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Optic Tectum of the Eastern Garter Snake, *Thamnophis sirtalis*. V. Morphology of Brainstem Afferents and General Discussion

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ABSTRACT

Brainstem neurons that project to the optic tectum of the eastern garter snake were identified by retrograde transport of horseradish peroxidase. The distribution and morphology of tectal afferent axons from the thalamus, pretectum, nucleus isthmi, and midbrain reticular formation were then studied by anterograde transport of horseradish peroxidase.

Diencephalic projections to the tectum arise from the ventral lateral geniculate complex ipsilaterally and the ventrolateral nucleus, suprapeduncular nucleus, and nucleus of the ventral supraoptic decussation bilaterally. Three pretectal groups (the lentiform thalamic nucleus, the lentiform mesencephalic-pretectal complex and the geniculate pretectal nucleus) give rise to heavy, bilateral tectal projections. Small neurons in nucleus isthmi and large reticular neurons in nucleus lateralis profundus mesencephali also give rise to bilateral projections. Caudal to the tectum, projections arise bilaterally from the pontine and medullary tegmentum, nuclei of the lateral lemniscus, the posterior colliculus, and the sensory trigeminal nucleus. A small contralateral projection arises from the medial vestibular complex.

Tectal afferents from the thalamus, pretectum, nucleus isthmi, and midbrain reticular formation had characteristic morphologies and laminar distributions within the tectum. However, these afferents fall into two groups based on their spatial organization. Afferents from the thalamus and nucleus isthmi arise from small neurons with spatially restricted, highly branched dendritic trees. Their axons terminate in single, highly branched and bouton-rich arbors about 100 μm in diameter. By contrast, afferents from the midbrain reticular formation and the pretectum arise from large neurons with long, radiate, and sparsely branched dendritic trees. Their axons course parallel to the tectal surface and emit numerous collateral branches that are distributed widely through the mediolateral and rostrocaudal extent of either the central or superficial gray layers. Each collateral bears several small, spatially disjunct clusters of boutons.

Key words: sensorimotor coding, tectal geometry, tectal afferent neurons

This is the fifth and last paper in a series on the light microscopic morphology of efferent, intrinsic, and afferent neurons of the optic tectum of the eastern garter snake, *Thamnophis sirtalis*. The preceding paper described the morphology of retinal terminal arbors in the tectum (Dacey and Ulinski, '86d). This paper concludes the analysis of tectal afferents with a description of the sources and morphology of nonretinal afferents.

Use of horseradish peroxidase (HRP) for retrograde tracing of neural connections has shown that a large number of visual and nonvisual brainstem nuclei project to the tectum in representatives of each vertebrate class (e.g., Wilczynski and Northcutt, '77; Edwards et al., '79; Gruberg et al., '79; Luiten, '81; Northcutt, '82; Smeets, '82; Hunt and Brecha,

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'84). Some afferents (like those from the midbrain nucleus isthmi/parabigeminal nucleus or the ventral lateral geniculate nucleus) are topographically organized (e.g., Hunt et al., '77; Gruberg and Udin; '78; Sherk, '79; Crossland and Uchwat, '79; Dacey, '80a; Mendez-Otero et al., '80; Sakamoto et al., '81). Other inputs (like those from the substantia nigra or the brainstem reticular formation) show no obvious point-to-point topography. Instead they show a discontinuous or patchy distribution in the tectum (Edwards and deOlmos, '76; Graybiel, '78b; Rhoades et al., '82; May and Hall; '84; review: Huerta and Harting, '84).

Further understanding of the organization of tectal afferents requires a detailed analysis of the synaptic and functional relation of specific afferents to identified classes of tectal neurons. Essential to this analysis is a knowledge of the morphology of afferent terminals and their spatial distribution in the tectum. This is especially important in the case of the nontopographic projections whose spatial organization and function are not clear. Previous Golgi studies provide some indication of a diverse morphology in putative tectal afferents (e.g., Ramón y Cajal, '11; Quiroga, '78; Dacey, '80b). However, it has been technically difficult to demonstrate these afferents in Golgi material and little is known about the morphology of afferents from an identified source. In this study, injections of HRP into the tectum are first used to identify the sources of tectal afferents in *Thamnophis sirtalis*, the eastern garter snake. Anterograde transport of HRP is then used to provide a more detailed description of the morphology of axons in several of these tectal projections.

METHODS

Protocols for iontophoretic injections of HRP, histochemistry, and serial section reconstructions are reported in the previous papers in this series (Dacey and Ulinski, '86a–d); 100 cases in which small injections of HRP were made directly into the tectum or into tectal afferent and efferent pathways were available for study. Bidirectional transport of HRP permitted the same cases that were used for analysis of tectal efferent neurons (Dacey and Ulinski, '86a,b) to be used to examine afferent connections.

Identification of retrogradely labeled neurons was made in 15 cases serially sectioned at 40 μm and examined with an oil immersion objective at a total magnification of 1,250×. Chartings of the positions of all labeled cells were then made on alternate 80-μm sections at lower magnification. Detailed camera lucida tracings (at a total magnification of 1,560×) were used to reconstruct the morphology of solid-filled tectal afferent neurons through 80- or 150-μm serial sections.

The complete pattern of retrograde labeling that results from injections of HRP into the tectum is presented first. This is followed by a more detailed description of the morphology of neurons that project to the tectum from the lateral thalamus, the pretectum, nucleus isthmi, and the nucleus lateralis profundus mesencephali.

Tectal afferents from the brainstem

Labeled neurons were observed in the brainstem from the rostral diencephalon to the medulla-spinal cord junction following injections of HRP into the tectum. No labeled neurons were observed in the telencephalon. The overall pattern of labeling was consistent in all 15 cases that were studied in detail. The results from one such case are described below and illustrated in Figures 1–4.

Abbreviations

Cer	Cerebellum
CG	Central gray
Co	Cochlear nucleus
cp	Cell plate of the ventral lateral geniculate nucleus
DF	Dorsal funiculus
DGN	Dorsal geniculate nucleus
DM	Dorsal medial nucleus
DTB	Dorsal tectobulbar tract
GP	Geniculate pretectal nucleus
HC	Habenular commissure
HP	Habenulopeduncular tract (fasciculus retroflexus)
IP	Interpeduncular nucleus
Ist	Nucleus isthmi
IT	Crossed isthmotectal pathway
LC	Locus coeruleus
LFB	Lateral forebrain bundle
LH	Lateral habenula
LL	Lateral lemniscus
LM	Nucleus lentiform mesencephalic nucleus
LPM	Nucleus lateralis profundus mesencephali
LT	Lentiform thalamic nucleus
MH	Medial habenula
MLF	Medial longitudinal fasciculus
Mot V	Motor nucleus of the trigeminal
MTTh	Medial tectothalamic tract
NDF	Nucleus of the dorsal funiculus
NLL	Nucleus of the lateral lemniscus
np	Neuropile of the ventral lateral geniculate nucleus
NTTh	Nucleus of the tectothalamic tract
NVSoD	Nucleus of the ventral supraoptic decussation
OT	Optic tract
Ov	Nucleus ovalis
Pag	Periaqueductal gray
PC	Posterior commissure
PCo	Posterior colliculus
Pd	Predorsal bundle
PD	Posterodorsal nucleus
Pr V	Principal nucleus of the trigeminal
Pt	Pretectal nucleus
RI	Inferior raphe
RID	Reticularis inferioris pars dorsalis
RIV	Reticularis inferioris pars ventralis
Ro	Nucleus rotundus
RSL	Reticularis superioris pars lateralis
RSM	Reticularis superioris pars medialis
Sp	Suprapeduncular nucleus
Sp V	Spinal nucleus of the trigeminal
TG	Tectogeniculate pathway
TrV	Spinal tract of the trigeminal
TTh	Tectothalamic tract
TThx	Crossed tectothalamic tract
VeVl	Ventrolateral vestibular nucleus
VeVm	Ventromedial vestibular nucleus
VGN	Ventral lateral geniculate nucleus
VH	Ventral hypothalamus
VL	Ventrolateral nucleus
Vr	Motor root of the trigeminal
VSoD	Ventral supraoptic decussation
VTB	Ventral tectobulbar tract
III	Oculomotor nucleus
IIIr	Root of the third cranial nerve
X	Motor nucleus of the vagus
XII	Hypoglossal nucleus

Layers of the optic tectum

SAC	Stratum album centrale
Sap	Stratum album periventriculare
SFGSa,b,c	Stratum fibrosum et griseum superficiale, sublaminae a, b and c
SGC	Stratum griseum centrale
SGP	Stratum griseum periventriculare
SO	Stratum opticum
SZ	Stratum zonale

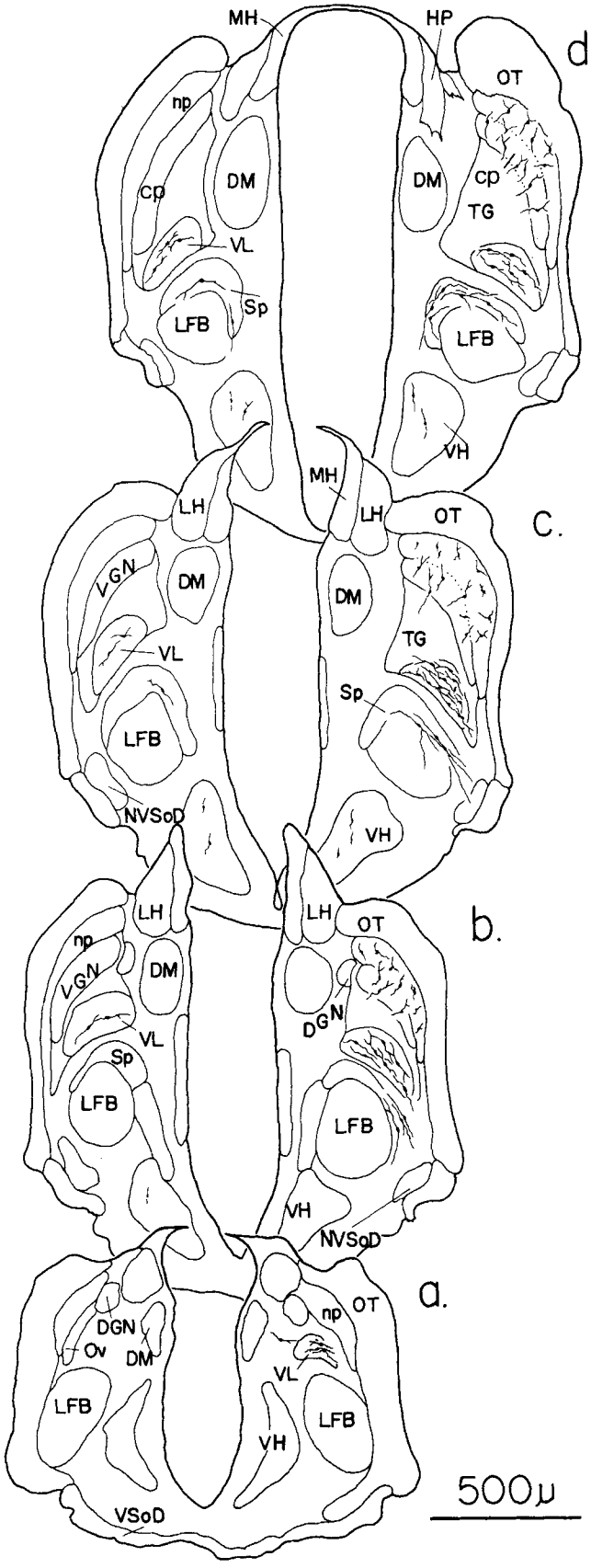


Fig. 1. Tectal afferents from the diencephalon retrogradely filled after injections of HRP into the tectum. Projections arise from the ventral lateral geniculate nucleus (VGN) ipsilaterally and the ventrolateral nucleus (VL), suprapeduncular nucleus (Sp) and the ventral hypothalamus (VH) bilaterally. The injection site is shown in Figure 3. Chartings were traced from alternate 80-μm coronal sections counterstained with cresyl violet.

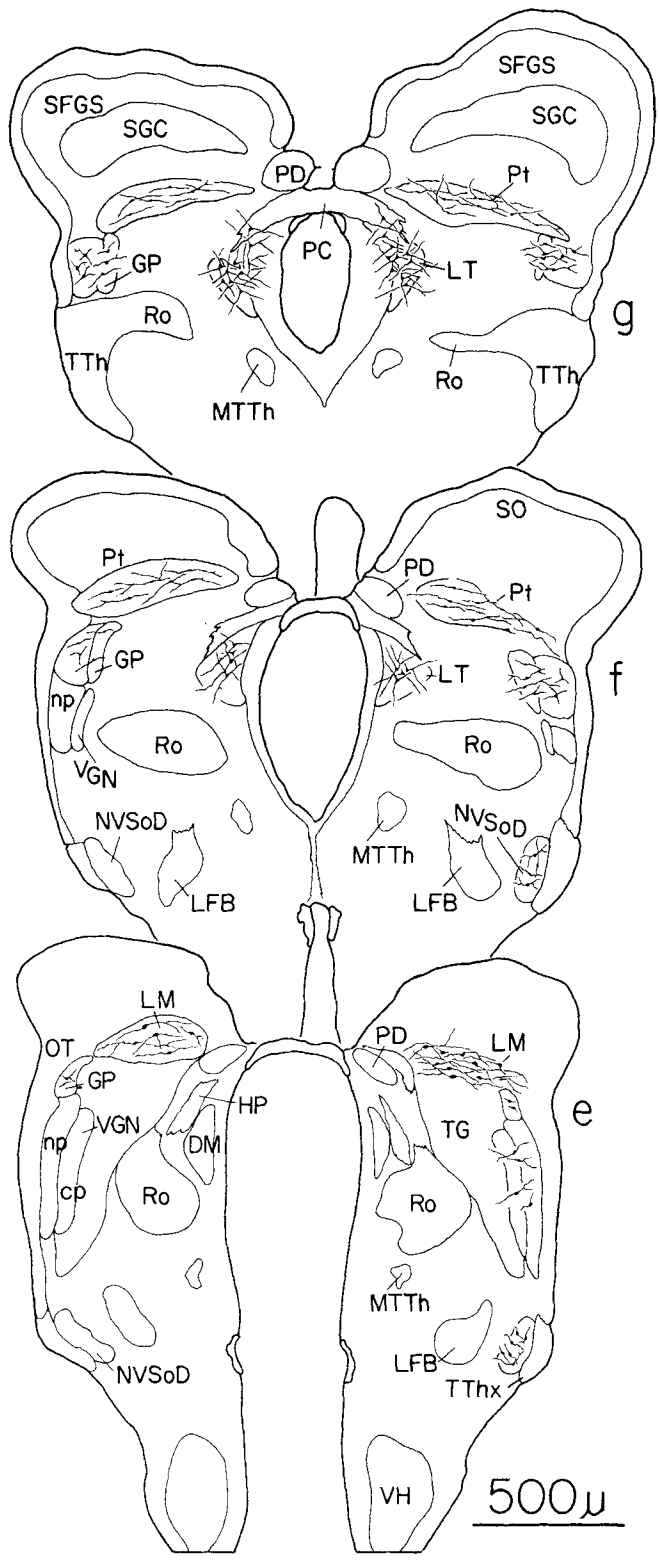


Fig. 2. Tectal afferents from the pretectum. The lentiform mesencephalic nucleus (LM), pretectal nucleus (Pt), geniculate pretectal nucleus (GP), and the lentiform thalamic nucleus (LT) give rise to bilateral projections. An ipsilateral projection arises from the caudal segment of the nucleus of the ventral supraoptic decussation (NVSoD). The injection site is shown in Figure 3. Chartings were traced from 80-μm serial sections counterstained with cresyl violet.

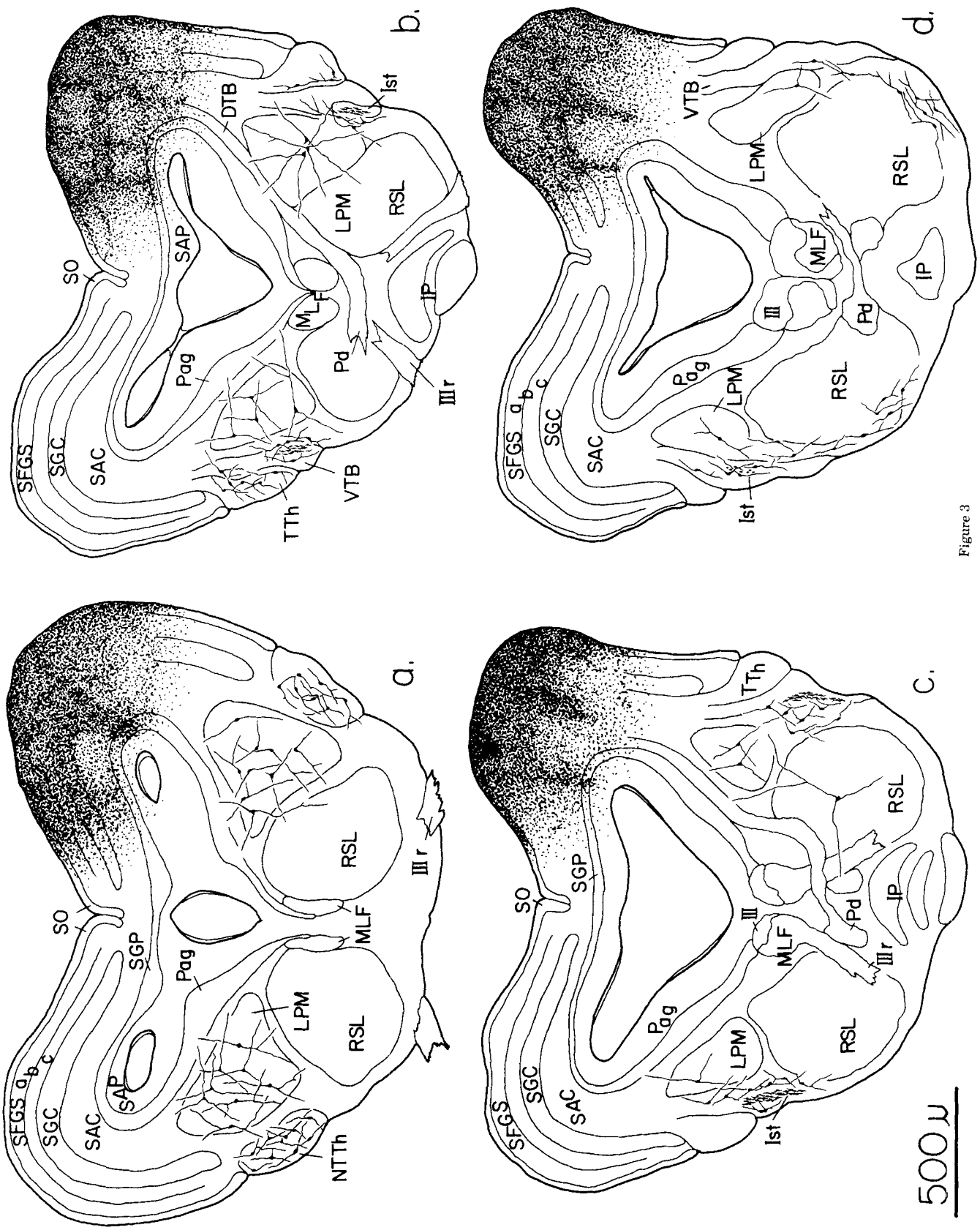

a.
SFGS a b c
SGC
SAC
SAP
SO
SGP
Pag
LPM
RSL
MLF
III r
NTTh
b.
SFGS
SGC
SAC
SO
SAP
Pag
DTB
LPM
RSL
MLF
Pd
IP
III r
TTh
VTB
Ist
c.
SFGS
SGC
SAC
SO
SGP
Pag
LPM
RSL
III
MLF
Pd
III r
IP
TTh
Ist
d.
SFGS a b c
SGC
SAC
Pag
LPM
III
RSL
MLF
Pd
IP
VTB
Ist
500 µ

Figure 3

Diencephalon. With the exception of a few labeled neurons in the ventral hypothalamus (VH, Fig. 1b–d) labeled neurons in the diencephalon are restricted to four ventral thalamic nuclei. The suprapeduncular nucleus contains solid-filled neurons bilaterally. They have small somata (8–12 μm in diameter) and long, radiate dendrites that appear to encapsulate the dorsal margin of the lateral forebrain bundle (Sp, Figs. 1b–d, 5A). The axons of suprapeduncular neurons extend ventromedially to enter the medial tectothalamic tract (MTTh). They pass caudally in this tract and then ascend to the stratum griseum centrale of the tectum via the dorsal tectobulbar tract (DTB).

