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Tectoreticular Pathways in the Turtle, *Pseudemys scripta*. II. Morphology of Tectoreticular Cells

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ABSTRACT

The morphology of tectoreticular neurons in turtles was examined with serial section reconstructions of neurons retrogradely filled with HRP. Six classes of tectal neurons project into the three tectobulbar pathways characterized in the preceding paper (Sereno, '85). (1) Large multipolar neurons with somata in the central gray layers, and with moderately branched dendrites sometimes spanning over a millimeter, project into the dorsal tectobulbar pathway, TBd. Their dendrites are covered with fine spicules and tend to arborize in the lower third of the superficial gray layers. (2) Medium-sized neurons with multiple radial dendrites and somata in the central white and upper periventricular layers probably project into the ipsilateral intermediate tectobulbar pathway, TBi. Their dendrites also bear fine spicules and usually reach the tectal surface. (3) Small radial cells in the periventricular layers, and (4) small bitufted radial cells in the superficial gray project into the small caliber component of the ipsilateral ventral tectobulbar pathway, TBv(sm). (5) Medium-sized central gray neurons with stratified dendrites, and (6) medium-sized central gray neurons with horizontal dendrites probably project into the medium caliber component of the ventral tectobulbar pathway, TBv(med). In contrast to TBd and TBi neurons, these last four classes emit a spray of long, filamentous dendritic appendages in the central gray and have dendritic arbors near the top of the superficial gray.

The morphology of the neurons described in this and the preceding paper is briefly discussed in light of current ideas about tectally mediated sensorimotor transformations.

Key words: tectum, sensorimotor, reticular formation, non-topographic, eye movements

The preceding study (Sereno, '85) used orthograde filling with horseradish peroxidase (HRP) to identify three tectobulbar pathways in pond turtles. A *dorsal pathway* (TBd; a key to nomenclature abbreviations precedes Fig. 1) crosses the midline at caudal midbrain levels to form the predorsal bundle. An *intermediate pathway* (TBi) courses through the lateral part of the ipsilateral reticular formation. A *ventral pathway* (TBv) courses along the ventral surface of the ipsilateral brainstem. Axons in each of the pathways collateralize extensively and terminate within several brainstem structures. Those in the dorsal pathway terminate mostly in the medial half of the pontine and medullary reticular formation while collaterals of axons in the intermediate and ventral pathways partly overlap in the lateral reticular formation. The present study uses retrograde filling with HRP and serial reconstruction to examine the laminar position and dendritic morphology of tectoreticular neurons. By restricting injections in the tegmentum or directly tracing axons into a pathway it was possible in a number of cases to determine which cell types contribute to each pathway. Together with the results of the previous paper, these findings permit a detailed characterization of tectoreticular neurons in turtles.

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Abbreviations

BON	Basal optic nucleus
Cereb	Cerebellum
CG	Central gray
dNPC	Dorsal nucleus of the posterior commissure
GP	Geniculate pretectal nucleus
ICo	Intercollicular nucleus
Imlf	Interstitial nucleus of the medial longitudinal fasciculus
Imc	Caudal magnocellular nucleus isthmi
Imr	Rostral magnocellular nucleus isthmi
Ip	Parvocellular nucleus isthmi
Mes V	Mesencephalic trigeminal nucleus
MLF	Medial longitudinal fasciculus
N. V	Trigeminal nerve
N. VI	Abducens nerve
N. VIII	Auditory-vestibular nerve
PC	Posterior commissure
PD	Nucleus posterodorsalis of the pretectum
PMc	Profundus mesencephali caudalis
PMr	Profundus mesencephali rostralis
PMv	Profundus mesencephali ventralis
Pt	Nucleus pretectalis
RID	Reticularis inferioris dorsalis
RM	Reticularis medius
RSL	Reticularis superioris lateralis
SAC	Stratum album centrale
SFGS	Stratum fibrosum et griseum superficiale (superficial gray)
SGC	Stratum griseum centrale (central gray)
SGP	Stratum griseum periventriculare (periventricular layers)
SN	Substantia nigra
SO	Stratum opticum
TBd(lg)	Dorsal tectobulbar pathway, large caliber component
TBd(sm)	Dorsal tectobulbar pathway, small caliber component
TBi	Intermediate tectobulbar pathway
TBv(med)	Ventral tectobulbar pathway, medium caliber component
TBv(sm)	Ventral tectobulbar pathway, small caliber component
Torc	Torus semicircularis, central nucleus
Torl	Torus semicircularis, laminar nucleus
TTh	Tectothalamic tract
VeDL	Dorsolateral vestibular nucleus
VeVL	Ventrolateral vestibular nucleus
III	Oculomotor nucleus
V ds	Descending trigeminal nucleus
V mot	Trigeminal motor nucleus
V mr	Mesencephalic root of the trigeminal nerve
V pr	Principal sensory trigeminal nucleus
V tr	Descending tract of the trigeminal complex
VI	Abducens motor nucleus
VII	Facial motor nucleus

