0270-6474/85/0506-1446$02.00/0

The Journal of Neuroscience
Vol. 5, No. 6, pp. 1446-1470
June 1985

Thalamic Projections to Areas 5a and 5b of the Parietal Cortex in the Cat: A Retrograde Horseradish Peroxidase Study[1]

CARLOS AVENDAÑO,[2] ESTRELLA RAUSELL, AND FERNANDO REINOSO-SUAREZ

Departamento de Morfología, Facultad de Medicina, Universidad Autónoma, 28029, Madrid, Spain

Abstract

The cytoarchitecture of areas 5a and 5b of the cat's parietal cortex was re-examined and the afferent connections from the thalamus were investigated using the horseradish peroxidase (HRP) retrograde transport technique. Single or multiple small injections of the enzyme were made in different points of these areas in the rostral sectors of the lateral and middle suprasylvian gyri. The cytoarchitecture of the cortical region affected by the injections was carefully assessed in each case, and the labeled neurons found in the thalamus were plotted on projection drawings of each histological section. A prominent projection to area 5a arises from the posterior (Po) and ventral lateral (VL) complexes; less substantial projections originate in the ventral anterior nucleus (VA), the lateral intermediate complex (LI), and the central lateral nucleus (CL). Projections to area 5b (and to the laterally adjacent area suprasylviana anterior) mainly arise from LI, the dorsal part of VL, and the caudodorsal part of VA and CL; a moderate projection was also found from Po, the pulvinar, and the lateral dorsal complex.

The main conclusions of this study are as follows. (*1*) The shape and extent of areas 5a and 5b show notable variations when only their projection on the convoluted cortical surface is considered; however, they are relatively constant when plotted on unfolded cortical maps. (*2*) The thalamic neurons projecting to areas 5a and 5b are organized according to a loose topographic plan, particularly noticeable in Po, VL and LI. In general, the rostral portion of this cortex (5a) receives projections from more ventral regions of the thalamus (mainly Po and VL), whereas the caudal part (5b) has connections from more dorsal regions (mainly LI and VA-VL). Moreover, the medial portions of these areas receive projections from lateral and ventral parts of the thalamic nuclei, whereas more dorsal and medial sectors of the thalamus project to the lateral portions of areas 5a and 5b. (*3*) When labeled thalamic cell populations resulting from cases with single injections in neighboring cortical loci were compared, no abrupt changes of labeling were observed; rather, we generally observed gradual transitions and overlaps, even across nuclear boundaries. (*4*) When only layers I and II of the cortex received the HRP, the number of labeled neurons and the intensity of their labeling decreased, their location in the thalamus was more restricted, and the mean size of the labeled cells was significantly smaller than that of the neurons labeled in the same regions after deep HRP injections.

Area 5 may be defined as a slender band of cortex, mediolaterally oriented, which abuts rostrally on the primary somatosensory cortex (SI),[3] thus forming the rostral part of the posterior parietal cortex. Early electrophysiological studies demonstrated that, in portions of this area, short-latency evoked potentials could be recorded after peripheral somatic sensory stimulation and that these responses were somatotopically organized to some degree (Marshall et al., 1941; Amassian, 1954; Darian-Smith et al., 1966). Electrical stimulation of area 5 also elicited topographically organized contralateral movements, even in the absence of motor and primary sensory cortices (Fleming and Crosby, 1955). These physiological findings suggested a close functional relationship of area 5 with the somatic sensory system, but their anatomical bases were poorly understood. In fact, for many years, the only subcortical structure which was known to project to area 5 was the lateral posterior complex of the thalamus (LP) (LeGros Clark and Boggon, 1935; Waller and Barris, 1937), a nucleus which was thought to lack any subcortical input other than that coming from other thalamic nuclei (Rose and Woolsey, 1943).

However, more recent findings have shown that the thalamic projections to area 5 arise not only from LP, but also from the ventrolateral complex (VL), nucleus ventralis anterior (VA), the posterior complex (Po), and the intralaminar nuclei, and that there are regional variations in these projections (Mizuno et al., 1975; Robertson, 1977; Tanji et al., 1978; Hendry et al., 1979; Niimi et al., 1979). None of these studies, however, have systematically explored the thalamic projections to different sectors of area 5, nor, with one

Received July 18, 1984; Revised October 9, 1984;
Accepted January 2, 1985

[1] We thank Dr. D. G. Amaral for his helpful comments on the manuscript, Maria Teresa Fernandez Yuste and Kris Trulock for preparing part of the photographic material, Carol Warren for revising the English text, and Mari Carmen Moncada for typing the manuscript. This work was supported in part by Comisión Asesora de Investigación Científica y Técnica Grant 4182/79.

[2] To whom correspondence should be addressed.

[3] The abbreviations used in the text are: AChE, acetylcholinesterase; AMLS, anteromedial lateral suprasylvian area; CeM, nucleus centralis medialis; CL, nucleus centralis lateralis; Cm, nucleus centromedianum; GLa, gyrus lateralis; GMMc, corpus geniculatum mediale, pars magnocellularis; GSs, gyrus suprasylvius; HRP, horseradish peroxidase; LD, lateral dorsal complex; LDM, lateral dorsal complex, pars medialis; LI, lateral intermediate complex; LIC, lateral intermediate complex, pars caudalis; LIO, lateral intermediate complex, pars oralis; LP, lateral posterior complex; LPl, lateral posterior complex, pars lateralis; Po, posterior complex; Pol, posterior complex, pars intermedia; PoL, posterior complex, pars lateralis; PoM, posterior complex, pars medialis; Pul, pulvinar; SAns, sulcus ansatus; SC, sulcus cruciatus; Sg, nucleus suprageniculatus; SL, sulcus lateralis; slf, supralemniscal field division of posterior complex; SSa, area suprasylviana anterior; SSp, sulcus splenialis; SI, primary somatosensory cortex; SII, area 2 praeinsularis; VA, nucleus ventralis anterior; VB, ventrobasal complex; VL, ventrolateral complex; Vm, nucleus ventromedialis; VP, ventroposterior complex; VPi, nucleus ventralis posteroinferior; VPl, nucleus ventralis posterolateralis.

exception (Tanji et al., 1978), have they provided satisfactory cytoarchitectonic correlations.

Area 5, which is composed of at least two different cytoarchitectonic sub-areas (Vogt and Vogt, 1919; Hassler and Muhs-Clement, 1964), is also heterogeneous in physiological characteristics (Lynch, 1980; Hyvärinen, 1982) and in its efferent projections to the thalamus (Robertson and Cunningham, 1981). The latter are topographically organized in different, although partially overlapping, domains, and largely reciprocate the thalamocortical connections. Although little is known about the functions of area 5 in the cat, some reports show that it is implicated in processing spatially organized somatic sensory input of different submodalities (Tanji et al., 1978; Dykes, 1983) and, perhaps, in integrating visuomotor behavior (Fabre and Buser, 1981).

In the present study we have investigated the anatomical organization of the thalamic projections to area 5 in the cat, using the horseradish peroxidase (HRP) retrograde axonal transport technique. As a preliminary step in this study, we have re-examined the cytoarchitecture of the cortex where area 5 is located. Special care was taken to correlate the distribution of labeled neurons in the thalamus with the topography and architecture of the injection loci in the cortex. The results of this study furnish evidence for a topographically organized, multinuclear thalamic projection to area 5. A preliminary report of these results has been given elsewhere (Avendaño et al., 1982).

Materials and Methods

This study was carried out on 18 adult cats of both sexes. Five animals were used for studying cortical cytoarchitecture. The remaining 13 animals received HRP injections in different regions of area 5 and were used to study the thalamocortical connections.

Cytoarchitectural study. The animals were deeply anesthetized with pentobarbital (Nembutal, Abbot) and perfused with cold saline (500 ml) followed by buffered 4% paraformaldehyde (1 to 2 liters). After removing the bone of the cranial vault, the brains were stereotaxically blocked *in situ*, removed, and kept in the same fixative for several weeks. Two brains were then frozen and cut in the coronal plane at 40 μm. Two other brains were embedded in paraffin and cut coronally at 20 μm. The fifth brain was embedded in celloidin and cut sagitally at 40 μm. Two series of each brain were collected; one was Nissl-stained with either cresyl violet or thionin and the other was stained using the Klüver-Barrera technique for simultaneous Nissl and myelin staining.

The coronal sections of the Nissl-stained series were projected on paper and outlines of the parietal cortex were drawn. Surface reconstructions were made from these projection drawings, and the cytoarchitectonic divisions plotted on the latter were transported to the former. The procedure for obtaining a two-dimensional reconstruction of this region of the cerebral cortex was based on a previous description by Jones and Wise (1977).

The area of the cortex occupied by areas 5a and 5b was measured in two cases using a digital planimeter, and values obtained were corrected for shrinkage (Table I). The correction factor was estimated from measurements of the shrinkage obtained by comparing distances between the tracks of two parallel stainless steel bars introduced at a known distance from each other prior to perfusion.

HRP study. In 12 animals anesthetized with Nembutal, one to six injections of a 50% (w/v) aqueous solution of HRP (Sigma type VI) were made with a 1-μl Hamilton syringe. All injections were placed in the right hemisphere under stereotaxic and topographic guidance through a fairly large craniotomy which allowed a good visual approach. The volume delivered in each injection was 60 nl. In an additional animal a small rectangle of filter paper, soaked in a solution of HRP, was applied to the cortical surface in the rostral portion of the lateral gyrus (GLa) (see "Results"). Table II shows the characteristics of the injections in each case.

After a 2-day survival, the animals were perfused through the ascending aorta with 300 ml of saline, followed by 2.5 liters of a solution of 1% paraformaldehyde and 1.25% glutaraldehyde in 0.1 M phosphate buffer (pH 7.3), and 1 liter of the same buffer with 10% sucrose. All solutions were kept on ice during the perfusion. A peristaltic pump was used, and the total perfusion time was maintained between 2 and 2.5 hr.

After perfusion, the brains were removed, quickly photographed, and immersed in phosphate buffer with 20% sucrose at 4°C for 1 to 3 days. They were then set on the freezing microtome, and two alternate series of 50-μm-thick sections were obtained, the intervals for each series being 250 μm. Both series were incubated in tetramethylbenzidine and processed according to the protocol of Mesulam (1978). One series was counterstained with thionin; the other was dehydrated, cleared, and coverslipped without prior counterstaining. At the level of the injection, additional sections were collected and reacted using diaminobenzidine as a substrate (Llamas and Martínez-Moreno, 1974). The lower sensitivity of this procedure yields a better definition of the "core" of the injection. This and other methods previously reported (Ramírez-Camacho et al., 1984) were used to identify accurately the cytoarchitecture of the region in which the HRP was injected. All sections were studied under bright- and darkfield illumination and labeled neurons were plotted on projection drawings of the histological sections. The stereotaxic planes were defined according to the atlas of Reinoso-Suárez (1961). The thalamic nuclear borders were determined for each individual section over low and high power microscopic examination, and the nomenclature of Reinoso-Suárez (1961), with modifications (Jones and Burton, 1974; Graybiel and Berson, 1980; see "Discussion"), was applied to the thalamic nuclei.

TABLE I

Area of cortex occupied by areas 5a and 5b in the right hemisphere of two cats

Case	Area 5a	Area 5b
G 66	45.5[a]	59.6
G 129	41.0	56.1

[a] Values are corrected for shrinkage and expressed in square millimeters.

TABLE II

Characteristics of HRP injections

Code No.	No. of Penetrations	Total Volume Injected (nl)	Location of the Injections
G 288	6	350	Whole mediolateral extent of area 5a. The most medial injection spread into area 1
G 309	3	180	Lateral half of area 5a (in GSs)
G 450	6	360	Whole mediolateral extent of area 5b. The most medial injection spread into area 7
G 456	3	180	Medial half of area 5a (in GLa). Slight spread into area 1
G 467	3	180	Medial half of area 5b (in GLa)
G 476	3	180	Lateral half of area 5b (in GSs)
G 520	1	60	Caudal SSa and rostral AmLS (in medial bank of SSs)
G 535	1	?	Small deposit in layers I and II of area 5a (in lateral bank of SL)
G 540	1	60	Lateral area 5b (in GSs)
G 541	1	60	Central part of areas 5a and 5b (in lateral bank of SL). HRP spread into underlying white matter
G 543	1	60	Ill-defined area (probably 5b) in medial face of the hemisphere
G 559	1	60	SSa (in medial bank of GSs)
G 565	Topical application		Layer I of the medial part of areas 5a and 5b (on GLa)

Results

Cortical cytoarchitecture. Hassler and Muhs-Clement's (1964) detailed study has been followed in identifying the cortical areas. Area 5a is most readily recognized by the large pyramidal cells which, interspersed among others of smaller size, form an irregular line within a relatively pale layer V. Area 5b, in contrast, has a wide layer V, with several lines of small and medium-sized pyramidal cells (Fig. 1). Although it certainly is characteristic, the appearance of

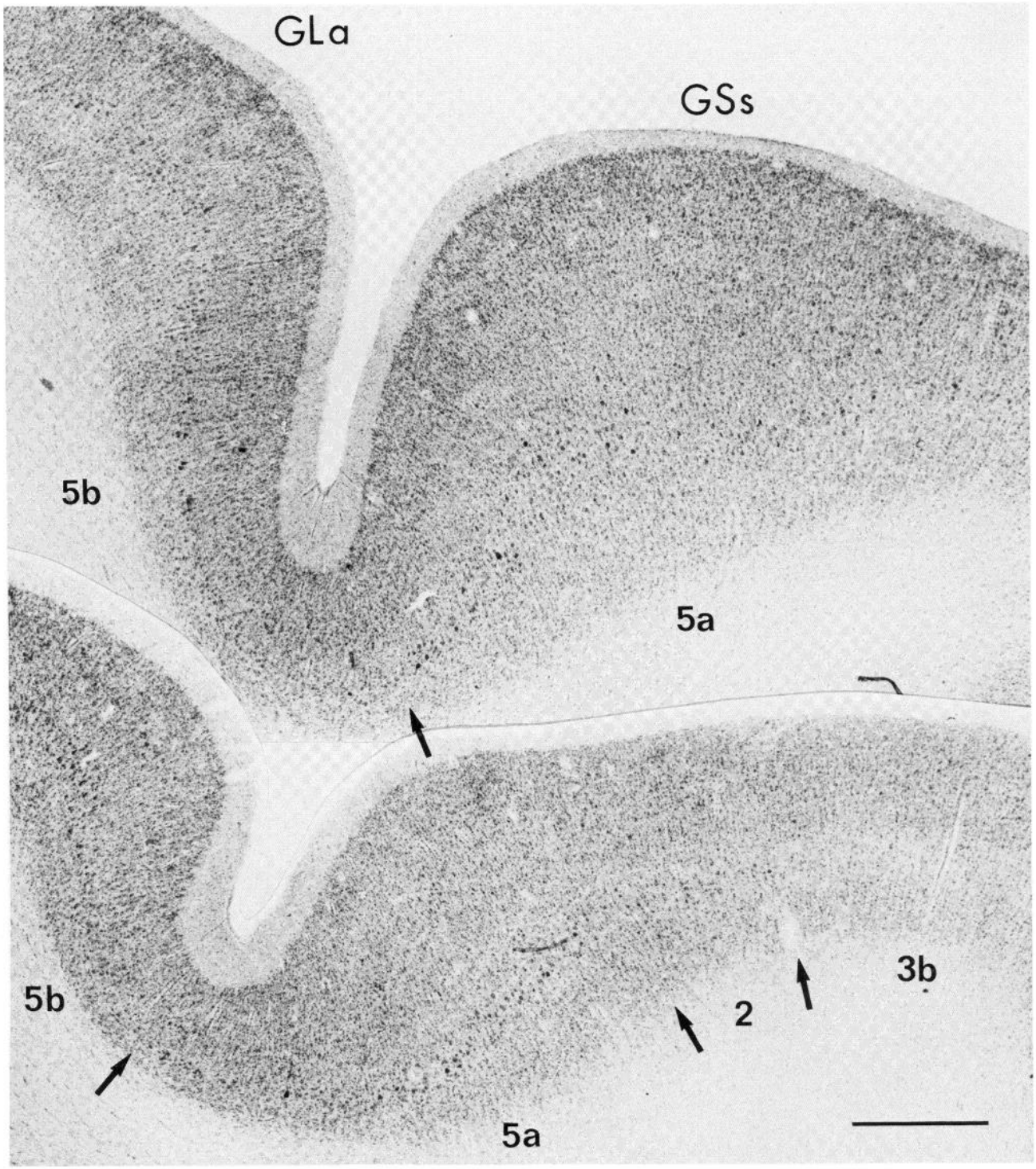

Figure 1. [4] Low power photomicrographs of 40-μm-thick cresyl violet-stained, frozen coronal sections through the rostral part of the lateral and middle GSs, approximately at stereotaxic planes +17 (*top*) and +20 (*bottom*). *Arrows* point to cytoarchitectonic borders. *Bar*: 1 mm.

layer V is not enough to identify these areas at all levels. The bottom of the lateral (SL) and ansate sulci (SNns), as well as the sections cut obliquely or tangentially to the cortical mantle (for example, at the junction of SAns and SL) introduces distortions such as disappearance of relevant pyramidal cells in layer V, or an irregular widening of this layer and changes in orientation of the pyramidal cells which make area 5a, in particular, less apparent. Other features noted by Hassler and Muhs-Clement (1964) then become useful to distinguish these areas, such as the thinner layer IV in 5a and, in area 5b, the palisades of neurons in layer VI. Disregarding some minor differences, the supragranular layers are similar in areas 5a and 5b.

[4] The abbreviations used in the figures are: *Am*, nucleus anteromedialis thalami; *Av*, nucleus anteroventralis thalami; *GL*, corpus geniculatum laterale; *LM*, nucleus lateralis medialis; *MD*, nucleus medialis dorsalis; *Pc*, nucleus paracentralis; *PcD*, postcruciate dimple; *PoR*, nucleus posterior of Rioch; *SAnL*, sulcus ansatus, ramus lateralis; *SAnM*, sulcus ansatus, ramus medialis; *SCo*, sulcus coronalis; *Sm*, nucleus submedius; *SSs*, suprasylvian sulcus; *VPm*, nucleus ventralis posteromedialis.

Area 5a is bound rostrally and medially by areas 1 and 2, of which the cytoarchitectonic features are quite distinct from those of area 5a. However, a narrow transition zone exists along practically the entire mediolateral extent of the boundary, making the delineation difficult at some points (see, for example, Fig. 1, *bottom*). Caudally, the boundary between areas 5b and 7 is relatively sharp on GLa and the medial bank of SL but is less distinct in the suprasylvian gyrus (GSs). On the medial face of the hemisphere, area 5b stretches backwards until merging gradually with area 7 (caudally) and with a poorly studied area between the rostral tip of the splenial sulcus (SSp) and the cruciate sulcus (SC), which Hassler and Muhs-Clement (1964) interpreted as a caudal enlargement of area 3a, but which actually differs substantially from it as it appears in the posterior sigmoid gyrus.

