; Figs 6a, 11), three small adjacent injections were placed in the trunk, forearm, and neck representations in S-I. Because the injections were closely spaced, they fused to form a single elongated injection site. As in case 84-54a, a zone of overlapping anterograde and retrograde label was in VPL. This label was continuous from the rostral to caudal extent of the nucleus (Fig. 11). Unlike case 84-54a, where the transported tracer was located more ventrally, labeled cell bodies and axon terminals in this case were found more dorsolaterally in VPL (compare Fig. 10 with Fig. 11). Pom also contained transported tracer. However, the label was located in the dorsalmost aspect of the nucleus at posterior levels. Finally, at rostral levels, both retrograde and anterograde label were found in the middle portions of VPI.

The results from the two cases support the conclusion that the forepaw is represented rostromedially, whereas the forearm and adjoining parts of the shoulder and neck are represented dorsally in VPL. A second representation of these body parts occurs dorsomedially in Pom. Thus, the overall representation in Pom parallels that in VP, with the body representations lateral to the face representations. Finally, at least some locations in S-I appear to have interconnections with VPI.

***The second somatosensory area, S-II.*** Injections of WGA-HRP were placed in the second somatosensory area in two gray squirrels (84-54b, 84-95). Both included portions of the forelimb, trunk, and hindlimb representations in S-II. However, the injection in case 84-54b was placed in slightly more proximal portions of the body representation than case 84-95 (Fig. 12a,b). In both cases, transported tracer was found in the ventroposterior nucleus, Pol, and Pom.

In case 84-95, an injection placed in the upper forelimb representation within S-II included portions of the trunk and caudal head representations (Fig. 12a). A zone of anterograde and retrograde label in VP included portions of both VPL and VPM. Label was apparent at all rostrocaudal levels of VP, but the label was most dense dorsolaterally in the nucleus (Figs. 13, 14a,b). Transported tracer was largely restricted to caudolateral levels of VPM. The location of label in VPM is consistent with the view that caudal face and scalp is represented dorsolaterally and caudally in VPM. In addition to label found in VPL and VPM, transported tracer was also found throughout all levels of Pol. Caudally, the label was located in the medialmost portion of Pol, whereas at intermediate and rostral levels the label was found more laterally. Labeled cells and terminations were also found in Pom. At caudal levels of the nucleus the label was in a middle portion, whereas farther rostrally, the label was located more dorsally.

In a second case, an injection centered in the shoulder representation spread into the trunk representation of S-II (Fig. 12b). A dense focus of labeled cells and terminations was found in dorsolateral VPL (Figs. 14c, 15). Label was found at all rostrocaudal levels of VPL. No label was found in VPM. As in case 84-95, labeled cell bodies and axon terminals were also found in Pol. However, the patches of transported tracer were not as widely distributed as in case 84-95. Instead, a focus of retrograde and anterograde label was found only in the dorsal aspect of rostral Pol. Patches of transported tracer were also found in Pom. At caudal levels of the nucleus, two patches, a small dorsal one and a larger middle one, were seen in the lateral aspect. More rostrally, the label was found in the laterodorsal portion of Pom (Fig. 15a).

***The parietal ventral area, PV.*** Three squirrels were used to determine the interconnections between the parietal ventral area of cortex and the thalamus (84-96, 84-115, 85-68). Although each case had injections centered in slightly different representations of body parts within PV, the labeled thalamic nuclei were similar across cases. Reciprocal connections were found with VP, VPI, Pol, and the internal division of the medial geniculate complex. In addition, anterograde label was found in the ventral division of the MG

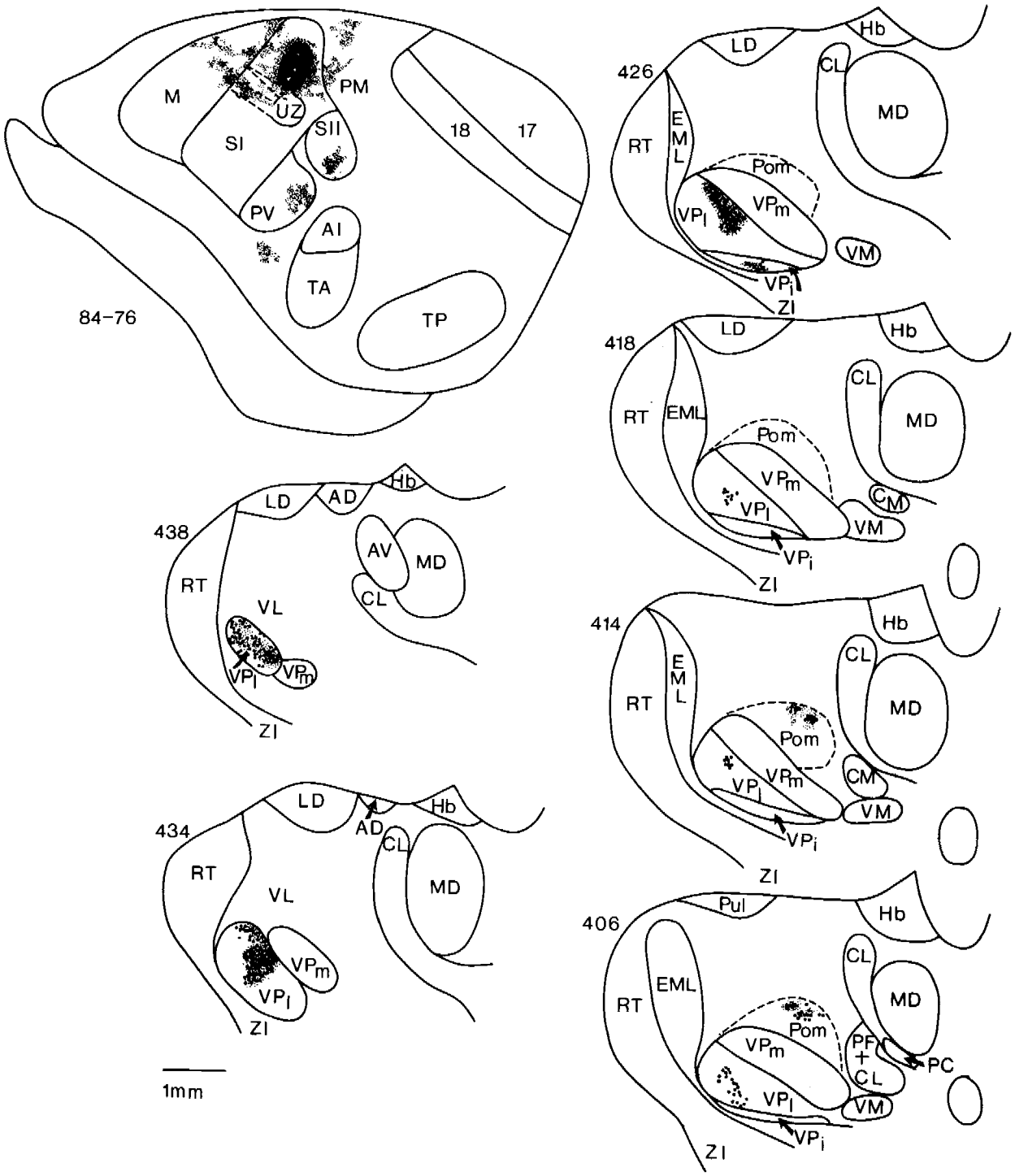



Fig. 11. Thalamic label after three small injections of WGA-HRP in the forearm, trunk, and neck representations in S-I. The labeled cell bodies and axon terminals are located more dorsolaterally in VPL than after a digit injection (compare with Fig. 10). Other label is in the dorsalmost aspect of Pom. Conventions as in Figure 7. See Abbreviations list.