MATERIALS AND METHODS

Twelve pond turtles (*Pseudemys scripta elegans* and *Chrysemys picta*) weighing 0.6–1.4 kg each were used. Animals were anesthetized with Brevital (Wang et al., '77) and then packed in ice for surgery. A craniotomy was performed and either a 1 μl Hamilton syringe with a sharpened tip or a micropipette was introduced into the brainstem tegmentum through the anterior cerebellum. Large pressure injections (0.2–0.6 μl) or large iontophoretic injections (2–4 μA for 30 minutes) of concentrated Sigma Type VI HRP in pH 8.6 Tris buffer were made into either the medial or lateral half of the pontine or medullary tegmentum. Several other animals received small iontophoretic injections (1 μA for 30 seconds) of HRP in the tectum from a micropipette with an internal tip diameter of 5–10 μm. Further histochemical processing of the brain tissue followed the procedures described in the preceding paper (Sereno, '85).

Plots of the distribution of labeled neurons were made by drawing every fourth serial section with a microprojector and entering all the granular and solid-filled cells from four consecutive sections on a single drawing. Soma outlines were drawn at twice the magnification of the sections to better illustrate their morphology. Every tectal cell labeled by an injection was plotted.

Single HRP-filled neurons were reconstructed with a drawing tube from a number of adjacent sections, usually under a 100× oil immersion objective (see Sereno, '85, for details). Some cells with dendritic fields greater than 1 mm in diameter were reconstructed with a 40× objective. A rough en face view of the dendritic tree was also reconstructed after correcting for the anisotropic shrinkage described previously (Sereno, '85). Finally, low-power tracings of each reconstructed cell and the section containing its soma were made with a drawing tube to illustrate the location of the high-power views.

RESULTS

The results are presented in two parts. First, cases with tegmental HRP injections are described, and illustrated at low magnification. Those experiments suggest that the somata of neurons projecting into each pathway have distinct and restricted laminar distributions. Second, the detailed morphology of the neurons is examined using serial reconstructions. The major finding is that six different classes of neurons project into the three pathways.

Laminar distribution of tectoreticular neurons

Figure 1 is representative of an injection confined principally to the left dorsal pathway (TBd). It mostly labeled neurons with large somata in the contralateral (right) tectum. A few granularly filled neurons with smaller somata are present in the ipsilateral tectum, probably as a result of the spread of HRP into the left intermediate (TBi) and ventral (TBv) pathways. Although the injection also appears to encroach on the right TBd, no large cells appear in the left tectum, suggesting that the right TBd did not transport significant amounts of HRP. It is thus unlikely that the right TBi and TBv—which are farther from the injection site—transported any HRP. Injections such as this labeled neurons in the contralateral stratum album centrale (SAC), in the lower half of the stratum griseum centrale (SGC), and occasionally in the stratum griseum periventriculare (SGP). Neurons were never labeled in the stratum fibrosum et griseum superficiale (SFGS) after a TBd injection. TBd injections consistently labeled more neurons in the caudolateral third than in the rostromedial two-thirds of the tectum.