Although cytoarchitectonic characteristics are basically consistent for each area, there are appreciable intra-areal regional variations. For example, in some animals, area 5a rostrally in the lateral bank of SL exhibits a relatively denser accumulation of large and medium-sized pyramidal cells in layer V. Also, in GLa, layer V in area 5b is usually comprised of larger, more abundant, and more tightly packed medium-sized neurons than in GSs (Fig. 2).

The extent and topography of areas 5a and 5b on the cortical surface change remarkably from animal to animal. Figure 3*B* shows two cases reproduced from Hassler and Muhs-Clement's (1964) illustrations, which differ substantially from each other. Two cases from our own material are likewise represented in Figure 4*A*. This variability, in addition to the well known variations in cerebral sulci and gyri (Hassler and Muhs-Clement, 1964; Kawamura, 1971), does not permit the identification of the locus of an injection exclusively from topographical landmarks. A more precise definition of the area and their relation to the gyri and sulci can be obtained from two-dimensional maps produced by unfolding the cortical mantle, as described above. Figure 4*B* presents two cases in which, despite notable differences in sulcal morphology, areas 5a and 5b correlate quite well both in their general shape and in the total area occupied by each of them (Table I).

Injections in area 5a. Two cases are representative of HRP injections in the medial (see Fig. 6, *G-456*) and lateral (see Fig. 7, *G-309*) halves of area 5a. Case G-456 received three injections evenly spaced in the rostral extreme of GLa. The most medial injection penetrated slightly into area 1 in the medial face of the hemisphere. Case G-309 also received three injections in the anterior part of GSs. All were confined to area 5a.

In both cases the labeled cells in the thalamus were distributed mainly in the posterior complex (Po) and VL. Other less extensively labeled nuclei were VA, the oral part of the lateral intermediate complex (LIO), and the periphery of the ventral posterior complex (VP) at some levels. Some labeled cells were also found in midline and intralaminar nuclei (particularly nucleus centralis lateralis (CL)), in the ventromedial nucleus (Vm), and in the caudal part of the lateral intermediate complex (LIC).

When area 5a was injected massively along its mediolateral extent (case G-288), practically all subdivisions of Po exhibited labeled neurons, with the exception of the intermediate part (Pol). However, labeling in the suprageniculate nucleus (Sg), the magnocellular part of the medial geniculate body (GMMc—its medioventral part, or slf;

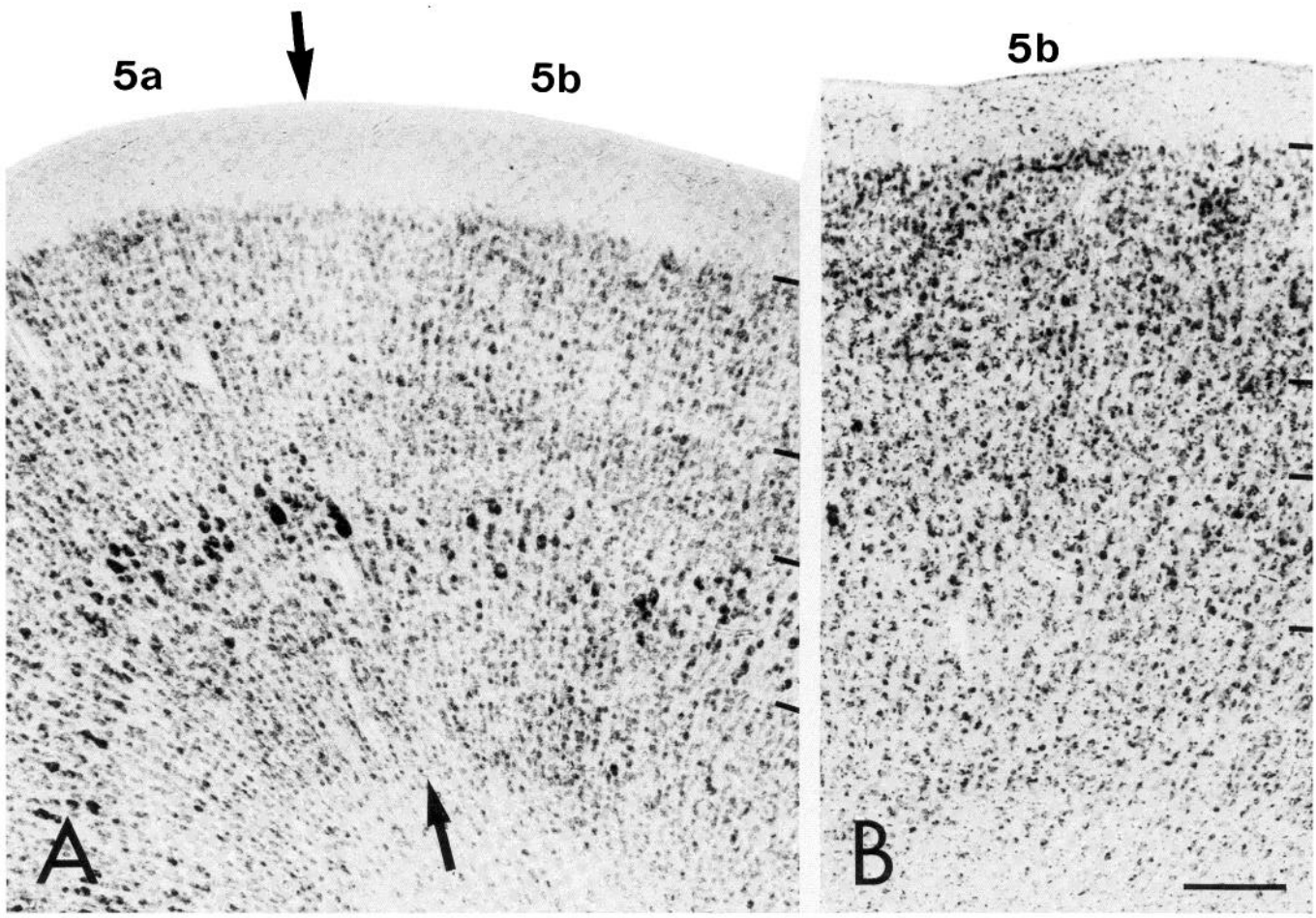

Figure 2. Photomicrographs of 40-μm-thick, cresyl violet-stained frozen coronal sections through the rostral part of the GLa (*A*: midline to the *left*) and the rostral part of the middle GSs (*B*). *Arrows* in *A* point to the cytoarchitectonic border between areas 5a and 5b. *Short bars* at the *right* of *A* and *B* mark limits between layers I, II-III, IV, V, and VI. Note that cytoarchitectonic differences between area 5b in GLa and in GSs have an effect most evidently on infragranular layers. *Calibration bar*: 250 μm.

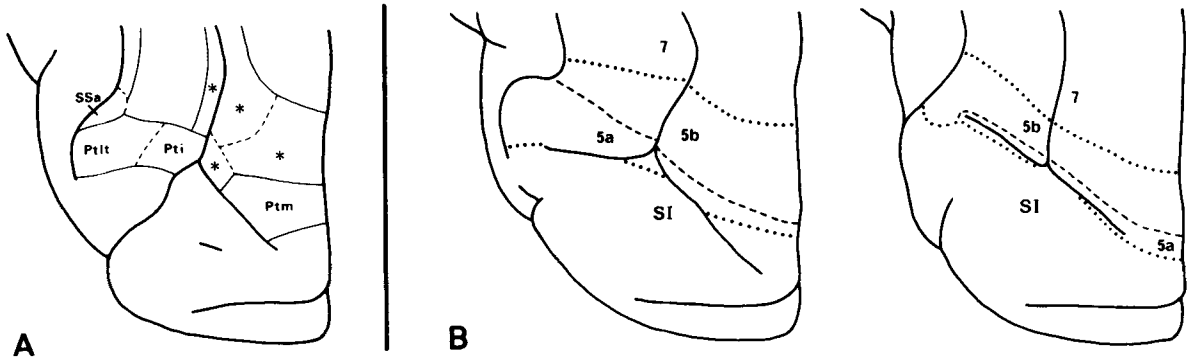

Figure 3. Cytoarchitectonic delineations on drawings of the dorsal surface of the rostral part of the cat's brain after Sanides and Hoffmann (1969; *A*) and Hasler and Muhs-Clement (1964; *B*), with slight modifications. In *A*, *asterisks* mark different sub-areas of the so-called "peristriate cortex;" other labeled areas correspond to the medial (*Ptm*), intermediate (*Pti*), and lateral (*Ptlt*) subdivisions of the "parietal integration belt," and to the anterior subdivision of the "suprasylvian sulcus belt" (*SSa*). Diagrams in *B* show two cases drawn after Hassler and Muhs-Clement (1964) in which sulcal morphology and shape and extent of areas 5a and 5b on the cortical surface differ remarkably.

see "Discussion"), and the ventral posteroinferior nucleus (VPi) was meager, whereas the medial posterior complex (PoM) and, to a lesser extent, the posterior complex, pars lateralis (PoL) were strongly labeled. In case G-309, injected laterally in area 5a, many labeled neurons forming irregular clumps were distributed throughout PoM, but labeling in PoL was almost absent (Fig. 5). In contrast, labeling was abundant in PoL and somewhat weaker in PoM when the most medial and rostral part of area 5a was injected (see Figs. 5*B* and 6).

The "spinal part" of VL (Jones and Burton, 1974) exhibited few labeled neurons in animals injected in area 5a. More dorsally, however, VL was densely filled with labeled cells. Rostrally, where VL and VA merge, labeled cells appeared more or less randomly scattered, sparing the dorsal zone of VA-VL, but extending ventrally and almost reaching the external medullary lamina. More caudally, the cells aggregated into clumps of irregular size and shape which reached the caudal end of VL. Labeled neurons were particularly sparse at the dorsomedial "corner" of VL, an area of ambiguous boundaries in many cases, which at some levels was included by Updyke (1983) as a part of his "lateral posterior complex shell region." A loose topographical organization was observed in VL cells projecting to area 5a: labeled neurons were more abundant in rostral and central-lateral sectors of VL after medial cortical injections and in caudal and central-medial sectors after lateral cortical injections (cf. Figs. 6 and 7).

A moderate number of labeled neurons was found in VP in all cats injected in area 5a. They formed a dorsal and rostral "cap" within the ventral posterolateral nucleus (VPl), but in case G-309 some neurons also appeared within the dorsolateral "shoulder" of the ventral posteromedial nucleus (see Fig. 5*A*). Labeling in VP was always topographically continuous with that in the neighboring nuclei, such as VL or PoM.

The lateral intermediate complex (LI) was consistently labeled after injections in area 5a. The labeled neurons were distributed ventrally in this complex, primarily occupying its oral division (LIO). In general, labeling in LIO and LIC abutted that in the adjacent VL.

Labeled cells in the midline and intralaminar nuclei were not numerous. A few intensely labeld neurons appeared most frequently in CL, but with no clear-cut topographical preference (Fig. 5*A*). Occasional labeled cells were found in the central medial (CeM) and paracentral nuclei, and only in case G-309 did a few labeled neurons appear in the rostral part of the centromedian nucleus (Cm). Labeled cells were also scarce in Vm.

Injections in area 5b. Figures 9, 10 and 13 illustrate three representative cats injected in area 5b. Case G-543 received one single injection in the medial face of the hemisphere, just anterior to the rostral tip of SSp. The needle entered obliquely to the surface, and the bottom of the injection appeared to involve the 5b border, slightly affecting a cytoarchitectonically ill-defined zone at the mergence of areas 5a, 3a, and 5b (see Figs. 4 and 8*A*). Case G-467 received three injections in GLa and the medial bank of SL, all of which remained within area 5b (Fig. 8*B*). Case G-540 received one injection in GSs behind a shallow lateral branch of the ansate sulcus. In this case the injection was centered superficially in area 5b, but it is possible that the upper layers of area 5a were slightly involved by the injection as well (Fig. 8*C*).

Basically, the same thalamic nuclei were labeled in areas 5a and 5b: some components of Po, VA, VL, LI, and some intralaminar nuclei, particularly CL. However, the topography and the magnitude of the projections from each of these nuclei were quite distinct in areas 5a and 5b. Furthermore, in animals injected in area 5b—and particularly those injected laterally, in GSs— the lateral dorsal complex (LD) and the pulvinar (Pul) also exhibited some labeled neurons. With the exception of case G-543, no labeled neurons appeared in VP after area 5b injections. Labeling in Vm and CeM was likewise meager in both groups of injections.

In Po, only PoM was consistently labeld after injections in area 5b. Labeled neurons were not abundant and formed irregular clumps throughout the nucleus. A few labeled neurons also appeared in VPi, but only in case G-543.

Labeling in VL, in contrast, was substantial and was distributed more dorsally and medially than that produced by area 5a injections. Our material does not allow us to establish a clear-cut topographic organization, although regional differences were found. For example, in cases G-450, massively injected in area 5b (see Fig. 20) and G-540, injected laterally and caudally in area 5b (Figs. 8*C* and 13) there appeared labeled neurons in the dorsomedial "corner" of VL (see Fig. 11*A*), whereas neurons labeled by more medial—and rostral—injections (cases G-467 and G-543) were found at more ventromedial sectors of VL and in the lateral sheet interposed between LI and VP (Figs. 9 and 10).

All injections in area 5b gave rise, at the level of the VA-VL junction, to an area of labeled neurons which merged dorsolaterally with others in the rostral tip of LIO and stretched medioventrally from there (Fig. 11*B*). Leaving aside a few occasional labeled neurons, the ventral half of VA-VL and VA proper (see "Discussion") were free of labeling.

Labeling in LI was particularly dense after injections in area 5b and exhibited a gross topographical organization. Medial and rostral injections in area 5b (case G-467) gave rise to a dense population of labeled neurons, mainly distributed in the rostral and lateral two-thirds of LIO at intermediate dorsoventral levels of the nucleus. The injection in the medial face of the hemisphere (G-543) resulted in labeled neurons at similar dorsoventral and mediolateral levels, but

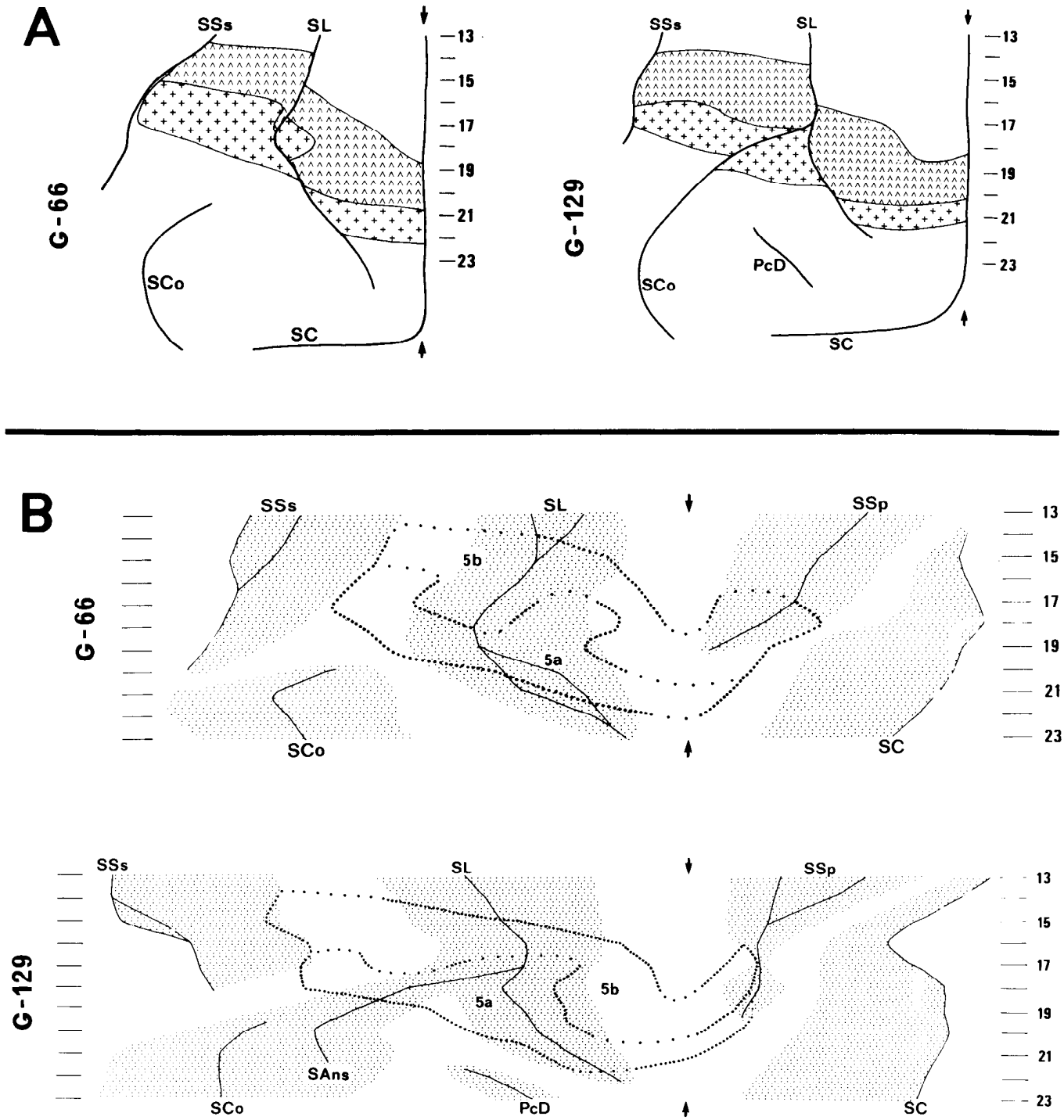

Figure 4. Diagrams showing the extent, shape, and correspondence with topographic landmarks of areas 5a and 5b in the right hemisphere of two different cats. *A*, Distribution of these areas (+, area 5a; Λ, area 5b) on the cortical surface. *B*, Projection of areas 5a and 5b on a flat map of the cortex obtained by unfolding gyri and sulci. *Shaded areas* and *continuous lines* in *B* represent, respectively, the banks and bottom of sulci. *Arrows* point to the dorsomedial "shoulder" of GLa, from which the cortex was unfolded. *Scales* on the *right* of each *drawing* represent stereotaxic planes.

more caudally situated (Fig. 12). The lateral cases, injected in GSs, had two separate populations of labeled cells, a small rostral and lateral one in LIO, topographically continuous rostrocaudally with labeled cells in VA-VL, and a larger one, caudomedially situated straddling LIO and LIC (see also Fig. 20).

In CL, both large and small cells were consistently labeled by injections in area 5b (Fig. 5C). In general, these cells tended to aggregate loosely in the lateral region of the caudal half of this nucleus, but scattered labeled neurons were often found at other levels. In LD, some labeled cells were found in the ventral part of its medial division (LDM), but only when GSs was injected. In these cases, a few labeled neurons appeared in Pul as well, distributing medially and rostrally in this nucleus (Fig. 13).