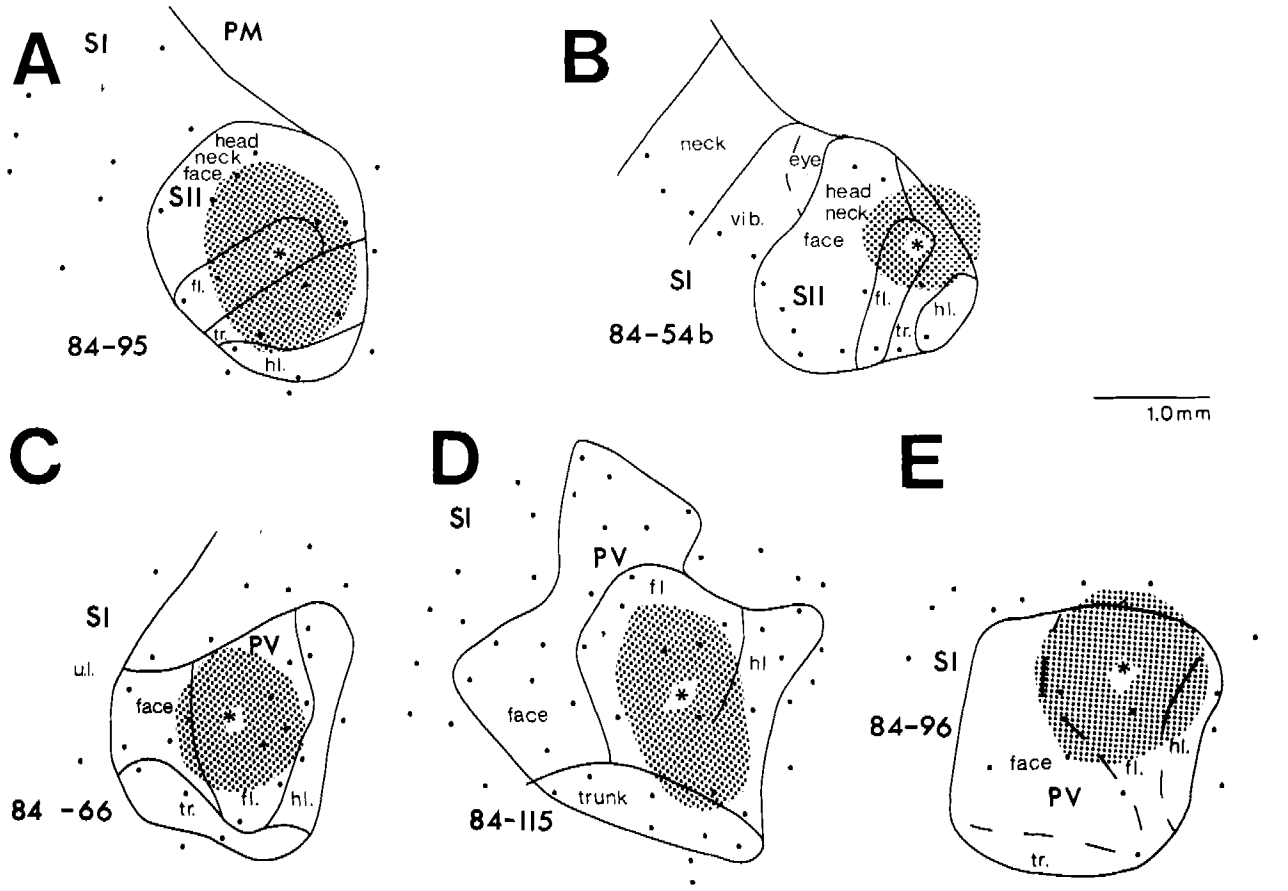



Fig. 12. Injection sites (stipple) in S-II (A, B) and PV (C, D, E) as they relate to physiologically identified representations of body parts. Injections were centered in the upper forelimb representation of S-II. However, one injection involves more of the head representation in S-II (A), whereas the other involves more of the trunk representation in S-II (B). Injections in PV were also centered in the forelimb representation. However, in C, portions of the face representation were involved in the injection site. In D, the injection spread into the caudal portions in PV involving parts of the hindlimb and trunk representations. The distal forelimb representation was injected in C; however, a portion of the hindlimb and face were also involved in the injection. In all figures, dots indicate electrode penetrations, asterisks mark where the injection pipette punctured cortex, and solid lines indicate boundaries between body part representations. Dorsal is to the top and caudal is right. See Abbreviations list.

complex, and in two cases, the suprageniculate nucleus.

Individual cases differed slightly in where the transported tracer was found in these nuclei. Case 84-66 had a relatively large injection of WGA-HRP that was centered in the representation of the forepaw, but it encompassed portions of the forelimb and face representations as well (Fig. 12c). The injection was completely restricted to PV. Labeled cell bodies and axon terminals were concentrated ventrally throughout the rostrocaudal extent of the central portion of VPL (Figs. 16, 17a,b). Injections in S-I (Fig. 10) suggest that this portion of VPL is devoted to the forepaw. Only sparse label was found in caudal VPM. VPI contained dense anterograde and retrograde label that was concentrated in the lateral aspect of the nucleus. The caudal portion of Pol also contained a patch of labeled cells and axon terminals. Dense label was found over much of MGi, and sparse anterograde label was found in the suprageniculate nucleus (SG).

Case 84-115 had an injection largely restricted to the forepaw representation, in PV, although there was some spread into portions of the trunk and hindlimb representations (Fig. 12d). A medioventral zone of anterograde and retrograde label extended throughout intermediate and caudal levels of VPL (Fig. 18). At most, only the caudomedial margin of VPM contained the tracer. Again, all levels of the lateral aspect of VPI contained both anterograde and retrograde label. Pol was also labeled, but only sparsely at intermediate levels. MGi contained both anterograde and retrograde label at more rostral levels, whereas MGv displayed only anterograde label most medially at rostral levels (Fig. 19a,b). Both anterograde and retrograde label was found in the suprageniculate nucleus as well.

In a third case (84-96), the injection was centered in the forepaw representation of PV. However, the tracer also spread into portions of the forelimb, face, and hindlimb representations (Fig. 12E). As in the other cases, VPL contained both labeled cell bodies and axon terminals. The label was more medial in VPL than in cases 84-66 and 84-115 (compare Figs. 13, 18, 20). The caudal portions of VPM also contained anterograde and retrograde label. A dense aggregation of labeled cell bodies and axon terminals was found in the lateral portion of VPI at rostral levels and across the mediolateral extent at intermediate and caudal levels (Fig. 17c). As in the previous cases, Pol contained

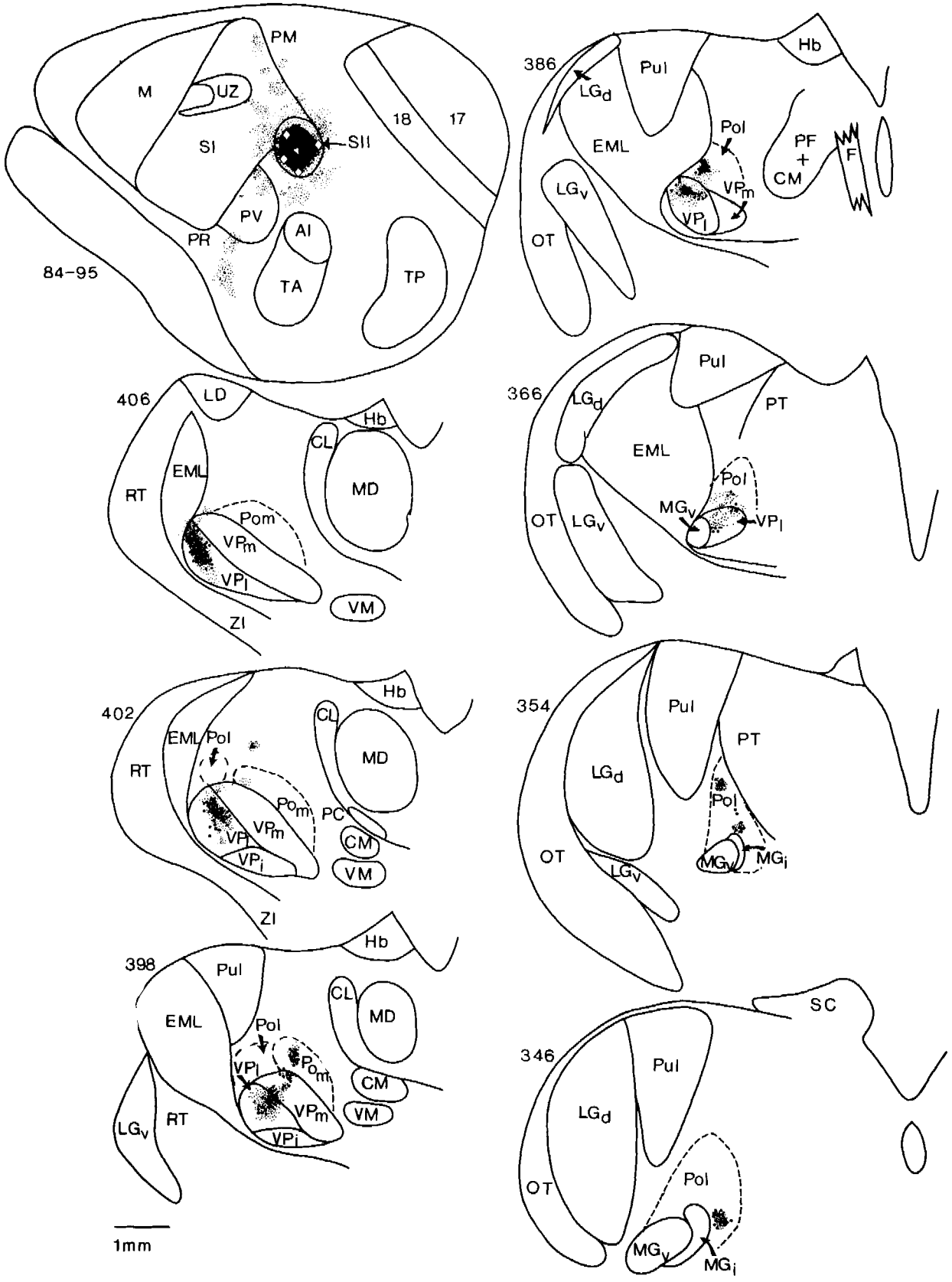



Fig. 13. Thalamic label after an injection of WGA-HRP centered in the upper forelimb representation of S-II (upper left). In this injection, portions of the face and trunk representations were also involved. Label is most dense dorsolaterally in VPL. In VPM label is restricted caudolaterally. Conventions as in Figure 7. See Abbreviations list.