The ventrolateral nucleus, situated just dorsal to the suprapeduncular nucleus, shows a heavy ipsilateral and light contralateral projection to the tectum (VL, Fig. 1a–d). Neurons have soma diameters of 10–15 μm and bushy, fusiform dendritic trees that appear restricted to the cytoarchitectonic boundaries of the ventrolateral nucleus. The axons of ventrolateral neurons reach the tectum by coursing dorsocaudally in the tectogeniculate pathway (TG, Fig. 1), directly through the pretectum and into the stratum album periventriculare (SAP).

The ventral lateral geniculate nucleus shows a heavy ipsilateral projection to the tectum (VGN, Figs. 1b–d,2e,7). The nucleus is divided into a cell-poor neuropile (np, Fig. 1) bounded laterally by the optic tract and a cell plate (cp, Fig. 1) bounded medially by the tectogeniculate pathway. The neuropile is a retinal terminal field (Halpern and Frumin, '73; du Lac and Dacey, '81).

The caudal portion of the nucleus of the ventral supraoptic decussation gives rise to an ipsilateral projection to the tectum (NVSoD, Figs. 2e,f,5B). It contains small, fusiform neurons situated along the medial edge of the crossed tectothalamic pathway (TThx, Fig. 2). Their dendrites extend radially into the tectothalamic fibers. Their axons could not be traced, but it is likely that they reach the tectum via the tectothalamic tract. This nucleus contains neurons that project directly to the retina (Halpern et al., '76).

Pretectum. The tectum receives a heavy, bilateral projection from four pretectal nuclei. The midline lentiform thalamic nucleus contains a heavily labeled aggregrate of large multipolar neurons (LT, Figs. 2f,g, 5D). These cells are wedged beneath the posterior commissure, but have long, radiate dendrites that extend medially into the tectogeniculate pathway. The geniculate pretectal nucleus contains an equally heavy aggregate of small, fusiform neurons (GP, Fig. 2e–g) whose dendrites extend laterally into the optic tract and medially into the tectogeniculate pathway. The pretectal nucleus contains labeled neurons distributed across the rostroventral face of the tectum between the geniculate pretectal and lentiform thalamic nucleus (Pt, Figs. 2f,g,5C). These neurons have comparatively small somata (6–10 μm in diameter) and long, thin dendrites that span the mediolateral extent of the nucleus. Finally, a distinct group of multipolar neurons are solidly filled just rostral to the pretectal nucleus in the large-celled mesencephalic lentiform nucleus (LM, Figs. 2e, 11).

Midbrain. The tectum receives heavy, bilateral projections from three groups of midbrain neurons. Densely labeled large multipolar neurons are present at the ventrolateral margin of the tectum embedded in the tectothalamic tract and are termed here the nucleus of the tectothalamic tract (NTTh, Fig. 3a,b). These neurons have thick dendrites that radiate within the tract and axons that ascend via this pathway to the stratum griseum centrale (SGC). A second group of labeled cells is present at the ventrolateral margin of the tectum caudal to the nucleus of the tectothalamic tract in the nucleus isthmi. Isthmotectal cells have small spherical somata (6–10 μm in diameter) or larger fusiform somata (12–18 μm in diameter) embedded in the fibers of the ventral tectobulbar tract (VTB). Finally, a massive field of large multipolar neurons are solidly filled in the nucleus lateralis profundus mesencephali (LPM, 3a–c). This reticular field is bordered laterally by the tectothalamic tract and the ventral tectobulbar tract and ventrally by reticularis superioris pars lateralis (RSL).

Caudal brainstem. The tectum receives a weak but consistent bilateral projection from the posterior colliculus and the nuclei of the lateral lemniscus (PCo and LL, Figs. 4a, 6D). Neurons in the posterior colliculus have small spherical somata (8–12 μm in diameter) and fusiform dendritic trees that appear oriented parallel to the collicular surface. Lemniscal neurons are similar to collicular neurons in shape and size, but their dendrites extend radially into the lateral lemniscus.

A moderate contralateral projection and a small ipsilateral projection arise from the spinal trigeminal nucleus (SpV; Figs. 4b,c,6C). Solid-filled neurons have bipolar dendritic trees that extend dorsolaterally across the nucleus. The axons of trigeminal neurons that project contralaterally pass ventromedially through the reticular formation, cross the midline below the predorsal bundle, and reach the ventral tectobulbar tract (arrows, Fig. 4d).

A distinct group of large multipolar neurons in the caudal medulla, situated lateral to the hypoglossal nucleus, projects bilaterally to the tectum. These neurons appear to be associated with the trigeminal spinal tract and have been indicated as part of the spinal trigeminal nucleus in Figure 4d. However, their large size and multipolar dendrites clearly distinguish them from neurons in the pontomedullary segments of the spinal trigeminal nucleus. They resemble specialized trigeminotectal relay neurons of the infrared system in the boid snakes (Newman et al. '80; Molenaar and Fizaan-Oostveen '80) in both their size and position.

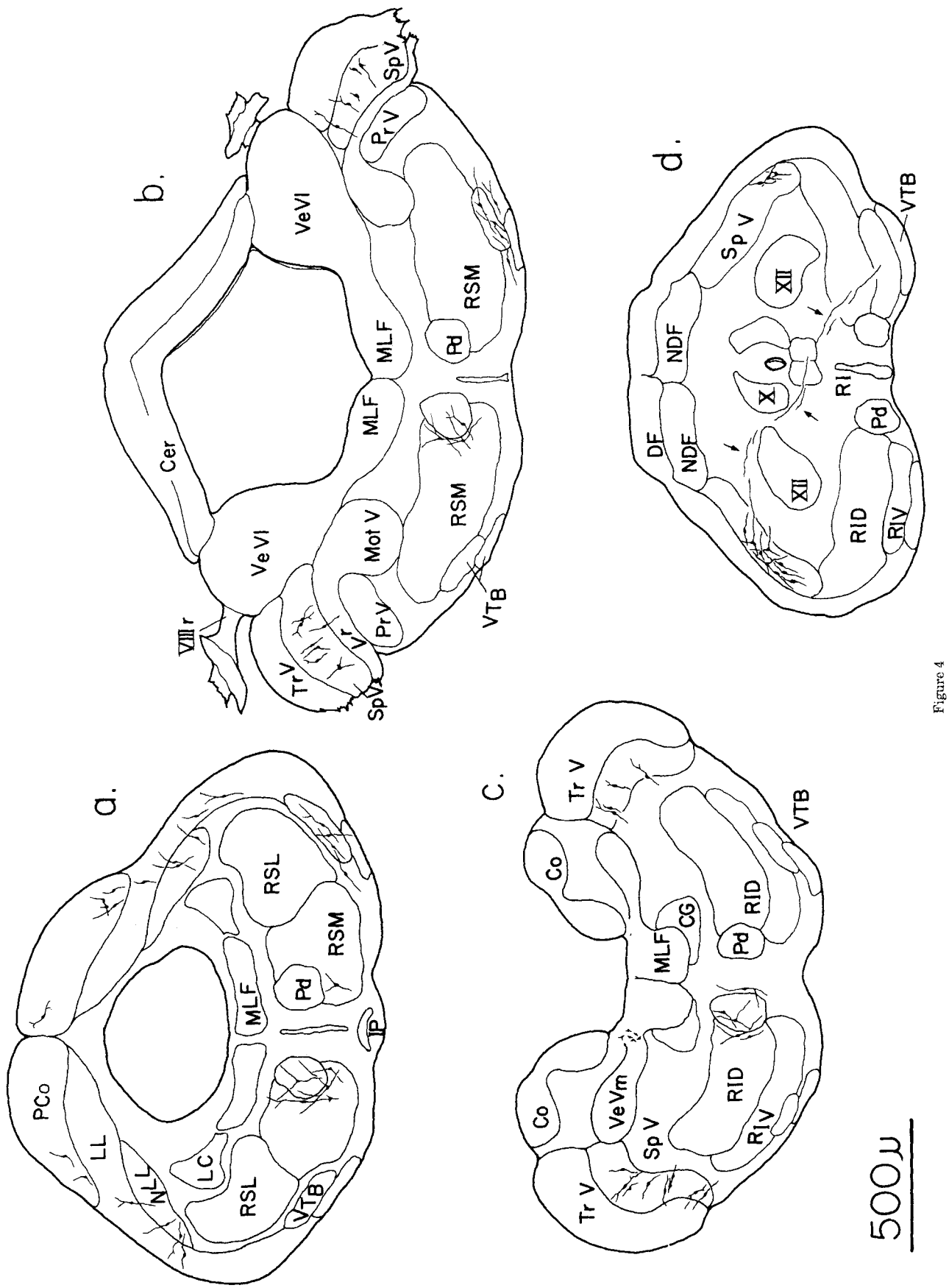
The ventromedial vestibular complex gives rise to a small, crossed tectal projection (VeVm; Fig. 4c). These neurons have small spherical somata (8–12 μm in diameter) and are located at the ventromedial margin of the nucleus. They showed only light granular HRP labeling and their dendrites were not observed.

Projections to the tectum arise from the pontine and medullary reticular formation in association with the crossed and ipsilateral tectobulbar pathways (Figs. 4a–c, 6A,B). Labeled neurons are embedded in or adjacent to the contralateral predorsal bundle or the ipsilateral ventral tectobulbar tract.

Morphology of afferents

In several cases, small injections of HRP into the tectum or into identified tectal afferent pathways demonstrated the morphology of dendrites or axons of neurons that project to the tectum. These results permit the following detailed description of the morphology of afferents arising

Fig. 3. Tectal afferents from the midbrain. Bilateral projections arise from the nucleus lateralis profundus mesencephali (LPM), the nucleus of the tectothalamic tract (NTTh), and the nucleus isthmi (Ist). Labeled neurons are also present within the ventral tectobulbar tract (VTB) bilaterally. The injection site is indicated by the stippling. Chartings were traced from alternate 80-μm coronal sections counterstained with cresyl violet.


a.
PCo
LL
NLL
LC
RSL
VTB
RSL
MLF
Pd
RSM
IP
b.
Cer
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MLF
MLF
Pd
RSM
RSM
Mot V
PrV
SpV
PrV
SpV
TrV
VIII r
VTB
c.
Tr V
Co
Co
VeVm
Sp V
MLF
CG
Pd
RID
RID
RIV
VTB
Tr V
d.
Sp V
NDF
DF
NDF
XII
X
XII
RI
Pd
RID
RIV
VTB
500μ

Figure 4

from the thalamus, pretectum, nucleus isthmi, and midbrain reticular formation.

Thalamotectal projections. Projections to the tectum from the thalamus arise via two pathways. Axons from the suprapeduncular nucleus and the nucleus of the ventral supraoptic decussation course in the medial tectothalamic pathway (MTTh; Fig. 2). Axons from the ventral lateral geniculate and the ventrolateral nucleus course in the tectogeniculate pathway (TG; Figs. 1, 2). Small injections of HRP into the tectogeniculate pathway filled two types of terminal arbors in the tectum.

A first type of terminal apparently arises from the lateral thalamus and reaches the tectum via the tectogeniculate pathway (Fig. 8). These arbors were filled from injections centered on the cell plate of the ventral lateral geniculate nucleus. The primary axons enter the tectum at its rostral pole, reach the stratum album centrale, and ascend vertically into the stratum griseum centrale. The arbors are characterized by a single cluster of boutons situated at the border of the strata fibrosum et griseum superficiale and griseum centrale. Some occupy an area as small as 25 μm in diameter (arbors c and g, Fig. 8). Others form larger, somewhat flattened sheets of boutons with short collaterals that extend for 75–100 μm in the mediolateral axis and 60–80 μm in the rostrocaudal axis of the tectum (arbors a, b, d–f, Fig 8). Arbors occasionally issue collaterals more deeply in the stratum griseum centrale (arbors b–d, Fig. 8).

The morphology of a cell plate neuron filled from injections of HRP into the tectum is shown in Figure 9. Cells of this type are the probable source of the terminal arbors filled from injections into the cell plate. They have fusiform dendritic fields, 75–100 μm in diameter, that extend laterally into the neuropile and medially into the tectogeniculate pathway. The axon (arrow, Fig. 9) arises from a soma or primary dendrite and travels dorsocaudally in the tectogeniculate pathway.

A second type of arbor filled after HRP injections into the lateral thalamus is shown in Figure 10. These axons are observed after larger injections that included much of the ventrolateral thalamic nucleus and the tectogeniculate pathway and may originate from the large multipolar neurons of the ventrolateral nucleus (Fig. 1). These axons pass through the pretectum and enter the strata griseum periventriculare and album periventriculare of the tectum. At their point of termination, single axons turn dorsally and extend vertically through the strata album and griseum centrale. The axons branch within these layers into several loosely arranged collaterals studded with boutons. Most terminal collaterals extend vertically and form cylindrical or conical arbors of diameters ranging from 50 to 150 μm. Some have single collaterals that extend horizontally away from the main terminal field (arrows, Fig. 10).

Pretectotectal projections. Small injections of HRP into the tectum solidly filled the dendrites and portions of the terminal axons of the large neurons of the lentiform mesencephalic nucleus (Fig. 11). The neuron indicated by the arrow in Figure 11 was reconstructed through serial sections and is shown in Figure 12. The soma is about 35 μm in diameter and issues five thick primary dendrites. These bifurcate into smooth secondary dendrites that radiate from the soma without further branching. The axon arises from the soma, courses medially, and emits two collaterals (straight arrows, Fig. 12) before crossing the midline in the posterior commissure. These collaterals ascend into the stratum fibrosum et griseum superficiale.

The morphology of axons arising from the lentiform mesencephalic nucleus is illustrated in Figure 13. One axon (a) was traced from the injection site through the posterior commissure to the contralateral nucleus where it gives rise to two collaterals. These give rise to three small terminal arbors (arrows, Fig. 13). One primary collateral was traced dorsocaudally into the stratum fibrosum et griseum superficiale for approximately 600 μm. This segment of the collateral gives off a series of terminal branches as it passes caudally. Each branch is heavily studded with boutons and courses mediolaterally for several hundred microns parallel to the tectal surface. Small tertiary branchlets arise from the terminal collaterals and extend dorsoventrally within the stratum fibrosum et griseum superficiale. This terminal pattern is illustrated for two other primary collaterals, shown at more caudal tectal levels, in Figure 13b and c.

Isthmotectal projections. Both crossed and ipsilateral isthmotectal cells were solid filled from tectal injections of HRP and their morphology is illustrated in Figure 14. These cells had either small spherical somata (6–10 μm in diameter) or larger fusiform somata (8–12 μm in diameter). The dendrites are highly branched and recurved. They bear short, globular appendages along their length and at their ends.

The crossed and ipsilateral projections arise from different populations of neurons within the nucleus isthmi. Axons from ipsilaterally projecting neurons arise from the soma or a primary dendrite (arrows, Fig. 14), exit the medial face of the nucleus, and turn dorsally into the stratum album centrale of the tectum without emitting collaterals or branching. Axons of crossed isthmotectal neurons also leave the nucleus medially (arrows Fig. 14) but turn ventrorostrally to join the dorsal aspect of the crossed tectothalamic tract (TThx). They follow this pathway rostrally and cross the midline in the ventral supraoptic decussation. It was thus possible to solidly fill the terminal arbors of the ipsilateral axons by making small injections into nucleus isthmi itself, and to fill the crossed projection by making injections into the ventral supraoptic decussation.

The morphology of axons traced to the tectum from injections of HRP into the ipsilateral nucleus isthmi is shown in Figure 15. Fine-caliber axons (less than 1.0 μm in diameter) course from the injection site into the stratum album centrale and ascend vertically through the strata griseum centrale and fibrosum et griseum superficiale to arborize in the strata zonale and opticum. The axon shown in Figure 15A arborizes heavily in the stratum opticum and forms a small cluster of terminals just below the pial surface in the stratum zonale. A second type of axon arising from ipsilateral isthmi is shown in Figure 15B. This axon is slightly larger in diameter (about 1 μm). It courses within the stratum griseum centrale giving rise to a series of widely spaced fine-caliber collaterals that ascend to the pial surface and, like the axons of the first type, arborize most heavily in the stratum zonale in single clusters of terminals. The clusters of different collaterals on a single axon are separated by gaps ranging from 20 to 100 μm so that the overall terminal

Fig. 4. Tectal afferents from the caudal brainstem. The posterior colliculus (PCo), nucleus of the lateral lemniscus (NLL), and the spinal nucleus of the trigeminal (Sp V) give rise to a bilateral projection. A small cluster of neurons in the vestibular complex (VeVm) project contralaterally. HRP-filled neurons are also embedded in the ventral tectobulbar tract (VTB) ipsilaterally and the predorsal bundle (Pd) contralaterally. Chartings were traced from 80-μm coronal sections.

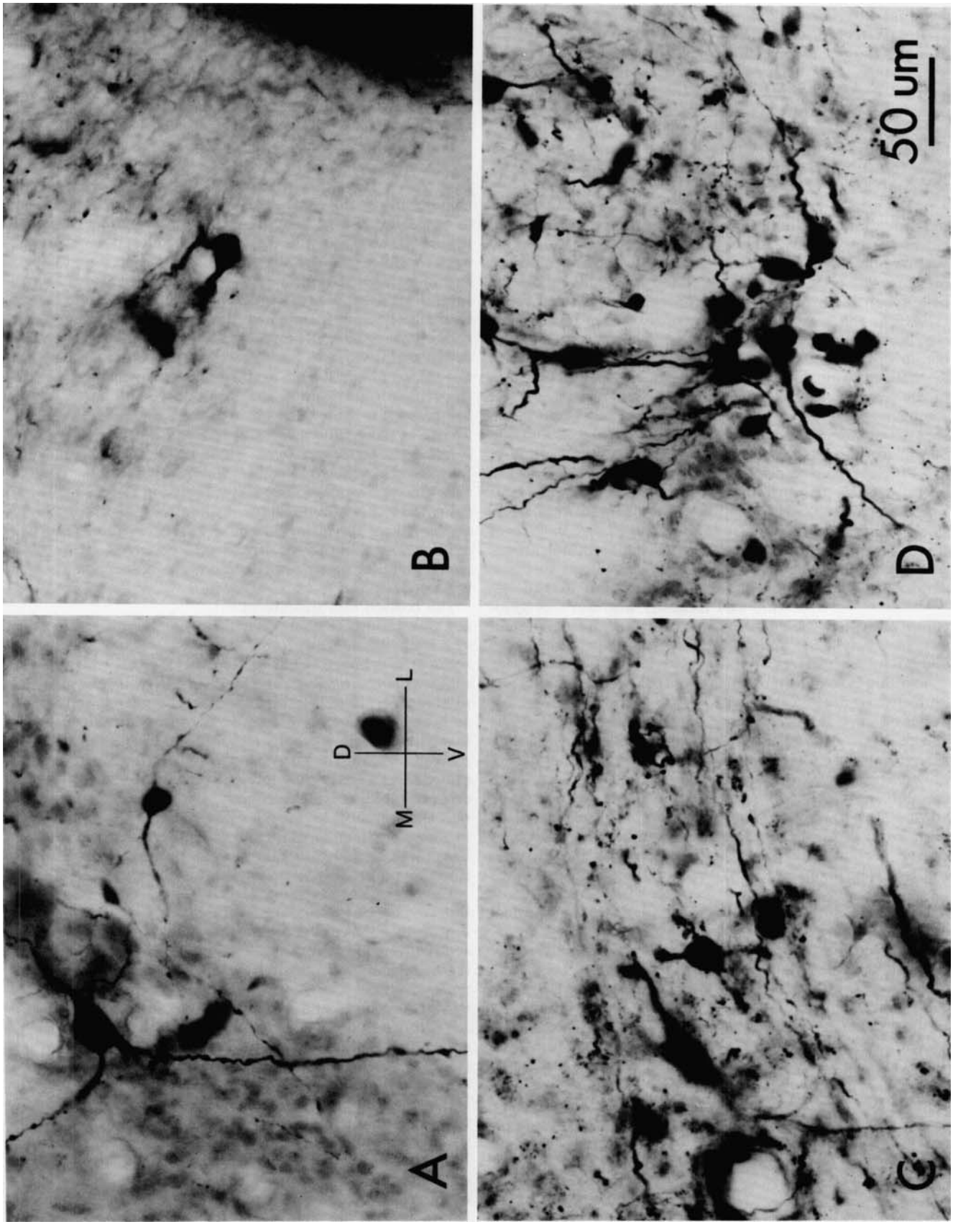

Fig. 5. Photomicrographs of retrogradely labelled tectal afferents from the ventral thalamus and the pretectum. A. The suprapeduncular nucleus. B. The nucleus of the ventral supraoptic decussation. C. The pretectal nucleus and D. The lentiform thalamic nucleus.