Injections in the medial bank of anterior suprasylvian sulcus. In two animals a single HRP injection was made in the medial bank of the suprasylvian sulcus. In case G-559 (Fig. 14) the injection was

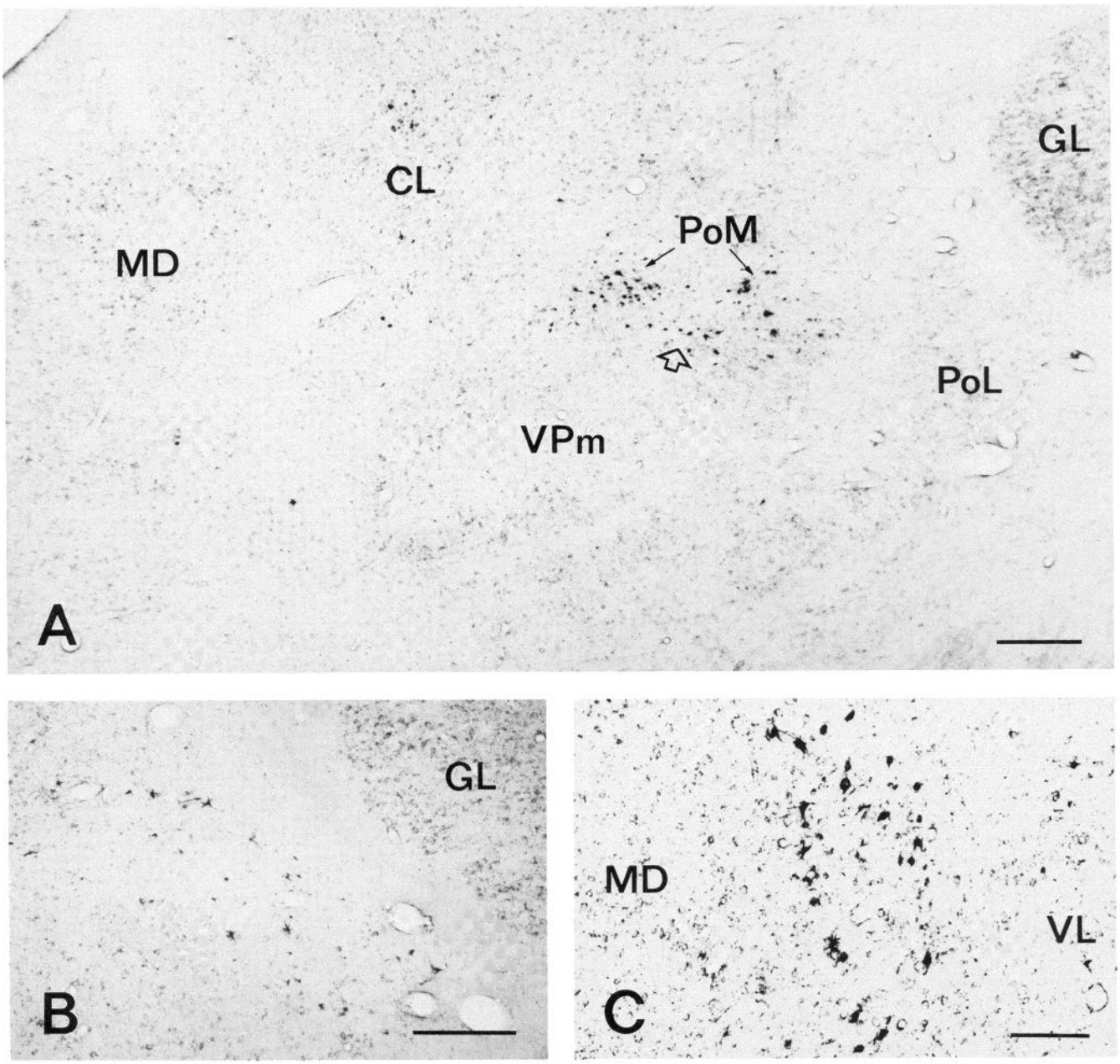

Figure 5. *A*, Photomicrograph showing labeled neurons in CL, PoM (*small arrows*), and the dorsal rim of nucleus ventralis posteromedialis (*VPm*) (*open arrow*) in case G 309, injected in the lateral part of area 5a. *B*, Photomicrograph showing labeled neurons in PoL in case G 288, which received six injections along the mediolateral extent of area 5a. *C*, Photomicrograph showing fairly numerous labeled neurons of various sizes in CL (*center*) in case G 450, injected in the medial and lateral parts of area 5b and in the most rostral and medial part of area 7. *Bars*: *A* and *B*, 500 μm; *C*, 250 μm.

confined to area suprasylvania anterior (SSa) of Sanides and Hoffman (1969). This cortical region is interposed between area 5a medially, area *2 praeinsularis* (Hassler and Muhs-Clement, 1964) or SII (Burton et al., 1982) laterally, area 2 rostrally, and the anteromedial lateral suprasylvian area (AmLS) (Palmer et al., 1978) caudally. The injection in G-520 (Fig. 15) was located more caudally, in the caudal part of SSa and in a region which topographically corresponds to the rostral part of AmLS as defined by Palmer et al. (1978). The HRP in this case spread also into the deep layers of the lateral part of area 5b. The close relationship of the retrograde thalamic labeling in these cases and those injected in various parts of area 5 justifies including them in the present study.

The location of labeled neurons in case G-559 practically reproduced that obtained after injections in area 5b in GSs (cf. Fig. 13); although the labeled neurons in LIC and LIO are more dorsally situated, there is an absence of labeled neurons in LDM and there is a small contingent of labeled cells in the lateral part of LP (LPl) in case G-559. Labeling in the thalamus was also similar in case G-520, although labeled neurons in LIO and LIC in this case were even more dorsally located, and some neurons also appeared in LDM. At caudal levels, however, the picture was remarkably different, because of the existence of a sizable amount of labeled cells in LPl and in the posterior nucleus of Rioch.

Thalamic projections to superficial layers of area 5. Thalamic cells which project specifically to the superficial layers of area 5 could be identified in two cases. In G-535 the tip of the needle fortuitously penetrated layer I of the cortex of the lateral bank of SL, resulting in a small injection of HRP in layers I and II (Figs. 16 and 18*A*). In G-565 a piece of filter paper soaked in a solution of HRP was placed on the surface of the anterior end of GLa, which previously had

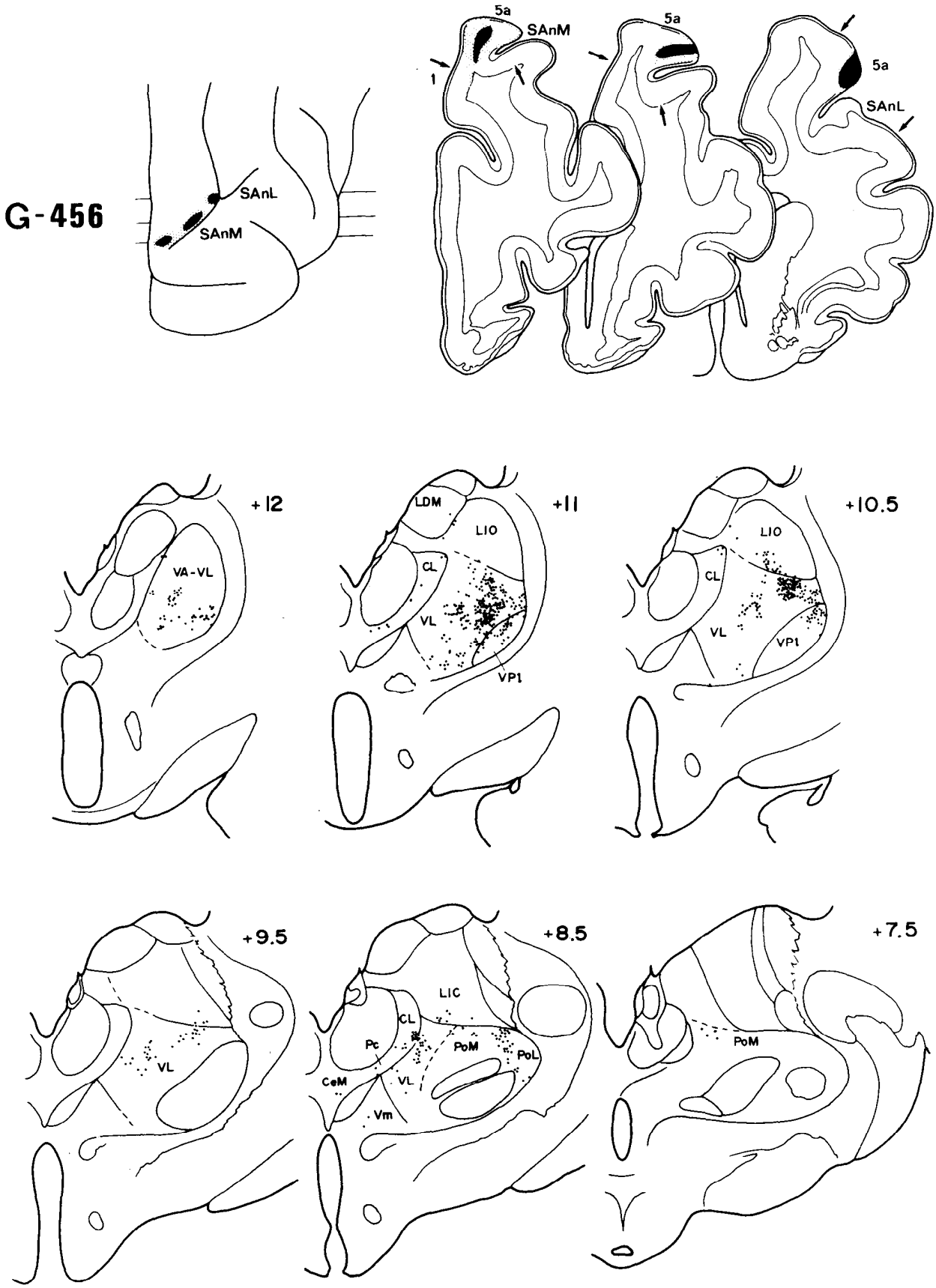

Figure 6. Semischematic illustrations showing localization of HRP injections in the cortex and retrogradely labeled cells in the thalamus in an animal which received three small injections in Gla, affecting the medial part of area 5a. Coronal sections at the *top right* are projection drawings from sections taken at levels indicated on the surface diagram (*top, left*) and are aligned from rostral to caudal; *arrows* point to cytoarchitectonic borders. Projection drawings through the diencephalon (*bottom rows*) are also aligned from rostral to caudal; stereotaxic levels (Reinoso-Suárez, 1961) are approximate and refer in all cases to the center of the thalamus. For abbreviations not used in the text, see Footnote 4.

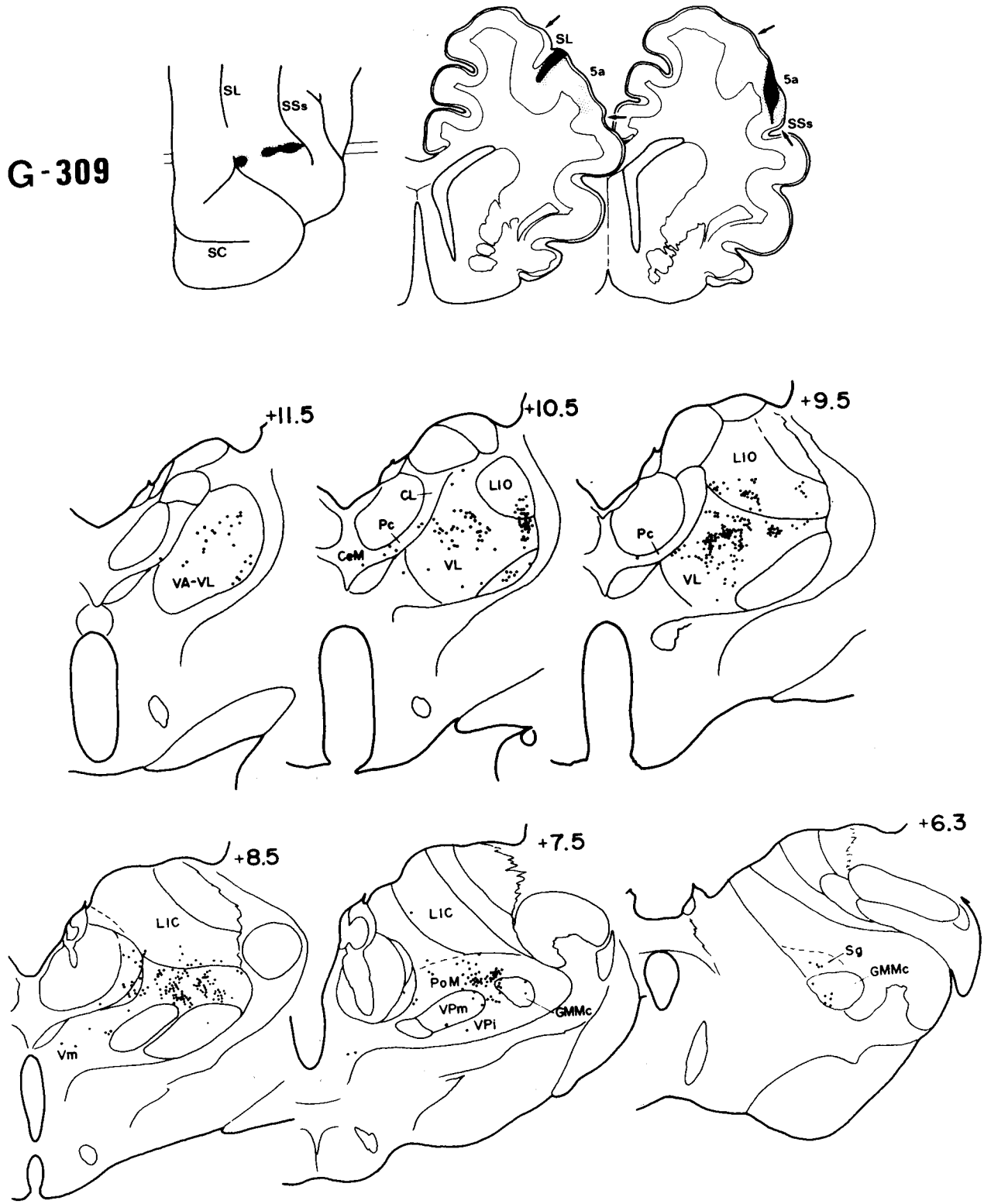

Figure 7. HRP injections and retrogradely labeled cells in an animal which received three small injections in GSs, affecting the lateral part of area 5a. Conventions are as in Figure 6.

been rubbed gently with a cotton-tipped applicator. In this case, the HRP apparently diffused only into layer I and indirectly produced a strong labeling of neuronal somata in layers II, III, and V, perhaps through a dendrosomatic transport (Figs. 17 and 18*D*).

Labeled neurons in the thalamus in both cases were relatively scarce, small in size, and, in general, only moderately filled with reaction product (Fig. 18, *B* and *E*). They were also located primarily in the rostral half of VL, but with a different distribution: central and medial in case G-535, and forming two separate clumps, one laterally and one ventromedially in case G-565. Occasional labeled neurons

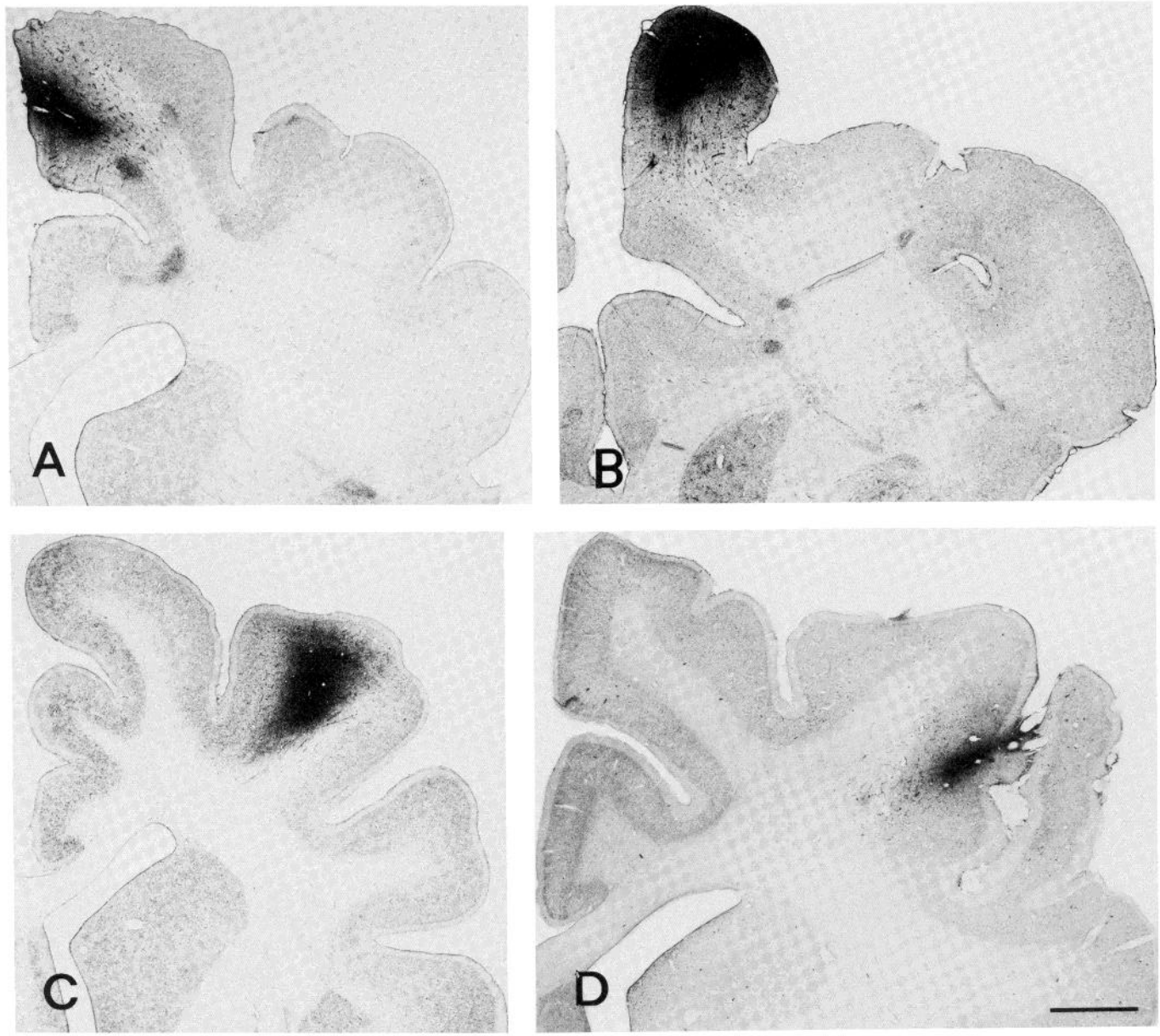

Figure 8. Photomicrographs of 50-μm-thick, thionin-stained coronal sections showing HRP injections in cases G 543 (*A*), G 467 (*B*), G 540 (*C*), and G 559 (*D*). *A, C,* and *D* correspond to animals which received single injections. *B* shows the central one of three injections which were placed in *Gla*. All cases were reacted with tetramethylbenzidine. *Bar:* 2 mm.

appeared in the ventrolateral part of Vm close to VL. In case G-565 a few labeled neurons were also seen in the ventral periphery of LIO, in continuity with those in VL, and occasional ones were found in Cm, CL, and PoM; a moderate number of faintly labeled neurons also appeared in the caudodorsal zones of VA.