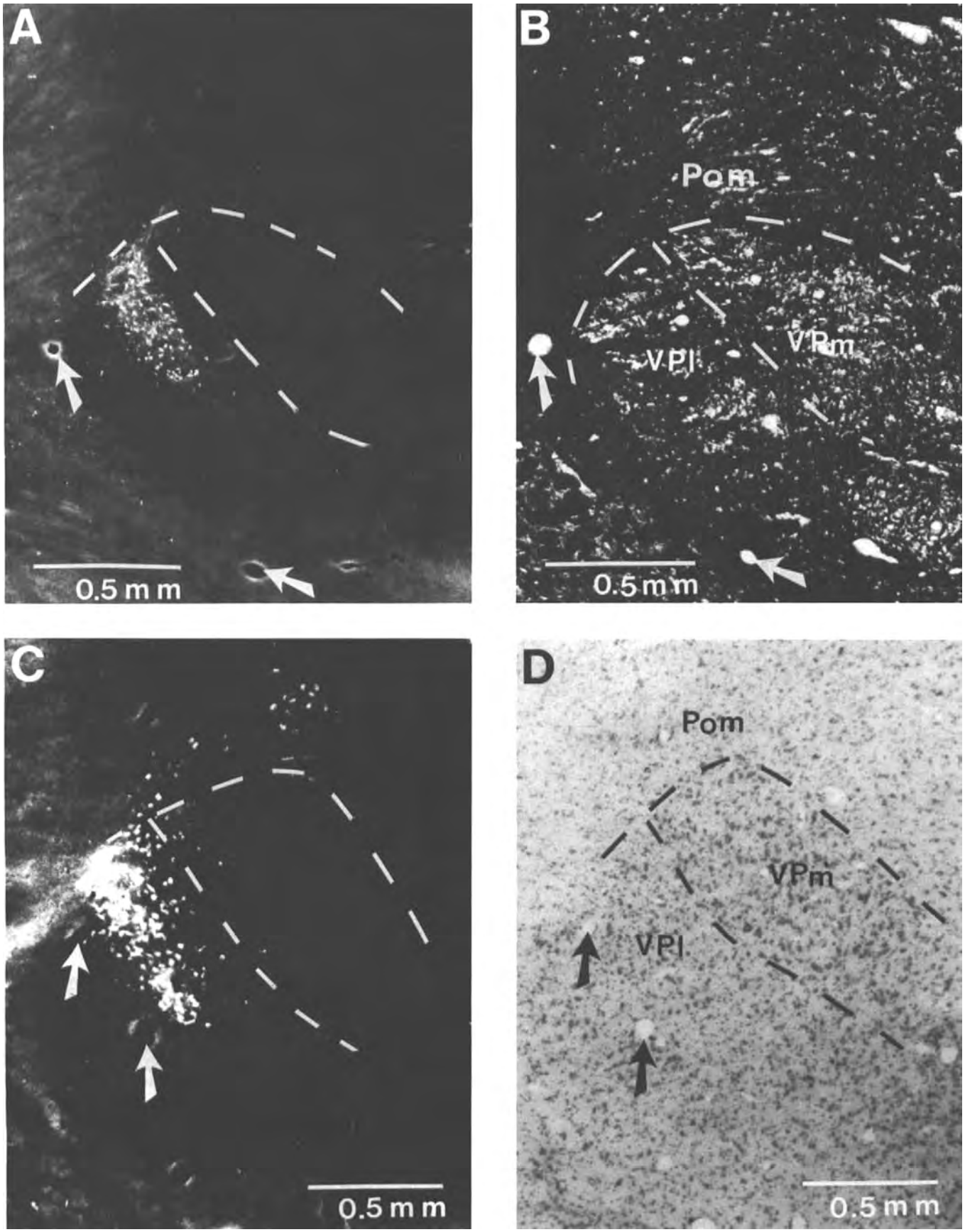



Fig. 14. Dark-field photomicrographs of anterograde and retrograde label in VPL after an injection in the forelimb representation in S-II in (A) case 84-95 and (C) case 84-54b. Adjacent sections reacted for CO (B) and stained for Nissl substance (D). Note the label located just dorsal to VP in Pom (C). In all figures dorsal is up and medial is right. Large arrows mark the same blood vessel in adjacent sections. See Abbreviations list.

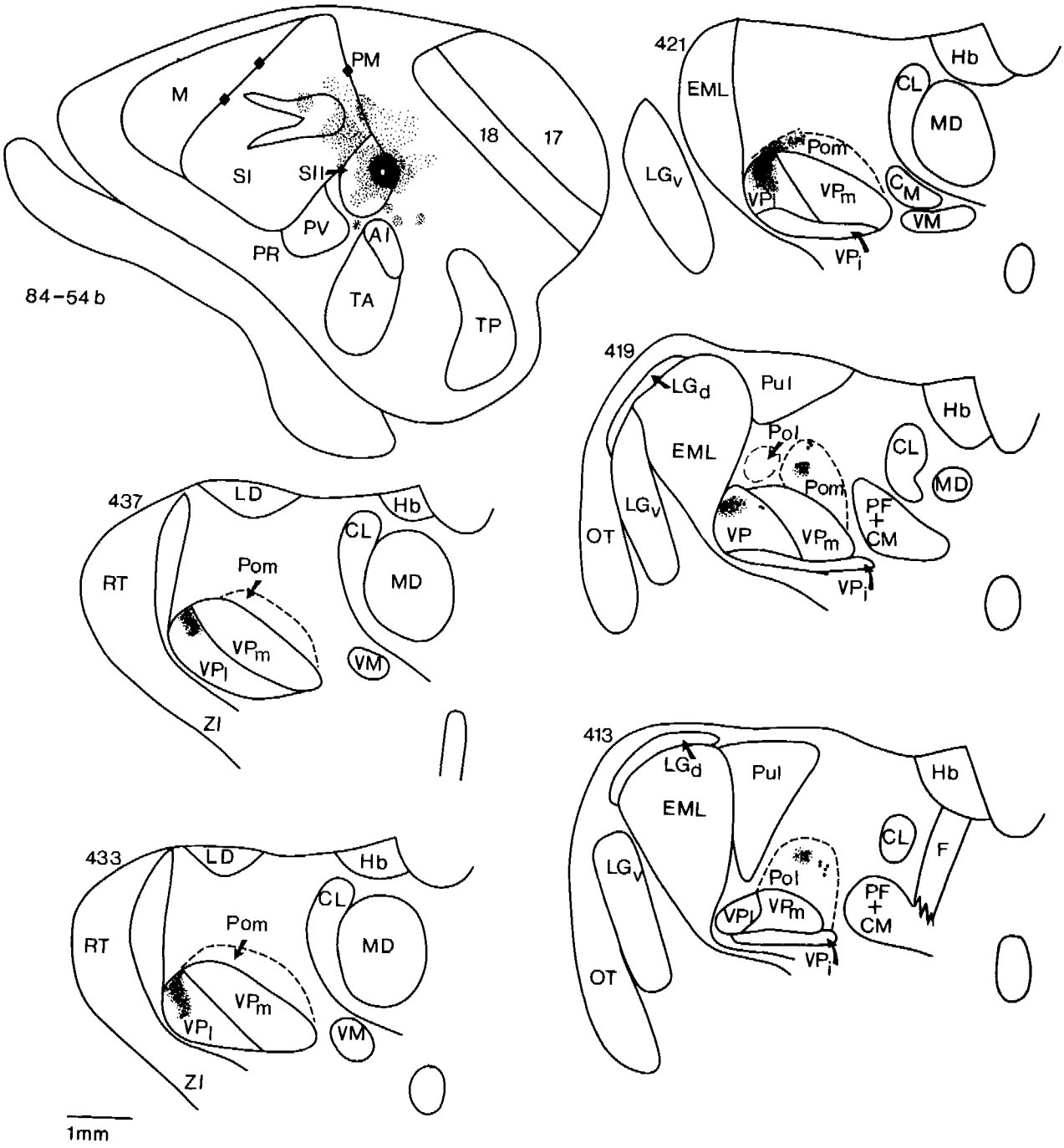



Fig. 15. Thalamic label after an injection of WGA-HRP in the forelimb representation in S-II (upper left). The injection spread into the adjacent trunk representation as well. Label is concentrated dorsolaterally in VPL. Conventions as in Figure 7. See Abbreviations list.

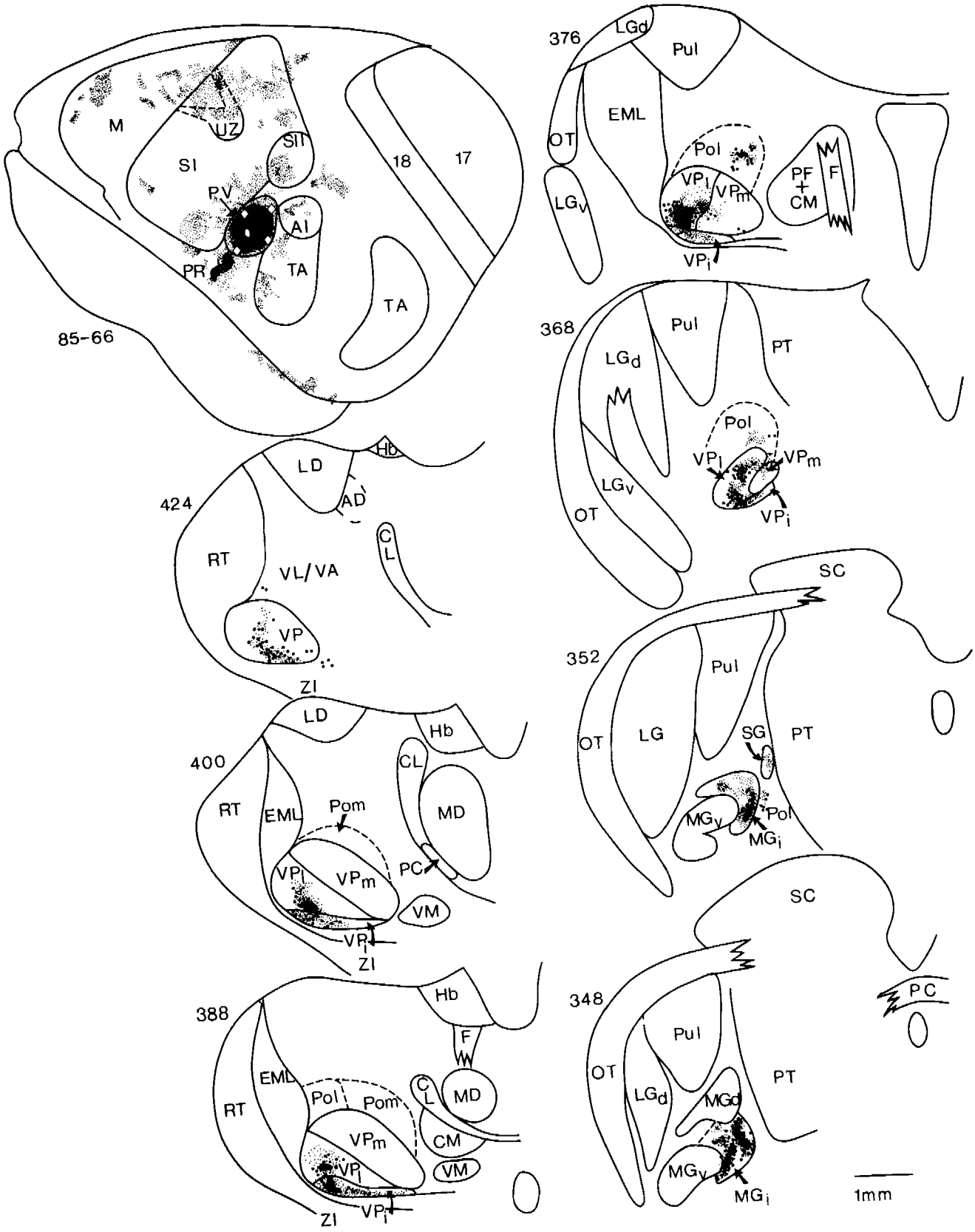



Fig. 16. Thalamic label after an injection centered in the forepaw representation of PV (upper left). A portion of the injection spread into the adjacent forearm and face representations in PV. The label is concentrated in the ventral portion of VPL at rostral through caudal levels. VPi and MGi are also heavily labeled, whereas only sparse amounts of transported tracer are found in Pol. High numbered sections are taken from rostral levels in the thalamus. Conventions as in Figure 7. See Abbreviations list.