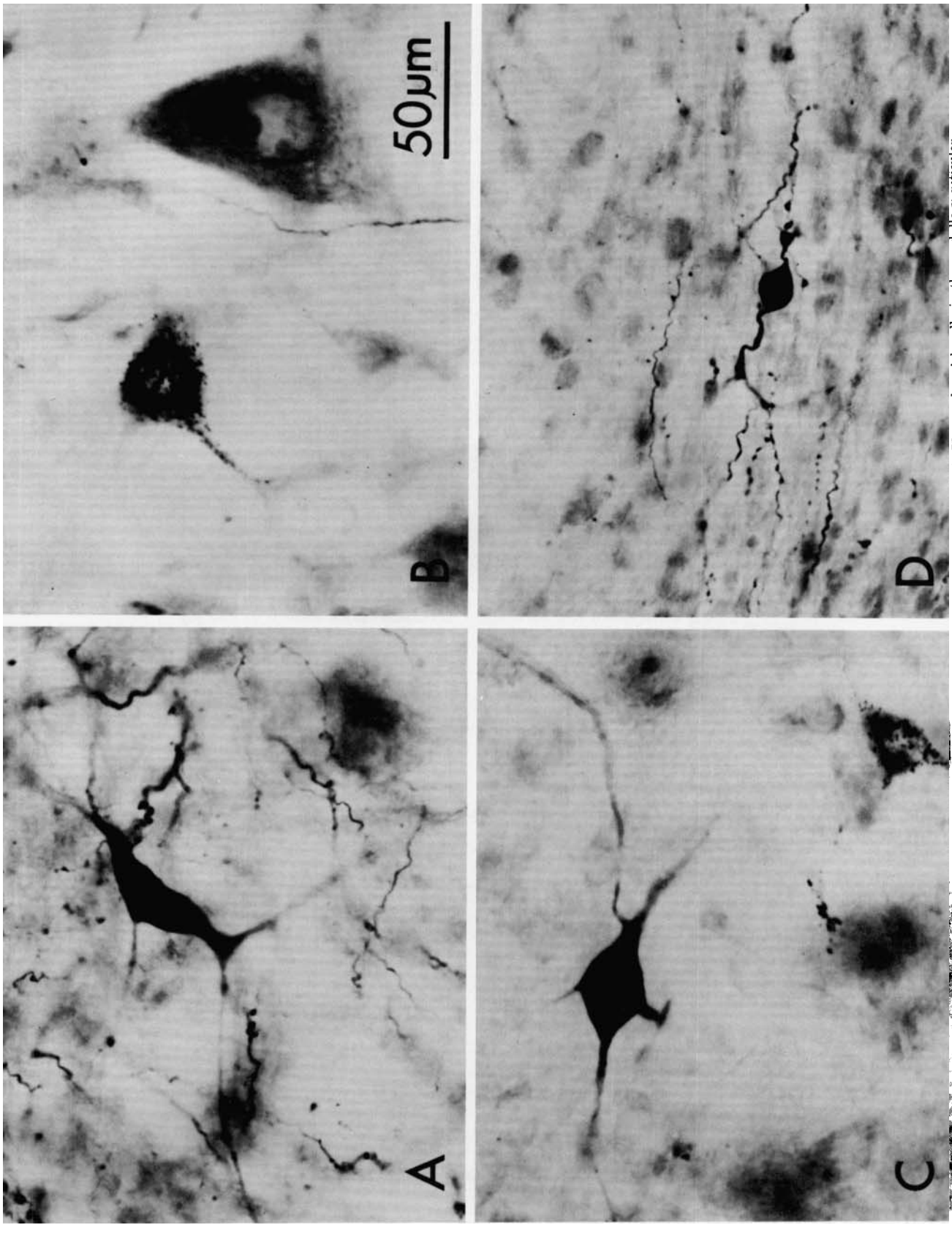

Fig. 6. Photomicrographs of retrogradely labelled tectal afferents from the caudal brainstem. A. The ventral tectobulbar tract in the pontine reticular formation. B. The predorsal bundle in the medullary reticular formation. C. The spinal trigeminal nucleus. D. The posterior colliculus.

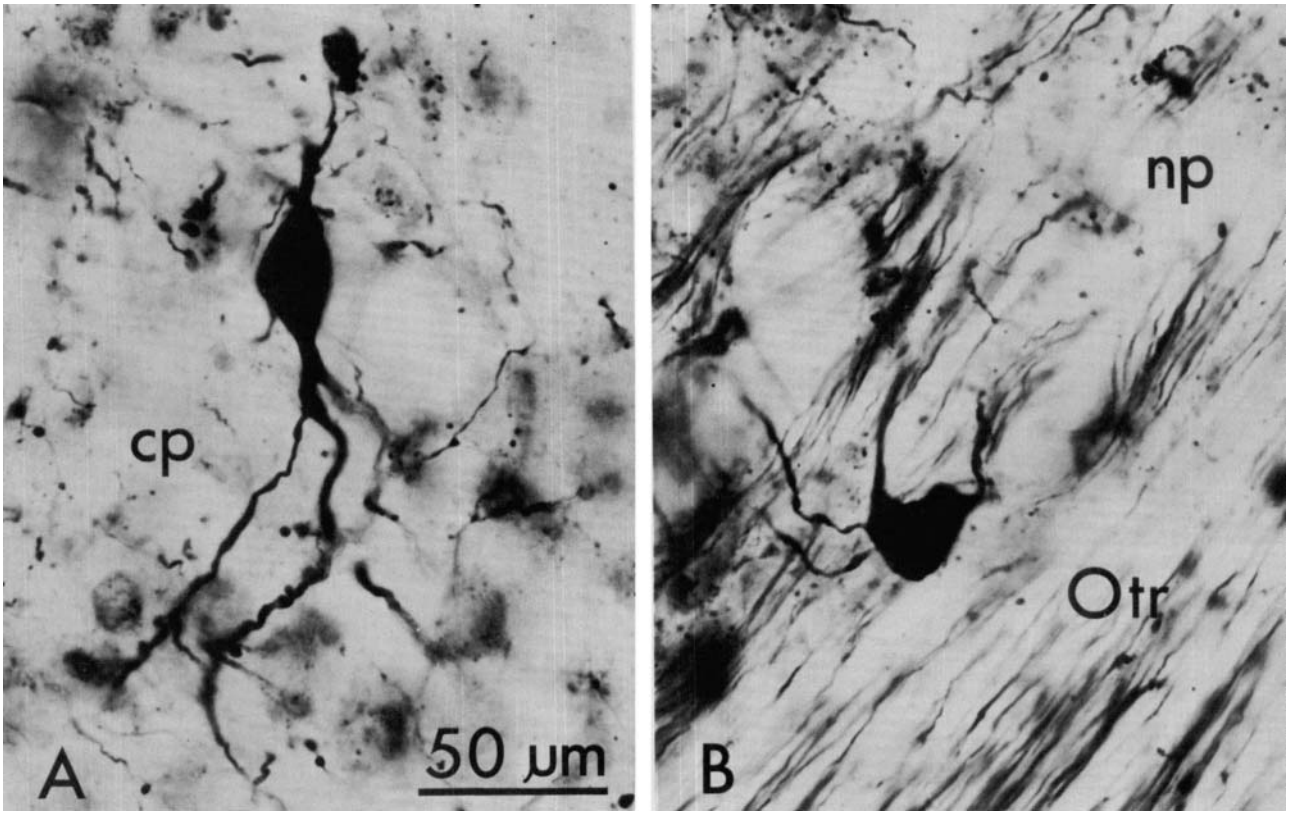

Fig. 7. Tectal afferents from the ventral geniculate nucleus. A. Neuron embedded in the optic neuropile (np) just medial to the optic tract (OT). B. A neuron located in the cell plate (cp) just medial to the neuropile.

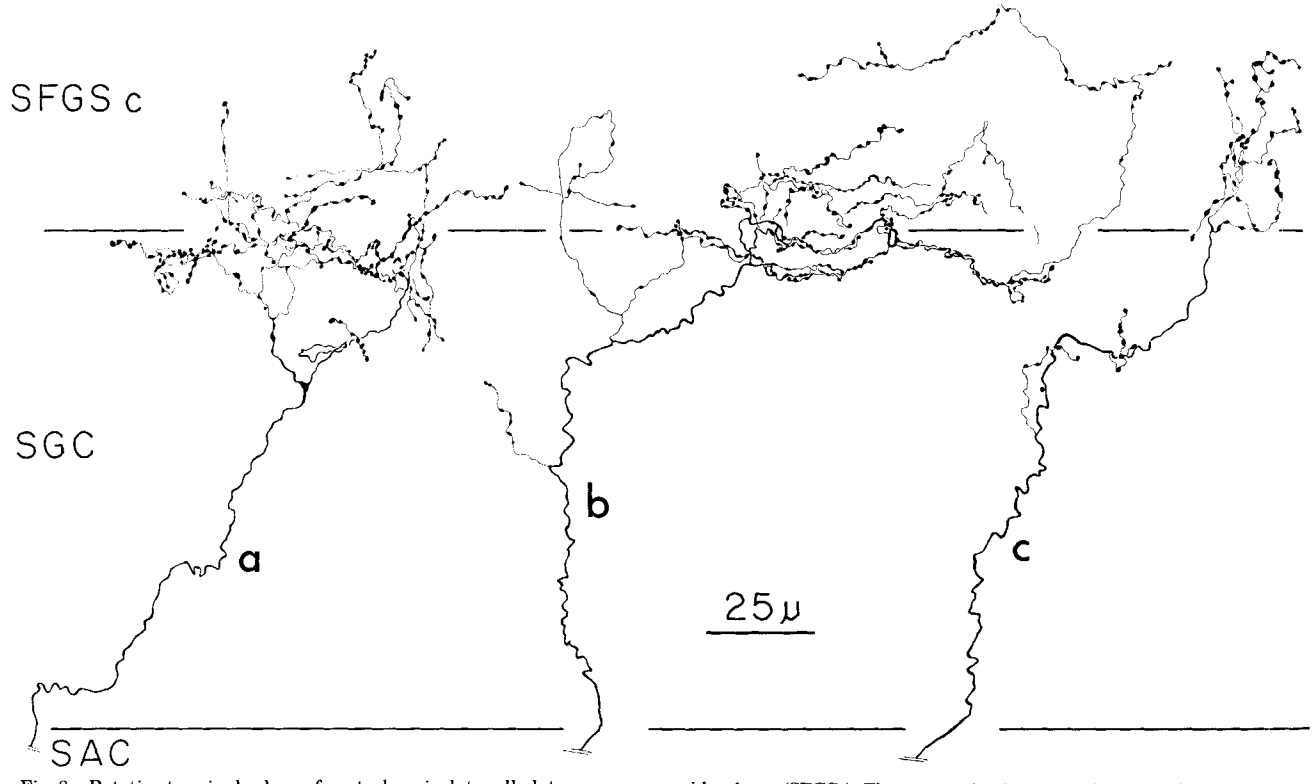

Fig. 8. Putative terminal arbors of ventral geniculate cell plate neurons. The parent axon ascends through the central layers of the tectum and arborizes as a single cluster of terminal boutons at the border of the stratum griseum centrale (SGC) and the stratum fibrosum et griseum superficiale, sublamina c (SFGSc). The terminal arbors may form small aggregrates (c and g) or larger flattened sheets (a, b, d–f). Some arbors emit a few collateral branches in the deep stratum griseum centrale (arbors e, b, and d).

distribution for a single axon is patchy and spread over 500 μm in the mediolateral axis and 250 μm in the rostrocaudal axis of the tectum.

Injections of HRP into the ventral supraoptic decussation retrogradely fill isthmi neurons and anterogradely fill crossed isthmotectal axons. After crossing the midline these fibers, along with the fibers of the crossed tectothalamic pathway, ascend dorsocaudally on the surface of the diencephalon below the optic tract. In the rostral midbrain they form a small bundle between the ventrolateral margin of the stratum opticum and the tectothalamic tract (IT, Fig. 17). Axons course medially into the stratum fibrosum et griseum superficiale from this position. Their morphology is shown in Figure 16. Fine-caliber axons (less than 1.0 μm in diameter) ascend vertically through the superficial layers to terminate just below the pial surface in the stratum zonale. The terminal arbor is composed of a dense network of fine collateral branches heavily laden with boutons. Collaterals often intertwine in small, cylindrical clusters of boutons about 10-20 μm in length and 2–5 μm in diameter (arrows, Fig. 16). In many of these arbors a few distinct collaterals are present at the border of the stratum opticum and the stratum fibrosum et griseum superficiale (arbors b–e in Fig. 16) The size of the arbors ranges from 80 to 100 μm in the mediolateral axis and from 40 to 80 μm in the rostrocaudal axis.

Nucleus lateralis profundus mesencephali. Injections of HRP into the deep tectal layers solidly fill large multipolar neurons in the opposite midbrain tegmentum. Large-caliber fibers coursing in the stratum album centrale cross the midline in the tectal commissure. They run in the contralateral stratum album centrale and pass ventrally to their neurons of origin in the midbrain tegmentum. In their course through the tectum these axons emit a series of terminal collaterals that arborize in the stratum griseum centrale. This pattern is illustrated in the low-magnification tracing in Figure 17. Segments of single axons are shown at higher magnification in Figure 18. The parent axons are about 2–3 μm in diameter, unbranched, and follow a relatively straight course across the lateromedial extent of the tectum. Single collaterals arise at irregular intervals and project vertically into the stratum album or griseum centrale where they arborize and bear distinct clusters of terminal boutons.

An example of a single neuron in the nucleus lateralis profundus mesencephali and part of its tectal projection is shown in Figure 19. This cell was reconstructed from several 80-μm serial sections but has been projected onto the section that contained the soma. The soma is smooth, about 25 μm in diameter, and gives off several thick, smooth dendrites that radiate into the tegmental gray. Each dendrite extends up to 400 μm before ending in a small, beaded arbor or terminal club. The axon arises from the soma and gives off a short collateral before proceeding dorsally into the stratum album centrale. Its first terminal collateral was filled and is shown in the inset in Figure 19. Two other collaterals were observed on this axon before it crossed in the tectal commissure. Each collateral gives rise to small clusters of boutons.

In some cases these clusters appeared to directly appose the somata and primary dendrites of tectoreticular neurons (Fig. 20). This relation was observed when injections of HRP into the midbrain tegmentum filled both reticulotectal axons anterogradely and tectoreticular cells retro-

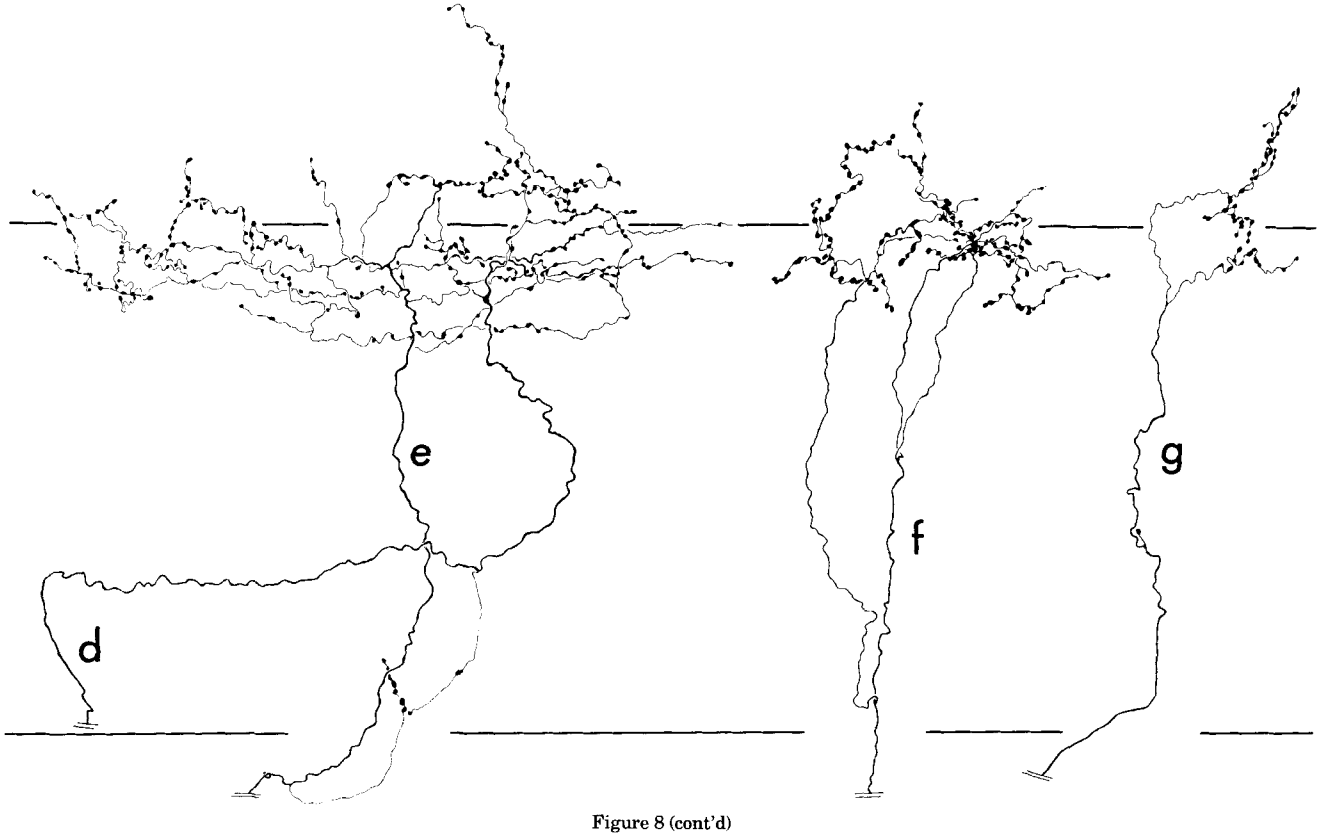

Figure 8 (cont'd)

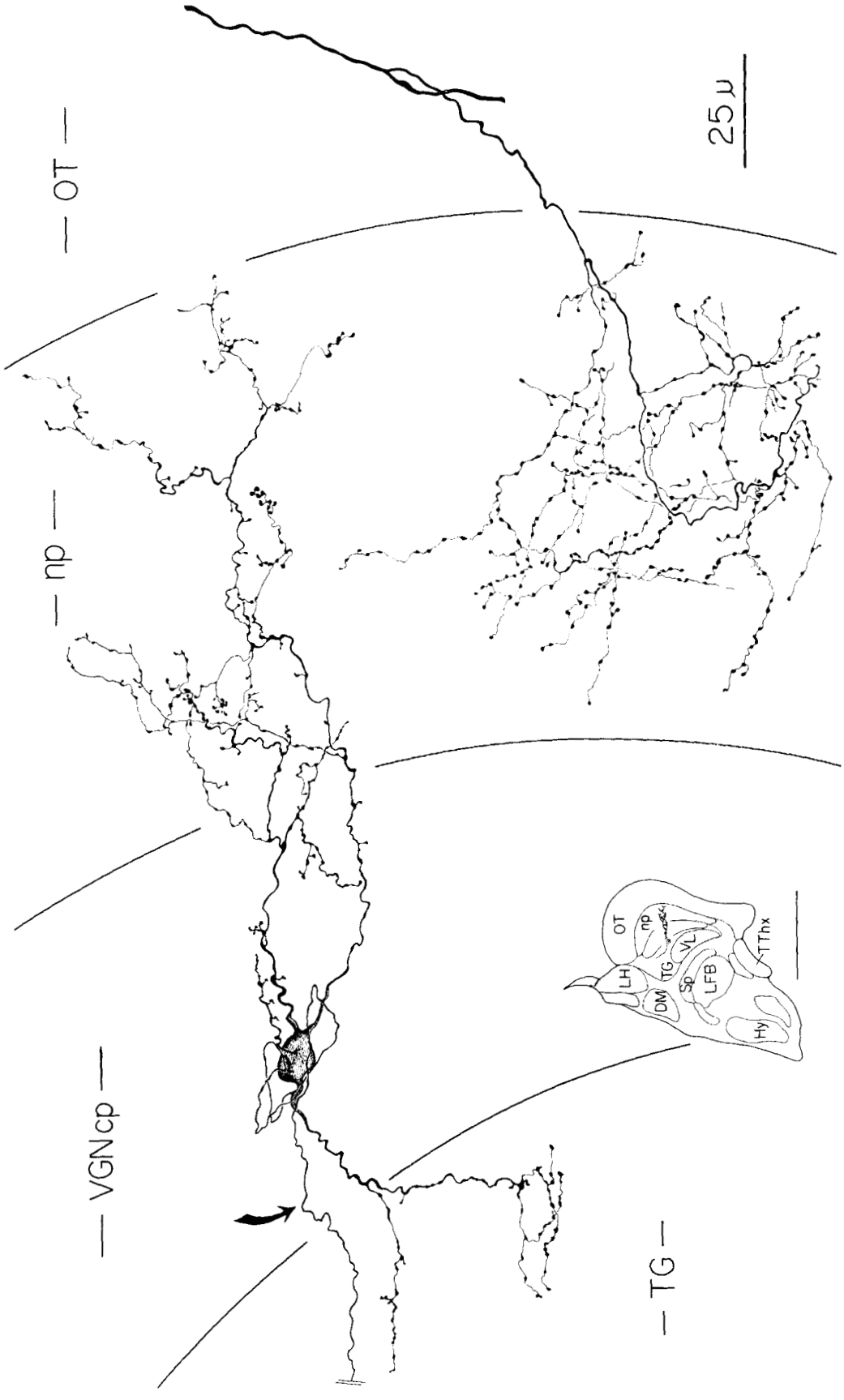

Fig. 9. A neuron of the ventral lateral geniculate cell plate retrogradely filled from injections of HRP into the tectum. Laterally directed dendrites occupy a narrow cylindrical space, approximately 75 μm in diameter in the retinorecipient neuropile (np). Medially directed dendrites arborize in the tectogeniculate pathway (TG). The axon of this cell (indicated by the arrow) was traced caudally in the tectogeniculate pathway to the stratum griseum centrale. An anterogradely filled optic tract axon and its collateral terminal arbor in the geniculate neuropile are also shown for comparison. The dimensions of the optic arbor closely match the dendritic field size of the geniculate cell.