From these data it seems that projections to layer I arise from several thalamic nuclei. This does not mean, however, that all thalamocortical neurons project to layer I. We should emphasize that fewer labeled neurons were found in case G-565 than in other cases, such as G-456, in which the HRP was injected at a similar level of GLa, but throughout the full depth of the cortex. In addition, the mean soma size of layer I-projecting neurons is significantly smaller than that of thalamocortical neurons labeled by deeper injections (for example, 198.2 ± 52.0 μm^2 in G-535 versus 257.0 ± 74.0 in G-541; see Figs. 18 and 19), which suggests that these projections arise, in part at least, from different populations of thalamic cells.

Discussion

Area 5 and the posterior parietal cortex. The posterior parietal cortex in the cat and other carnivores is a portion of homotypical isocortex situated behind SI, rostral to perivisual and medial to periauditory areas. Brodmann (1909) identified three main divisions of this cortex in the kinkajou: areas 5, 7, and 51, the latter being apparently unique to this species. Subsequently, Vogt and Vogt (1919) subdivided areas 5 and 7 into 5a, 5b, 7a, and 7b in *Cercopithecus*. In the cat, Winkler and Potter (1914) and Gurewitsch and Chatschaturian (1928) first attempted to map the cortical areas according to the system of Brodmann (1909), but their findings differed substantially from each other and were also at variance with Brodmann's (1909) study. More recently, Hassler and Muhs-Clement (1964) divided the posterior parietal areas in the cat into areas 5a, 5b, and 7, and their description has been widely used thereafter.

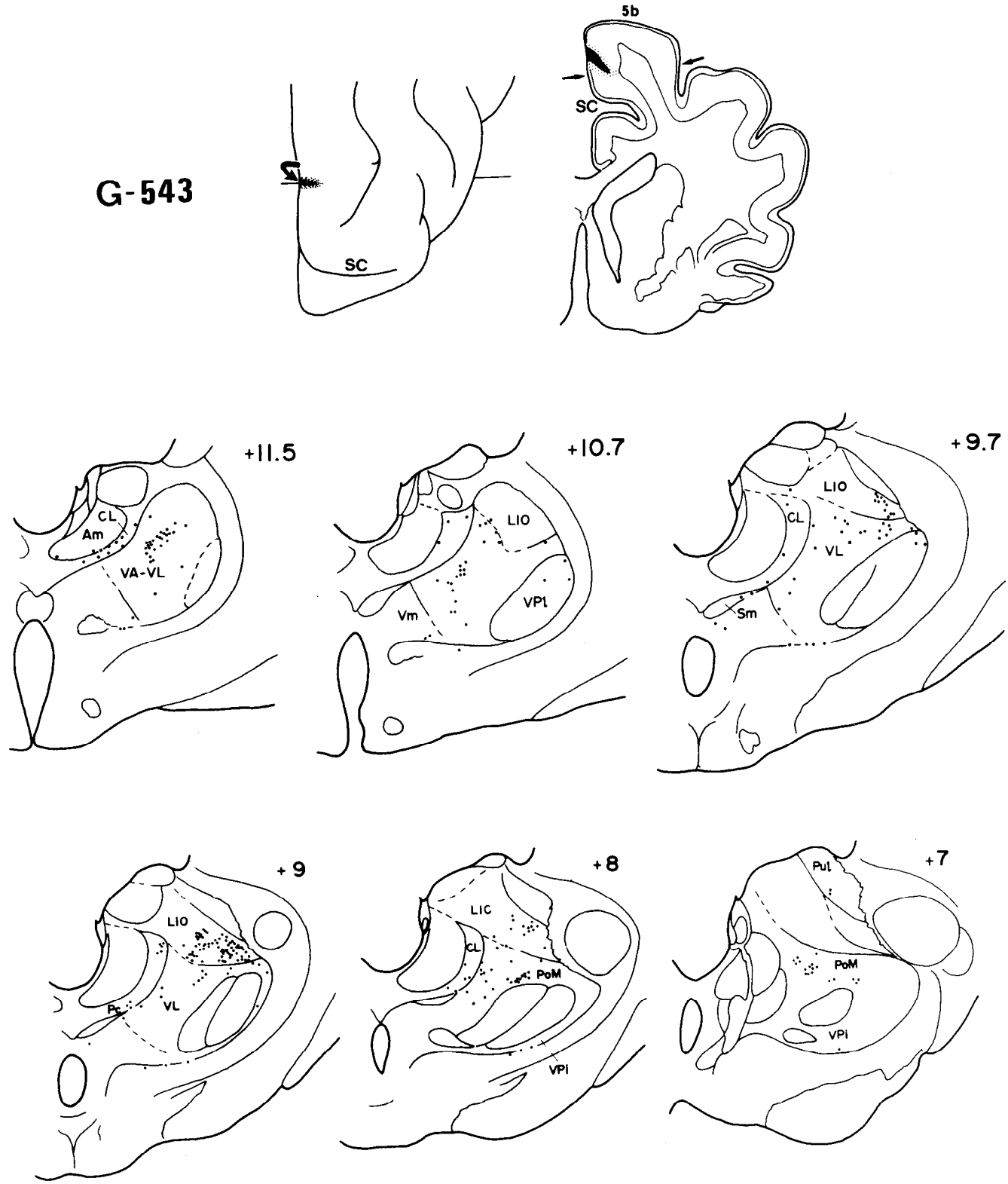

Figure 9. Thalamic labeled cells in an animal with a single HRP injection in the medial face of the hemisphere, mainly affecting area 5b. Conventions are as in Figure 6.

Despite its wide use, Brodmann's (1909) terminology has not been accepted by all, mainly to avoid establishing interspecies homologies of cortical areas, particularly in relation to the "association" cortex (Sanides and Hoffman, 1969). To circumvent this problem, topographically based terms were chosen by others (Von Economo and Koskinas, 1925; Von Bonin and Bailey, 1947). For the cat, Sanides and Hoffman (1969) coined the terms "integration cortex" or "integration belt" to designate the cortex of the anterior and middle GSs and the rostral portion of GLa, a region which largely coincides with Brodmann's areas 5 and 7. This "belt" was

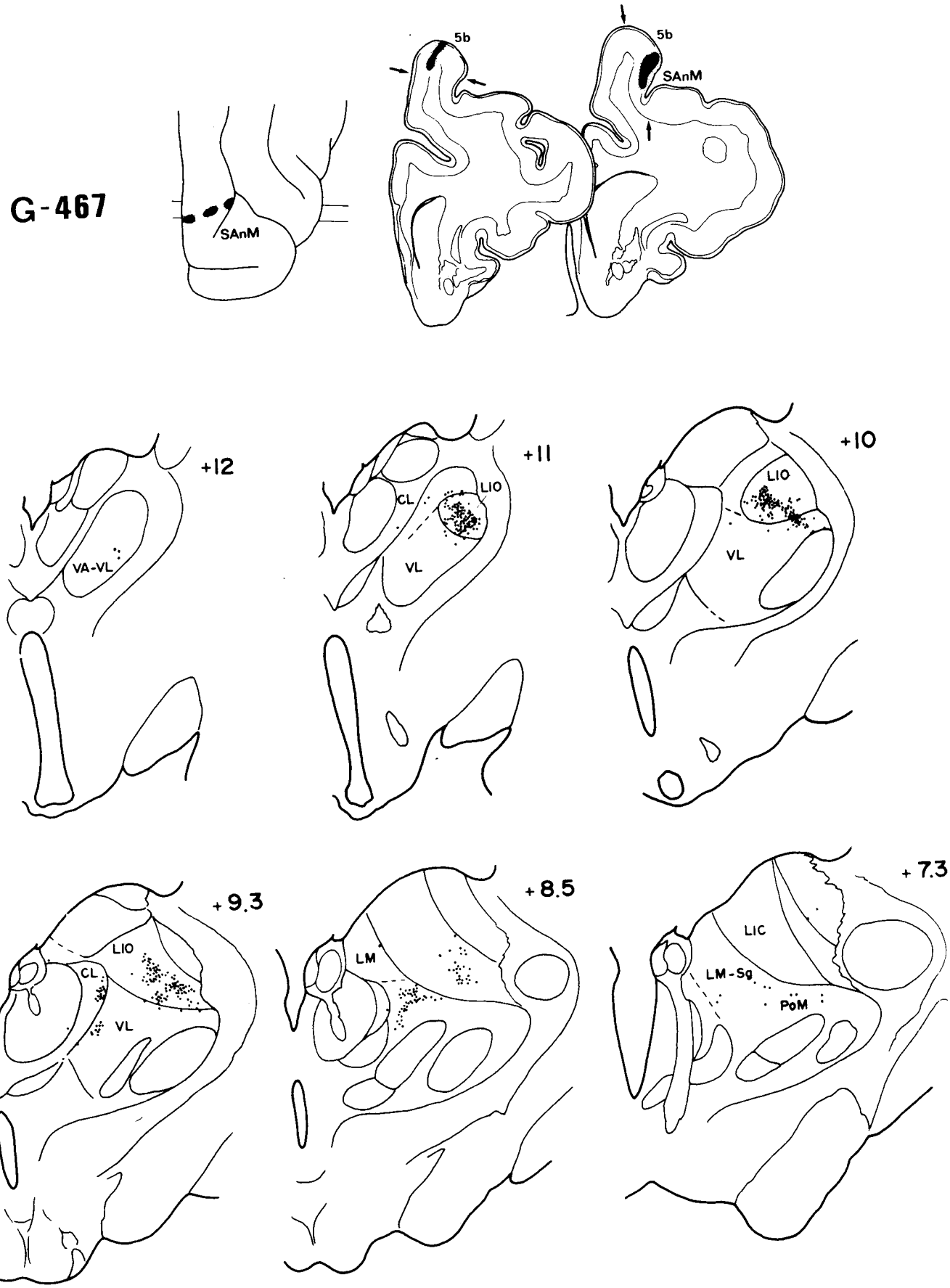

Figure 10. Thalamic labeled cells in an animal which received three small HRP injections in GLa, affecting the medial part of area 5b. Conventions are as in Figure 6.

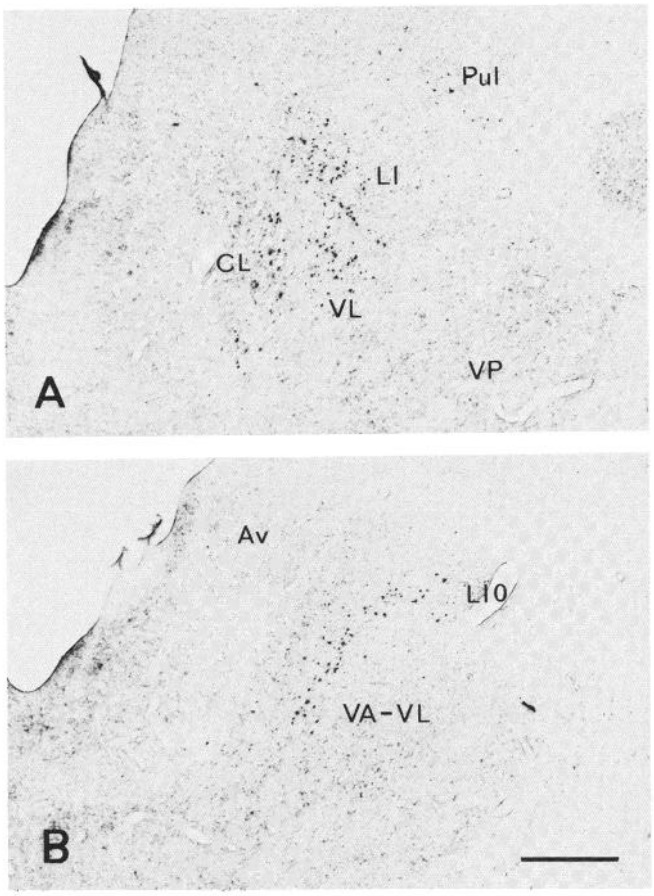

Figure 11. Low power photomicrographs from two levels of the thalamus in case G 540 (see Fig. 13), showing labeled neurons in CL, VL, LIO, Pul, and the dorsocaudal part of VA. *Bar:* 1 mm.

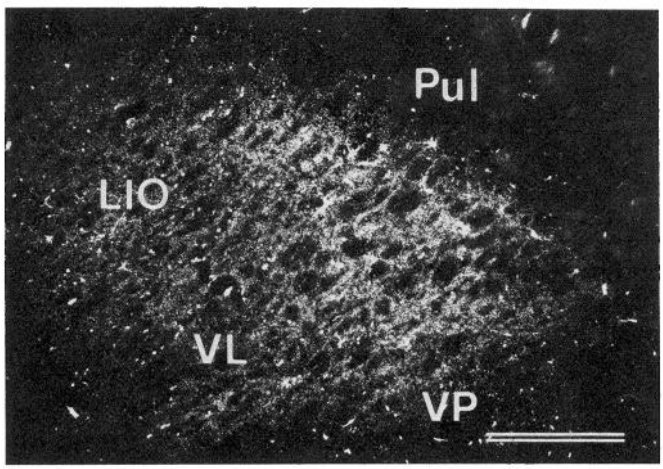

Figure 12. Darkfield photomicrograph of a lateral sector of the thalamus at the level of the caudal part of LIO in case G 543, which was injected in the most medial part of area 5b. In addition to many labeled neurons, mainly located in LIO, a dense, fine precipitate due to anterograde transport is observed in LIO and in the dorsolateral part of VL. *Bar:* 500 μm.

divided into three divisions, parietal, suprasylvian, and suprasylvian sulcus belts, each of which was further subdivided on topographical grounds (Fig. 3*A*). Although it is not possible to separately equate each of Sanides and Hoffman's (1969) divisions with Brodmann's, area 5 as a whole corresponds most closely to the parietal integration belt. There are, however, two important differences. The first one is that Sanides and Hoffman (1969) separated the parietal integration belt into two parts by a tongue of "peristriate cortex" which protruded rostrally toward the medial bank of the ansate sulcus; and the second is that for these authors the major changes in cytoarchitecture in this region proceed from medial to lateral, whereas for Hassler and Muhs-Clement (1964) the progression runs from rostral to caudal.

We have chosen Brodmann's nomenclature in our work for several reasons. (*1*) Our findings show that the major cytoarchitectonic changes take place in a rostral-to-caudal progression, that is, areas 1-2, 5a, 5b, and 7. This fact notwithstanding, regional differences can also be observed within areas 5a and 5b in their mediolateral extent. (*2*) An "equivalency" (see Sanides and Hoffman, 1969) between areas 5a and 5b in cats and primates is supported by connectional and physiological findings, as will be commented on below. Accepting homonymous areas as "equivalent" across species should not imply that they are "homologous" or "analogous" in the full sense (Campbell and Hodos, 1970). Consequently, naming "area 5" a part of the cerebral cortex does not necessarily imply that this area must have a common phylogenetic ancestor and exhibit all and only the same functions in both species. (*3*) Finally, Brodmann's nomenclature has been extensively used in the cat in many laboratories.

Projections from Po. In the broadest sense, Po ecompasses several aggregates of differently shaped neurons which together form a shell around the ventrobasal complex (VB) and separate it from the medial geniculate and the LP-LI (Rose and Woolsey, 1958; Jones and Powell, 1971; Jones and Burton, 1974; Updyke, 1983). Thus defined, Po would include Pol, PoL, PoM, Sg, VPi, and even the VL-spinal zone (Jones and Burton, 1974; Berkley, 1980) which dorsally and medially surrounds the dorsal half of VP. The ventrocaudal part of PoM, as defined by Jones and Burton (1974), lies medioventrally to GMMc and was called by Updyke (1983) the "supralemniscal field" division of Po (slf). In our figures no distinction has been made between slf and GMMc.

Before the introduction of axoplasmic transport techniques, the cortical projections attributed to Po were mostly to "secondary" auditory and periauditory areas (Rose and Woolsey, 1958; Heath and Jones, 1971; Graybiel, 1973). However, Rose and Woolsey (1958) raised the possibility that a part of the somesthetic cortex (SII) received projections from the rostral parts of Po and considered this thalamic region ideally suited for "tactile and auditory interconnections." In fact, recent studies have demonstrated that the projections from Po are widely distributed in the cerebral cortex with a remarkable degree of topographic specificity (Bentivoglio et al., 1983). In the somatosensory cortex, all of its subdivisions receive projections from PoM, but although this projection to SI is meager (Spreafico et al., 1981), it is much larger to SII (Spreafico et al., 1981; Roda and Reinoso-Suárez, 1983) and SIV (Roda and Reinoso-Suárez, 1983). Also, PoM projects weakly to the motor cortex (Morán et al., 1982).

The existence of a direct projection from Po to area 5 was first reported in the cat (Robertson, 1978; Tanji et al., 1978) and in the monkey (Pearson et al., 1978), and was thereafter confirmed in a number of species (Hendry et al., 1979; Niimi et al., 1979; Donoghue and Ebner, 1981; Miyata and Sasaki, 1983; Neylon and Haight, 1983). Reports in the cat describe PoM as the only subdivision of Po projecting to area 5 and, more specifically, to area 5a (Tanji et al., 1978; Hendry et al., 1979). Our results show that PoM is the major source of projections from Po to area 5 and that these projections are particularly abundant to area 5a. However, area 5b also receives some projections from clumps of neurons in PoM, and projections to area 5a arise also from PoL. The difference between our findings and those of Tanji et al. (1978) may be explained by the fact that these authors injected only the lateral part of area 5a which, in accordance with our results, receives connections from PoM but not from PoL.