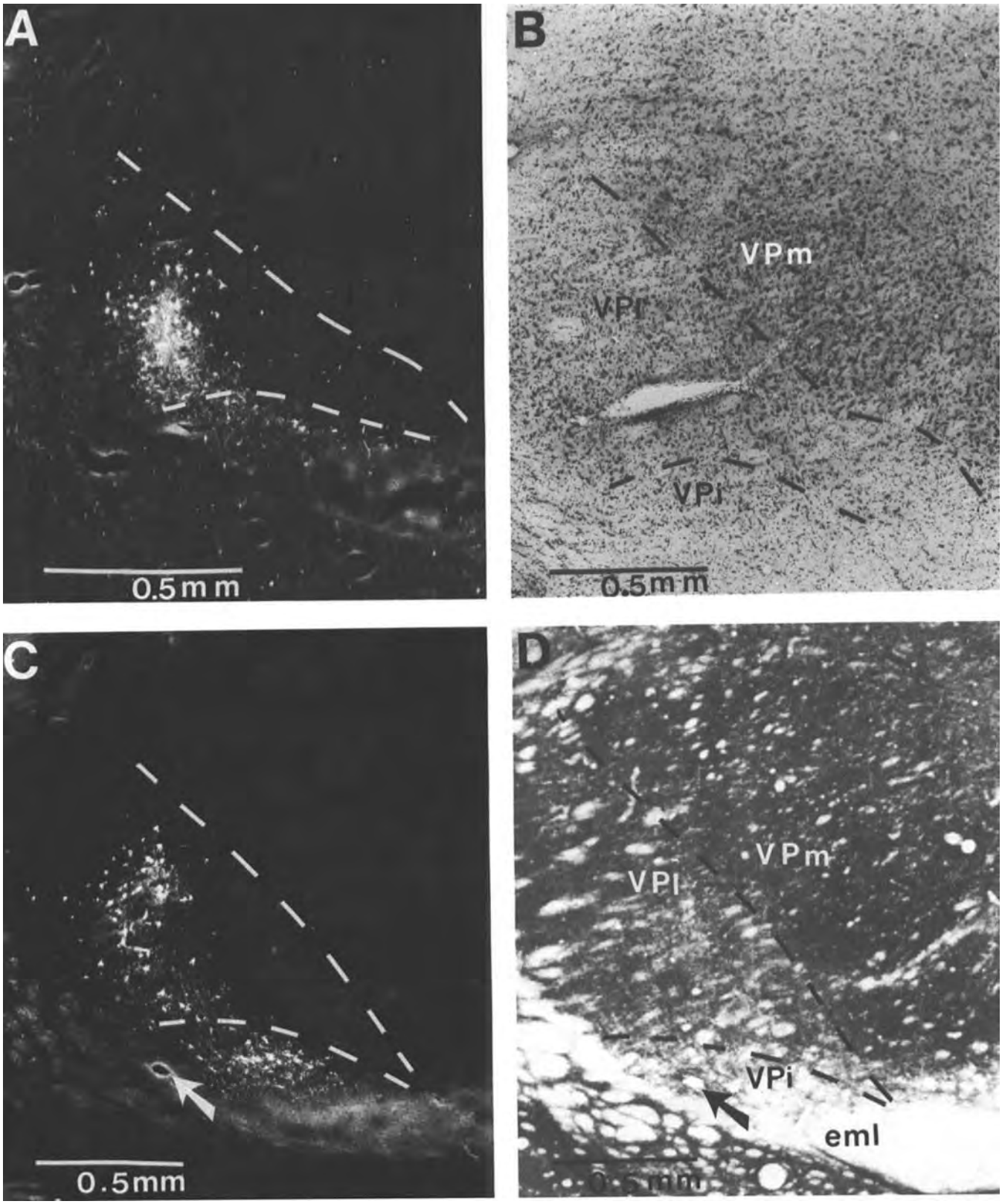



Fig. 17. Dark-field photomicrographs of transported tracer in VPL and VPi after injections in the forelimb representation in PV in (A) case 84-66 and (C) case 84-96. Adjacent Nissl-stained (B) and cytochrome oxidase reacted (D) sections illustrate these thalamic nuclei. Dorsal is to the top and medial is right. Large arrows mark the same blood vessel in adjacent sections for each case. See Abbreviations list.

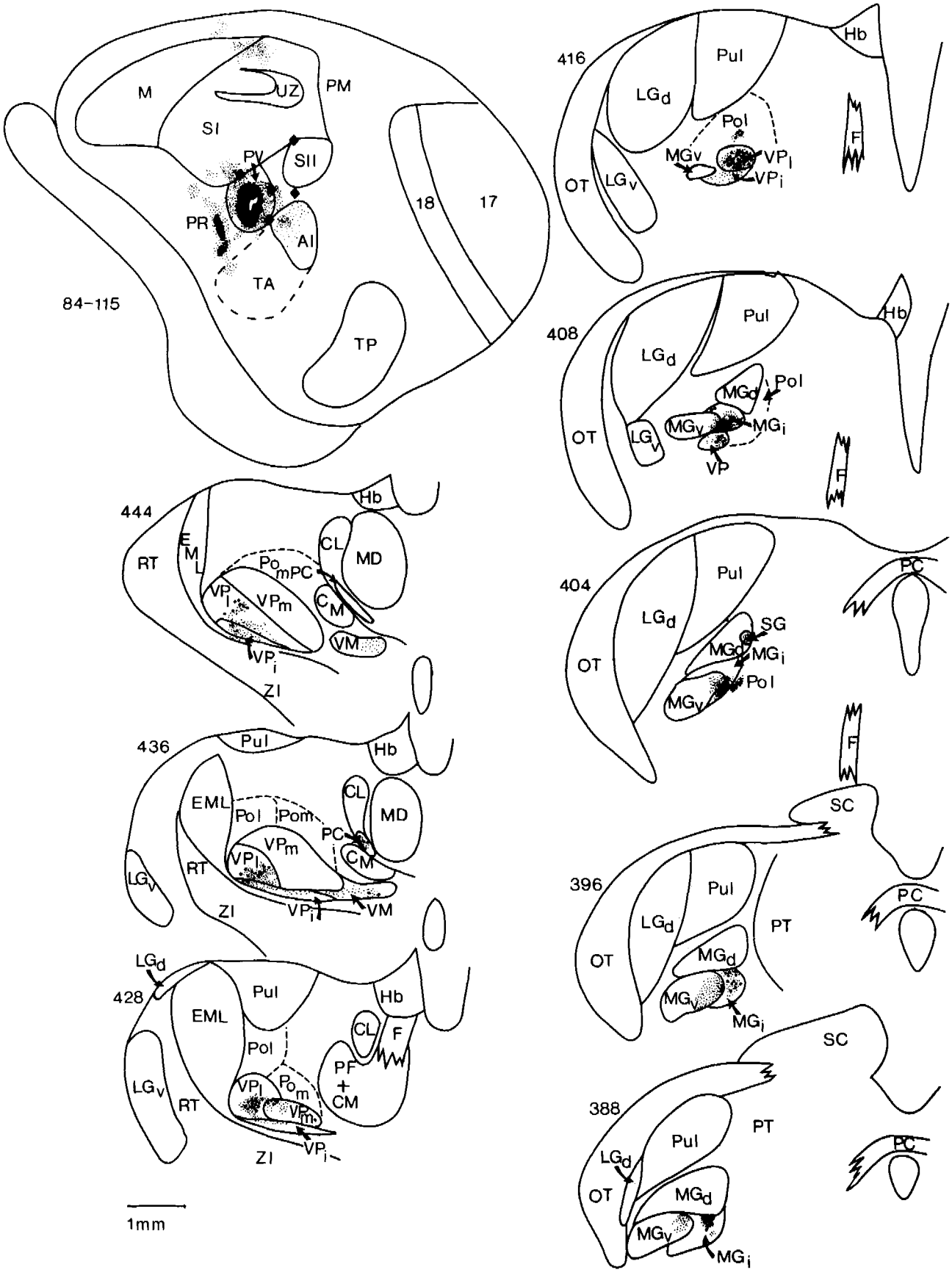



Fig. 18. Thalamic label after an injection of WGA-HRP that is almost completely restricted to the forepaw representation in PV. A dense aggregation of labeled cell bodies and axon terminals is in the medial-ventral portion of VPL. Also, portions of VPi and MGi are labeled. Only anterograde label was in MGv. Sections are numbered from caudal to rostral. Conventions as in Figure 7. See Abbreviations list.