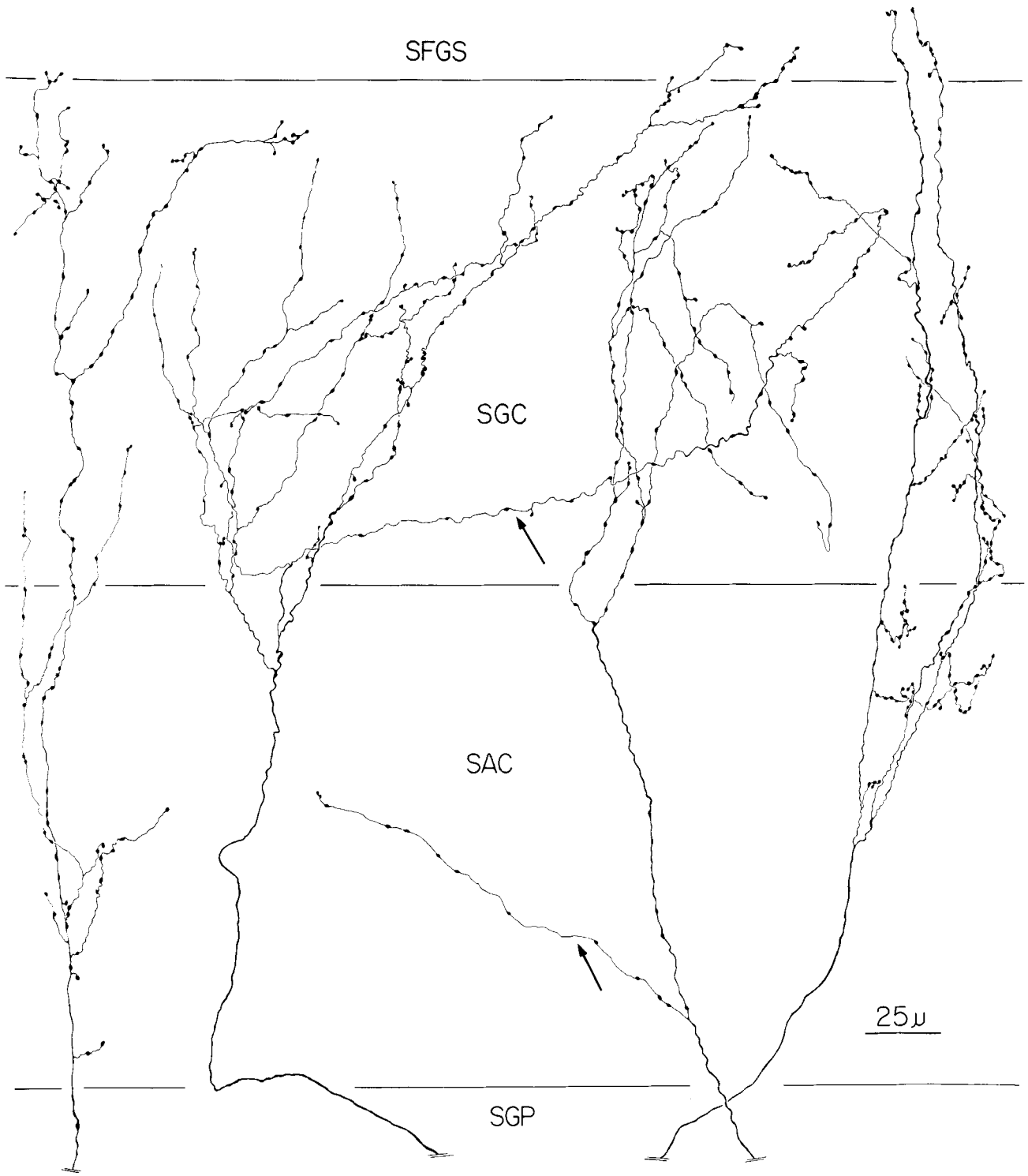

Fig. 10. Putative terminal arbors of neurons of the ventrolateral nucleus. The parent axons ascend from the periventricular gray (SGP) and form vertically oriented arbors in the central white and gray layers. In contrast to the terminals shown in Figures 8–10 these arbors are sparsely branched and show a lower density of terminal boutons. A few collateral branches extend horizontally away from the main terminal arbor (arrow).

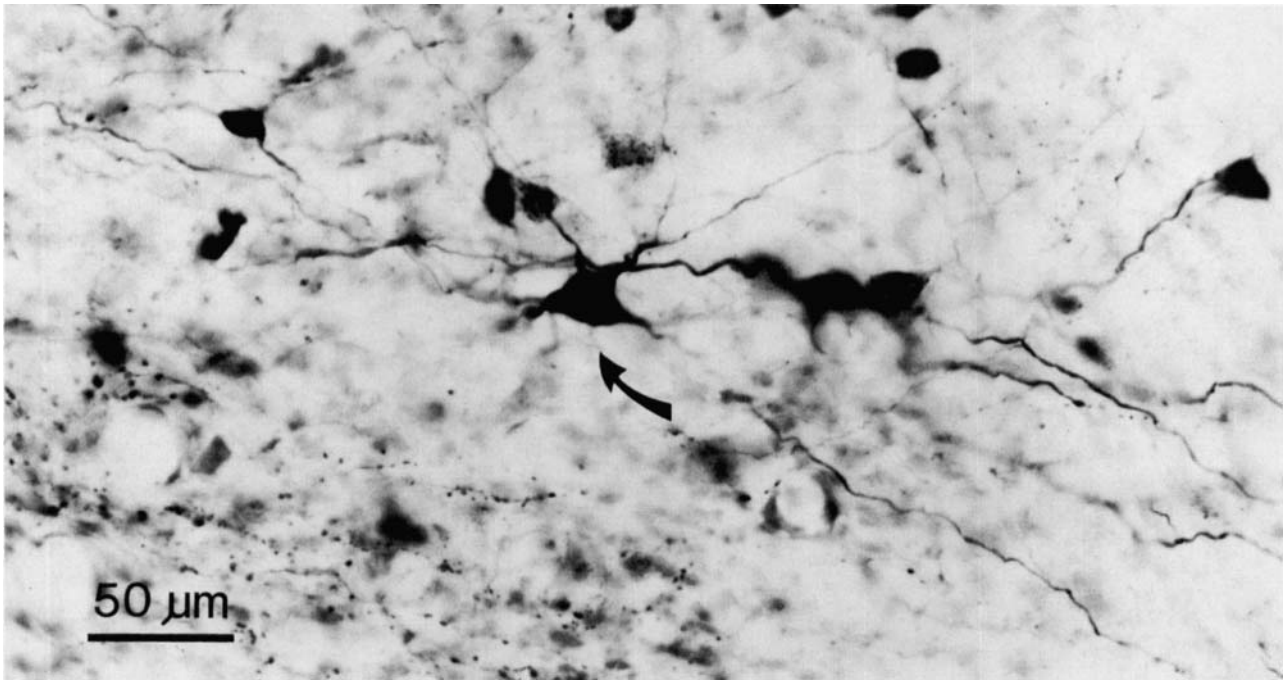

Fig. 11. Large multipolar cells of the lentiform mesencephalic nucleus (LM) retrogradely filled after injections of HRP into the contralateral tectum. A camera lucida reconstruction of the cell indicated by the arrow is shown in Figure 12.

gradely. The contact appears highly specific with many boutons of a single terminal cluster apposing the somata and dendrites of a single tectoreticular cell.

DISCUSSION

The present results conclude a description of the dendritic and axon morphology of efferent, intrinsic, and afferent tectal neurons at the light microscopic level (Dacey and Ulinski, 86a–d). The Discussion will comment on the sources and morphology of the afferents to the tectum in *Thamnophis*. It is followed by a General Discussion that considers the relevance of some of the major findings of the series to the function of the optic tectum.

Sources of tectal afferents in *Thamnophis*

We present a comparative review of tectal afferent organization in reptiles elsewhere (Ulinski et al., '86), and another similar review has been published recently (Northcutt, '84), so only a few general points concerning the results in *Thamnophis* will be considered here. First, nucleus isthmi has been clearly identified for the first time in a snake. As in other species, isthmi is a small-celled nucleus located in the midbrain at the caudolateral margin of the tectum that gives rise to a bilateral, topographically organized tectal projection. Second, a dorsal thalamic projection to the tectum has not been observed in *Thamnophis*. A projection from the dorsal thalamus to the tectum has been suggested in the rattlesnake *Crotalus viridus* where the "pars dorsalis" of the geniculate nucleus is reported to project to the tectum (Gruberg et al., '79). However, these cells appear equivalent to our ventral lateral geniculate nucleus, which apparently lacks a telencephalic projection (du Lac et al., '86). Third, as expected, *Thamnophis* does not show the highly specialized trigeminotectal projections present in the infrared-sensitive snakes (Kishida et al., '80; Molenaar and Fizaan-Oostveen, '80; Newman et al., '80). However, *Thamnophis* does receive a direct projection from the spinal nucleus of the trigeminal and from large cells of unknown connection in the caudal medulla (Fig. 4d), which appear similar in structure and position to the nucleus reticularis caloris identified in *Crotalus*. Fourth, no telencephalic projections to the tectum were observed in *Thamnophis* or in *Crotalus* (Gruberg et al., '79). This contrasts with results in other reptiles where there is evidence from anterograde degeneration studies for a corticotectal projection (Hall et al., '77; Elprana et al., '80). However, these findings should be considered tentative since the cortical cells of origin have not yet been identified in any reptile. Thus, with the possible absence of a telencephalic projection, the overall pattern of projections from the brainstem to the tectum in *Thamnophis* resembles that demonstrated in all other species examined.

Morphology of afferents

The morphology of axons afferent to the tectum has been described in Golgi material (e.g., Ramón y Cajal, '11; Quiroga, '78; Dacey, '80b). These studies suggest that tectal afferents vary in the morphology of their terminal arbors. However, due to the limitations of the Golgi method, it has been virtually impossible to characterize these axons in detail or to relate them to their cells of origin. By contrast, the use of HRP filling in this and the preceding paper provides a detailed description of the morphology of afferents to the tectum from the retina and several brainstem nuclei. The relative sizes, distribution, and structure of these arbors is summarized in Figure 21. They can be

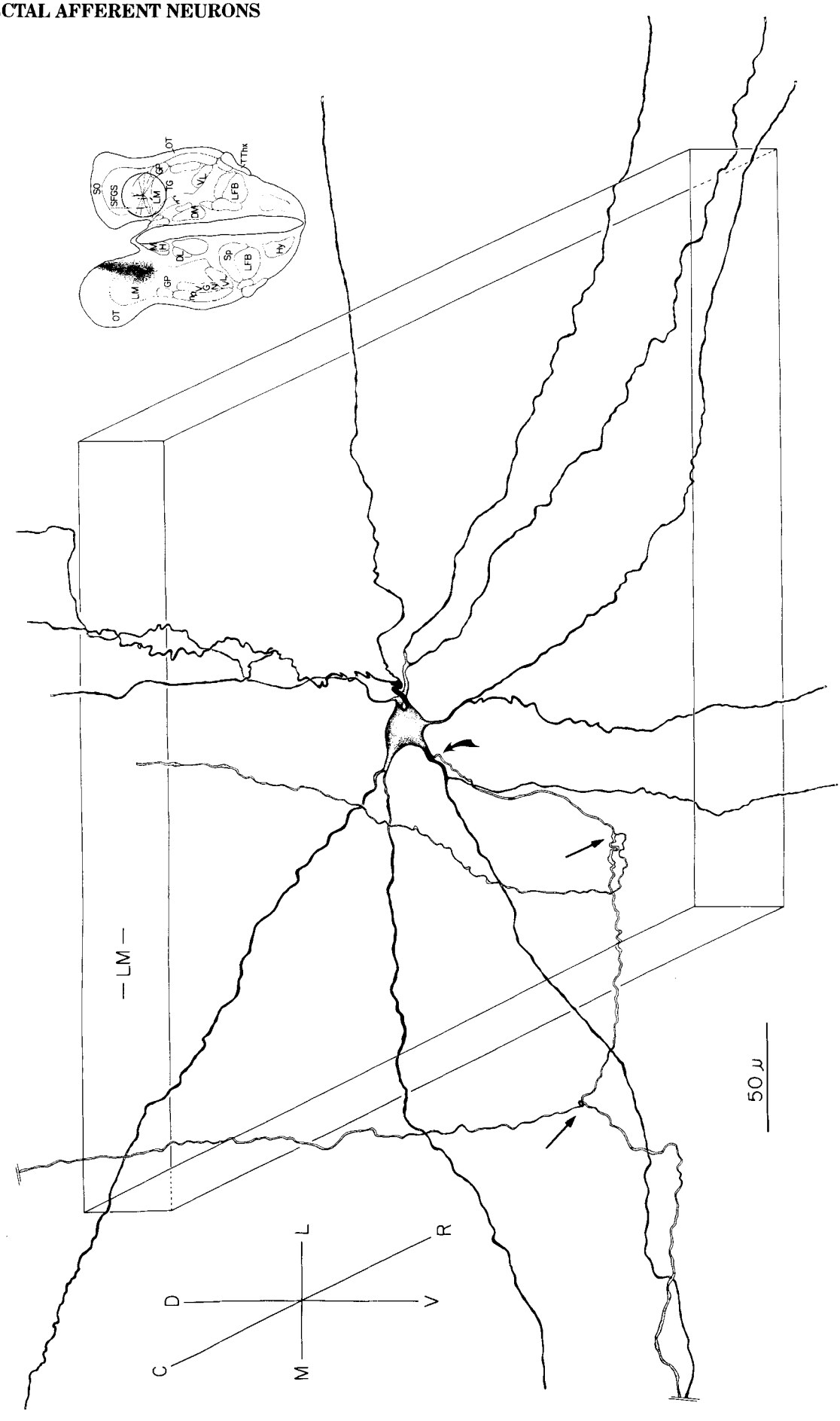

Fig. 12. Lentiform mesencephalic pretectal cell retrogradely filled from injections of HRP into the tectum. The dendrites are long, smooth, and unbranched and radiate for at least 250 μm from the soma. The axon (curved arrow) emits primary collaterals (straight arrows) that ascend into the stratum fibrosum et griseum superficiale. The parent axon crosses the midline in the posterior commissure. The inset at the upper right of the figure shows the injection site (stippling) and the position of this cell in the pretectum (circled area)

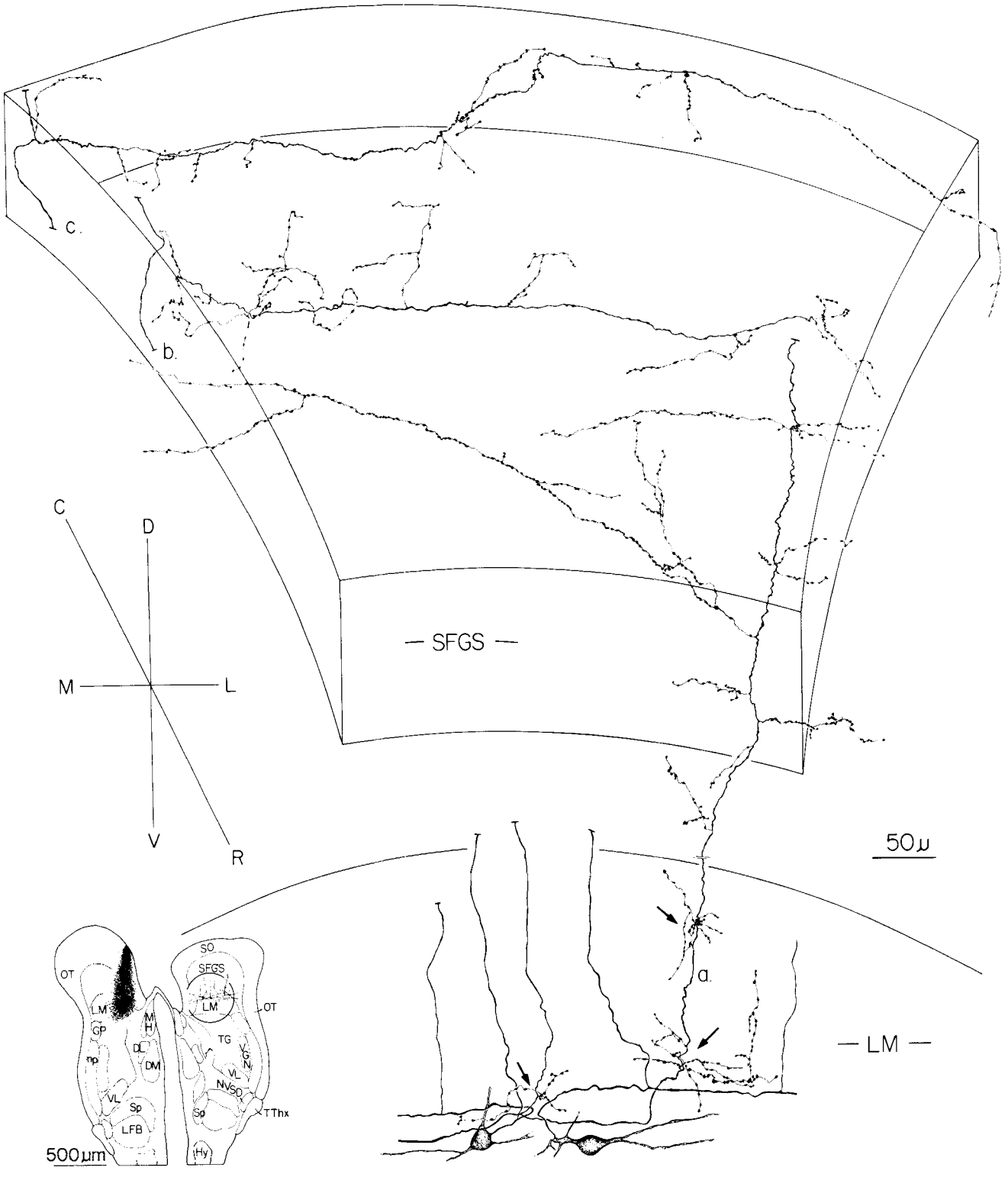

Fig. 13. Anterogradely filled tectal afferent terminals arising from cells of the lentiform mesencephalic nucleus (LM) after injections of HRP into the contralateral pretectal region. Primary axons were traced from the injection site (stippled area in inset at lower left) across the midline in the posterior commissure to cells of origin in the lentiform mesencephalic nucleus (circled area in inset at lower left). Primary collaterals from these axons emit short terminal branches in the pretectum that bear small clusters of boutons (arrows). The collaterals ascend into the tectum (a–c) and were traced up to 600 μm rostrocaudally within the stratum fibrosum et griseum superficiale. They give rise to terminal branches that course mediolaterally. These branches emit short branchlets that extend dorsoventrally within the stratum fibrosum et griseum superficiale. C-R, caudal-rostral; M-L, medial-lateral; D-V, dorsal-ventral.