The finding of labeled cells in PoL after area 5a injections was not

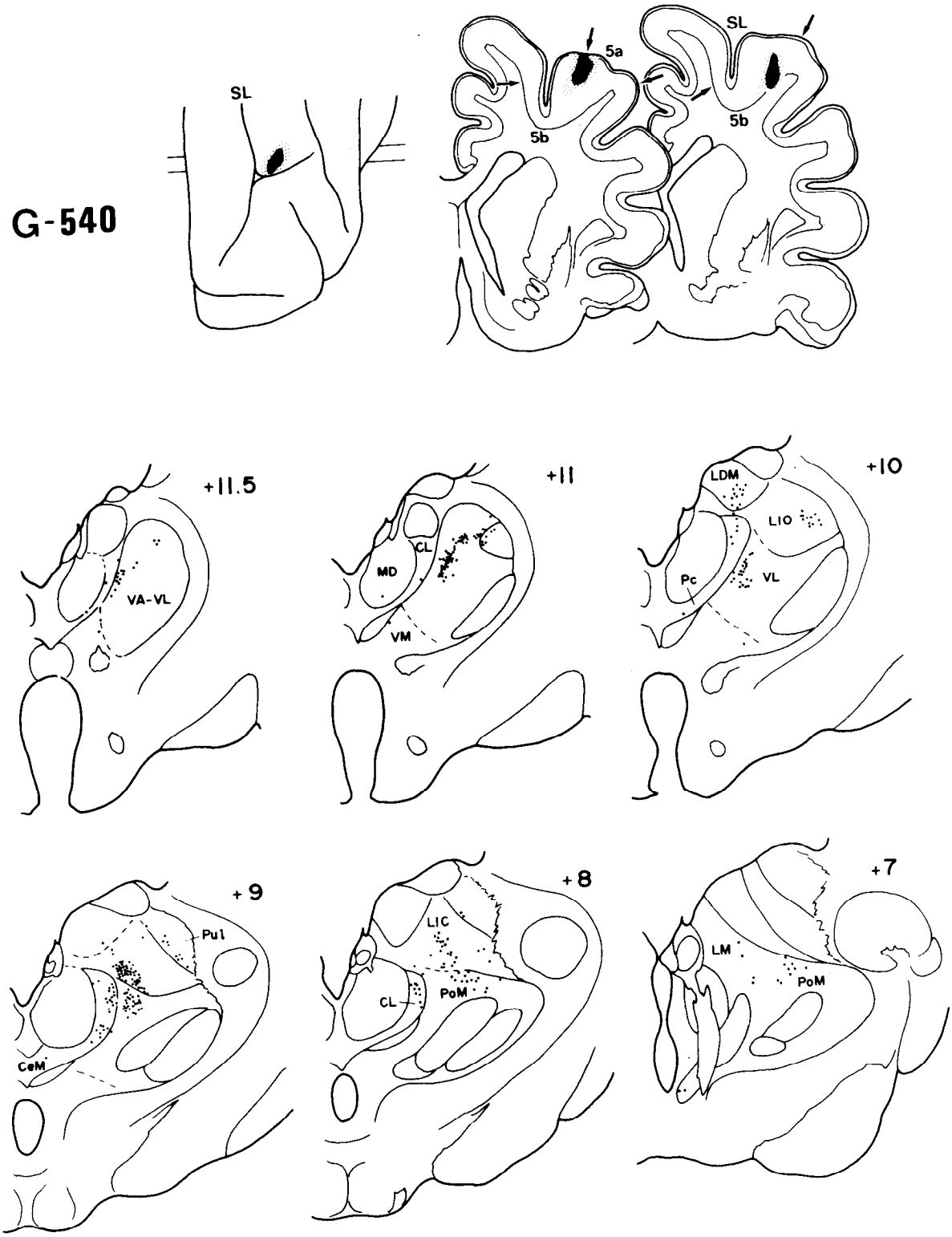

Figure 13. Thalamic labeling in an animal which received a single HRP injection in GSs, mainly affecting the lateral part of area 5b. Conventions are as in Figure 6.

unexpected, since cells activated by somatic stimuli have been recorded in this nucleus (Guilbaud et al., 1977; Blum and Gilman, 1979). Also, PoL projects to SII (Spreafico et al., 1981; Bentivoglio et al., 1983; Roda and Reinoso-Suárez, 1983), SIV (Roda and Reinoso-Suárez, 1983), and area 4 (Morán et al., 1982). In areas 4, SII, SIV, and 5a there is a recognizable somatotopy, and it is noteworthy that PoL seems to project mainly to the cortical sectors representing the caudal parts of the body; that is, the upper bank of SC (Nicoullon and Rispal-Padel, 1976; Morán et al., 1984), the caudal part of SII (Spreafico et al., 1981; Burton et al., 1982), the caudal part of SIV (Clemo and Stein, 1982; Roda and Reinoso-Suárez, 1983), and the medial part of area 5 (present findings).

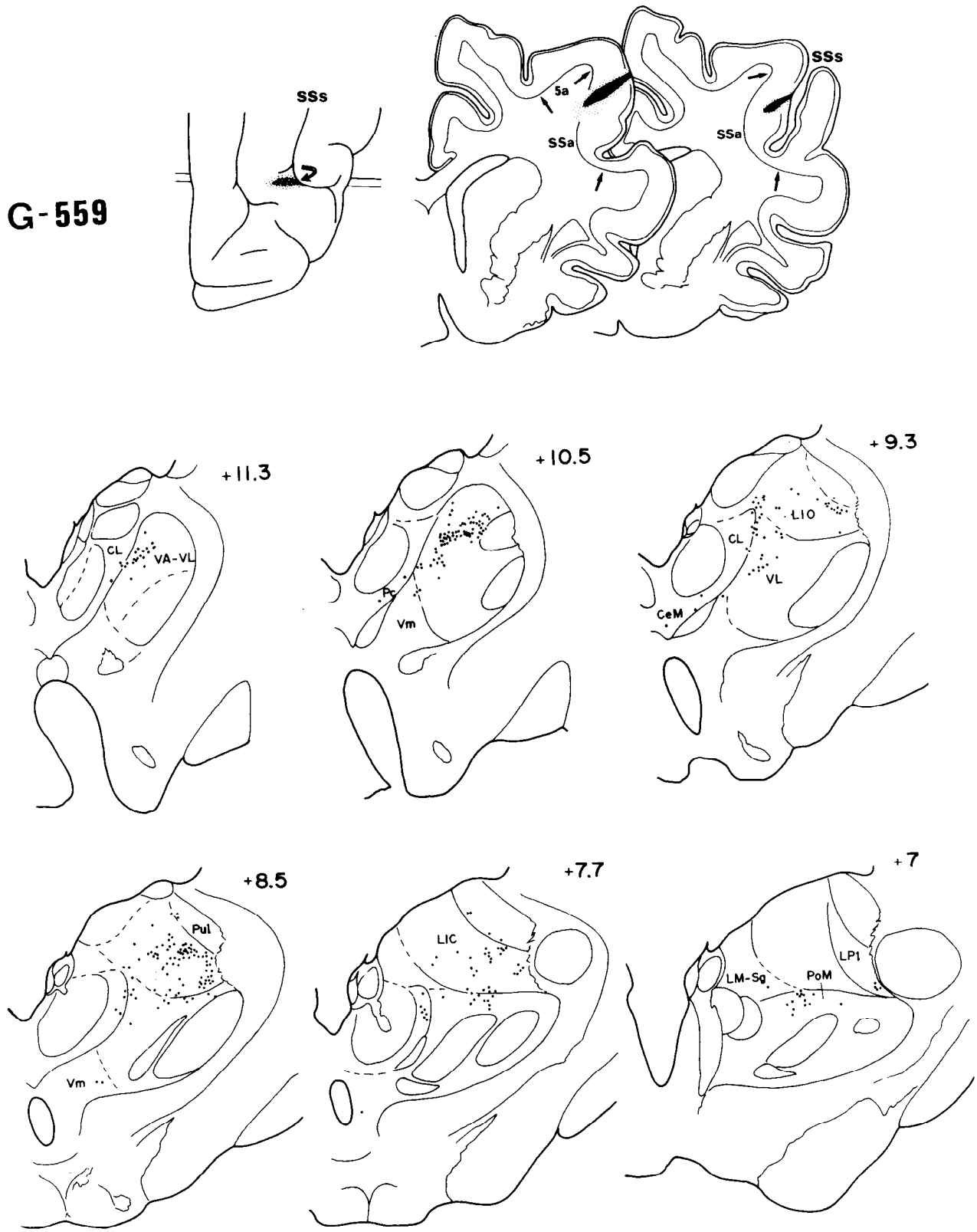

Figure 14. Injection locus and thalamic labeled neurons in an animal which was injected singly in the medial bank of the anterior suprasylvian sulcus, affecting area SSa of Sanides and Hoffman (1969). Conventions are as in Figure 6.

The response properties of Po neurons upon somatic stimulation show large receptive fields, and early descriptions failed to recognize a somatotopical organization of afferents in Po from the spinal cord or the dorsal column nuclei (Boivie, 1971a, b; Jones and Burton, 1974). However, fibers from different parts of SI distribute to different sectors of Po (Rinvik, 1968b). More recently, a loose topographic organization has been reported for the projections to PoM from the dorsal column nuclei, the lateral and rostral parts of PoM mainly

Figure 15. Injection locus and thalamic labeled neurons in an animal which received a single injection in the medial bank of the suprasylvian sulcus, slightly more caudal to that shown in Figure 14, which affects SSa and AmLS. Conventions are as in Figure 6.

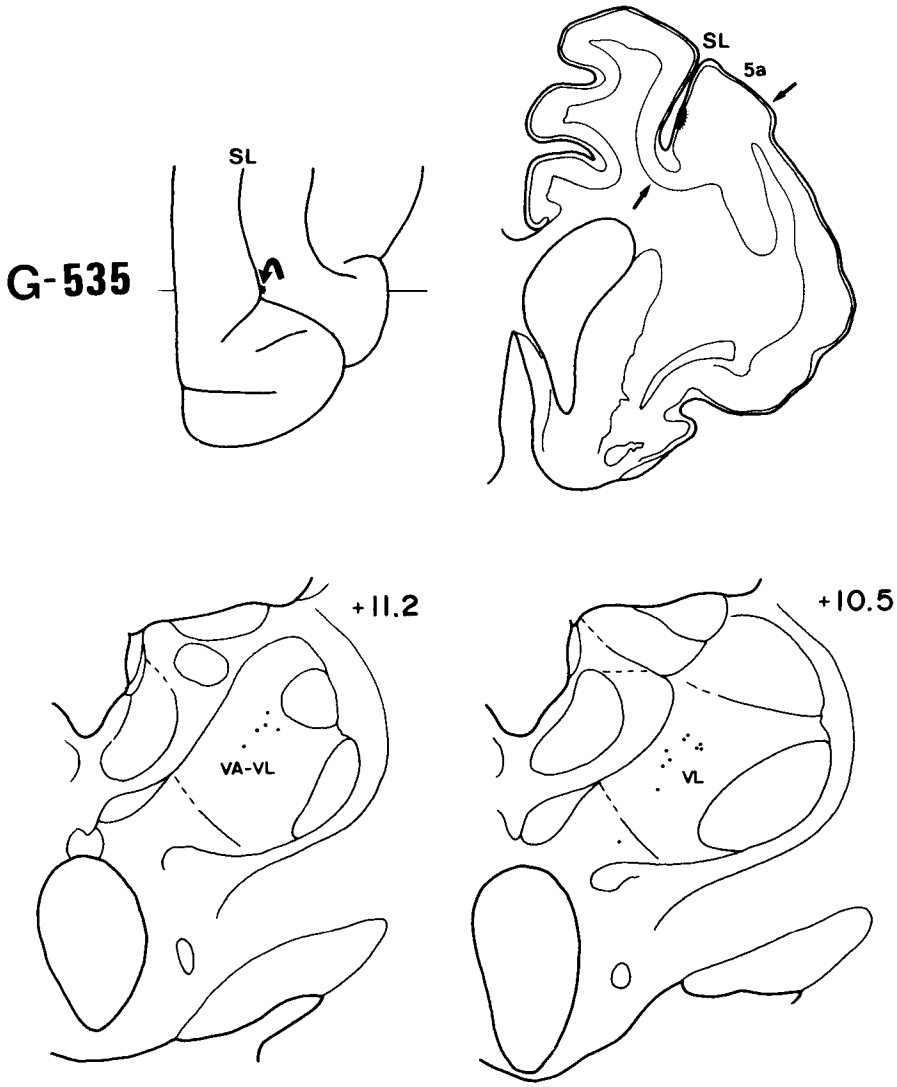

Figure 16. Thalamic labeled neurons produced by a small injection in the lateral bank of the lateral sulcus, which affects layers I and II of area 5a. Conventions are as in Figure 6.

receiving projections from the gracile nucleus, and the caudal and medial parts receiving mixed connections from the gracile and cuneate nuclei (Berkley, 1980). Since spinothalamic and lemniscal projections end without discontinuities in PoL and PoM, it is reasonable to speculate that the somatic input to PoL arises from the hindlimb, which would agree well with the PoL projection onto the medial part of area 5a, as shown here.

The significance of Po projections to area 5 remains elusive. Among the different sensory modalities which converge on Po neurons, nociceptive input has perhaps the greatest effect on ongoing neuronal activity (Guilbaud et al., 1977). Furthermore, SII, an important cortical target for Po, was implicated in the experience of pain (Berkley and Palmer, 1974). Since there are no indications of area 5 neuron responses to noxious stimuli, it is possible that PoM and PoL—or their thalamic counterpart in the monkey—are responsible at least in part for the cutaneous responses which are recorded in a sizable proportion of neurons in area 5a (Sakata et al., 1973; Mountcastle et al., 1975; Tanji et al., 1978).

Projections from VL and VA. It is no longer possible to regard VL as a unique entity, in carnivores at least, although no consensus has yet been reached as to what subdivisions in this complex can be made on sound morphological, connectional, or functional grounds. A conservative criterium was followed in the figures presented in this work, labeling as VL the territory lying between VP, LI, Vm, and the intralaminar complex, that continues caudally into Po and rostrally merges with VA (Rioch, 1929; Jasper and Ajmone-Marsan, 1954; Reinoso-Suárez, 1961). At least three major subdivisions can be distinguished in this territory. First, the so-called "spinal portion" of VL (Jones and Burton, 1974), also called VB/VL border zone by Berkley (1980; see also Updyke, 1983), caps dorsally, medially, and rostrally the rostral part of VPl and is caudally continuous with PoM, PoL, and VPi. This region is characterized by a mixed population of small and medium-sized neurons with some outlying larger VP cells (Jones and Burton, 1974), and it is an important target for spinothalamic fibers (Boivie, 1971b; Jones and Burton, 1974; Berkley, 1980).

Second, VL merges with VA, rostrally, but the boundary between both varies considerably from animal to animal. This boundary is more easily identified by differences in cell packing density and distribution of fiber bundles than by cell morphology. In the cat, VA cells are somewhat larger than those in VL, but the change in cell size, particularly in coronal sections, is not abrupt (Rinvik, 1968a; Berman and Jones, 1982). In the cat and the dog, a caudodorsal extension of cells which caps the rostral pole of LIO has been commonly included in VA (Rioch, 1929; Jasper and Ajmone-Marsan, 1954; Reinoso-Suárez, 1961; Berman and Jones, 1982; Updyke, 1983). However, on the basis of different corticothalamic afferents, Rinvik (1968a) ascribed this sector to VL in the cat. In the dog, Sakai et al. (1983) observed that this sector differed substantially from more rostral sectors of VA in cell packing density and in acetylcholinesterase (AChE) staining, which was moderately positive, as in VL, whereas VA was AChE negative. These findings, which are

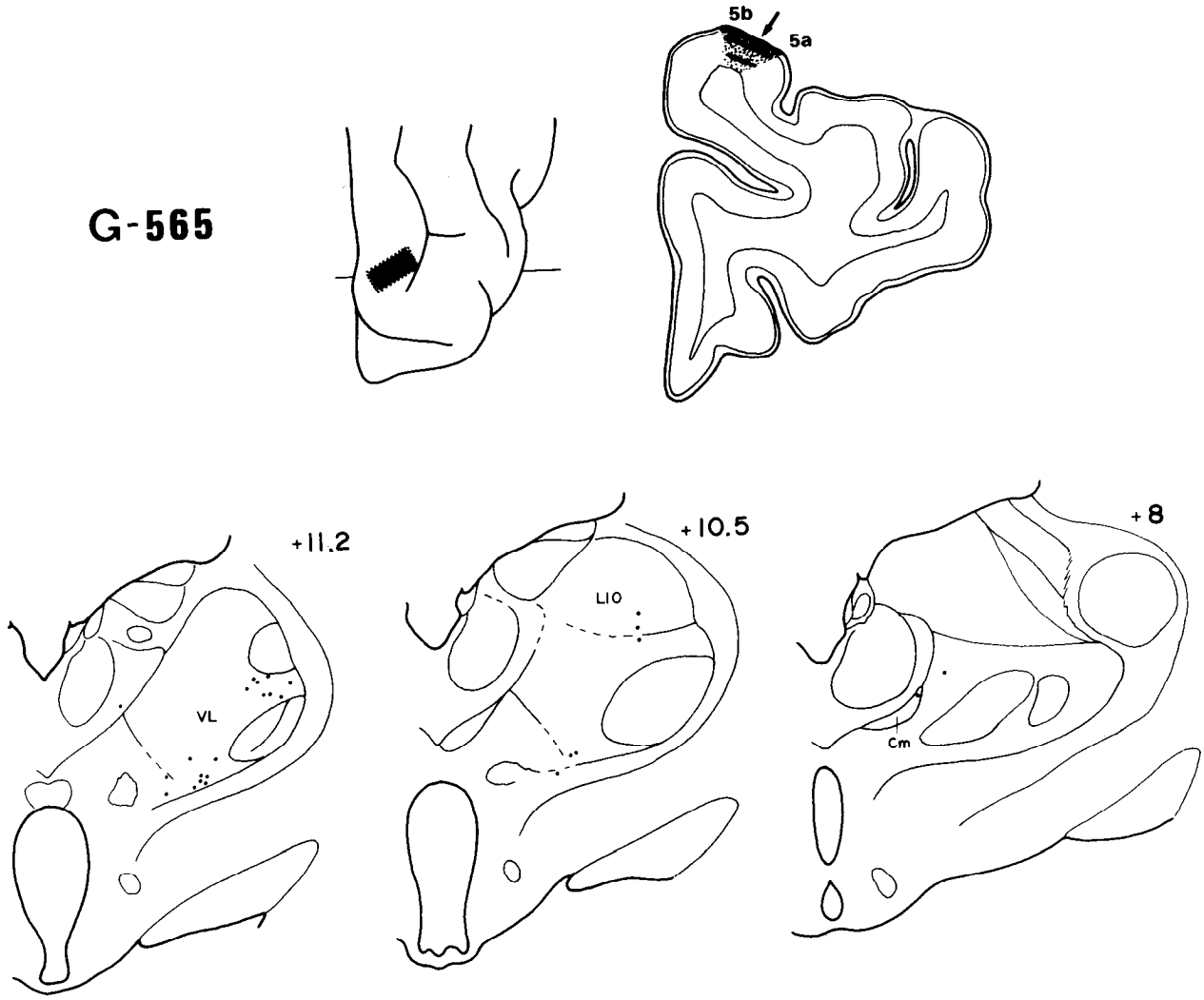

Figure 17. Superficial application of HRP in the rostral part of GLa, affecting layer I of areas 5a and 5b. Only labeled neurons observed in counterstained sections were plotted in the drawings of the thalamus. A moderate number of very weakly labeled neurons was found also in VA-VL in non-counterstained sections. These were not represented in this diagram. Other conventions are as in Figure 6.

consistent with data from the cat (Graybiel and Berson, 1980; C. Avendaño and E. Rausell, unpublished observations), led Sakai et al. (1983) to consider this sector as a "dorsal division" of VL. Whenever this sector is present in our figures, the whole area of the ventral nuclei has been labeled "VA-VL."