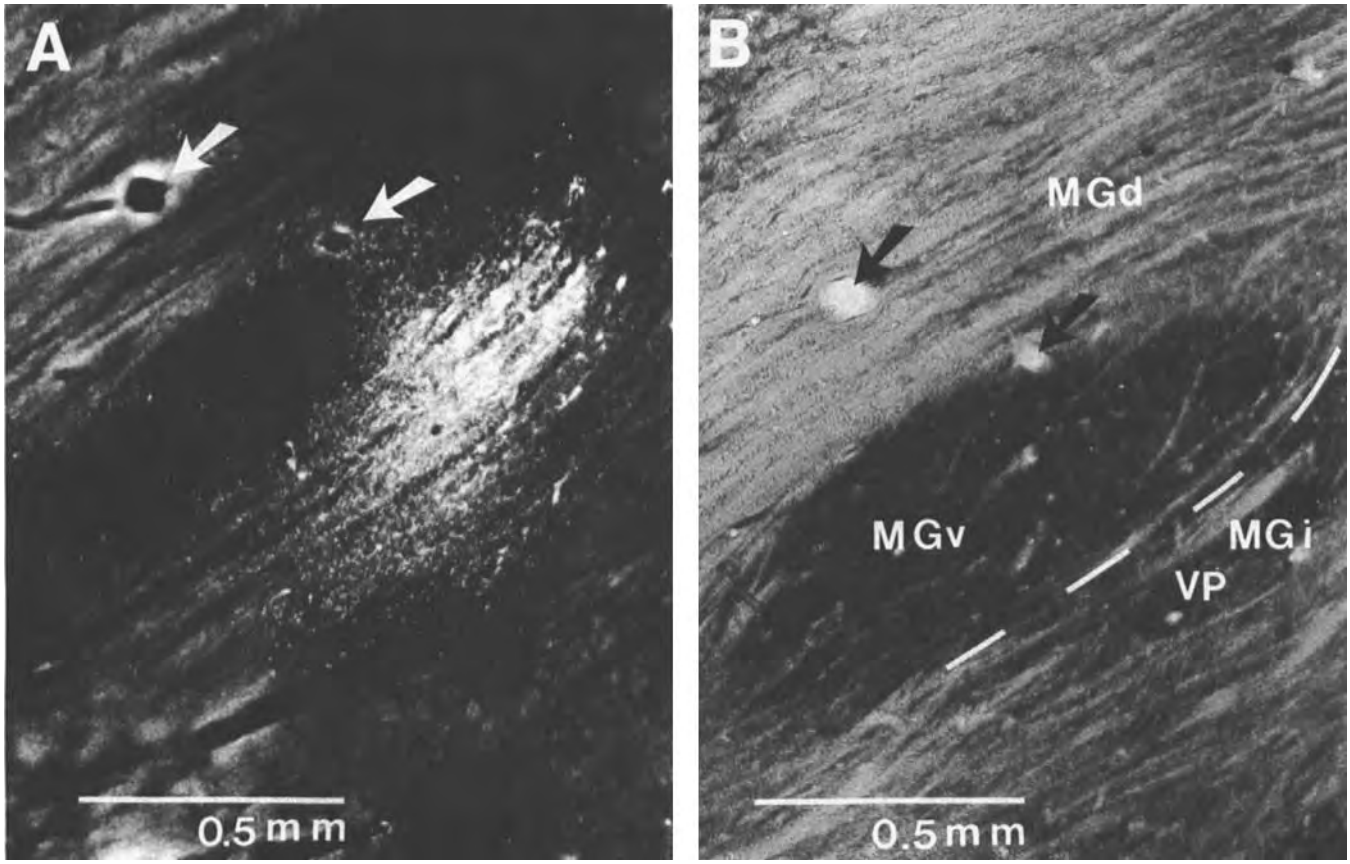



Fig. 19. A dark-field photomicrograph of labeled neurons and axon terminals in the medial geniculate nucleus after an injection in PV (A) and the adjacent cytochrome oxidase reacted section viewed under light-field illumination (B). Dense amounts of both anterograde and retrograde label are in MGi, whereas MGv contains only a sparse amount of anterograde label. Large arrows mark the same blood vessel in the adjacent section; a dotted line marks the division between MGi and MGv. Dorsal is to the top and medial is right. See Abbreviations list.

both anterograde and retrograde label at intermediate levels. Finally, moderately dense reciprocal connections were demonstrated in MGi. Only a light dusting of anterograde label was found in the rostral pole of MGv.

Together, results from these three cases support the evidence from the S-I injections that a somatotopic organization exists in VP, with the face and head represented in VPM, and the forelimb in central and medial VPL. In addition, a crude representation is suggested in VPI, with the forelimb lateral to the representation of the head. Connections with Pol were limited or scattered and no clear somatotopic pattern was apparent. Likewise, interconnections were widespread over MGi with no obvious somatotopy.

## DISCUSSION

The present report describes thalamic connections of three subdivisions of somatosensory cortex in squirrels. Connections of S-I, S-II, and a newly discovered field, PV (Krubitzer et al., '86), were revealed by placing injections of a bidirectionally transported tracer, WGA-HRP, in cortex and examining the thalamus for labeled cells and axons.

In this type of study, there are two general problems that complicate interpretations of results. First, it is often difficult to be certain that injection sites (or lesions in degeneration studies) are confined to specific cortical regions. This problem is less critical for larger fields with obvious architectonic boundaries such as S-I, but it can be serious for small fields with less obvious boundaries such as S-II and PV. We minimized the difficulty of localizing the injection site by: (1) using microelectrode mapping procedures to identify boundaries of fields, (2) marking boundaries with microlesions for later identification in brain sections, and (3) cutting and processing brain sections parallel to the surface of the artificially flattened cortex so that the full extent of injected label could be readily appreciated and related to marker lesions, electrophysiological results, and cortical myeloarchitecture. In the present study, injection sites can be seen as confined within each of three somatosensory fields, S-I, S-II, and PV.

The second general problem in studies of corticothalamic connections is in defining thalamic nuclei. This problem

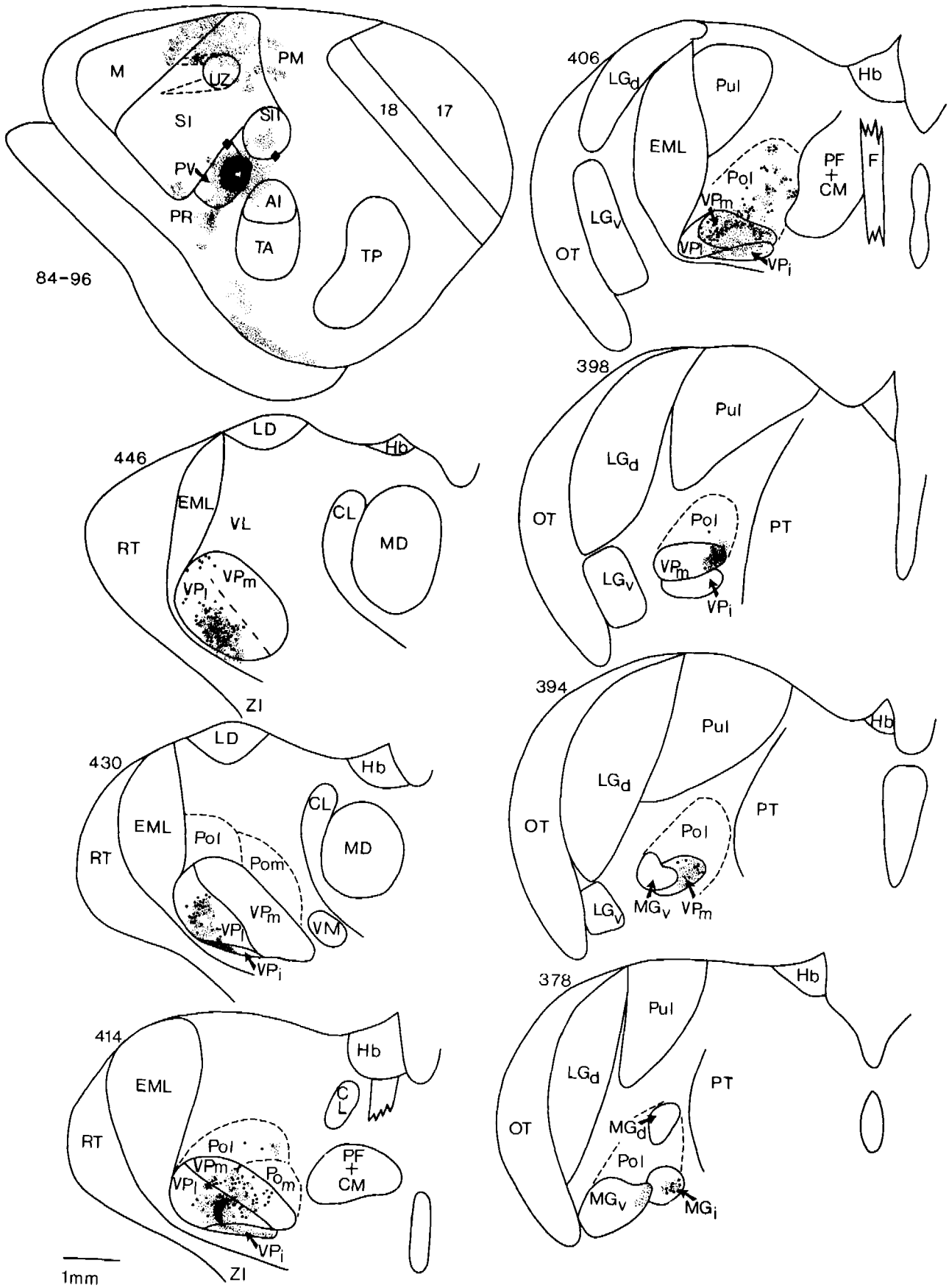



Fig. 20. Thalamic label after an injection in the forearm representation in PV. The injection also spread into the face representation in PV. Note the heavy concentration of label in the medial portion of VPL and sparser amounts of label in VPM. Conventions as in Figure 7. See Abbreviations list.

has two aspects. First, architectonic subdivisions of the thalamus are not always obvious. The common gray squirrel offers some advantages in this regard in that subdivisions of the thalamus are more clearly differentiated than in most rodents (e.g., see Kaas et al., '72). The difficulty of making architectonic distinctions can be further minimized by using more than one procedure for revealing thalamic structures. In the present study, brain sections prepared for cytoarchitecture, myeloarchitecture, or cytochrome oxidase patterns were examined, and each procedure uniquely helped define some features of thalamic organization. Second, even under favorable conditions for determining architectonic boundaries, some uncertainties often remain over what constitutes a thalamic nucleus.