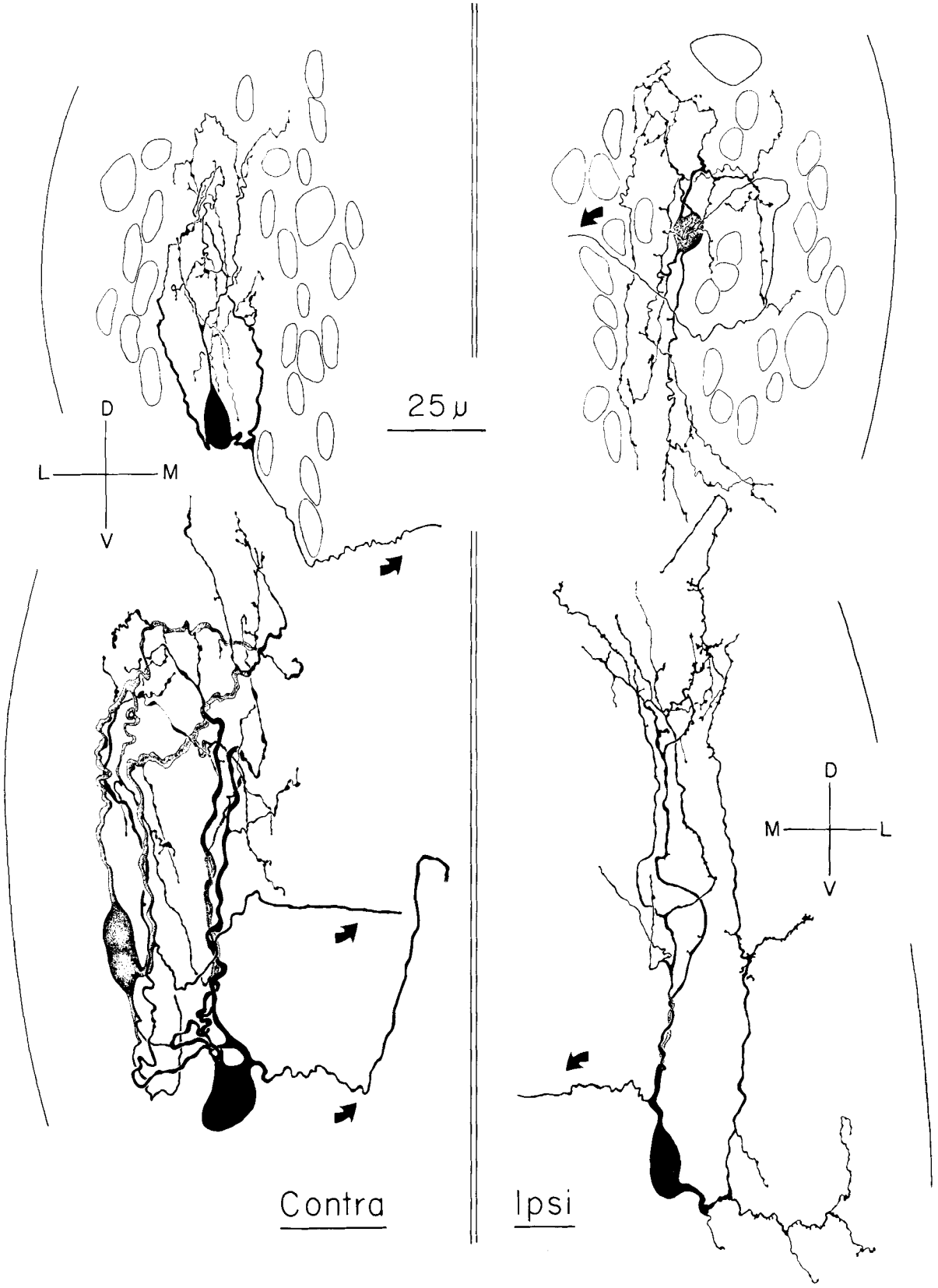

Fig. 14. Isthmotectal cells retrogradely filled from injections of HRP into the tectum. Both contralateral (Contra) and ipsilateral (Ipsi) projections arise from both small (shown at top of figure) and large neurons (shown at the bottom of figure). The dendrites of isthmotectal cells often recurve and intertwine. The axons of these cells are indicated by arrows. Outlines of the somata of a few counterstained isthmi neurons are included in the top tracings. The curved lines indicate the lateral surface of the brainstem. M-L; medial-lateral; D-V, dorsal-ventral.

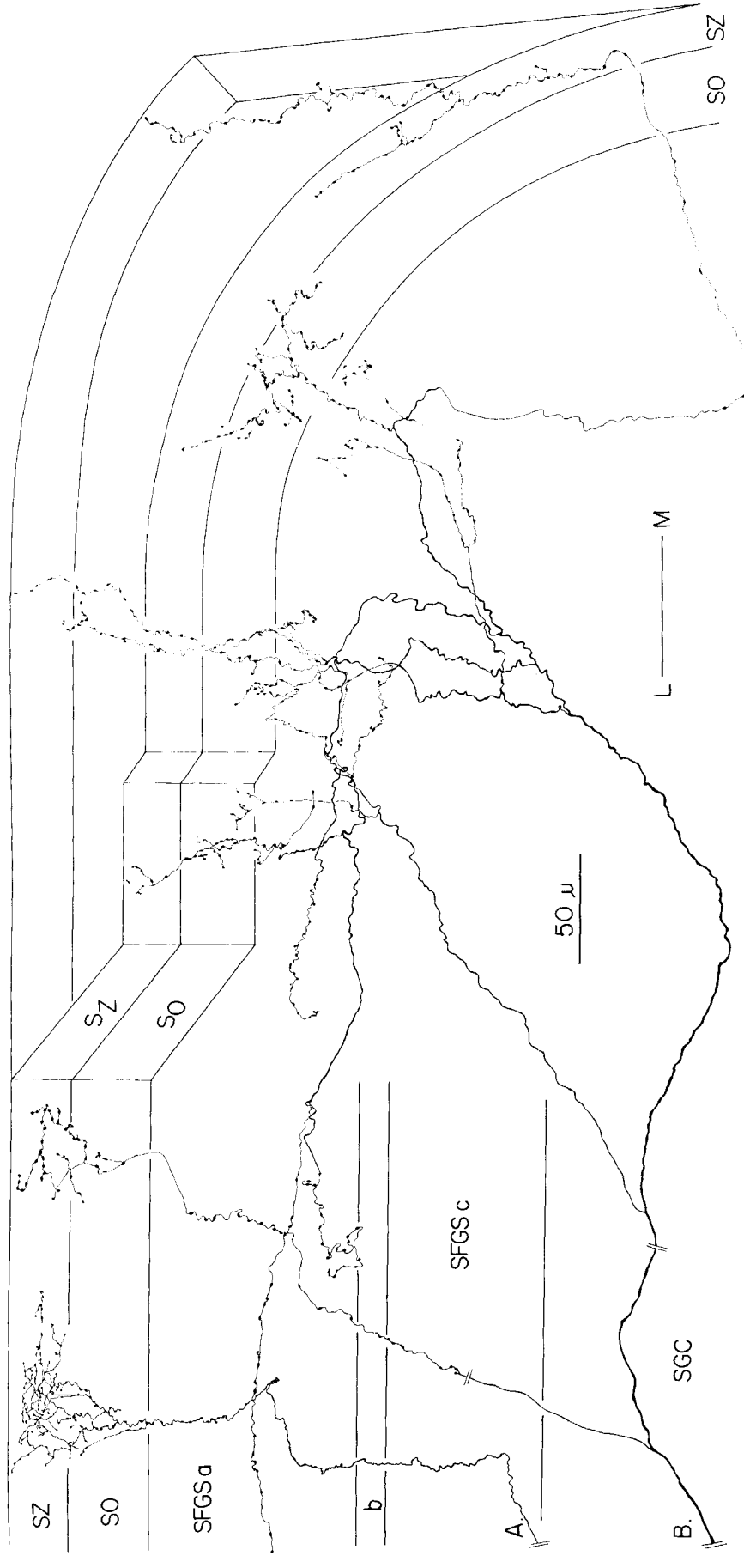

Fig. 15. Tectal afferent axons anterogradely filled from injections of HRP into nucleus isthmi. These fine-caliber axons ascend through the superficial gray and arborize principally in the stratum opticum (SO) and stratum zonale (SZ). Two types of terminal arbors were observed. The first type (A) derives from a fine-diameter fiber (less than 1 μm) and forms a single bushy arbor of about 80–100 μm in diameter. The second type (B) arises from a larger-diameter axon (about 1 μm) that gives rise to multiple thin collaterals. Each of these collaterals issues and widely branched terminal arbors that are patchily distributed over an area of several hundred microns.

divided into two broad groups by the size and shape of their terminal arbors.

Spatially restricted arbors. This first group includes afferents from the retina, ventral lateral geniculate nucleus, ventrolateral nucleus, and nucleus isthmi. Axons from these structures form single arbors in which the terminal boutons are restricted to a relatively small volume, but each arbor is distinct in the details of its structure and laminar distribution.

The retinotectal axons share a characteristic preterminal and terminal branching pattern that gives rise to ellipsoidal terminal arbors varying in size from 50 to 150 μm along their long axes. Single arbors are restricted to one of three distinct sublayers in the superficial tectum. Variation in parent axon diameter and terminal bouton size was observed among the arbors; however, arbors of all sizes and axon calibers were present in each of the three retinorecipient sublayers. Arbors deriving from the nucleus isthmi overlap the retinal arbors in the stratum zonale and show a similar size range, but are distinguished by their branching pattern and bouton distribution. The terminal branchlets of these arbors give rise to distinct, intertwined clusters of small boutons (less than 0.5 μm in diameter). Similar topographically organized isthmotectal arbors have been observed in birds (Ramón y Cajal, '11; Hunt et al., '77) and turtles (Sereno, '83); restriction of the crossed isthmotectal projection to the stratum zonale has also been observed in cats (Graybiel, '78a) and frogs (Gruberg and Udin, '78). Ventral geniculate cell plate neurons have arbors with a characteristic loose branching pattern in sublayer c of the stratum fibrosum et griseum superficiale. These arbors also are similar in size to the retinal arbors but are distinct in that they are restricted to the ventral half of the sublayer and show a clustering of terminal branchlets at the dorsal border of the stratum griseum centrale. By contrast, the putative arbors of ventrolateral nucleus neurons showed small, loose clusters of boutons distributed radially through most of the stratum griseum and album centrale.

Spatially distributed arbors. Embedded within this ordered framework of spatially restricted afferent arbors is a second type of afferent terminal which, by contrast, has a relatively widespread distribution in the tectum. These spatially distributed axons originate from neurons with large somata and large, sparsely branching dendritic trees in the lentiform mesencephalic nucleus of the pretectum, the nucleus lateralis profundus mesencephali of the midbrain reticular formation, and an unidentified subgroup of cells from the nucleus isthmi. Each shows a divergent projection within the tectum via multiple terminal collaterals. However, like the spatially restricted arbors, each also shows a laminar segregation, albeit a much broader one.

Axons of the lentiform mesencephalic nucleus neurons give rise to a terminal zone that spans the stratum fibrosum et griseum superficiale. Single reconstructed axons within this terminal zone course over much of the rostrocaudal extent of the tectum and give rise to several terminal collaterals. These collaterals are thin and extend for long distances parallel to the tectal surface, bearing small boutons "en passant" and occasional small bouton clusters.

The thicker-caliber lateralis profundus axons extend through the stratum griseum and album centrale and give rise to stout collaterals that ascend or descend vertically and bear distinct clusters of large boutons. These terminal clusters appear to appose the somata and primary dendrites of tectoreticular neurons.

Large-caliber isthmotectal axons branch widely, emitting a number of terminal collaterals that ascend to the stratum zonale where they form disjunct terminal arbors spread over an area of several hundred microns. A similar pattern of divergent branching of single HRP-filled axons has also been observed recently in a component of the isthmotectal projection of turtles (Sereno, '83).

The disjunct terminal collaterals of single axons shown in *Thamnophis* suggest the probable anatomical basis for the patchy or discontinuous distribution of many of the tectal afferents observed in autoradiographic studies (review: Huerta and Harting, '84). Recent studies of the nigrotectal projection in hamsters (Rhoades et al., '82) and in grey squirrels (May and Hall, '84) that used anterograde transport of HRP to demonstrate the projection also observed a patchy terminal field and concluded that it derived from terminal collaterals of nigrotectal axons. The present study, by reconstructing single axons, has shown that this pattern derives from multiple, irregularly spaced collaterals of *single* axons within the overall terminal field.

GENERAL DISCUSSION

The results of this and the preceding four papers (Dacey and Ulinski, '86a–d) have used extracellular injections of HRP to demonstrate the morphology of neurons that are efferent, intrinsic, and afferent to the optic tectum in the garter snake. Our approach has been to reconstruct single HRP-filled cells from serial sections so as to arrive at a composite view of the complete morphology of connectionally identified neurons at the light microscopic level. The results do not permit conclusions about the synaptic contacts among tectal neurons. However, they do permit an analysis of the spatial relations among tectal neurons that is essential for understanding the kinds of neural transformations that occur in the tectum. This section reviews the relation of the major findings to the problem of sensorimotor coding in the tectum.

Sensorimotor coding

It is generally accepted that the optic tectum (or superior colliculus) is involved in the production of natural orienting movements in response to sensory stimuli. In frogs, for example, the tectum is involved in orienting the body toward a visual stimulus (reviews: Ingle, '82; Grobstein et al., '83). In cats, the tectum mediates movements of the eyes, head, pinnae, and vibrissae toward visual, auditory, or somatosensory stimuli (Stein and Clamann, '81; reviews: Harris, '80; McIlwain, '82). In monkeys, the tectum is involved in the generation of rapid, reflexlike saccadic eye movements to visual targets (Schiller and Maunsell, '84; review: Wurtz and Albano, '80). In heat-sensitive snakes (whose tecta contain a topographic map of pit organ infrared receptors), the tectum is involved in localizing warm-blooded prey with the aid of infrared cues (Terashima and Goris, '75; review: Hartline, '84).

Evidence that the optic tectum is involved in the production of orienting movements derives principally from the finding that low-level electrical stimulation restricted to the tectum elicits orienting movements to a point in space that corresponds to the position of the electrode in the retinotopic map contained in the tectum. This result has led to the idea that the tectum participates in a transfor-

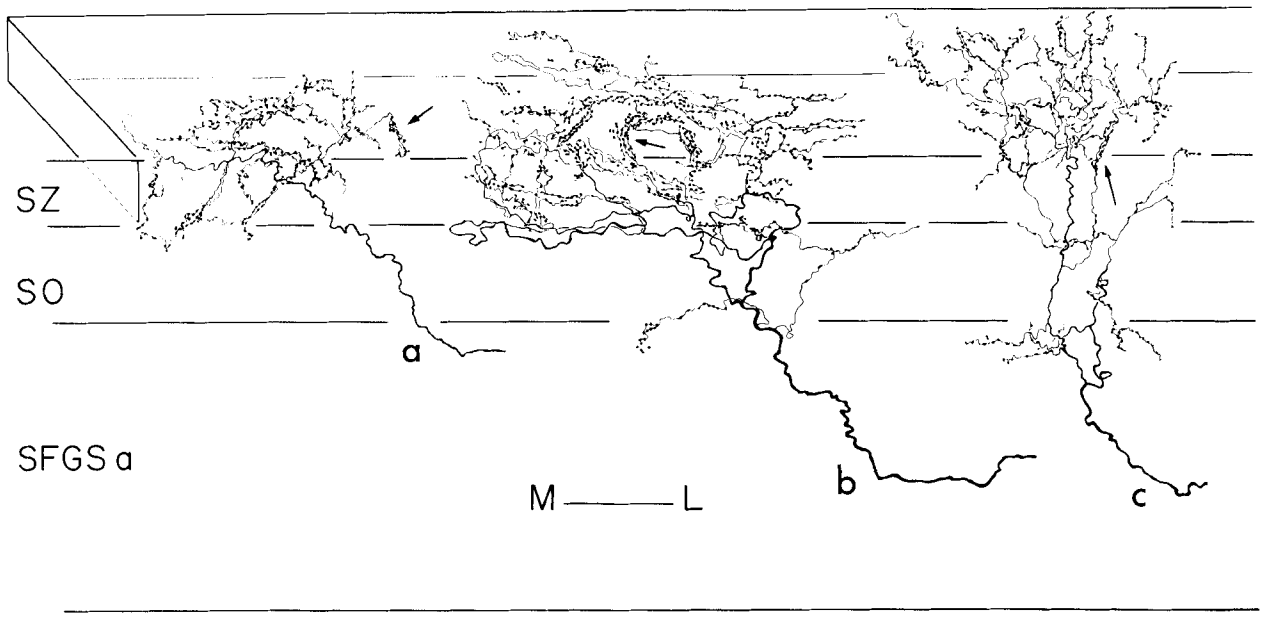

Fig. 16. Tectal afferent axons anterogradely filled after injections of HRP into the ventral supraoptic decussation. These axons form the crossed isthmotectal projection. Single parent axons ascend through the stratum fibrosum et griseum superficiale and terminate in single bushy arbors (about 80–100 μm in width) within the stratum zonale (SZ). Terminal branchlets intertwine to produce dense clusterings of terminal boutons (arrows). Many of the arbors emit a few collaterals that terminate at the border of the stratum opticum (SO) and the stratum fibrosum et griseum superficiale (a, b, e, f).

mation from topographically organized sensory inputs to a motor output (Ingle and Sprague, '75; Edwards, '80; Wurtz and Albano, '80; Ingle, '82; McIlwain, '82; Hall and May, '84). The neural mechanisms underlying this proposed sensorimotor transformation are not known, but they must—at least in part—involve interactions among the tectal neurons.

One possibility is that a sequence of topographically organized connections provides a functional link from the superficial layers of the tectum to the deeper layers of the tectum and in turn to the premotor centers of the brainstem (Sprague, '75; Comer and Grobstein, '78). Activation of a particular tectal locus by a sensory stimulus in a given region of visual space could then be linked to a specific movement that orients the animal to the appropriate region of the external world. The simplest neuronal model of this type requires a sequence of connections from a specific region of the tectum through the brainstem and to a particular population of motor neurons. The model can be tested by a variety of techniques. Anatomical studies should demonstrate a sequence of point-to-point connections from the superficial layers of the tectum through the brainstem to the vicinity of the motor neuron pools. Physiological studies should demonstrate the existence of restricted receptive or "movement" fields in neurons throughout this sequence. Behavioral studies should demonstrate that restricted lesions of the structures in the proposed sequence abolish orienting to particular regions of the external world.

However, recent experimental work has failed to support this concept of tectal sensorimotor coding. Anatomical studies have been unable to demonstrate such topographic intratectal connections (Edwards, '80; May and Hall, '84; Masino et al., '84). Physiological studies have drawn attention to the lack of a clear spatial topography in the deep tectum. A consistent finding is the presence of units with extremely large receptive fields in the deep tectal layers (reviews: McIlwain, '76; Goldberg and Robinson, '78; Chalupa, '84; Grusser-Cornehls, '84; Jassik-Gerschenfeld and Hardy, '84). Similarly, the motor-related discharge of tectal units in monkeys (their movement fields) occurs prior to a wide range of movements (Sparks et al., '76; Sparks and Mays, '80). Behavioral studies have shown that partial lesions of the tectum do not eliminate orienting movements of specific direction and amplitude, but instead have subtle effects on all orienting movements. In frogs, partial lesions of the tectum or its descending pathways produce a systematic "undershooting" in the orienting component of the prey capture sequence (Grobstein et al., '83). In monkeys, saccadic eye movements are not abolished by small tectal lesions. They instead fall short of their intended target and show an increased latency to onset (Wurtz and Goldberg, '72; Mohler and Wurtz, '77; Albano and Wurtz, '82). Similarly, it has been shown that focal injections of GABA agonists or antagonists produce either an increase or decrease in the latency, accuracy, and velocity of saccadic eye movements that is graded with the size of the injection of these substances (Hikosaka and Wurtz, '85). Thus, several lines of evidence suggest that the sensorimotor transformation does not involve a series of simple point-to-point or topographic connections.