Third, the rest of VL ("principal division," in Sakai et al., 1983), while forming the bulk of the nucleus, is by no means homogeneous in structure. Medium-sized cells predominate, but small cells are also found ubiquitously. A distinct border with the VL "spinal zone" is lacking, whereas the boundary with LI is variable in position and definition, especially at the VL dorsomedial "corner" where CL, VL, and LI meet. This sector, which was included by Updyke (1983) within LP (or LI), is clearly outlined in some animals but very imprecise in others.

Our findings show that, together with Po, VL is the main source of thalamic projections to area 5a and also is an important one to area 5b and SSa. There are notable topographic differences in these projections, however. The medial part of area 5a (in GLa) receives a prominent projection from the "principal" part of VL, a moderate projection from the "spinal" part, and only a meager projection from the "dorsal" part. The input from VL to GLa decreases sharply when HRP is located in area 5b, just caudal to area 5a, and the labeled neurons then occupy more dorsal levels of VL (Fig. 20). Lateral area 5a injections (in GSs) likewise label many neurons in VL, in similar proportions in its three parts, but in a somewhat more medial and dorsal location than after medial area 5a injections. Lateral 5b—and SSa—injections, in turn, reveal a projection from the "principal" part of VL similar to that of medial area 5b, but they also give rise to a much larger population of labeled cells in the "dorsal" part of VL.

VL projections to area 5 were first described by Smaha et al. (1969), although this finding was later interpreted as artifactually produced by the passage of the lesioning electrode through the cortex (Strick, 1973). More recently, projections from VL or from the caudodorsal part of VA to area 5 in the GSs have been repeatedly confirmed (Mizuno et al., 1975; Robertson, 1975, 1977, 1978; Bentivoglio et al., 1978; Hendry et al., 1979; Niimi et al., 1979), although there are several discrepancies in these reports. For example, in contrast with our results, Robertson (1977) described more abundant projections from VL to area 5b than to area 5a, and only a light projection from VA to the lateral part of area 5b. Also, whereas Tanji et al. (1978) reported a scanty projection from VA to area 5a in GSs, which is consistent with our results, Hendry et al. (1979) described a fairly large projection from the caudodorsal part of VA to the same region (see their Fig. 6). Moreover, on the basis of data obtained from the same case, these authors stated that labeled neurons in the "principal" part of VL distributed outside the region of VL labeled by injections in area 4, a finding which is in conflict with other reports (Morán et al., 1982, 1985). It is likely that these

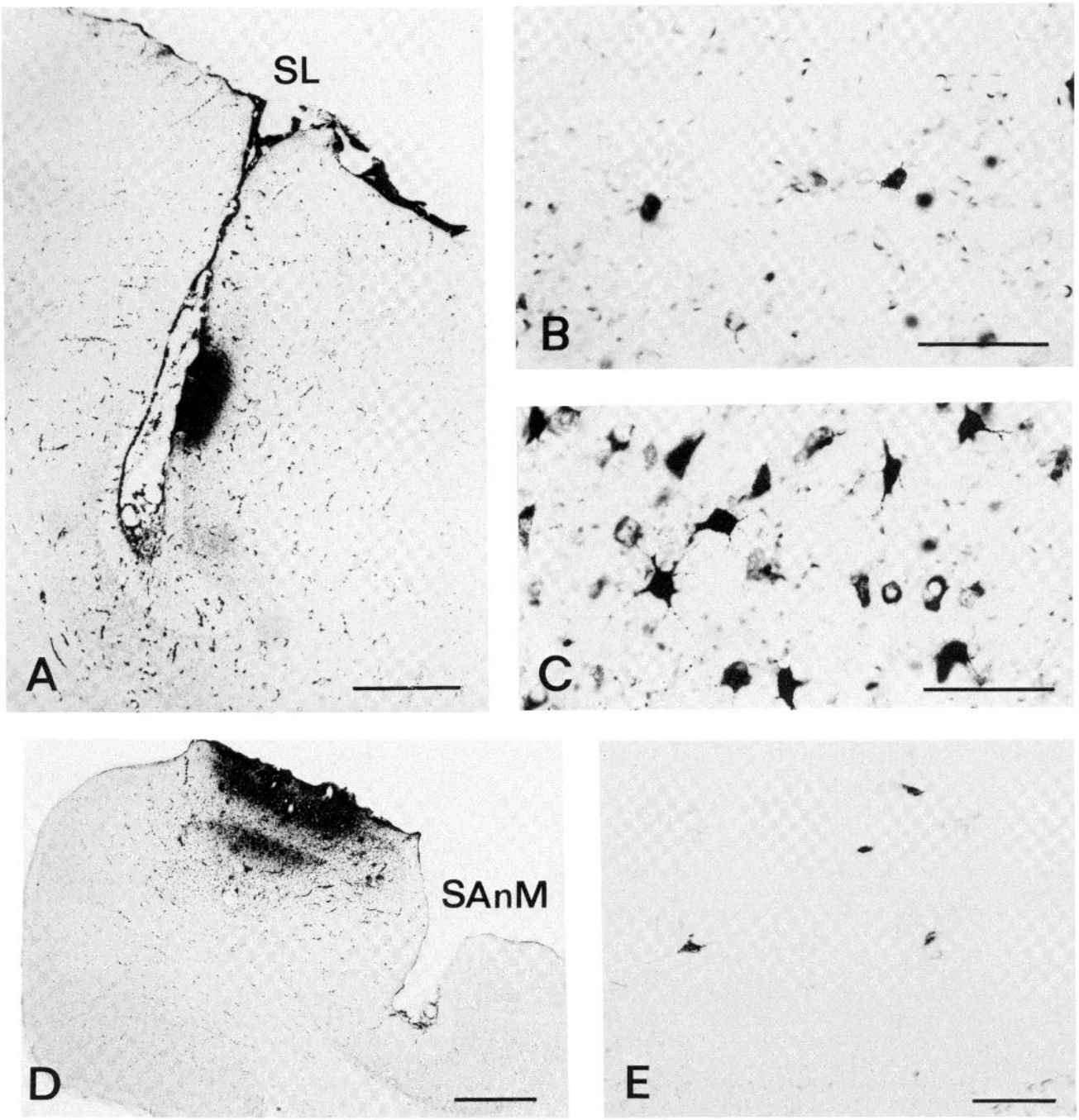

Figure 18. A and *B*, Photographs of the injection site and of two labeled neurons in VL in case G-535 (see Fig. 16). *C*, Labeled neurons in the same region of VL as in *B*, in case G-541, which received a deep HRP injection in the lateral bank of the lateral sulcus. Note the larger size of many of these neurons compared to those in *B*. *D*, HRP deposit in layer I on the top of GLa in case G-565 (see Fig. 17); the dark bands in layers II-III and V correspond to neuronal bodies probably labeled through dendrosomatic transport from layer I. *E*, Small, weakly labeled neurons in the ventrolateral part of VL in case G-565. *Bars: A* and *D*, 1 mm; *B*, *C*, and *E*, 100 μm.

discrepancies can be accounted for by the fact that Hendry et al. (1979) did not explore the medial sectors of area 5a, and by a probable caudal spread of HRP into area 5b, since in none of our "pure" injections in area 5a or 5b is there a combination of labeling in VA, VL, CL, and Po such as that reported by these authors after a lateral area 5a injection. The topographic coincidence of labeled neurons in VL after area 4 and area 5a injections is remarkable, as well as the considerable overlap between the VL regions labeled by area 5b and area 6 injections. If a difference must be pointed out, it regards the slightly more ventral location of labeled neurons and their larger occupation of the VL "spinal" zone after area 4 injections, and the ventromedial displacement of the labeled cells, approaching Vm, after area 6 injections (M. A. Morán, C. Avendaño, and F. Reinoso-Suarez, manuscript in preparation).

Both the "dorsal" and the "principal" zones of VL receive an important contingent of monosynaptic afferents from the deep cerebellar nuclei (see references in Hendry et al., 1979; see also Kultas-Ilinsky and Ilinsky, 1983; Sakai et al., 1983). The former mediate recruiting responses in the posterior parietal cortex, probably including area 5b (Sasaki et al., 1972; Oka et al., 1982). Many

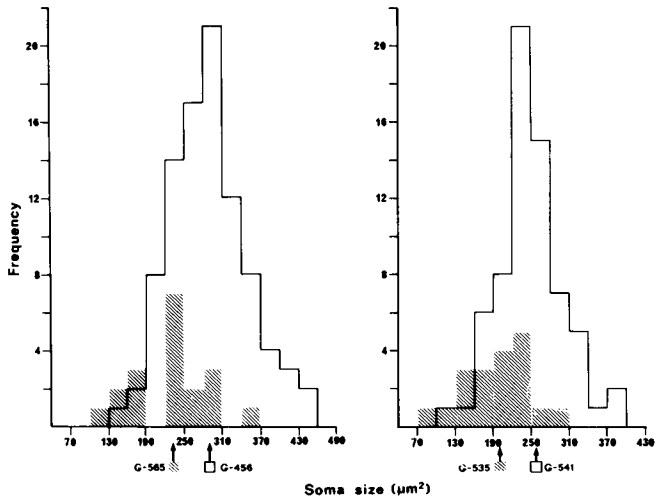

Figure 19. Histograms showing the soma size of labeled thalamic neurons after superficial cortical deposits of HRP (*shaded bars*). Only labeled cells in VL (case G-532, *right histogram*) or in VL + LIO (case G-565, *left histogram*) were measured. Similar measurements were made on neurons labeled after deep HRP injections in corresponding topographical and areal locations. All labeled neurons appearing in these nuclei in every fifth section were plotted in those cases with superficial deposits of HRP, whereas all labeled neurons within a 300,000-μm^2 field at topographically matching loci, in the same number of sections, were measured in cases with deep injections. *Arrows* point to mean values for each case. The difference for each pair of cases was significant at $p < 0.005$ (Student's t test). Values were not corrected for shrinkage.

neurons in GSs which receive projections from the "dorsal" VL project, in turn, to the pontine nuclei (Mizuno et al., 1973; Steriade et al., 1978), thus establishing an oligosynaptic circuit between the cerebellum and, most probably, area 5b. The involvement of this cortical region in the motor system is strengthened by the fact that the same caudodorsal sector of VA also projects to the premotor cortex (Strick, 1973; Vedovato, 1978; Avendaño and Llamas, 1984), and because areas 6 and 5b entertain topographically organized corticocortical connections (see references in Jones et al., 1978; Isorna, 1983).

The cerebellar projections to the "principal" part of VL arise largely from the nucleus interpositus and distribute in VL with a gross somatotopic organization (Angaut, 1973; Nakano et al., 1980). The nucleus interpositus receives a somototopically organized projection from the paramedian lobule of the cerebellum (Courville et al., 1973) which, in turn, receives a wealth of proprioceptive impulses somatotopically organized (see references in Brodal, 1981). It is likely that input from deep receptors may reach area 5 through this cerebellothalamocortical path, and this could lend an anatomical substrate to the large proportion of joint responses recorded from the rostral part of area 5 (see references in Mountcastle et al., 1975, and Dykes, 1983). Area 2 also exhibits many units which are activated by joint stimulation, but the most likely thalamic relay in this case is the dorsal part of VP and, perhaps, the adjoining VL "spinal" zone (Albe-Fessard, 1967; Yin and Williams, 1976; Ramírez-Camacho et al., 1984). Moreover, the qualitative features of joint responses in areas 2 and 5a are not the same (Mountcastle et al., 1975), which would favor other structures as candidates for the relay of deep somatic input to area 5a, such as Po, "principal" VL, or even corticocortical connections from SI and area 4.

Projections from LI. In the present work LI and its subdivisions, LIO and LIC, have been named after the terminology of Graybiel and Berson (1980). These authors borrowed these terms from Rioch (1929), although their subdivisions do not exactly match those of Rioch (1929) and are based on variations in AChE stain and connectional patterns rather than on cyto- and myeloarchitecture.

Our results show that projections to area 5 from LI are organized in a complicated pattern (see Fig. 21). Area 5a receives projections only from LIO, whereas area 5b is connected from LIO, LIC, and, to a much lesser extent, the adjoining Pul. Projections to the medial part of areas 5a and 5b arise from a relatively continuous population of neurons in LIO, which are more ventrally placed and fewer in number in area 5a than in area 5b cases. In the latter, they are more dorsally located and are much more abundant. In contrast, the lateral portions of areas 5a and 5b (and, to some extent, SSa) receive projections from two more-or-less separate cell populations, one in the rostral sectors of LIO and the other located caudoventrally in LIO and—in the cases of area 5b injections—in LIC. Lateral injections in areas 5a and 5b differ, however, in the more dorsal and medial location of the labeled cells in area 5b cases: at rostral levels, labeled cells in these cases are continuous medially with cells labeled in VA-VL, whereas in area 5a cases they merge ventrally with labeled cells in VL. Labeled cells in Pul were observed only after lateral area 5b and SSa injections and, in all cases, concentrated in the medial border of the rostral part of this nucleus.

Graybiel (1972) provided the first evidence for the existence of a topographical organization in the projections from LP, LI, and Pul to areas 5 and 7. In all cases in which there were degenerating fibers in area 5 (no distinction between areas 5a and 5b was made), the lesions had affected the ventral parts of LIO and LIC. These projections to area 5 have been better delineated in recent years with the HRP technique in the cat (Mizuno et al., 1975; Robertson, 1977, 1978; Tanji et al., 1978; Hendry et al., 1979; Niimi et al., 1979; Oka et al., 1982) and other species (Pearson et al., 1978; Jones et al., 1979; Donoghue and Ebner, 1981; Miyata and Sasaki, 1983). However, none of these studies gives a complete view of these projections, and several inconsistencies can be found. For example, Tanji et al. (1978) described only "occasional small clusters of labeled cells" in LP after a small injection in the lateral part of area 5a, whereas an apparently similar case of Hendry et al. (1979) produced many labeled neurons in the dorsal part of LP (probably corresponding to LIO). However, as was noted above, it seems that in this case the HRP injection also involved area 5b. Niimi et al.'s (1979) results are difficult to evaluate, but it seems that they attribute a larger number of projections from LP to area 5a than to area 5b in GLa, which would contrast markedly with our results. Closer agreement exists between our findings and those briefly reported by Robertson (1978).

The functional implications of the LI-area 5 projections are far from clear. LI receives afferents from a number of subcortical structures, most notably from the pretectum, the deep layers of the superior colliculus, the pedunculopontine tegmental nucleus, the oculomotor complex, the parabrachial nuclei, some components of the brainstem reticular formation, and the lateral cerebellar nucleus (see Rodrigo-Angulo and Reinoso-Suárez, 1983, 1984), but the largest contingent of afferents derives from the cerebral cortex and follows a fairly strict reciprocal pattern (see references in Robertson and Cunningham, 1981; see also Fig. 21).

On the basis of the afferent connections from structures related to the extrageniculate visual system, Updyke (1983) proposed the existence of a continuous visual field representation in his caudal and rostral layers of the lateral division of LP (equivalent to the present LPl, and large parts of LIC and LIO). A careful analysis of published material shows that neither subcortical nor cortical afferents related to the geniculate or extrageniculate visual system terminate in significant quantity in the region of LIO and LIC connected with area 5. Projections from the retina, the superficial layers of the superior colliculus, and the pretectum end in LPl, the medial part of LP, or Pul (see Graybiel and Berson, 1980; Updyke, 1983). Corticothalamic afferents from areas 17, 18, 19, 20, and 21, and most of the lateral suprasylvian areas distribute only in caudal, dorsal, and/or lateral sectors, sparing to a large extent the area 5-related region of LIC (Updyke, 1977, 1981; Graybiel and Berson, 1980; Berson and Graybiel, 1983; Raczkowski and Rosenquist, 1983). AmLS is an exception, since it sends a heavy projection to a sector

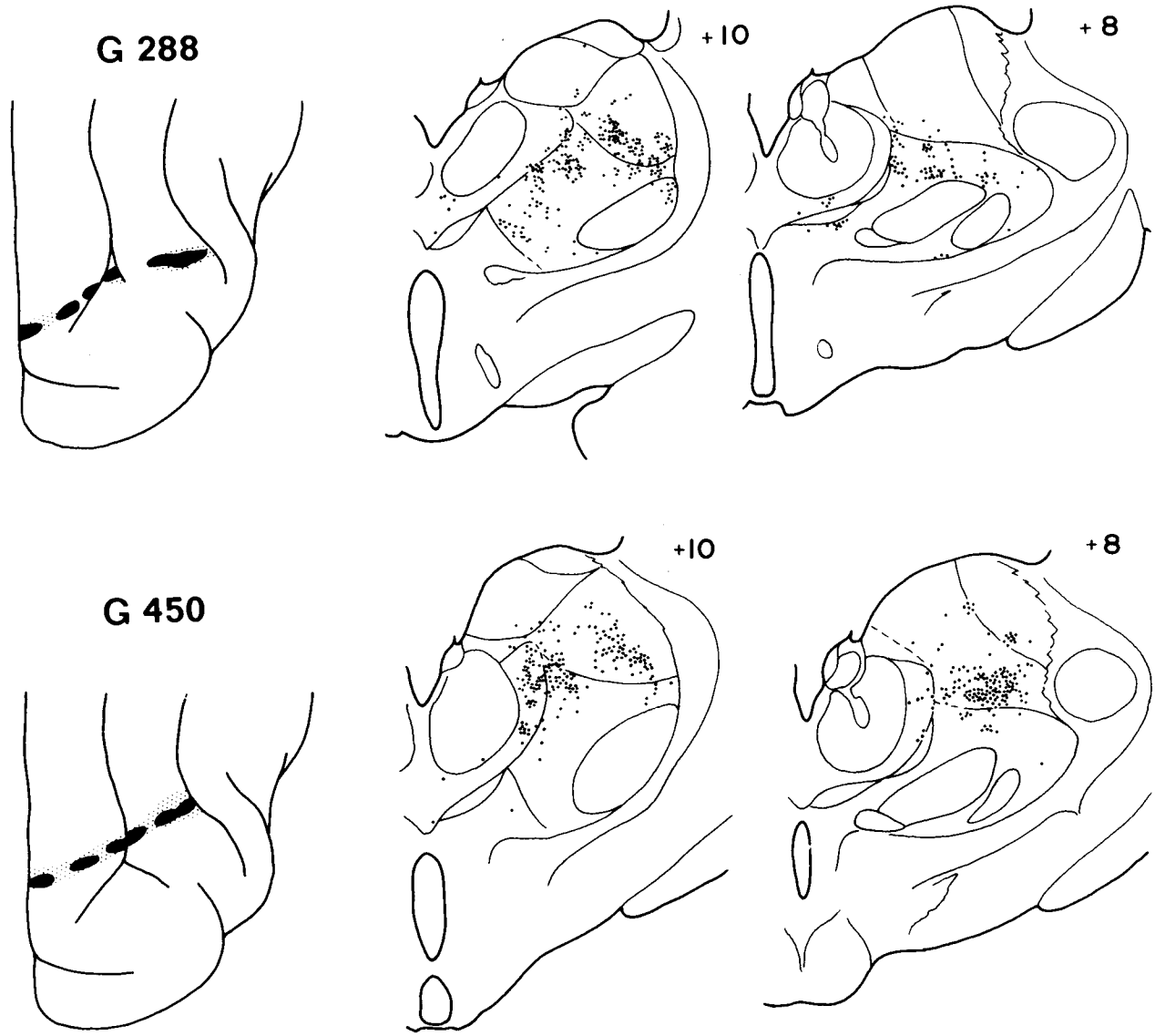

Figure 20. Semischematic diagram showing thalamic labeled neurons at two corresponding stereotaxic levels in two animals, injected in the full mediolateral extent of area 5a (G 288)) and 5b (G 450). Note the overall dorsal shift of the labeled neurons in the latter in comparison with the former.

of LIC (Updyke, 1981; Berson and Graybiel, 1983) which widely overlaps the region of this nucleus projecting to areas 5b and SSa. Visual units have also been found in rostral parts of LIC, some exhibiting somatovisual or even somatoauditory-visual convergence (Avanzini et al., 1980), but their long response latencies make it unlikely that these units represent relays in a "parallel" transmission to the cortex of extrageniculate visual input. Field- and single-unit analyses performed on a cortical region probably including area 5b have also shown polysensory responses and convergence in the cat (Bental and Bihari, 1963; Thompson et al., 1963; Dubner and Rutledge, 1964). However, area 7 involvement in these studies cannot be precluded, because of the lack of precise topographic and architectonic correlates. Data from monkeys indicate that visually responsive units are virtually lacking in area 5a, are scarce in area 5b, and increase in number steadily from the rostral limit of area 7 (Mountcastle et al., 1975).