In the present study, we define VP (VPM and VPL) as a characteristic group of darkly staining and densely packed cells in the ventral thalamus. VP is also distinct as a nucleus with high reactivity for cytochrome oxidase (Fig. 3). This definition of VP appears to be consistent with how the nucleus has been distinguished in other rodents (e.g., Lund and Webster, '67; McAllister and Wells, '81; Jones, '85) and mammals in general (for review see Welker, '73). However, the present VP is smaller than the VP (or VB) composed of both a "core" of densely packed, darkly stained neurons and a "shell" of more scattered, less darkly stained neurons of some investigators (e.g., Spreafico et al., '83; Friedman and Jones, '81; Jones and Friedman, '82). We include these architectonically distinct "fringe" regions in nuclei other than VP, and evidence from patterns of connections supports this judgment (see below).

Another uncertainty relates to the ventral group of scattered, pale-staining cells we term the ventroposterior inferior nucleus, VPI. The problem here is not in defining the nucleus, since VPI is clearly distinct from VP. Rather, there is some danger in naming the region since homologies are thereby assumed without fully satisfactory evidence. The present VPI in squirrels has the location just ventral to VP and the appearance of VPI described in primates (e.g., Jones, '85) and carnivores (e.g., Herron, '83; Rinvik, '68), although the region designated as VPI in raccoons and monkeys is clearly larger and more impressive than our VPI in squirrels. Jones ('85) has preferred not to define a VPI in rodents and has implied that VPI really only exists in primates. The present study provides some experimental support, architectural and anatomical, for a nucleus residing just ventral to the ventral posterior nucleus. Based on location and cytoarchitecture, this nucleus strongly resembles the VPI nucleus so clearly demonstrated by connections with S-II in raccoons (Herron, '83) and monkeys (Friedman et al., 1983; Friedman and Murray, '86; Manzoni et al., '84; Krubitzer and Kaas, '86). On the other hand, some of the major cortical connections are different from those described for raccoons and monkeys, which suggests that this nucleus may not be homologous to VPI. However, we use the term VPI because connections obviously can change in evolution, and it would be remarkable if VPI exists only in primates, and even more remarkable if VPI occurs in both primates and carnivores and not other mammals.

The difficulties of differentiating and identifying nuclei are even greater for parts of the somatosensory thalamus dorsal and dorsocaudal to VP. In squirrels, the architectonic evidence suggests the existence of two nuclei, one lateral to the other, and connection patterns with cortex support this conclusion. Yet, the two nuclei are not sharply differentiated from each other or from all of the adjacent regions of the thalamus, so that boundaries and even numbers of subdivisions of the somatosensory thalamus remain uncertain. These difficulties also exist in other mammals, and the region of the thalamus dorsal to VP has been subdivided in various ways by different investigators. In monkeys, much of this region has been included in the ventroposterior shell (Friedman and Jones, '81; Jones and Friedman, '82) or the ventroposterior superior nucleus (Dykes et al., '81; Kaas et al., '84; Cusick et al., '85). In cats, the comparable region has been described as including parts of LP, VL, and the posterior group, Po (e.g., Garraghty et al., '87), the shell of VP and/or medial (Pom) and lateral (Pol) divisions of the posterior group (Spreafico et al., '83; Burton and Kopf, '84), and the ventroposterior superior nucleus (VPS) and ventroposterior oral (VPO) nucleus (Dykes, '83). In rats, it is now common to describe medial (Pom) and lateral (Pol) divisions of the posterior group (e.g., McAllister and Wells, '81; Jones, '85). Because the lateral and medial nuclei in squirrels have the general locations and appearances of Pol and Pom of rats, and they, indeed, may correspond to these nuclei as defined in rats and perhaps even other mammals such as cats, we have referred to them as Pol and Pom. However, other possibilities exist, (see following Discussion), and because of the uncertainties, we use these terms with the expectation that they may be replaced after a better understanding and a consensus on the subdivisions and homologies of the somatosensory thalamus emerge.

## The organization and cortical connections of the somatosensory thalamus

The experimental results help answer several questions about thalamic organization in squirrels and other mammals. The first issue is how to subdivide the somatosensory thalamus. Information relevant to this issue was generated by comparing connection patterns with thalamic architecture.

***The ventroposterior nucleus (VP).*** The largest and undoubtedly most significant nucleus of the somatosensory thalamus is the ventroposterior nucleus. In most mammals, VP is easily recognized by its densely packed, darkly stained neurons. The ventroposterior nucleus is particularly obvious in squirrels (Fig. 1). According to most definitions, VP contains a single systematic representation of cutaneous receptors, and it is well established that VP is densely and reciprocally interconnected in a somatotopic manner with primary somatosensory cortex, S-I (Table 1). Architectonic features and described patterns of connections support the conclusion that we have correctly identified VP in squirrels.

The connection pattern also revealed aspects of the somatotopic organization of VP in squirrels. Injections confined to the representation of the face in S-I demonstrate that the labeled dorsomedial division of VP is the ventroposterior medial subnucleus (VPM), since VPM is known to represent the face and head in other mammals (see Welker, '73). Injections confined to the representation of the body in S-I labeled a ventrolateral region thereby identified as the ventroposterior lateral (VPL) subnucleus of VP. As in other rodents such as rats (e.g., McAllister and Wells, '81), VPM is larger than VPL, demonstrating the relative importance of sensory information from the vibrissa, lips, and nose in rodents. The present results are consistent with a previous finding that lateral and medial lesions in somatosensory

TABLE 1. Thalamic Connections of Somatosensory Cortex

| Study | Mammal | Lesion or injection | Connected target |
|---|---|---|---|
| **Rodents** | | | |
| Price and Webster, '72 | rat | S-I | VP + "LPl" |
| Suporta and Kruger, '77 | rat | S-I | VP |
| Wise and Jones, '77 | rat | S-I | VP + Pom |
| White and DeAmicis, '77 | mouse | S-I | VP + Po |
| Donoghue et al., '79 | rat | S-I | VP + Pom |
| Caviness and Frost, '80 | mouse | VP | "area 3" (S-I) |
| | | PO | "area 40a" (S-II?) |
| | | Pom | "area 40"(PV + PR?) |
| Bold and Neafsy, '84 | rat | S-II | VP + Po |
| Weinberg et al., '84 | rat | S-II | Po + VP |
| Donaldson et al., '75 | rat | VP | S-I |
| **Carnivores** | | | |
| Macchi et al., '59 | cat | S-I | VP |
| | | S-II | VP |
| Hand and Morrison, '72 | cat | VP | S-I, S-II |
| | | PO | S-II, other |
| Ralston and Sharp, '73 | cat | S-I | VP, Pom |
| | | S-II | VP, Pom |
| Jones and Burton, '74 | cat | S-I | VP, Pom |
| Kosar and Hand, '81 | cat | S-I | VP |
| | | S-II | VP |
| Spreafico et al., '81 | cat | S-I | VP, Pom |
| | | S-II | VP, Pol, Pom, MGm, VPI |
| Fisher et al., '83 | cat | S-I | VP |
| | | S-II | VP (caudal) |
| Herron, '83 | raccoon | S-I | VP |
| | | S-II | VPI |
| Warren and Pubols, '84 | raccoon | S-I | VP, Po |
| Jones and Powell, '69 | cat | VP | S-I, S-II |
| Herron and Dykes, '81 | cat | VPI | S-II, S-I |
| **Primates (recent studies)** | | | |
| Nelson and Kaas, '81 | Macaque | 3b | VP |
| | | 1 | VP |
| Pon and Kaas, '85 | Macaque | 1 | VP, Pul |
| | | 2 | VPS, VP, Pul |
| Jones and Friedman, '82 | Macaque | "VP core" (VP) | 3b, 1 |
| | | "VP shell" (VPS) | 3a, 2 |
| Lin et al., '79 | Owl monkey | 3b | VP |
| | | 1 | VP |
| Mayner and Kaas, '86 | Cebus | 3b | VP, Pul |
| | | 1 | VP, Pul |
| Burton and Jones, '76 | Macaque | S-II | VP |
| | | Ig | SG |
| Burton, '84 | Macaque | S-II | VP, VPI |
| Manzoni et al., '84 | Macaque | S-II | VPI |
| Friedman and Murray, '86 | Macaque | S-II | VPI, VL, Po |
| | | Ig | SG, Po, MGl, VPI, Pul |
| Krubitzer and Kaas, '86 | Marmoset | S-II | VPI, VP |
| Burton and Carlson, '86 | Galago | S-II | VP, VPI, Po |
| **Marsupials** | | | |
| Neylon and Haight, '83 | Bush-tailed Possum | S-I | VP, Po |
| Donoghue and Ebner, '81 | Virginia Opossum | S-I | VP, VL |
| | | | "CIN" (Po?) |
| Robards and Ebner, '77 | Virginia Opossum | S-II | VP, Po, MGi |

koniocortex (S-I) of squirrels result in retrograde cell degeneration in medial and lateral sectors of VP, respectively (Kaas et al., '72).

When the connection patterns revealed by the present study are considered in more detail (Fig. 21), it is apparent that the caudal head and neck, lateral face and nose, and lips are represented in a roughly dorsoventral sequence in VPM, whereas the forepaw is medial to the hindpaw and the paws ventral to more proximal body parts in VPL. Thus, the somatotopic pattern in VP of squirrels at least roughly corresponds to that commonly reported for other mammals (see Welker, '73).