Alternatively, it has been suggested that the information about tectal position needed for orienting movements is encoded in the graded activation of a large population of tectal neurons (McIlwain, '76, '82; Sparks and Mays, '81; Middlebrooks and Knudsen, '84; Wize and Irvine, '85). In this scheme, topographic input to the tectum results in the activation of a widespread population of tectal units with large, overlapping fields. Information about the position of the stimulus in the tectum is coded in the spatial pattern of activity in these units. A slight shift in the position of a

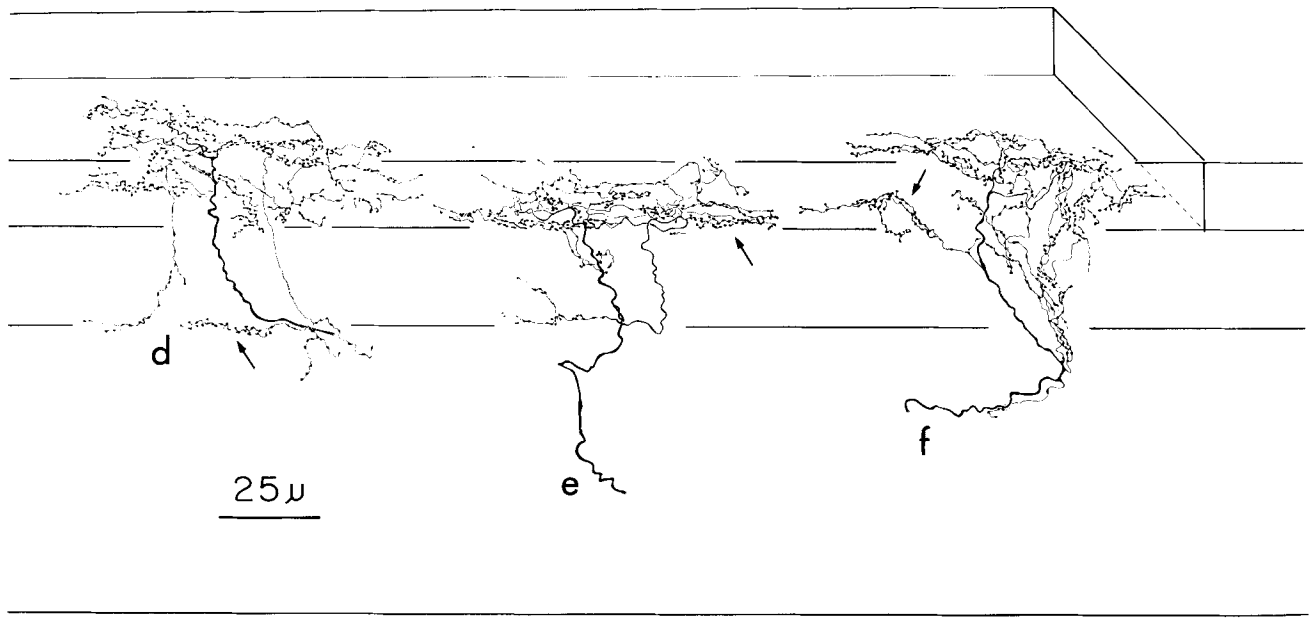

Figure 16 (cont'd)

stimulus is linked to a corresponding shift in the spatial distribution of activity in the tectum. Information about tectal position used in generating a movement signal is then extracted from this distributed representation.

However, the neural organization that could underlie such a graded population coding mechanism is not understood. A major difficulty has been in developing a detailed concept of the intrinsic organization of the tectum that includes an idea of the spatial relations among connectionally identified classes of neurons. This information is essential for determining the kinds of neural transformations that take place within the tectal circuitry. The results of this series provide a relatively comprehensive light microscopic picture of the morphology of tectal neurons and their connections in a single species. In the following, these results are used to develop a concept of tectal organization that considers the spatial organization or geometry of tectal neurons, and to outline a general hypothesis about how this geometry may provide a mechanism for graded population coding.

Neuronal geometry of the tectum

Tectal neurons can be divided into three broad groups by the size, shape, and distribution of their dendrites and axons: (1) spatially restricted neurons, (2) spatially mixed neurons, and (3) spatially distributed neurons. These groups are summarized diagrammatically in Figure 22. Each type of neuron has distinct anatomical features and could play a specific role in tectal function.

(1) *Spatially restricted neurons* have both dendritic fields and terminal axon arbors that are relatively small, or restricted, in size. A crossed tectoisthmi cell is illustrated in Figure 22 as an example of this kind of geometry. The tectogeniculate, ipsilateral tectoisthmi efferent, type B intrinsic, and the thalamotectal and isthmotectal afferent neurons are also spatially restricted. Each of these neurons shows a narrow, fusiform or globular dendritic tree, and spherical or rodlike axon arbors. The tectogeniculate, tectoisthmi, and type B cells all have narrow, cylindrical dendritic trees that extend into the retinorecipient layers of the tectum and are comparable in size (about 80–100 μm in diameter) to the terminal arbors of retinal ganglion cells. The intrinsic collaterals of these cells form narrow arbors of about the same width and in vertical alignment with their dendritic fields. The extrinsic collaterals of these axons also give rise to small, bushy arbors that are comparable in size to the dendritic trees of likely target neurons in nucleus isthmi and the thalamus. Similarly, the isthmal and thalamic afferents to the tectum form single, small arbors that are comparable in width to the retinal arbors and the dendritic trees of the spatially restricted tectal neurons.

It seems clear that the spatially restricted neurons determine a set of projections that preserve point-to-point topographic information necessary on the input side of the sensorimotor transformation. In *Thamnophis* there is a clear spatial match between the widths of the topographically organized retinal and nonretinal terminal arbors and the narrow, radial dendritic trees of the spatially restricted and the spatially mixed tectal neurons. This type of spatial match between the size of retinal terminals and likely target neurons in the superficial layers of the tectum has also been recently shown in the grey squirrel (May, '81) and is apparent in Golgi studies of other vertebrates (e.g., Ramón y Cajal, '11; Quiroga, '78). Intracellular recording and staining studies in a variety of species show that these cells have small receptive fields (Niida et al., '80; Ogawa and Takahashi; '81; Hardy et al., '83; McCrea and Grobstein, '83; Mooney et al., '84).

(2) *Spatially mixed neurons* have spatially restricted dendritic trees but spatially distributed axon arbors. These neurons include the tectorotundal (shown in Fig. 22), the tectoisthmobulbar efferent, and the type C and D intrinsic neurons. All of these neurons have narrow, vertically aligned dendritic fields that are similar in width (about 80–100 μm) to the dendritic trees of the spatially restricted neurons and axon terminals. The tectoisthmobulbar cell

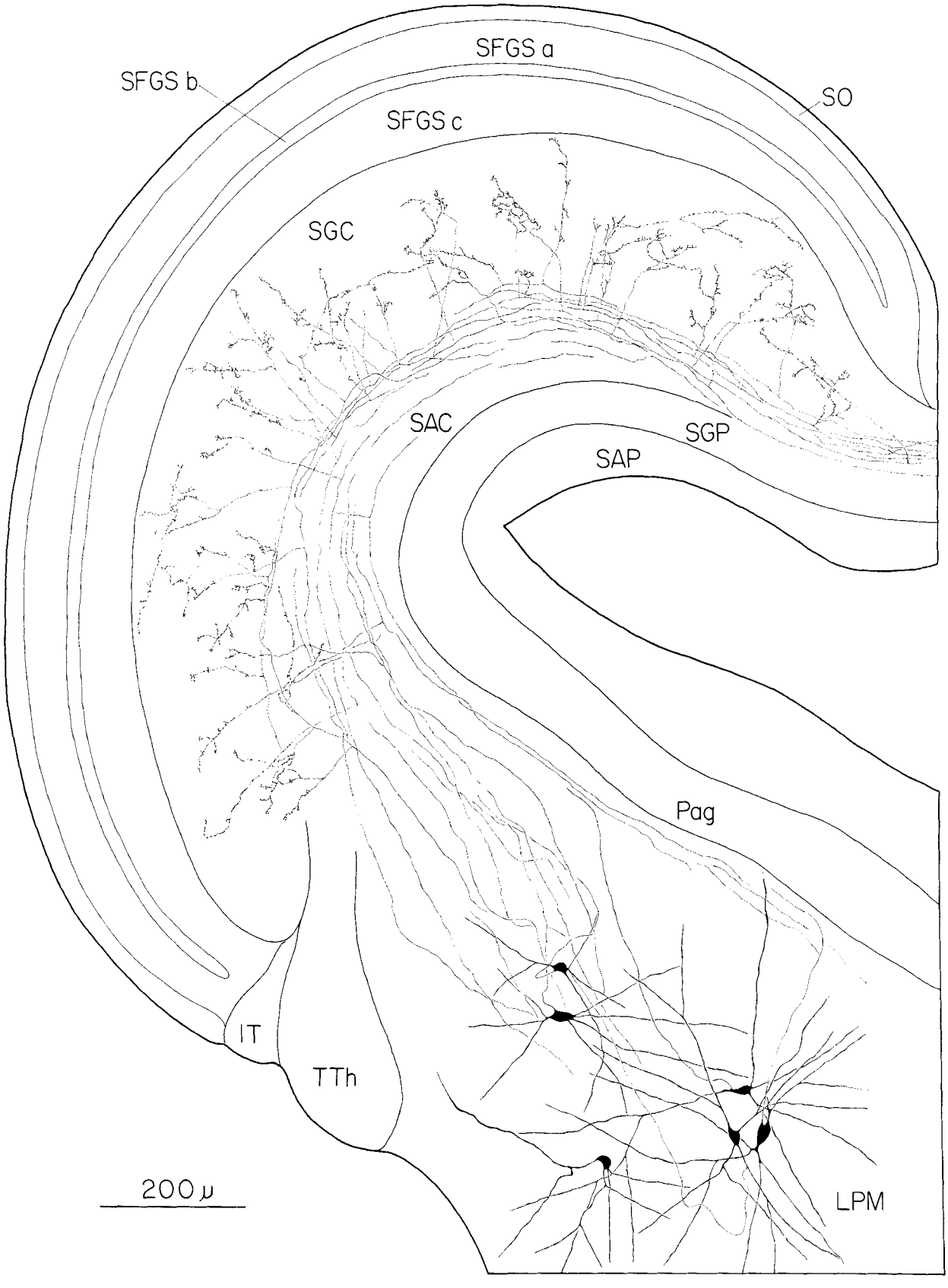

Fig. 17. Tectal afferents from nucleus lateralis profundus mesencephali (LPM) retrogradely filled from injections of HRP into the opposite tectal hemisphere. Large-caliber axons arise from the multipolar cells of LPM and ascend into the stratum album centrale (SAC), course medially, and cross the midline in the tectal commissure. Multiple terminal collaterals arise from each parent axon and ascend radially into the stratum griseum centrale (SGC) but do not extend into the superficial retinorecipient layers.

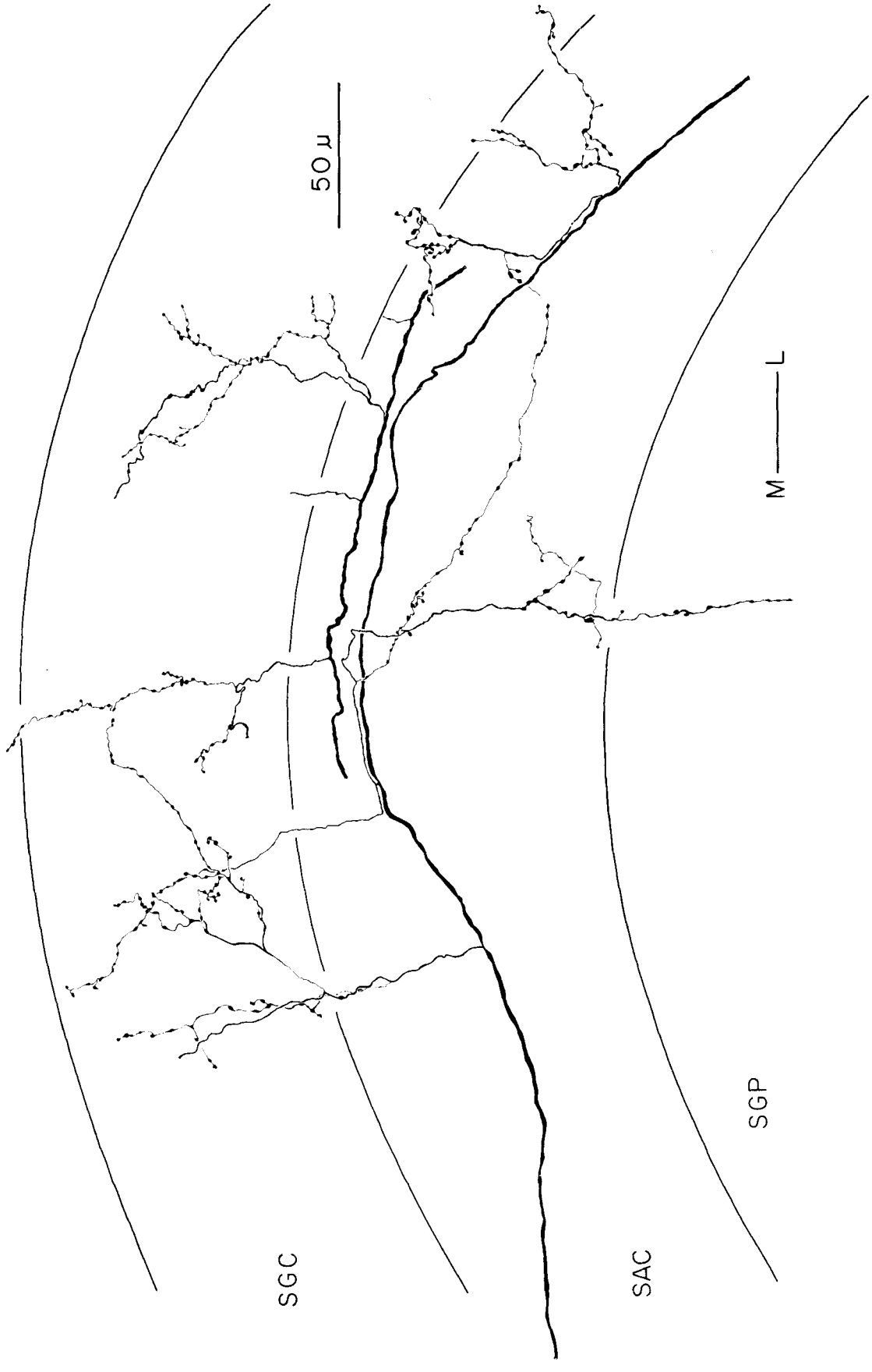

Fig. 18. Segments of single axons of lateralis profundus mesencephali cells in the tectum. These axon segments were traced through serial sections back to their parent cells in LPM in the case shown in Figure 17. A single axon issues multiple primary collaterals that in most instances ascend into the stratum album centrale (SAC) and the stratum griseum centrale (SGC). Each collateral bears clusters of large terminal boutons. M-L, medial-lateral; SGP, stratum griseum periventriculare.

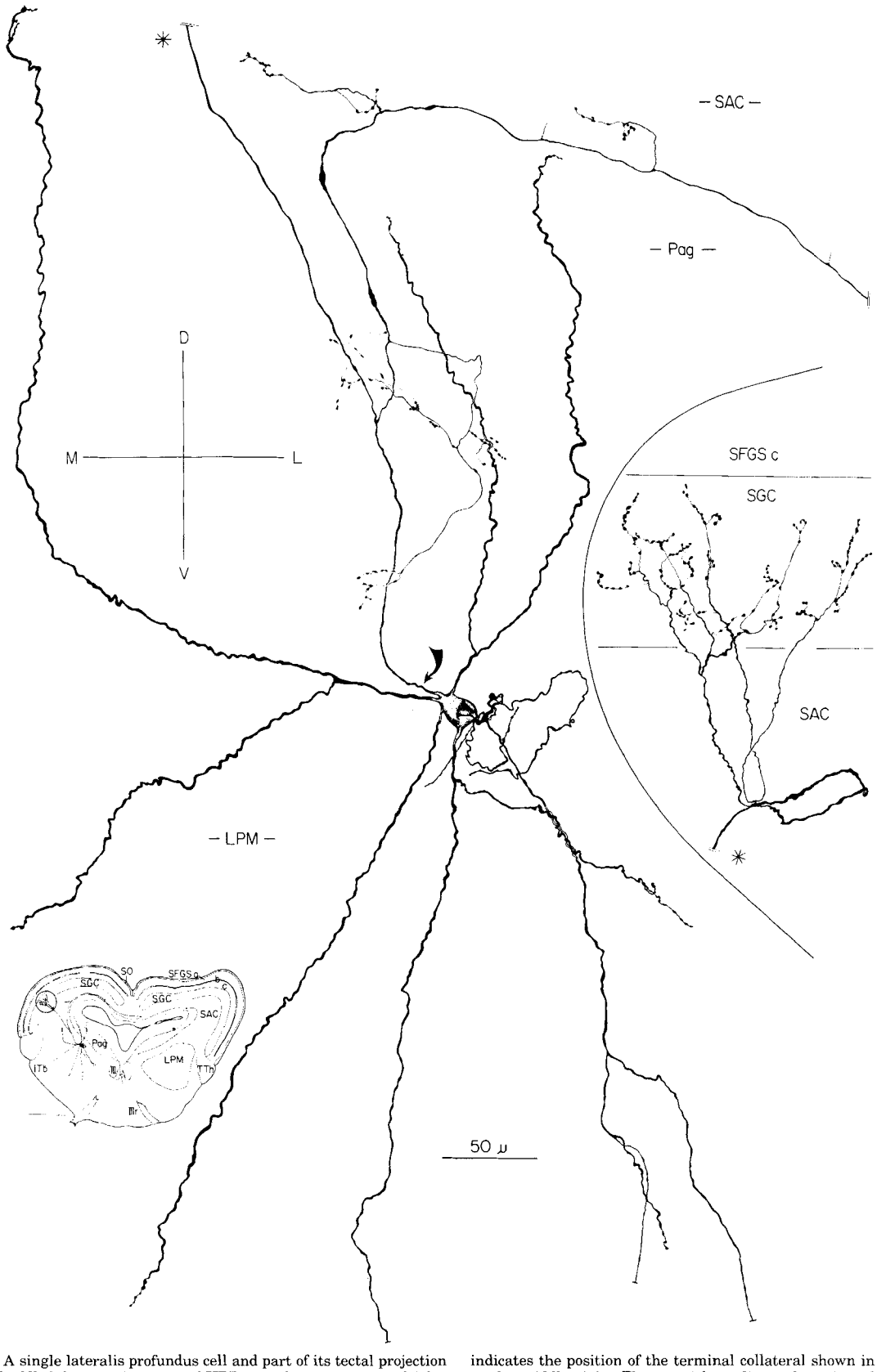

Fig. 19. A single lateralis profundus cell and part of its tectal projection retrogradely filled from an injection of HRP into the opposite tectal lobe. This large multipolar cell and its axon were reconstructed through five 80-μm serial sections. The inset at the lower left shows the position of the cell in the section that contained the cell body. The circled area in the inset indicates the position of the terminal collateral shown in the second inset at the middle right. The asterisks indicate the point where the primary collateral was separated from its terminal arbor for illustrative purposes. The origin of the axon is indicated by the arrow. D–V, dorsal-ventral; M–L, medial-lateral.