It seems then that a spatially organized visual input to the region of LI which projects to area 5 is probably minimal. Although LP, the caudal and dorsal sectors of LIC, and, partly at least, Pul are directly implicated in conveying and integrating different aspects of visual information, LIO and the rostroventral sectors of LIC are more likely engaged in polysensory-motor integration, also including visuomotor functions. In this regard, the stimulation of LIC and LIO evokes eye movements independently of the integrity of the superior colliculus (Crommenlinck et al., 1977; Wilson and Goldberg, 1980), and the ablation of a portion of the GSs including area 5b and rostral area 7 severely impairs certain behavioral tasks involving visuomotor guidance which are not affected by more caudal area 7 lesions (Fabre and Buser, 1981). Furthermore, the close relationship of most of the subcortical afferents of LI with the motor system (see above) and the finding of a substantial projection to certain parts of the motor cortex from LIO and rostral LIC (Morán et al. 1982) also speak in favor of an important role of this thalamic region in sensory-motor integration.

Projections from the intralaminar complex. The delineation of the intralaminar nuclei is relatively straightforward and little discrepancy has existed about it in the literature (Jasper and Ajmone-Marsan, 1954; Reinoso-Suárez, 1961; Rinvik, 1968a; Berman and Jones, 1982).

Present findings point to CL as the main source of intralaminar projections to area 5. These projections are more abundant to area 5b and to GSs than to area 5a and GLa. The whole projection field of CL includes the striatum, some parts of the motor and premotor cortices, the posterior parietal cortex, and some visual cortical areas

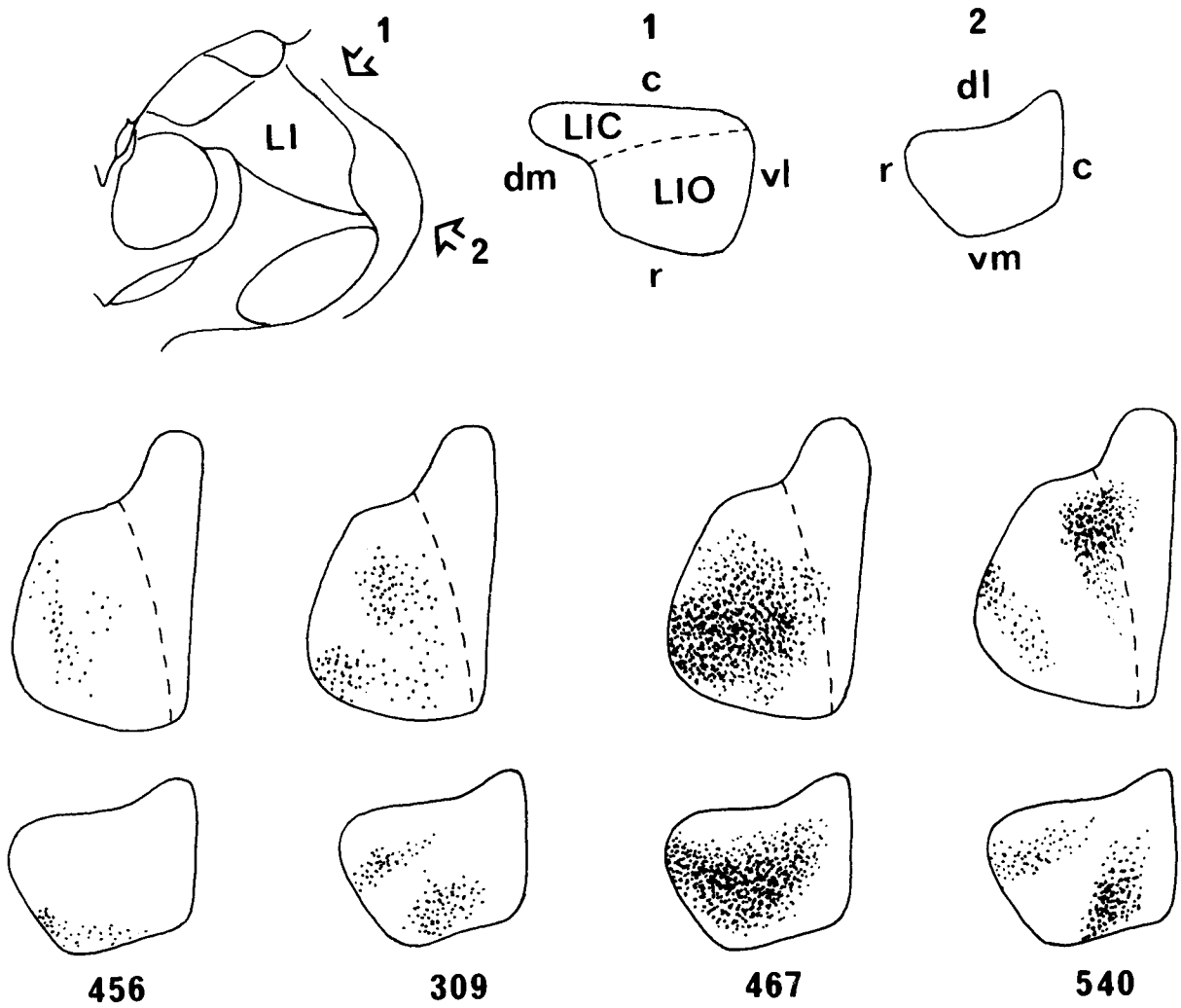

Figure 21. Schematic diagram showing the approximate distribution of labeled neurons in LIO and LIC in four representative cases with HRP injections in the medial (G 456) and lateral (G 309) parts of area 5a, and in the medial (G 467) and lateral (G 540) parts of area 5b. The *upper row* of drawings shows a coronal section of the thalamus through LI (*left*) and two spatial reconstructions of LI, from dorsolateral (*1; middle*) and ventrolateral (*2; right*) perspectives. *c*, caudal; *dl*, dorsolateral; *dm*, dorsomedial; *r*, rostral; *vl*, ventrolateral; *vm*, ventromedial. The approximate distribution of labeled neurons is shown as clouds of dots in similar spatial reconstructions of LI in the *lower two rows* of drawings.

(Jones and Leavitt, 1974; Itoh and Mizuno, 1977; Kennedy and Baleydier, 1977; Macchi et al., 1977; Tanji et al., 1978; Vedovato, 1978; Hendry et al., 1979; Niimi et al., 1979; Macchi and Bentivoglio, 1982; Morán et al., 1982; Cavada and Reinoso-Suárez, 1983).

Despite the large projection field of the intralaminar nuclei taken as a whole, it is no longer possible to consider them, and particularly CL, as a "diffuse" system. On anatomical grounds, there is a recognizable topographic plan in the CL efferent projection. For example, the striatal projections arise from dorsal and medial sectors of the nucleus (Bentivoglio et al., 1983); projections to area 5 arise mainly from lateral sectors (Hendry et al., 1979; present findings); and a certain regional preference also exists in CL projections to areas 4 and 6 (Vedovato, 1978; Morán et al., 1982), although a strict topographic organization such as that reported by Itoh and Mizuno (1977) is probably too exaggerated. Moreover, only a small proportion of individual cells in CL send widely branching fibers into separate target fields (Van der Kooy, 1979; Bentivoglio et al., 1981, 1983; Jinnai and Matsuda, 1981; Steriade and Glenn, 1982).

A large variety of subcortical inputs converge in CL. The most prominent are from the spinal cord, a number of brainstem reticular structures, superior colliculus, pretectum, substantia nigra, periaqueductal gray, and the deep cerebellar nuclei, some of which, at least, reportedly end in different sectors of the nucleus (see Hendry et al., 1979, and Martínez-Bermejo, 1983, for discussion and references). However, the projections from CL to area 5 do not seem to arise from any particular sector of CL related to one or another input. For example, in agreement with a previous report (Hendry et al., 1979), the projection from CL to area 5 originates from both the caudally placed large neurons, on which the spinothalamic cells are said to terminate (Mehler, 1966; Jones and Burton, 1974), and the smaller cells, more widely distributed within the nucleus.

Although other sensory inputs to CL should not be disregarded (Blum and Gilman, 1979), the spectrum of the afferent and efferent connections of this nucleus is suggestive of its playing an important role in organizing some aspects of visuo- and somatomotor behavior. Available data that show a complex integrative function of CL in visuomotor behavior favor this view (Schlag and Schlag-Rey, 1971; Hunsperger and Roman, 1976; Schlag et al., 1980).

Superficial thalamocortical projections. Recently, it has been shown that most, if not all, thalamic nuclei have a heterogeneous population of thalamocortical neurons in regard to their laminar projection pattern in the cortex (see Caviness and Frost, 1980 and Avendaño and Llamas, 1984). Moreover, it was conclusively demonstrated that there were morphological differences in the thalamic neurons projecting to different layers. Using superficial applications of HRP onto the striate cortex of the tree shrew and a prosimian,

Carey et al. (1979) found labeled cells inthe lateral geniculate nucleus of smaller size than after deep injections. More recently, Penny et al. (1982) found that the cells projecting to layers I and II of the cat's somatosensory and motor cortices were significantly smaller than those labeled after injections in, or deep to, layers III and IV (the mean areas for the whole sample were 160 versus 338 μm^2). Interestingly, these authors also found that the mean area of cells projecting to layers I and II changed depending on the cortical area of injection. In our cases, the distribution and size of VL-labeled neurons are similar to those obtained by Penny et al. (1982) after injecting superficial layers of area 4.

Taken together with previous reports (Oka et al., 1982; Rieck and Carey, 1982; see also Avendaño and Llamas, 1984), our findings indicate that the neurons projecting to superficial layers of the cortex vary both in distribution and size, depending on the cortical region considered. Moreover, there is evidence for the existence of different neuronal populations in the thalamus which are differentiable by the distribution of their terminals in superficial, middle, or deep layers of the cortex, and which may or may not coincide with cytoarchitectonically defined nuclei.

A comment on the topographic organization of the thalamic neurons projecting to area 5. As described above, the distribution of labeled neurons in Po, VL, and LI following HRP injections in area 5 exhibits regional preferences depending on the location of the injections. Although these preferences do not reach the discreteness found in the projections from sensory relay nuclei to primary sensory areas, they allow the identification of two basic gradients in the spatial organization of these projections, which are particularly evident in VL and LI. One is a ventral-to-dorsal gradient corresponding to a rostral-to-caudal positioning of the HRP in the cortex. The other is a less noticeable medial-to-lateral gradient corresponding to a lateral-to-medial location of the injection, both in areas 5a and 5b. This gradient is also observed in Po. These gradients are not pure, since a simultaneous shift in the rostrocaudal dimension is also noticeable, especially in LI. The existence of a crude topological correspondence between the thalamus and area 5 which, as far as is known, respects somatotopy, is in keeping with a number of previous reports (Robertson, 1977; Pearson et al., 1978; Hendry et al., 1979).

If the overall topographic organization of the thalamic projections to area 5 is considered, two additional features stand out. First, the labeled neurons produced by single or multiple injections in the cortex often form a spatially continuous population which may cross nuclear borders. Second, when adjacent portions of the cortex are injected, even if entering a different cytoarchitectonic area, there is a gradual shift of the labeled cell population in the thalamus (Fig. 20) which is not random but takes place according to the above-mentioned gradients (see also Avandaño and Llamas, 1984). This global organization recalls Kieveit and Kuypers' (1977) thalamic "bands" of labeled neurons produced by frontal lobe injections of HRP in the monkey, although, at least regarding present findings in the cat, the thalamic populations of labeled cells are rather loose, with considerable overlapping, and at some levels may branch, giving rise to diverging groups of cells.

References

Albe-Fessard, D. (1967) Organization of somatic central projections. Contrib. Sens. Physiol. *2:* 101–167.

Amassian, V. E. (1954) Studies on organization of somesthetic association areas, including a single unit analysis. J. Neurophysiol. *17:* 39–56.

Angaut, P. (1973) Bases anatomo-fonctionelles des interrelations cérébello-cérébrales. J. Physiol. (Paris) *67:* 53–116.

Avanzini, G., G. Broggi, S. Franceschetti, and R. Spreafico (1980) Multisensory convergence and interaction in the pulvinar-lateralis posterior complex of the cat's thalamus. Neurosci. Lett. *19:* 27–32.

Avendaño, C., and A. Llamas (1984) Thalamic and non-thalamic direct subcortical projections to association areas of the cat's cerebral cortex. In *Cortical Integration,* F. Reinoso-Suárez, and C. Ajmone-Marsan, eds., pp. 195–221, Raven Press, New York.

Avendaño, C., J. Rodríguez-Sanz, E. Rausell, and G. Vigall (1982) Thalamic projections to the anterior portions of the lateral and middle suprasylvian gyri (areas 5 and 7) in the cat. Neurosci. Lett. Suppl. *10:* 53.

Bental, E., and B. Bihari (1963) Evoked activity of single neurons in sensory association cortex of the cat. J. Neurophysiol. *26:* 207–214.

Bentivoglio, M., G. Macchi, P. Rossini, and E. Tempesta (1978) Le proiezioni talamo-corticali del nucleo ventrale anteriore: Studio mediante il trasporto assonale retrogrado di HRP nel gatto. Arch. Ital. Anat. Embriol. *83:* 111–127.

Bentivoglio, M., G. Macchi, and A. Albanese (1981) The cortical projections of the thalamic intralaminar nuclei, as studied in cat and rat with the multiple fluorescent retrograde tracing technique. Neurosci. Lett. *26:* 5–10

Bentivoglio, M., M. Molinari, D. Minciacchi, and G. Macchi (1983) Organization of the cortical projections of the posterior complex and intralaminar nuclei of the thalamus as studied by means of retrograde tracers. In *Somatosensory Integration in the Thalamus,* G. Macchi, A. Rustioni, and R. Spreafico, eds., pp. 337–363, Elsevier-North Holland Publishing Co., Amsterdam.

Berkley, K. J. (1980) Spatial relationships between the terminations of somatic sensory and motor pathways in the rostrl brainstem of cats and monkeys. I. Ascending somatic sensory inputs to lateral diencephalon. J. Comp. Neurol. *193:* 283–317.

Berkley, K. J., and R. Parmer (1974) Somatosensory cortical involvement in responses to noxious stimulation in the cat. Exp. Brain Res. *20:* 363–374.

Berman, A. L., and E. G. Jones (1982) *The Thalamus and Basal Telencephalon of the Cat.A Cytoarchitectonic Atlas with Stereotaxic Coordinates,* The University of Wisconsin Press, Madison, WI.

Berson, D. M., and A. M. Graybiel (1983) Subsystems within the visual association cortex as delineated by their thalamic and transcortical affiliations. Prog. Brain Res. *58:* 229–238.

Blum, P. S., and S. Gilman (1979) Vestibular, somatosensory and auditory input to the thalamus of the cat. Exp. Neurol., *65:* 343–354.

Boivie, J. (1971a) The termination in the thalamus and the zona incerta of fibres from the dorsal column nuclei (DCN) in the cat. An experimental study with silver impregnation methods. Brain Res. *28:* 459–490.

Boivie, J. (1971b) The termination of the spinothalamic tract in the cat. An experimental study with silver impregnation methods. Exp. Brain Res. *12:* 331–353.

Brodal, A. (1981) *Neurological Anatomy,* Ed. 3, Oxford University Press, London.

Brodmann, K. (1909) *Vergleichende Lokalisationslehre der Gross-hirnrinde in ihren prinzipien Dargestellt auf Grund des Zellenbaues,* J. A. Barth, Leipzig.

Burton, H., and E. G. Jones (1976) The posterior thalamic region and its cortical projection in New World and Old World monkeys. J. Comp. Neurol. *168:* 249–302.

Burton, H., G. Mitchell, and D. Brent (1982) Second somatic sensory area in the cerebral cortex of cats: Somatotopic organization and cytoarchitecture. J. Comp. Neurol. *210:* 109–135.

Campbell, C. B. G., and W. Hodos (1970) The concept of homology and the evolution of the nervous system. Brain Behav. Evol. *3:* 353–367.

Carey, R. G., D. Fitzpatrick, and I. T. Diamond (1979) Layer I of striate cortex of *Tupaia glis* and *Galago senegalensis:* Projections from thalamus and claustrum revealed by retrograde transport of horseradish peroxidase. J. Comp. Neurol. *186:* 393–438.

Cavada, C., and F. Reinoso-Suárez (1983) Afferent connections of area 20 in the cat studied by means of the retrograde axonal transport of horseradish peroxidase. Brain Res. *270:* 319–324.

Caviness, V. S., and D. O. Frost (1980) Tangential organization of thalamic projections to the neocortex in the mouse. J. Comp. Neurol. *194:* 335–367.