The major target of VP in rodents, S-I, actually contains two types of cortex. In rats (Welker, '71; Chapin and Lin, '84) and squirrels (Kaas et al., '72; Sur et al., '78; Krubitzer et al., '86), a systematic representation of the body surface is contained in a sheet of granular and densely myelinated cortex that is basically homuncular in shape, whereas re-

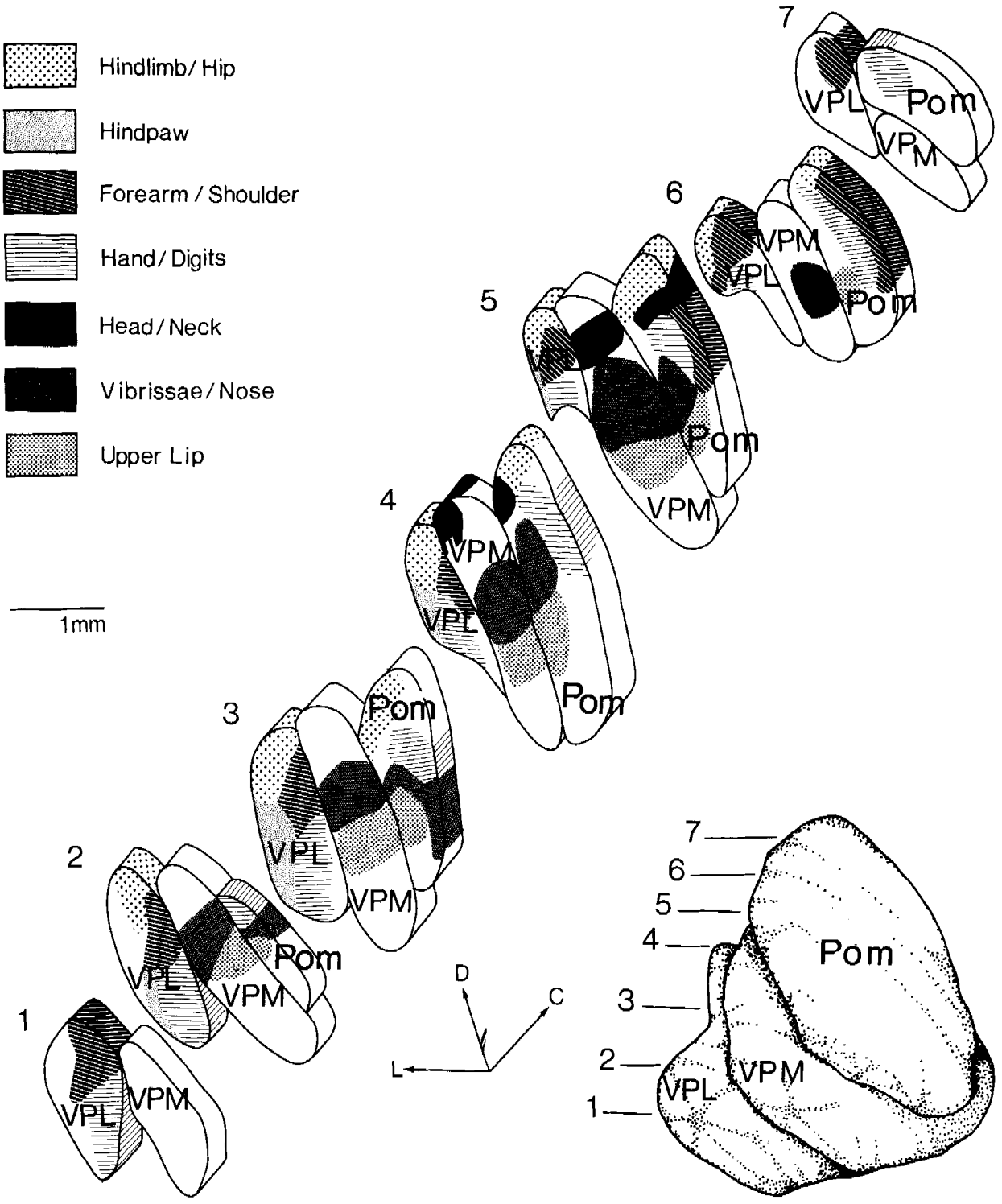



Fig. 21. The representations of body parts in VPL, VPM, and Pom based on data in previous figures. Note that the representation in Pom closely mirrors that in VP. Nuclei are shown as a rostrocaudal series of slabs from a coronal series above, and the levels of the sections are shown on a three-dimensional reconstruction below.

gions of dysgranular and lightly myelinated cortex separate the representations of major body parts within this homunculus. There is evidence in rats (Wise and Jones, '78; Akers and Killackey, '78; Olavarria et al., '84) that VP projections are largely or exclusively in the granular zones of S-I, rather than the dysgranular zones that are relatively unresponsive to somatosensory stimuli in anesthetized animals (see Chapin and Lin, '84; Sur et al., '78; Welker, '76). The present study does not address the issue of the possible restriction of VP projections to granular cortex in S-I, since all injections included granular cortex. However, squirrels have a large, central dysgranular zone (see Krubitzer et al., '86; Sur et al., '78; Kaas et al., '72), and a preliminary report of Gould ('81) suggests that whereas the large dysgranular zone has some input from VP, it is greatly reduced in comparison to granular SI. In the present investigation, injections in S-I that may have spread into portions of the dysgranular unresponsive zone showed additional connections with VPI (cases 84-50, 84-76). The connectional and architectonic differences in the granular and dysgranular zones raise the issue of considering dysgranular S-I as a field separate from S-I.

A second target of major interconnection of VP in squirrels is S-II. Interconnections between VP and S-II have been described for several mammalian species (see Table 1), and such interconnections appeared to be a basic component of the mammalian somatosensory system. Recently, however, the prominence and even the existence of the VP to S-II projection has become a matter of controversy. Initially, Herron ('83) reported that injections of HRP into S-II of raccoons did not label cells in VP, but rather labeled cells ventral to VP in VPI. Subsequently Herron and Dykes ('81) found that injections in VPI of cats labeled S-II. More recently, a major projection from VPI to S-II has been demonstrated in several species of primates (Table 1). However, projections from VP to S-II have been commonly reported in cats, and even in primates some projections from VP to S-II can be demonstrated (see Table 1). The present report supports the conclusion that projections from VP to S-II are a widespread and thereby probably primitive feature of the mammalian somatosensory system. In some lines of specialization, most notably in the raccoon branch of carnivores and in most primates, the VP projections have apparently been reduced and replaced to a large extent by VPI inputs (see VPI section below).

The results of lesion studies support the conclusion that VP projections to S-II have become reduced in importance in some primates. Large lesions of the anterior parietal cortex in macaque monkeys, including S-I proper (3b) and adjoining areas 3a, 1, and 2, render S-II unresponsive to somatosensory stimuli (Pons et al., '87). In contrast, lesions of S-I in cats (Manzoni et al., '79) and rabbits (Woolsey and Wang, '45) do not inactivate S-II. The implication of these ablation studies is that VP inputs remain an important parallel source of cutaneous receptor input to S-II of cats and rabbits, but not to S-II of monkeys.

In addition to the interconnections between VP and S-I and S-II, VP is also interconnected with PV. Based on location and relative position to S-I and S-II, PV resembles the granular insular (Ig) region in monkeys. However, injections in Ig in monkeys have not revealed connections with VP. Rather this region appears to be strongly interconnected with the suprageniculate nucleus, and less strongly with other parts of the posterior group, VPI, MGi, and the medial pulvinar (Friedman et al., '86). Yet, because PV is interconnected with at least some of these nuclei in squirrels, the possibility of homology between PV and Ig is somewhat supported by thalamocortical connection patterns.

In cats, the fourth somatosensory representation, S-IV, is in the relative position of PV of squirrels and Ig of monkeys. Both PV (Krubitzer et al., '86) and S-IV (Clemo and Stein, '83) have an inverted somatotopic representation of the body and contain neurons responsive to auditory stimuli. Some cortical connections of PV and S-IV are similar, but others appear to be different (see Krubitzer et al., '86). Likewise, some of the thalamic connections of S-IV (Burton and Kopf, '84), such as those with medial and lateral divisions of the posterior group and MGi, resemble those of PV. But unlike PV, S-IV does not appear to have connections with VP. We conclude that the many similarities between PV of squirrels and S-IV of cats suggest a homology between the two fields, but the evidence is too limited to be completely compelling.

Since we investigated the connections of only areas S-I, S-II, and PV, it remains possible that VP in squirrels projects to other regions of the cortex in addition to these three cutaneous representations. More widespread connections have been described in other mammals. In monkeys, VP projects to areas 1 and 2, in addition to S-I proper or area 3b (for review see Pons and Kaas, '85; Kaas, '83). Furthermore, there is evidence that some neurons branch and project to both areas 3b and 1 (Cusick et al., '85). In cats, there is some evidence that VP projects to a representation caudal to S-I termed S-III (Garraghty et al., '87). Thus, somatosensory cortex medial to S-II and caudal to S-I in squirrels possibly has some input from VP.

***The ventroposterior inferior nucleus (VPI).*** In gray squirrels, we distinguish a group of small pale-staining neurons ventral to VP, the ventroposterior inferior nucleus, VPI. Whereas VPI has not been previously described in rodents, or in most mammals, VPI became a standard nucleus of the thalamus of monkeys after being denoted in the popular atlases of Olszewski ('52) and Emmers and Akert ('63). Subsequently, a VPI nucleus has been described in cats (Rinvik, '68) and raccoons (Herron, '83). As in monkeys and carnivores, the region we designate as VPI in squirrels contains relatively few neurons and is crossed by many fibers of passage. Overall, this ventral group of neurons is so unimpressive in most mammals that Jones ('85) concluded that VPI is "really only distinct in the primate brain" and that the existence of VPI in other mammals is doubtful. However, the VPI region is clearly distinguishable from VP in many species, and the connections of the VPI region do appear to differ from those of VP. Nevertheless, apparent differences in cortical connections of VPI raise the question of whether the region denoted as VPI is the same nucleus across species.

Early speculations based on large lesions or injections in monkeys said that VPI projects to the dysgranular insular cortex (Roberts and Akert, '63; Burton and Jones, '76).