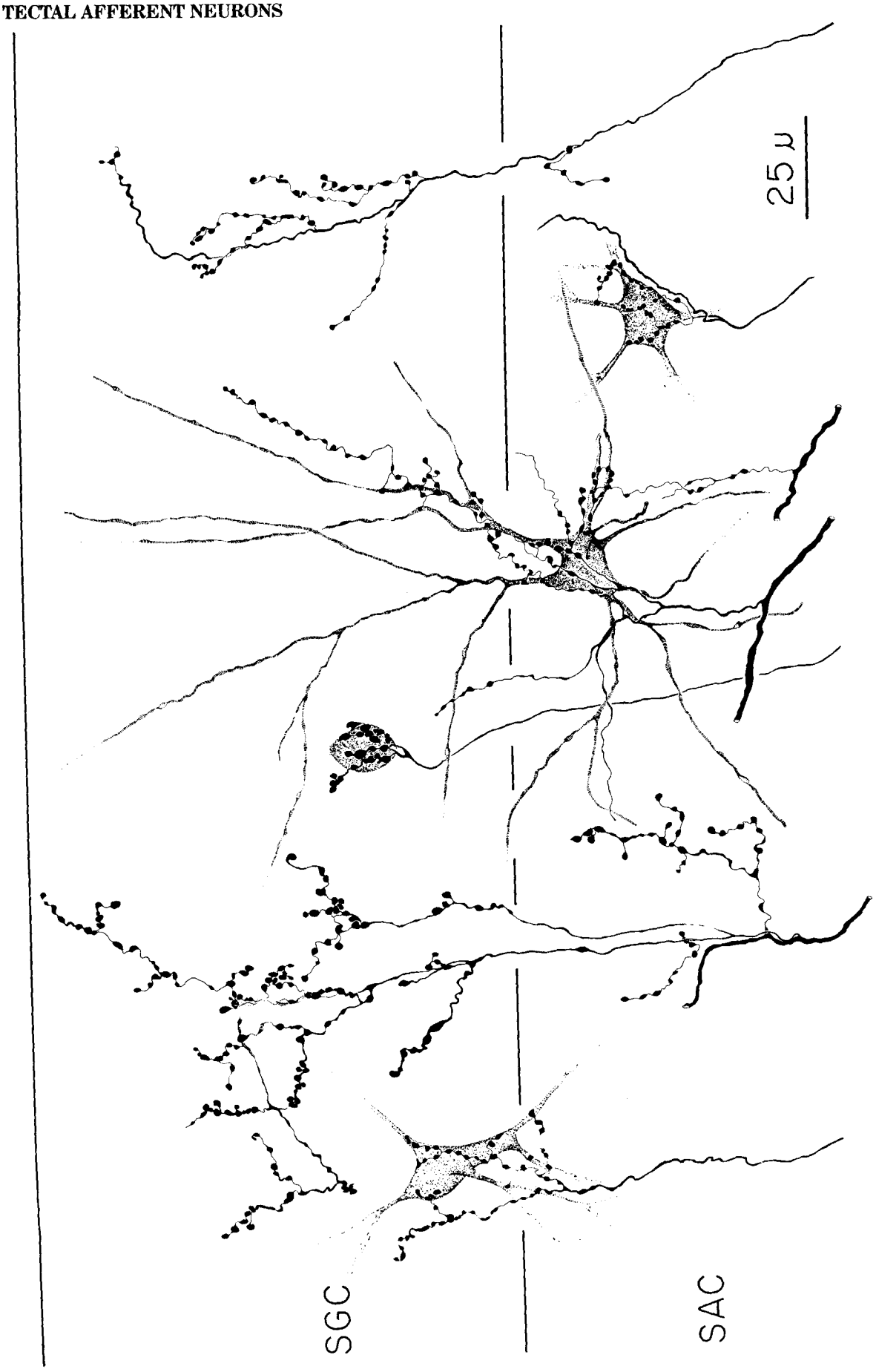

Fig. 20. Tectal afferent terminals anterogradely filled from injections of HRP into the midbrain tegmentum. The morphology and distribution of these arbors match that shown to arise from lateralis profundus mesencephali neurons. Tectobulbar neurons were also retrogradely filled from the injections and are illustrated as stippled profiles. The terminal boutons of these afferents appear apposed to the somata and primary dendrites of the labeled tectobulbar cells.

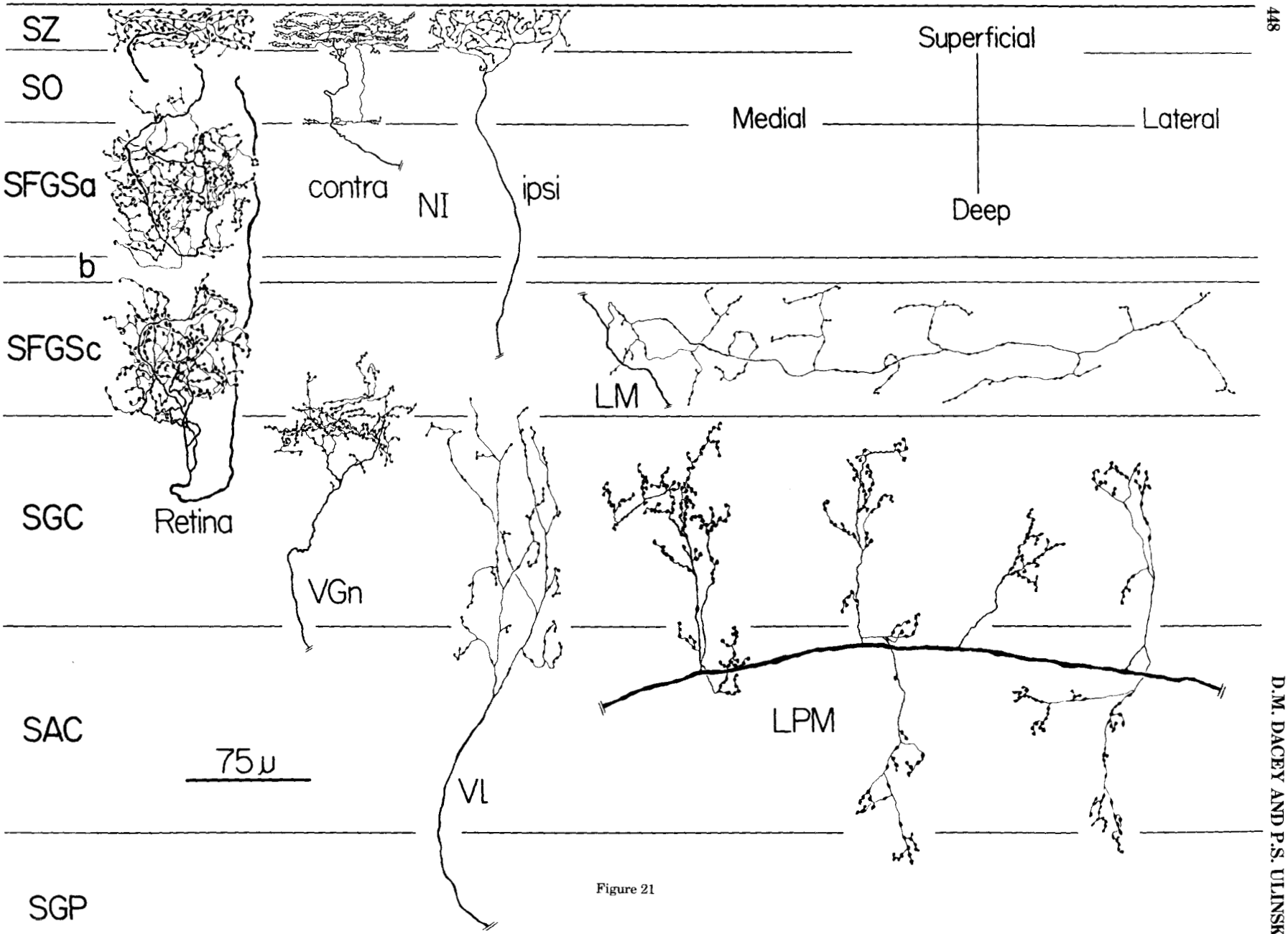
SZ
SO
SFGSa
b
SFGSc
SGC
SAC
SGP
Retina
contra
NI
ipsi
Superficial
Medial
Lateral
Deep
LM
VGn
VI
LPM
75 μ

Figure 21

has a spatially restricted axon terminal in nucleus isthmi that is similar in shape and size to that of the other tectoisthmi projection, but its collateral to the reticular formation shows a spatially distributed geometry like that of the other tectobulbar axons. Single axons of tectorotundal cells extend widely throughout nucleus rotundus and the lack of topography in this projection has been well documented (Dacey and Ulinski, '83). The intrinsic axon collaterals of the tectorotundal, type C, and type D intrinsic neurons all share a spatially distributed projection into the deep tectal layers. The intratectal collaterals of these neurons have a widespread horizontal distribution that extends at least 500 μm outside of the cells' dendritic fields. In the type C and D intrinsic neurons these axons are asymmetric, extending either medially (type C) or laterally (type D) away from the cell's dendritic field.

The organization of the spatially mixed neurons suggests involvement in a spatial transformation within the tectum. The tectorotundal and type C intrinsic neurons have restricted dendritic fields, are likely to receive retinal input, and have relatively small receptive fields. However, their intratectal axon collaterals have a widespread distribution in the deep tectal layers and could have a divergent input to a large population of tectobulbar cells whose dendrites are restricted to the deep tectum. Physiological studies of single tectal units in cats and monkeys may provide some insight into this type of organization. Microstimulation of the type used to elicit natural orienting movements leads to the transsynaptic activation of tectoreticular cells up to 3 mm from the stimulation site (McIlwain, '82). Similarly, the large movement fields of saccade-related burst neurons in the monkey indicate that a large population of tectoreticular cells is activated prior to a movement (Sparks and Mays, '80). This activation could be mediated by the convergence of several types of spatially mixed neurons upon the large, overlapping dendritic fields of tectoreticular cells and is consistent with the existence of extremely large receptive fields of deep tectal units in all vertebrate classes. Spatially distributed intrinsic tectal connections have not been observed in cats, but they have recently been observed in hamsters (Mooney et al., '84,'85), turtles (Sereno and Ulinski, '85), and frogs (McCrea and Grobstein, '83) in HRP-filled neurons. The results in *Thamnophis* suggest that the intratectal connections are markedly asymmetric. The axon arbors of the type C neurons are medially displaced from their dendritic trees whereas the intrinsic projections of the type D neuron are laterally displaced. It is thus possible that these neurons mediate a transsynaptic spread of excitation or inhibition either medially or laterally away from an initial stimulus point. This could result in a systematic relation between the position of a stimulus and the spatial distribution of resulting activity.

(3) *Spatially distributed* neurons have much larger dendritic trees than the spatially restricted neurons and highly collateralized axons that do not show a point-to-point or topographic organization. The crossed tectobulbar cell illustrates this type of geometry in Figure 22. The ipsilateral tectobulbar, type A intrinsic, and the tectal afferent neurons of the midbrain reticular formation and pretectum are also spatially distributed. The type A intrinsic neurons have long, horizontally radiating dendrites and axon collaterals that cut across the vertical topographic organization of the retinorecipient layers. Electron microscopic studies suggest that the varicose dendrites of horizontal cells are presynaptic to the radial dendrites of other tectal cells and postsynaptic to retinal terminals. The entire horizontal cell dendritic tree thus receives convergent input from retinal terminals and can potentially influence a large number of tectal cells via its dendritic output or its axon. The tectobulbar cells have similarly widespread dendritic trees in the deeper tectal layers. Reconstructed axons of these cells are highly collateralized and extend from the midbrain to the caudal medulla and spinal cord. Single collaterals show a sparse distribution of boutons that are widely distributed in a given terminal zone. Similarly, tectal projecting neurons in the nucleus lateralis profundus mesencephali and the lentiform mesencephalic nucleus have large, sparsely branching dendritic fields and single axons that collateralize in the tectum to produce a sparse but widespread distribution of terminal boutons.

The anatomy of the spatially distributed neurons suggests involvement in a transformation from spatial coordinates to a code in the temporal domain expressed in the discharge frequency of target neurons. Recent hypotheses about the role of the tectum in generating a movement signal suggest a spatial to frequency transformation of this type must be involved (Sparks and Mays, '81; McIlwain, '82; Wurtz and Albano, '80). Thus, the evidence from recent studies of the oculomotor system in cats and monkeys show that the discharge frequency of midbrain and pontine reticular neurons is correlated with motor neuron discharge frequency and movement amplitude (review: Robinson, '81). The geometry of the tectobulbar axons suggests a neural mechanism that could accomplish such a spatial to frequency transformation. Because of their distributed geometry, target neurons in the brainstem reticular formation could receive convergent input from a large population of these tectobulbar cells. Assuming linear and spatial summation, the number of tectal cells active could be represented in the synaptic drive to the target neuron, and, presumably its discharge frequency. Variations in the number of tectobulbar neurons with tectal position or variation in the number of terminal boutons from a single axon in a given terminal zone could produce a synaptic weighting factor that would reflect the spatial distribution of tectal activity. There is some evidence for an increased density of tectobulbar neurons in the caudolateral tectum (Edwards and Henkel, '78; Sereno and Ulinski, '85), where peripheral visual fields and larger movement amplitudes are represented. Reconstructions of tectoreticular axons in cats (Grantyn and Grantyn, '82), turtles (Sereno, '85), and in *Thamnophis* (Dacey and Ulinski, '86a) all suggest that bouton numbers from individual axons may vary significantly. However, the relation of cell number or bouton number to tectal position has not yet been studied systematically in any species.

Fig. 21. Tectal afferent arbors. This figure summarizes the morphology and laminar distribution of retinal terminals (Dacey and Ulinski, '86d) and the major afferents from the brainstem. All arbors show a characteristic laminar position. Terminals from the retina, ventral lateral geniculate nucleus (VGN), ventrolateral nucleus (VL), and the nucleus isthmi (Ist) contralateral and ipsilateral projections) occupy spatially restricted cylindrical domains 65–85 μm in diameter. By contrast, axons from the pretectal nucleus, lentiformis mesencephali (LM), and the nucleus lateralis profundus mesencephali (LPM) and a second arbor type from the nucleus isthmi (not shown; see Fig. 15) show a widespread horizontal and rostrocaudal distribution in the superficial and deep tectum, respectively. The arbors have been drawn semischematically and approximately to scale.

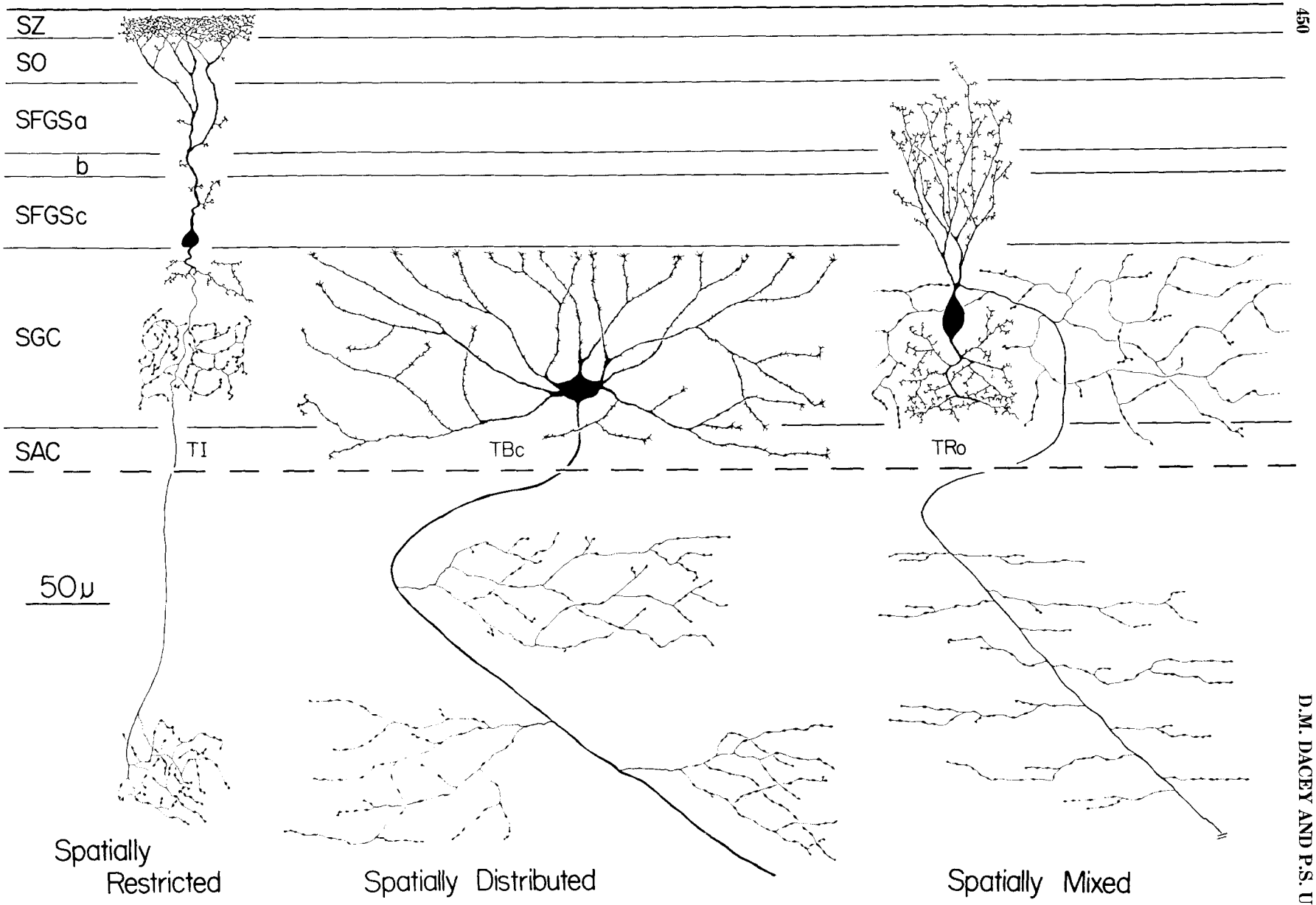

Fig. 22. Geometries of tectal neurons. Tectal neurons can be divided into three broad groups by the spatial organization of their dendrites and axon arbors. Examples of each group are illustrated semischematically in this figure, which is based on the results presented in Dacey and Ulinski ('86a, b). (1) *Spatially restricted neurons* have narrow, radial dendritic trees and single, compact terminal axon arbors. A tectoisthmi neuron (TI) is shown as an example of this type of morphology. (2) *Spatially mixed neurons* have narrow, radial dendritic trees like that of the spatially restricted neurons but have axon arbors with a divergent or widespread terminal distribution. A tectorotundal neuron (TRo) is shown as an example of this type of morphology. (3) *Spatially distributed neurons* have widespread dendritic fields and highly collateralized axon arbors. A crossed tectobulbar neuron (TBc) is shown as an example of this type of morphology.