Clemo, H. R., and B. E. Stein (1982) Somatosensory cortex: A "new" somatotopic representation. Brain Res. *235:* 162–168.

Courville, J., N. Diakiw, and A. Brodal (1973) Cerebellar corticonuclear projection in the cat: The paramedian lobule. An experimental study with silver methods. Brain Res. *50:* 25–46.

Crommenlinck, M., A. Roucoux, and M. Meulders (1977) Eye movements evoked by stimulation of lateral posterior nucleus and pulvinar in the alert cat. Brain Res. *124:* 361–366.

Darian-Smith, I., J. Isbister, H. Mok, and T. Yokota (1966) Somatic sensory cortical projection areas excited by tactile stimulation of the cat: A triple representation. J. Physiol. (Lond.) *182:* 671–689.

Donoghue, J. P., and F. F. Ebner (1981) The organization of thalamic projections to the parietal cortex of the Virginia opossum. J. Comp. Neurol. *198:* 365–388.

Dubner, R., and L. T. Rutledge (1964) Recording and analysis of converging

input upon neurons in cat association cortex. J. Neurophysiol. *27:* 620–634.

Dykes, R. W. (1983) Parallel processing of somatosensory information: A theory. Brain Res. Rev. *6:* 47–115.

Fabre, M., and P. Buser (1981) Effects of lesioning the anterior suprasylvian cortex on visuomotor guidance performance in the cat. Exp. Brain Res. *41:* 81–88.

Fleming, J. F. R., and E. C. Crosby (1955) The parietal lobe as an additional motor area. J. Comp. Neurol. *103:* 485–512.

Graybiel, A. M. (1972) Some ascending connections of the pulvinar and nucleus lateralis posterior of the thalamus in the cat. Brain Res. *44:* 99–125.

Graybiel, A. M. (1973) The thalamo-cortical projection of the so-called posterior nuclear group: A study with anterograde degeneration methods in the cat. Brain Res. *49:* 229–244.

Graybiel, A. M., and D. M. Berson (1980) Histochemical identification and afferent connections of subdivisions in the lateralis posterior-pulvinar complex and related thalamic nuclei in the cat. Neuroscience *5:* 1175–1238.

Guilbaud, G., D. Caille, J.M. Besson, and G. Benelli (1977) Single unit activities in ventral posterior and posterior group thalamic nuclei during nociceptive and non-nociceptive stimulations in the cat. Arch. Ital. Biol. *115:* 38–56.

Gurewitsch, M., and A. Chatschaturian (1928) Zur Cytoarchitektonik der Großhirnrinde der Feliden. Z. Anat. Entwicklungsgesch. *87:* 100–138.

Hassler, R., and K. Muhs-Clement (1964) Architektonischer Aufbau des sensomotorischen und parietalen Cortex der Katze. J. Hirnforsch. *6:* 377–420.

Heath, C. J., and E. G. Jones (1971) An experimental study of ascending connections from the posterior group of thalamic nuclei in the cat. J. Comp.Neurol. *141:* 397–426.

Hendry, S. H. C., E. G. Jones, and J. Graham (1979) Thalamic relay nuclei for cerebellar and certain related fiber systems in the cat. J. Comp. Neurol. *185:* 679–714.

Hunsperger, R. W., and D. Roman (1976) The integrative role of the intralaminar system of the thalamus in visual orientation and perception in the cat. Exp. Brain Res. *25:* 231–246.

Hyvärinen, J. (1982) *The Parietal Cortex of Monkey and Man,* Springer-Verlag, Berlin.

Isorna, S. (1983) Proyecciones cortico-corticales a las áreas 5 y 7 en el gato. Doctoral thesis, Universidad Autónoma, Madrid.

Itoh, K., and N. Mizuno (1977) Topographical arrangement of thalamocortical neurons in the centrolateral nucleus (CL) of the cat, with special reference to a spino-thalamo-motor cortical path through the CL. Exp. Brain Res. *30:* 471–480.

Jasper, H. H., and C. Ajmone-Marsan (1954) *A Stereotaxic Atlas of the Diencephalon of the Cat,* National Research Council of Canada, Ottawa.

Jinnai, K., and Y. Matsuda (1981) Thalamocaudate projection neurons with a branching axon to the cerebral motor cortex. Neurosci. Lett. *26:* 95–99.

Jones, E. G., and H. Burton (1974) Cytoarchitecture and somatic sensory connectivity of thalamic nuclei other than the ventrobasal complex in the cat. J. Comp. Neurol. *154:* 395–432.

Jones, E. G., and R. Y. Leavitt (1974) Retrograde axonal transport and the demonstration of non-specific projections to the cerebral cortex and striatum from thalamic intralaminar nuclei in the rat, cat and monkey. J. Comp. Neurol. *154:* 349–378.

Jones, E. G., and T. P. S. Powell (1971) An analysis of the posterior group of thalamic nuclei on the basis of its afferent connections. J. Comp. Neurol. *143:* 185–216.

Jones, E. G., and S. P. Wise (1977) Size, laminar and columnar distribution of efferent cells in the sensory-motor cortex of primates. J. Comp. Neurol. *175:* 391–438.

Jones, E. G., J. D. Coulter, and S. P. Wise (1978) Intracortical connectivity of architectonic fields in the somatic sensory, motor and parietal cortex of monkeys. J. Comp. Neurol. *181:* 291–348.

Jones, E. G., S. P. Wise, and J. D. Coulter (1979) Differential thalamic relationships of sensory-motor and parietal cortical fields in monkeys. J. Comp. Neurol. *183:* 833–882.

Kawamura, K. (1971) Variations of the cerebral sulci in the cat. Acta Anat. *80:* 204–221.

Kennedy, H., and C. Baleydier (1977) Direct projections from thalamic intralaminar nuclei to extra-striate visual cortex in the cat traced with horseradish peroxidase. Exp. Brain Res. *28:* 133–139.

Kievit, J., and H. G. J. M. Kuypers (1977) Organization of the thalamo-cortical connexions to the frontal lobe in the rhesus monkey. Exp. Brain Res. *29:* 299–322.

Kultas-Ilinsky, K., and I. A. Ilinsky (1983) Subdivisions of motor related thalamic nuclei in the cat based on their connectivity and ultrastructure. Soc. Neurosci. Abstr. *9:* 1230.

LeGros Clark, W. E., and R. H. Boggon (1935) The thalamic connections of the parietal and frontal lobes of the brain in the monkey. Philos. R. Soc. Lond. Trans. (Biol.) *224:* 313–359.

Llamas, A., and E. Martínez-Moreno (1974) Modificaciones al método del transporte axonal retrógrado de la horseradish peroxidase en el sistema nervioso central del gato adulto. An. Anat. *23:* 431–443.

Lynch, J. C. (1980) The functional organization of posterior parietal association cortex. Behav. Brain Sci. *3:* 485–534.

Macchi, G., and M. Bentivoglio (1982) The organization of the efferent projections of the thalamic intralaminar nuclei: Past, present and future of the anatomical approach. Ital. J. Neurol. Sci. *2:* 83–96.

Macchi, G., M. Bentivoglio, C. D'Atena, P. Rossini, and E. Tempesta (1977) The cortical projections of the thalamic intralaminar nuclei restudied by means of the HRP retrograde axonal transport. Neurosci. Lett. *4:* 121–126.

Marshall, W. H., C. N. Woolsey, and P. Bard (1941) Observations on cortical somatic sensory mechanisms of cat and monkey. J. Neurophysiol. *4:* 25–43.

Martínez-Bermejo, M. A. (1983) Proyecciones aferentes a los núcleos intralaminares del tálamo. Un estudio en el gato con el método del transporte axonal retrógrado de la HRP. Doctoral Thesis, Universidad Autónoma, Madrid.

Mehler, W. R. (1966) Some observations on secondary ascending afferent systems in the central nervous system. In *Pain,* R. S. Knighton and P. R. Dumke, eds., pp. 11–32, Little, Brown & Co., Boston.

Mesulam, M. -M. (1978) Tetramethylbenzidine for horseradish peroxidase neurohistochemistry. A non-carcinogenic blue reaction-product with superior sensitivity for visualizing neuronal afferents and efferents. J. Histochem. Cytochem. *26:* 106–117.

Miyata, M., and K. Sasaki (1983) HRP studies on thalamocortical neurons related to the cerebello-cerebral projection in the monkey. Brain Res. *274:* 213–224.

Mizuno, N., K. Mochikuzi, C. Akimoto, R. Matsushima, and K. Sasaki (1973) Projections from the parietal cortex to the brain stem nuclei in the cat, with special reference to the parietal cerebro-cerebellar system. J. Comp. Neurol. *147:* 511–522.

Mizuno, N., A. Konishi, M. Sato, S. Kawaguchi, T. Yamamoto, S. Kawamura, and M. Yamawaki (1975) Thalamic afferents to the rostral portions of the middle suprasylvian gyrus in the cat. Exp. Neurol. *48:* 79–87.

Morán, A., C. Avendaño, and F. Reinoso-Suárez (1982) Thalamic afferents to the motor cortex in the cat. A horseradish peroxidase study. Neurosci. Lett. *33:* 229–233.

Mountcastle, V. B., J. C. Lynch, A. Georgopoulos, H. Sakata, and C. Acuña (1975) Posterior parietal association cortex of the monkey: Command functions for operations within extrapersonal space. J. Neurophysiol. *38:* 871–908.

Nakano, K., T. Takimoto, T. Kayahara, Y. Takeuchi, and Y. Kobayashi (1980) Distribution of cerebellothalamic neurons projecting to the ventral nuclei of the thalamus: An HRP study in the cat. J. Comp. Neurol. *194:* 427–439.

Neylon, L., and J. R. Haight (1983) Neocortical projections of the supragenticulate and posterior thalamic nuclei in the marsupial brush-tailed possum, *Trichosurus vulpecula* (Phalangeridae), with a comparative commentary on the organization of the posterior thalamus in marsupial and placental mammals. J. Comp. Neurol. *217:* 357–375.

Nieoullon, A., and L. Rispal-Padel (1976) Somatotopic localization in cat motor cortex. Brain Res. *105:* 405–422.

Niimi, K., H. Matsuoka, and H. Matsumoto (1979) Thalamic afferents to the anterior part of the lateral gyrus in the cat studied by retrograde axonal transport of horseradish peroxidase. Proc. Jpn. Acad. *55:* 357–361.

Oka, H., J. Ito, and M. Kawamura (1982) Identification of thalamocortical neurons responsible for cortical recruiting and spindling activities in cats. Neurosci. Lett. *33:* 13–18.

Palmer, L. A., A. C. Rosenquist, and R. J. Tusa (1978) The retinotopic organization of lateral suprasylvian visual areas in the cat. J. Comp. Neurol. *177:* 237–256.

Pearson, R. L. A., P. Brodal, and T. P. S. Powell (1978) The projection of the thalamus upon the parietal lobe in the monkey. Brain Res. *144:* 143–148.

Penny, G. R., K. Itoh, and I. T. Diamond (1982) Cells of different sizes in the ventral nuclei project to different layers of the somatic cortex in the cat. Brain Res. *242:* 55–65.

Raczkowski, D., and A. C. Rosenquist (1983) Connections of the multiple

visual cortical areas with the lateral posterior-pulvinar complex and adjacent thalamic nuclei in the cat. J. Neurosci. *3:* 1912–1942.

Ramírez-Camacho, R., C. Avendaño, and F. Reinoso-Suárez (1984) Thalamic projections to the anterior suprasylvian and posterior sigmoid cortex: An HRP study of the "vestibular areas" of the cerebral cortex in the cat. Brain Res. Bull. *12:* 245–252.

Reinoso-Suárez, F. (1961) *Topographischer Hirnatlas del Katze,* Merck A.G., Darmstadt.

Rieck, R., and R. G. Carey (1982) Ventrl thalamic projections to layer I of parietal cortex. Anat. Rec. *202:* 157A–158A.

Rinvik, E. (1968a) A re-evaluation of the cytoarchitecture of the ventral nuclear complex of the cat's thalamus on the basis of corticothalamic connections. Brain Res. *8:* 237–254.

Rinvik, E. (1968b) The corticothalamic projection from the pericruciate and coronal gyri in the cat. An experimental study with silver impregnation methods. Brain Res. *10:* 79–119.

Rioch, D. McK. (1929) Studies on the diencephalon of Carnivora. I. The nuclear configuration of the thalamus, epithalamus and hypothalamus of the dog and cat. J. Comp. Neurol. *49:* 1–119.

Robertson, R. T. (1975) Thalamic projections to parietal cortex. Soc. Neurosci. Abstr. *1:* 1046.

Robertson, R. T. (1977) Thalamic projections to parietal cortex. Brain Behav. Evol. *14:* 161–184.

Robertson, R. T. (1978) Thalamic projections to areas 5 and 7 of parietal cortex in the cat. Soc. Neurosci. Abstr. *4:* 79.

Robertson, R. T., and T. J. Cunningham (1981) Organization of corticothalamic projections from parietal cortex in cat. J. Comp. Neurol. *199:* 569–585.

Roda, J. M., and F. Reinoso-Suárez (1983) Topographical organization of the thalamic projections to the cortex of the anterior ectosylvian sulcus in the cat. Exp. Brain Res. *49:* 131–139.

Rodrigo-Angulo, M. L., and F. Reinoso-Suárez (1983) Topographical organization of the brainstem afferents to the lateral posterior-pulvinar thalamic complex in the cat. Neuroscience *7:* 1495–1508.

Rodrigo-Angulo, M. L., and F. Reinoso-Suárez (1984) Cerebellar projections to the lateral posterior-pulvinar thalamic complex in the cat. Brain Res. *322:* 172–176.

Rose, J. E., and C. N. Woolsey (1943) A study of thalamocortical connections in the rabbit. Bull. Johns Hopkins Hosp. *73:* 65–128.

Rose, J. E., and C. N. Woolsey (1958) Cortical connections and functional organization of the thalamic auditory system of the cat. In *Biological and Biochemical Bases of Behavior,* H. F. Harlow and C. N. Woolsey, eds., pp. 127–150, University of Wisconsin Press, Madison, WI.

Sakai, S. T., and G. B. Stanton, and D. Tanaka, Jr. (1983) The ventral lateral thalamic nucleus in the dog: Cytoarchitecture, acetylthiocholinesterase histochemistry, and cerebellar afferents. Brain Res. *271:* 1–9.

Sakata, H., Y. Takaoka, A. Kawarasaki, and H. Shibutani (1973) Somatosensory properties of neurons in the superior parietal cortex (area 5) of the rhesus monkey. Brian Res. *64:* 85–102.

Sanides, F., and J. Hoffmann (1969) Cyto- and myeloarchitecture of the visual cortex of the cat and of the surrounding integration cortices. J. Hirnforsch. *11:* 79–104.

Sasaki, K., Y. Matsuda, S. Kawaguchi, and N. Mizuno (1972) On the cerebello-thalamo-cerebral pathway for the parietal cortex. Exp. Brain Res. *16:* 89–103.

Schlag, J., and M. Schlag-Rey (1971) Induction of oculomotor responses from thalamic internal medullary lamina in the cat. Exp. Neurol. *33:* 498–508.

Schlag, J., M. Schlag-Rey, C. K. Peck, and J. P. Joseph (1980) Visual responses of thalamic neurons depending on the direction of gaze and the position of targets in space. Exp. Brain Res. *40:* 170–184.

Smaha, L. A., W. W. Kaelber, and R.R. Maharry (1969) Efferent projections of the nucleus ventralis lateralis. An experimental study in the cat. J. Anat. *104:* 33–40.

Spreafico, R., N. L. Hayes, and A. Rustioni (1981) Thalamic projections to the primary and secondary somatosensory cortices in cat: Single and double retrograde tracer studies. J. Comp. Neurol. *203:* 67–90.

Steriade, M., and L. L. Glenn (1982) Neocortical and caudate projections of intralaminar thalamic nuclei and their synaptic excitation from midbrain reticular core. J. Neurophysiol. *48:* 352–371.

Steriade, M., A. Kitsikis, and G. Oakson (1978) Thalamic inputs and subcortical targets of cortical neurons in areas 5 and 7 of the cat. Exp. Neurol. *60:* 420–442.

Strick, P. L. (1973) Light microscopic analysis of the cortical projection of the thalamic ventrolateral nucleus in the cat. Brain Res. *55:* 1–24.

Tanji, D. G., S. P. Wise, R. W. Dykes, and E. G. Jones (1978) Cytoarchitecture and thalamic connectivity of third somatosensory area of cat cerebral cortex. J. Neurophysiol. *41:* 268–284.

Thompson, R. F., R. H. Johnson, and J. J. Hoopes (1963) Organization of auditory, somatic sensory, and visual projections to association fields of cerebral cortex in the cat. J. Neurophysiol. *26:* 343–364.

Updyke, B. V. (1977) Topographic organization of the projections from cortical areas 17, 18 and 19 onto the thalamus, pretectum and superior colliculus in the cat. J. Comp. Neurol. *173:* 81–122.

Updyke, B. V. (1981) Projections from visual areas of the middle suprasylvian sulcus onto the lateral posterior complex and adjacent thalamic nuclei in cat. J. Comp. Neurol. *201:* 477–506.

Updyke, B. V. (1983) A reevaluation of the functional organization and cytoarchitecture of the feline lateral posterior complex, with observations on adjoining cell groups. J. Comp. Neurol. *219:* 143–181.

Van der Kooy, D. (1979) The organization of the thalamic, nigral and raphe cells projecting to the medial vs. lateral caudate-putamen in rat. A fluorescent retrograde double labeling study. Brain Res. *169:* 381–387.

Vedovato, M. (1978) Identification of afferent connections to cortical area 6aβ of the cat by means of retrograde horseradish peroxidase transport. Neurosci. Lett. *9:* 303–310.

Vogt, C., and O. Vogt (1919) Allgemeinere Ergebnisse unserer Hirnforschung. J. Psychol. Neurol. (Leipzig) *25:* 279–462.

Von Bonin, G., and P. Bailey (1947) *The Neocortex of Macaca mulatta,* University of Illinois Press, Urbana.

Von Economo, C., and G. N. Koskinas (1925) *Die Cytoarchitektonik der Hirnrinde der erwachsenen Menschen,* Springer-Verlag, Berlin.

Waller, W. H., and R. W. Barris (1937) Relationships of thalamic nuclei to the cerebral cortex in the cat. J. Comp. Neurol. *67:* 317–341.

Wilson, J. S., and S. J. Goldberg (1980) Inputs of the pulvinar and lateral posterior nucleus into the abducens nucleus of the cat. Exp. Neurol. *68:* 72–86.

Winkler, C., and A. Potter (1914) *An Anatomical Guide to Experimental Researches on the Cat's Brain,* W. Versluys, Amsterdam.

Yin, T. C. T., and W. J. Williams (1976) Dynamic response and transfer characteristics of joint neurons in somatosensory thalamus of the cat. J. Neurophysiol. *39:* 582–600.