In squirrels, label was found in VPI after an injection in S-I involving the dysgranular unresponsive zone and after injections in PV, whereas injections in S-II did not label VPI. The cortical connections of VPI in other mammals are not well established, but a major projection in raccoons and monkeys is to S-II. Herron ('83) demonstrated that in raccoons, where VPI is particularly well developed, a major

projection of VPI is to S-II. In closely related cats, there is some evidence for interconnections of VPI with S-II (Rinvik, '68; Herron and Dykes, '81), but a recent study (Burton and Kopf, '84) fails to describe any labeled neurons in VPI after S-II injections. Limited electrophysiological evidence suggests that VPI relays pacinian receptor information in monkeys (Dykes et al., '81), and many neurons in S-II of cats appear to be responsive to pacinian receptor stimulation (Ferrington and Rowe, '80; Fisher et al., '83). In primates, the evidence is now extensive that a major projection of VPI is to S-II (Table 1). We conclude that S-II is the principle target of VPI in primates, raccoons, and possibly cats, but not in squirrels. This difference in some of the connections raises the possibilities that the regions identified as VPI in squirrels and primates are not homologous, that S-II has not been correctly identified in all mammals, or that connections of VPI have undergone major modifications in some lines of evolution.

Connections of VPI with PV in squirrels and Ig in monkeys (Friedman and Murray, '86), a possible homologue of PV, support the conclusion that VPI in rodents and VPI in monkeys are homologous. However, it is also possible that part of the lateral nucleus of the Po complex with connections with S-II in squirrels corresponds to VPI of monkeys. Parts of the Po complex and VPI are very similar in appearance, with the major difference being that of position. Jones ('85) has suggested that parts of Po and VPI are a single nucleus in monkeys, and Kaas et al. ('84) postulated that VPI in squirrel monkeys extends dorsocaudally to include regions of Po of other investigators. Perhaps the true homologue of VPI of monkeys is located in a more caudal or more dorsal position relative to VP in other mammals.

***The dorsal somatosensory nuclei, Pol and Pom.*** The architectonic and the connectional evidence supports the conclusion that there are two somatosensory nuclei just dorsal to VP in squirrels. Because they have been identified in other rodents as Pol and Pom (see Jones, '85) and to avoid confusion, we have temporarily termed them Pol and Pom (Fig. 2). Both Pol and Pom project strongly to S-II; Pol projects additionally to PV whereas Pom has a projection to S-I (Fig. 2).

Because injections were placed in the representations of different body parts in S-I, the projections of Pom to S-I revealed that Pom contains a systematic representation of the body (Fig. 22). The somatotopic organization of Pom roughly parallels that of VP. Thus, the hindlimb regions of S-I were interconnected with dorsolateral portions of Pom, the head with central Pom, and the face with ventromedial Pom. Whereas a second representation of the body surface has been reported in the thalamus of rats (Emmers, '65), this representation was described as being located in caudal VP, and therefore it does not appear to be the equivalent of Pom.

***Pom as Pom, the anterior pulvinar, or VPS.*** As noted above, Pom in squirrels is in the relative position and has the general architectonic appearance of the region known as Pom in rats and cats (see Jones, '85). In part, Pom is defined by somatosensory terminations from the spinothalamic tract (see Lund and Webster, '67; Berkley, '80), and since the distribution of these inputs are yet unknown for squirrels, some caution seems justified in equating Pom in squirrels with Pom in rats and cats. Yet there are major similarities in the cortical connections of the two thalamic regions. As for Pom in squirrels, connections of Pom with

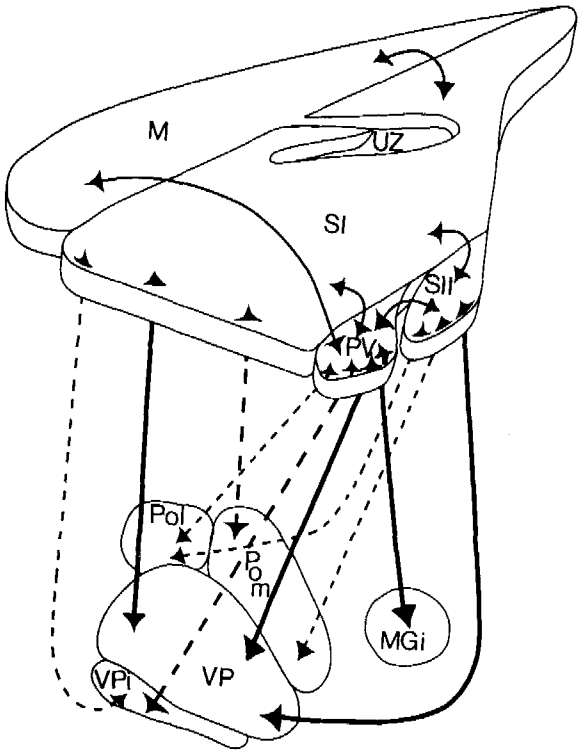



Fig. 22. Thalamocortical and corticocortical connections of the somatosensory system of squirrels. Solid lines, thick dotted lines, and thin dotted lines indicate major, intermediate, and minor interconnections, respectively. See Abbreviations list.

S-I and S-II have been described for rats and cats (Table 1). Such connections may be part of a general mammalian pattern, since even in the Virginia opossum, the region of Pom projects to S-I (Donoghue and Ebner, '81) and S-II (Robards and Ebner, '77). If Pom in squirrels corresponds to Pom of rats and cats, connections of Pom with cortex medial to S-II and caudal to S-I might also exist in squirrels, since such projections have been demonstrated for Pom of cats (Garraghty et al., '87; Tanji et al., '78; Robertson and Cunningham, '81). A Pom region has been identified in monkeys, but this part of the primate thalamus apparently differs from Pom of cats and rats in that it projects to the cortex caudal to S-II rather than S-II or S-I (3b) (Burton and Jones, '76).

An intriguing recent suggestion by Jones ('85) is that the anterior pulvinar of monkeys is equivalent to at least part of Pom. The anterior pulvinar of monkeys, with no designated homologue in nonprimates, projects broadly to somatosensory cortex (see Pons and Kaas, '85), and there is evidence that the projections include both S-I proper, area 3b (Cusick and Gould, '86), and possibly S-II (Friedman and Murray, '86). Thus, Pom connected with both S-I and S-II in squirrels may be homologous with part or all of the anterior pulvinar of monkeys. Another possibility is that the ventroposterior superior (VPS) nucleus (see Pons et al., '86; Cusick et al., '85, part of the VP "shell" of Jones and Friedman, '82) is a homologue of Pom in squirrels. VPS contains a systematic representation of the body (see Kaas

et al., '84), much like that of Pom. In addition, major projections of VPS are to cortical areas 3a and 2. In some ways, the dysgranular zones of S-I in rodents, with connections with Pom, architectonically resemble area 3a of monkeys.

***Pol as Pol, Pol plus Poi, or Pol plus VPI.*** A caudolateral region of the thalamus just dorsal to VP was found to project densely to PV and less densely to S-II in squirrels (Fig. 22). We termed this region Pol, and it is roughly in the location of Pol of rats and cats (Jones, '85). However, an intermediate posterior nucleus, Poi, is sometimes also distinguished in this region in cats, and Pol in squirrels appears to overlap some of the expected position of Poi. The Poi region of cats has input from the inferior colliculus (e.g., Kudo and Niimi, '80), but thalamic projections of the inferior colliculus have not been determined in squirrels. Cortical connections of the Pol and Poi regions in cats include cortex in the region of some of the auditory fields (Anderson et al., '80) as well as the S-II region (Table 1). There may also be interconnections with S-IV (Burton and Kopf, '84) and S-III (Tanji et al., '78; Garraghty et al., '87). The connections of the lateral portion of the Po region of onkeys are somewhat unclear, but there is evidence that lateral Po relates to insular cortex, including the granular (Ig) region just rostral to S-II (Jones and Burton, '76). This similarity with Pol projections to PV supports the possibility that PV and the somatosensory representation in Ig are homologues (see Krubitzer et al., '86). As noted previously, the lateral division of Po in squirrels is similar in architectonic appearance to VPI. Likewise, the possible homology of VPI in squirrels and VPI in carnivores and primates was also discussed. Because no connections between VPI and S-II were observed in squirrels, this hypothesis seemed less likely. However, if indeed all or part of Pol is included in VPi, than the discrepancy in results can be accounted for since Pol in squirrels does project to S-II.

***The internal (magnocellular) nucleus of the medial geniculate complex, MGi.*** The internal or magnocellular division of the medial geniculate complex, MGi can be recognized with considerable certainty in a range of mammalian species because of its distinctive cytoarchitecture and myeloarchitecture (Fig. 1). The present study demonstrates interconnections between MGi and PV in squirrels. This MGi projection to PV may provide the auditory activation that was noted within most of the field (Krubitzer et al., '86). The MGi nucleus in monkeys, tree shrews, and cats projects broadly to auditory and adjacent insular fields (e.g., Anderson et al., '80; Burton and Jones, '76; Oliver and Hall, '78) including Ig (Friedman et al., '86). Hence, the projection to PV from MGi lends further support to the proposition that PV and IG are homologous.

## Summary and conclusions

The results further reveal the complexity of the anatomical framework for processing somatosensory information in squirrels (Fig. 22). The three mapped somatosensory representations in the cortex (S-I, S-II, PV) are cortically interconnected and have connections with other fields as well (Krubitzer et al., '86). In addition, each of the three fields is interconnected with several thalamic nuclei. Early concepts that each cortical field has exclusive input from a single thalamic nucleus (for review see Friedman and Murray, '86) clearly do not apply even for the primary field, S-I.

The somatosensory thalamus of squirrels appears to contain as many as five or more nuclei, two with somatotopic representations of the body. For two of these nuclei, VP and MGi, homologies with nuclei of the same name in other mammals seem certain. Homologies of the regions we term VPI, Pol, and Pom in squirrels are less certain. We suggest that the region we term VPI in squirrels is homologous to VPI in cats and monkeys, but there are reasons for considering other possibilities. Pol may correspond to Pol, Pol plus Poi, or Pol plus VPI of other mammals, whereas Pom may be the homologue of Pom, the anterior pulvinar, or VPS. We stress, however, that subdivisions of the somatosensory thalamus may have emerged independently in some lines of mammalian evolution, and thus do not have true homologues in other lines.

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