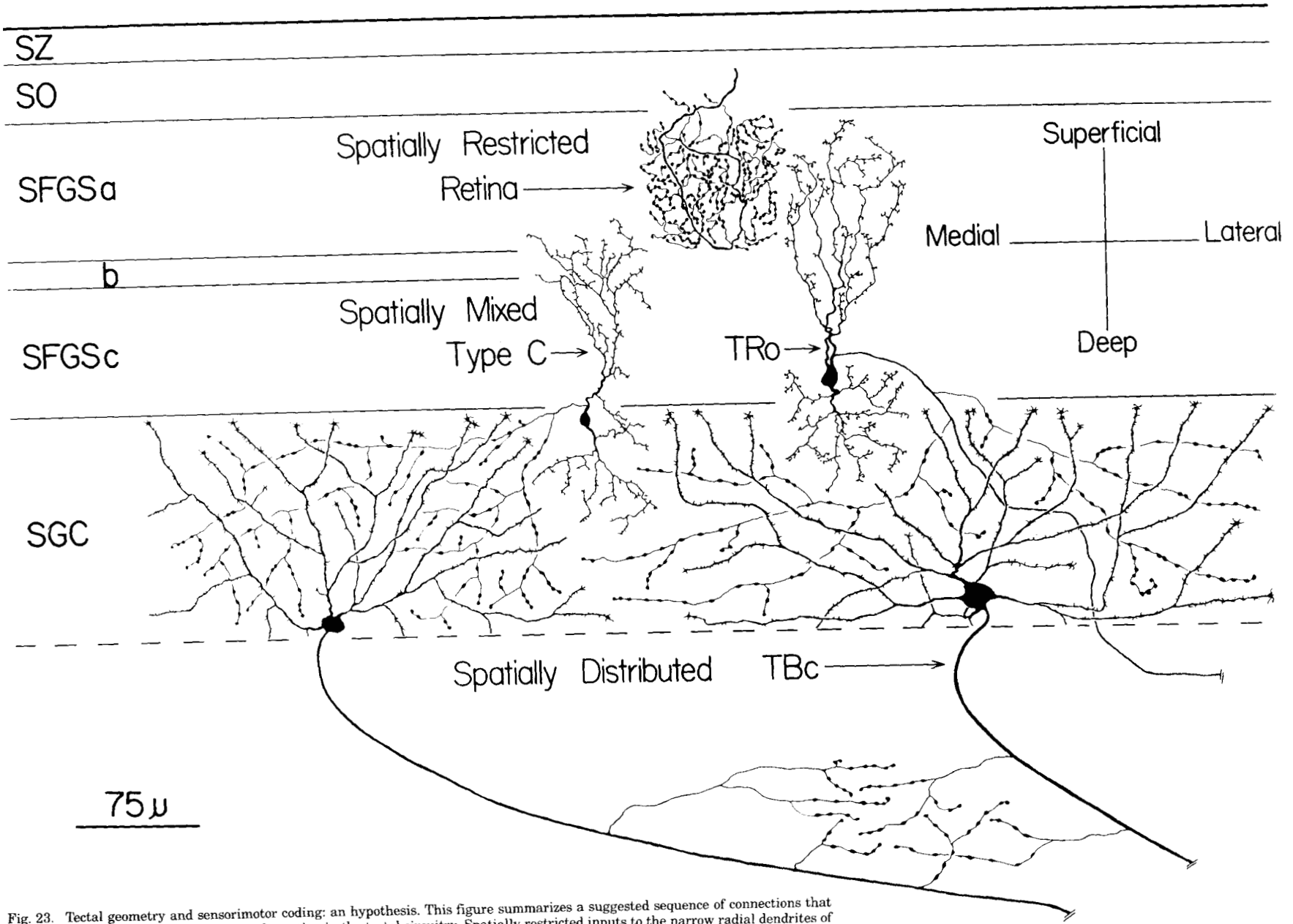

Fig. 23. Tectal geometry and sensorimotor coding: an hypothesis. This figure summarizes a suggested sequence of connections that could subserve a spatial to frequency transformation in the tectal circuitry. Spatially restricted inputs to the narrow radial dendrites of spatially mixed neurons may preserve retinotopic order in the superficial layers. This is illustrated as retinal input to the type C intrinsic neurons and the tectorotundal efferent neurons. However, the widespread intratectal connections of these neurons to the deep tectum determine a nontopographic spatial transformation that encodes information about tectal position in the size and spatial distribution of an activated population of tectobulbar neurons (TBc). This pattern is encoded temporally as discharge frequency in brainstem target neurons via summation of convergent inputs from the spatially distributed axons of tectobulbar cells.

Summary: Neuronal geometry and sensorimotor coding

The above ideas lead to a general hypothesis about the neural organization linking topographically organized sensory maps in the tectum to the motor-related discharge of neurons in the brainstem reticular formation. The hypothesis is summarized schematically in Figure 23; it suggests at least three synaptic steps in the tectal portion of the postulated sensorimotor transformation. The first involves a preservation of topographic order in the superficial layers of the tectum. This is illustrated as a connection between the spatially restricted retinal arbors and the narrow dendritic trees of the spatially mixed tectorotundal (TRo) and type C intrinsic neurons. The second step is a spatial transformation in which activity at a given location in the superficial layers is represented as a widespread spatial pattern of activity in the deep tectal layers. This transformation is accomplished by the widely spreading intratectal connections of the spatially mixed neurons to the dendrites of the spatially distributed neurons such as the crossed tectobulbar cells (TBc). In the final step the spatial pattern of activity of tectobulbar neurons undergoes a space to frequency transformation and is represented as the discharge frequency of brainstem premotor neurons. This is accomplished by spatial summation of convergent inputs from the axons of tectobulbar cells. This proposed circuitry, of course, does not include all of the neurons that have been described in these studies, nor do these studies consider all the problems of structure and function in the tectum. This circuitry does, however, constitute a model of the tectal sensorimotor transformation that is stated in terms of anatomically defined populations of tectal neurons and considers the role of neuronal geometry in a space to frequency transformation.

The hypothesis outlined above suggests that there are major lateral interconnections among specific populations of tectal neurons and it predicts that the total spatial pattern of these interconnections is critical for the behaviorally relevant output of the tectum. Thus an important area of future work will be to assess in detail the effects of inactivating small regions of tectum on the response properties of motor-related tectal cells and on the movements elicited by microstimulation of the tectum.

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LITERATURE CITED

Albano, J.E., and R.H. Wurtz (1982) Deficits in eye movements following ablation of the monkey superior colliculus, pretectum and posterior medial thalamus. J. Neurophysiol. *48:*318–337.

Chalupa, L.M. (1984) Visual physiology of the mammalian superior colliculus. In H, Vanegas (ed): Comparative Neurology of the Optic Tectum. New York: Plenum Press, pp. 775–818.

Comer, C., and P. Grobstein (1978) Prey acquisition in atectal frogs. Brai. Res. *153:*217–221.

Crossland, W.J., and C.J. Uchwat (1979) Topographic projections of the retina upon the ventral lateral geniculate nucleus in the chick. J. Comp. Neurol. *185:*87–106

Dacey, D.M. (1980a) Reciprocal tectogeniculate connections in a snake, (*Thamnophis sirtalis*). Neurosci. Abstr. *6:*748.

Dacey, D.M. (1980b) Intrinsic organization of the optic tectum in snakes: The optic terminal layer. Anat. Rec. *196:*40a.

Dacey, D.M., and P.S. Ulinski (1983) Nucleus rotundus in a snake, *Thamnophis sirtalis*: An analysis of a non-retinotopic projection. J. Comp. Neurol. *216:*175–191.

Dacey, D.M., and P.S. Ulinski (1986a) Optic tectum of the eastern garter snake, *Thamnophis sirtalis*: I. Efferent pathways. J. Comp. Neurol. *245:*1–28.

Dacey, D.M., and P.S. Ulinski (1986b) Optic tectum of the eastern garter snake, *Thamnophis sirtalis*: II. Morphology of efferent cells. J. Comp. Neurol. *245:*198–237.

Dacey, D.M., and P.S. Ulinski (1986c) Optic tectum of the eastern garter snake, *Thamnophis sirtalis*: III. Morphology of intrinsic neurons. J. Comp. Neurol. *245:*283–300.

Dacey, D.M., and P.S. Ulinski (1986d) Optic tectum of the eastern garter snake, *Thamnophis sirtalis*: IV. Morphology of afferents from the retina. J. Comp. Neurol. *245:*301–318.

duLac, S., and D.M. Dacey (1981) Relation of the retina and optic tectum to the lateral geniculate complex in garter snakes, *Thamnophis sirtalis;*. Neurosci. Abst. *7:*460.

duLac, S., D.M. Dacey, and P.S. Ulinski (1986) Lateral geniculate complex in the eastern garter snake, *Thamnophis sirtalis;* I. Cytoarchitecture and afferent connections. In preparation.

Edwards, S.B. (1980) The deep cell layers of the superior colliculus: Their reticular characteristics and structural organization. In J.A. Hobson and M.S.B. Brazier (eds): The Reticular Formation Revisited. New York:Raven Press, pp. 193–210

Edwards, S.B., and J.S. deOlmos (1976) Autoradiographic studies of the midbrain reticular formation: Ascending projections of the nucleus cuneiformis. J. Comp. Neurol. *165:*417–432.

Edwards, S.B., C.L. Ginsburgh, C.K. Henkel, and B.E. Stein (1979) Sources and subcortical projections to the superior colliculus in the cat. J. Comp. Neurol. *184:*309–330.

Edwards, S.B., and C.K. Henkel (1978) Superior colliculus connections with the extraocular motor nuclei in the cat. J. Comp. Neurol. *179:*451–468.

Elprana, D., F.G. Wouterlood, and V.E. Alones (1980) A corticotectal projection in the lizard (Agama agama). Neurosci. Lett. *18:*251–256.

Goldberg, M.E., and D.L. Robinson (1978) Visual system: superior colliculus. In R.B. Masterson (ed): Handbook of Behavioral Neurobiology, Vol. 1. New York: Plenum Press, pp. 119–164.

Grantyn, A., and R. Grantyn (1982) Axonal patterns and sites of termination of cat superior colliculus neurons projecting in the tecto-bulbospinal tract. Exp. Brain Res. *46:*243–256.

Graybiel, A.M. (1978a) A satellite system of the superior colliculus: The parabigeminal nucleus and its projection to the superficial collicular layers. Brain Res. *145:*365–374.

Graybiel, A.M. (1978b) Organization of the nigrotectal connection: An experimental tracer study in the cat. Brain Res. *143:*339–348.

Grobstein, P.C., C. Comer, M. Hollyday, and S.M. Archer (1978) A crossed isthmotectal projection in *Rana pipiens* and its imvolvement in the ipsilateral visuotectal projection. Brain Res. *156:*117–123.

Grobstein, P.E., C. Comer, and S.K. Kostyk (1983) Frog prey capture behavior: Between sensory maps and directed motor output. In J-P. Ewert, R.R. Capranica, and D.J. Ingle (eds): Advances in Vertebrate Neuroethology. New York: Plenum Press, pp. 331–348.

Gruberg, E.R., and B. Udin (1978) Topographic projections between nucleus isthmi and the tectum of the frog *Rana pipiens*. J. Comp. Neurol. *179:*487–500.

Gruberg, E.R., E. Kicliter, E.A. Newman, L. Kass, and P.H. Hartline (1979) Connections of the tectum of the rattlesnake *Crotalus viridis*: An HRP study. J. Comp. Neurol. *188:*31–42.

Grusser-Cornehls, U. (1984) The neurophysiology of the amphibian optic tectum. In H. Vanegas (ed): Comparative Neurology of the Optic Tectum. New York: Plenum Press, pp. 211–246.

Hall, J.A., R.E. Foster, R.F. Ebner, and W.C. Hall (1977) Visual cortex in a turtle (*Pseudemys scripta* and *Chrysemys picta*). Brain Res. *130:*197–216.

Hall, W.C., and P.J. May (1984) The anatomical basis for sensorimotor transformations in the superior colliculus. In W.D. Neff (ed): Contributions to Sensory Physiology. Orlando: Academic Press, pp. 1–40.

Halpern, M., and N. Frumin (1973) Retinal projections in a snake (*Thamnophis sirtalis*). J. Morphol. *141:*359–382.

Halpern, M., R.T. Wang, and D.R. Coleman (1976) Centrifugal fibers to the eyes in a nonavian vertebrate: Sources revealed by horseradish peroxidase studies. Science *194:*1185–1187.

Hardy, O., N. Leresche, and D. Jassik-Gerschenfeld (1983) Possible neuronal circuits in the pigeon's optic tectum: An intracellular recording labelling study. Neurosci. Abstr. *9:*819.

Harris, L.M. (1980) The superior colliculus and movements of the head and eyes in cats. J. Physiol. (Lond.) *300:*367–391.

Hartline, P.H. (1984) The optic tectum of reptiles: neurophysiological stud-

ies. In H. Vanegas (ed): Comparative Neurology of the Optic Tectum. New York: Plenum Press, pp. 601–618.

Hikosaka, O., and R.H. Wurtz (1985) Modification of saccadic eye movements by GABA-related substances. I. Effects of muscimol and bicuculline in monkey superior colliculus. J. Neurophysiol. *53:*266–291.

Huerta, M.F., and J.K. Harting (1984) The mammalian superior colliculus: studies of its morphology and connections. In H. Vanegas (ed): Comparative Neurology of the Optic Tectum. New York: Plenum Press, pp. 687–774.

Hunt, S.P., and N. Brecha (1984) The avian optic tectum: a synthesis of morphology and biochemistry. In H. Vanegas (ed): Comparative Neurology of the Optic Tectum. New York: Plenum Press, pp. 619–648.

Hunt, S.P., P. Streit, H. Kunzle, and M. Cuenod (1977) Characterization of the pigeon isthmo-tectal pathway by selective uptake and retrograde movement of radioactive compounds and by Golgi-like horseradish peroxidase labelling. Brain Res. *129:197–212.*

Ingle, D.J. (1982) Organization of visuomotor behavior in vertebrates. In D.J. Ingle, M.A. Goodale, and R.J.M. Mansfield (eds): Analysis of Visual Behavior. Cambridge: MIT Press, pp. 67–109.

Ingle, D.J., and J.M. Sprague (1975) Sensorimotor functions of the midbrain tectum. Neurosci. Res. Prog. Bull. *13:*173–288.

Jassik-Gerschenfeld, D., and O. Hardy (1984) The avian optic tectum: Neurophysiology and behavioral correlations. In H. Vanegas (ed): Comparative Neurology of the Optic Tectum. New York: Plenum Press, pp. 649–686.

Kishida, R., F. Amemiya, T. Kusunoki, and S.-I. Terashima (1980) A new tectal afferent nucleus of the infrared sensory system in the medulla oblongata of crotaline snakes. Brain Res. *195:*271–279.

Luiten, P.G.M. (1981) Afferent and efferent connections of the optic tectum in the carp (*Cyprinus carpio*). Brain Res. *220:*51–65.

Masino, T., S.K. Kostyk, and P. Grobstein (1984) Laterality of tectal efferent projections in *Rana pipiens*. Neurosci. Abstr. *10:*60.

May, P.J. (1981) Characterization of cells projecting from the superficial grey layer of the superior colliculus. Anat. Rec. *199:*165A.

May, P.J., and W.C. Hall (1984) Relationships between the nigrotectal pathway and the predorsal bundle. J. Comp. Neurol. *226:*357–376.

McCrea, R. A., and P. Grobstein (1983) Anatomical and electrophysiological characteristics of the neurons in the frog tectum receiving optic inputs. Neurosci. Abstr. *9:*818.

McIlwain, J.T. (1976) Large receptive fields and spatial transformations in the visual system. Int. Rev. Physiol. *10:*223–248.

McIlwain, J.T. (1982) Lateral spread of neural excitation during microstimulation in intermediate gray layer of cat's superior colliculus. J. Neurophysiol. *47:*167–178.

Mendez-Otero, R., C.E. Rocha-Miranda, and V.H. Perry (1980) The organization of the parabigemino-tectal projections in the opossum. Brain Res. *198:*183–189.

Middlebrooks, J.C., and E.I. Knudsen (1984) The neural code for auditory space in the cat's superior colliculus. J. Neurosci. *4:*2621–2634.

Mohler, C.W., and R.H. Wurtz (1977) Role of striate cortex and superior colliculus in visual guidance of saccadic eye movements in monkeys. J. Neurophysiol. *40:*74–94.

Molenaar. G.J., and J.L.F.P. Fizaan-Oostveen (1980) Ascending projections from the lateral descending and common sensory trigeminal nuclei in python. J. Comp. Neurol. *189:*555–572.

Mooney, R.D., B.G. Klein, M.F. Jacquin, and R.W. Rhoades (1984) Dendrites of deep layer somatosensory superior colliculus neurons extend into the superficial laminae. Neurosci. Abstr. *10:*158.

Mooney, R.D., B.G. Klein, and R.W. Rhoades (1985) Correlations between the structural and functional characteristics of neurons in the superficial laminae in the hamster's superior colliculus. J. Neurosci. *5:*2989–3009.

Newman E.A., E.R. Gruberg, and P.H. Hartline (1980) Infrared trigeminotectal pathway in the rattlesnake and the python. J. Comp. Neurol. *191:*465–478.

Niida, A., H. Oka, and K.S. Iwata (1980) Visual responses of morphologically identified tectal neurons in the crucian carp. Brain Res. *201:*361–371.

Northcutt, R.G. (1982) Localization of neurons afferent to the optic tectum in longnose gars. J. Comp. Neurol. *204:*325–335.

Northcutt, R.G. (1984) Anatomical organization of the optic tectum in reptiles. In H. Vanegas (ed): Comparative Neurology of the Optic Tectum. New York: Plenum Press, pp. 547–600.

Ogawa, T., and Y. Takahashi (1981) Retinotectal connectivities within the superficial layers of the cat's superior colliculus. Brain Res. *217:*1–11.

Quiroga, J.C. (1978) The tectum opticum of *Pantodactylus schreiberii* (Teiidae, Lacertillia, Reptilia). J. Hirnforsch. *19:*109–131.

Ramón y Cajal, S. (1911) Histologie du Système Nerveux de l'Homme et des Vertébrés. Vol. 2. Paris: A. Maloine (reprinted in 1955 by Consejo Superior de Investigaciones Cientificas, Instituto Ramón y Cajal, Madrid).

Rhoades, R.W., D.C. Kuo, J.D. Polcer, S.E. Fish, and T.J. Voneida (1982) Indirect visual cortical input to the deep layers of the hamster's superior colliculus via the basal ganglia. J. Comp. Neurol. *208:*239–254.

Robinson, D.A. (1981) The use of control systems analysis in the neurophysiology of eye movements. Ann. Rev. Neurosci. *4:*463–503.

Sakamoto, N., H. Ito, and S. Ueda (1981) Topographic relations between the nucleus isthmi and the optic tectum in a teleost, *Navodon modestus*. Brain Res. *224:*225–234.

Schiller, P.H., and J.H. Maunsell (1984) The effect of superior colliculus and frontal eye field lesions on saccadic latency in the monkey. Neurosci. Abstr. *10:*60.

Sereno, M.I. (1983) Dendritic and axonal morphology of tectal-projecting neurons in the isthmus region of a turtle, *Pseudemys scripta*. Neurosci. Abstr. *9:*818.

Sereno, M.I. (1985) Tectoreticular pathways in the turtle, *Pseudemys scripta*. I. Morphology of tectoreticular axons. J. Comp. Neurol. *233:*48–90.

Sereno, M.I., and P.S. Ulinski (1985) Tectoreticular pathways in the turtle, *Pseudemys scripta*. II. Morphology of tectoreticular cells. J. Comp. Neurol. *233:*91–114.

Sherk, H. (1979) Connections and visual field mapping in cat's tectoparabigeminal circuit. J. Neurophysiol. *42:*1656–1668.

Smeets, W.J.A.J. (1982) The afferent connections of the tectum mesencephali in two chondrichthyans, the shark, *Scyliorhinus canicula* and the ray *Raja clavata*. J. Comp. Neurol. *205:*139–152.

Sparks, D.L., and L.E. Mays (1980) Movement fields of saccade related burst neurons in the monkey superior colliculus. Brain Res. *190:*39–50.

Sparks, D.L., and L.E. Mays (1981) The role of the monkey superior colliculus in the control of saccadic eye movements: a current perspective. In A.F. Fuchs and W. Becker (eds): Progress in Oculomotor Research, Vol. 12. Amsterdam: Elsevier, pp. 137–144.

Sparks, D.L., R. Holland, and B.L. Guthrie (1976) Size and distribution of movement fields in the monkey superior colliculus. Brain Res. *113:*21–34.

Sprague, J.M. (1975) Mammalian tectum: Intrinsic organization, afferent connections and integrative mechanisms. Anatomical substrate. Neurosci. Res. Prog. Bull. *13:*204–213.

Stein, B.E., and H.P. Clamann (1981) Control of pinna movements and sensorimotor register in cat superior colliculus. Brain Behav. Evol. *19:*180–192.

Terashima, S., and R.C. Goris (1975) Tectal organization of pit infrared reception. Brain Res. *83:*490–494.

Ulinski, P.S., D.M. Dacey, and M.I. Sereno (1986) Optic tectum. In C. Gans and R.G. Northcutt (eds): Biology of the Reptilia. New York: Academic Press, in press.

Wilczynski, W., and R.G. Northcutt (1977) Afferents to the optic tectum of the leopard frog: an HRP study. J. Comp. Neurol. *173:*219–230.

Wize, L.Z., and D.R.F. Irvine (1985) Topographic organization of interaural intensity difference sensitivity in deep layers of cat superior colliculus: Implications for auditory spatial representation. J. Neurophysiol. *54:*185–211.

Wurtz, R.H., and M.E. Goldberg (1972) Activity of the superior colliculus in behaving monkey. IV. Effects of lesions on eye movements. J. Neurophysiol. *35:*587–596.

Wurtz, R.H., and J.E. Albano (1980) Visual-motor functions of the primate superior colliculus. Ann. Rev. Neurosci. *3:*189–226.