These findings were confirmed by small tectal injections (less than 250 μm in diameter) that produced solid-filled neurons adjacent to the injection site in several cases. These neurons were occasionally situated so that their axons did not pass through the site. Several such neurons were identified as contributing to the dorsal pathway because their axons could be traced out of the tectum (through lightly labeled efferent bundles) until they crossed the midline and turned caudally into the predorsal bundle. The photomicrographs in Figure 6A and B show one of these small injection sites and a solid-filled TBd neuron from a nearby section. As expected, neurons such as this one had large somata located in the SAC and lower SGC.

Figure 2 is representative of an injection confined mostly to the intermediate and ventral pathways. It labeled many

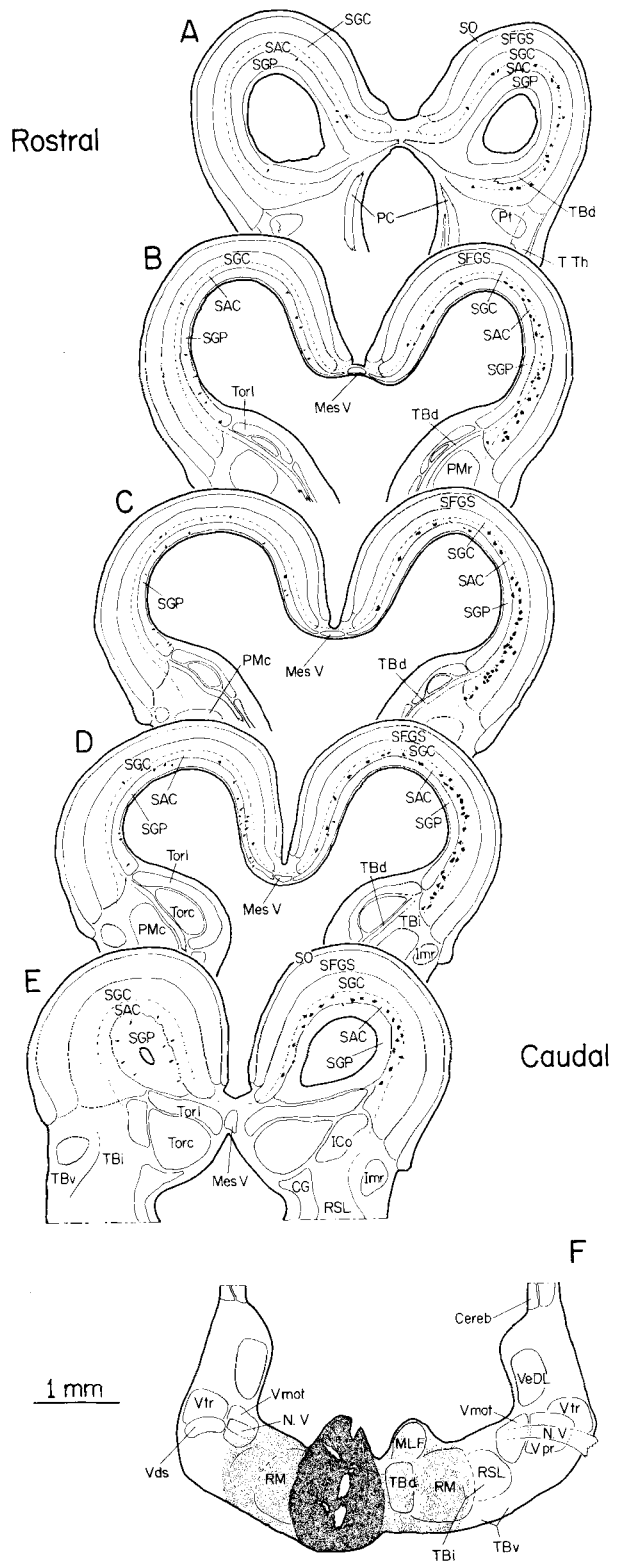


Fig. 1. Neurons labeled in tectum after a dorsal pathway (TBd) injection in the medial tegmentum. The somata of most of the solid-filled and granular-filled neurons are large and are located contralateral to the injection in the stratum album centrale (SAC) and the stratum griseum centrale (SGC). A few small, granularly filled neurons appear ipsilaterally, possibly as a result of the spread of the injection into the left lateral tegmentum. No large neurons appear ipsilaterally, suggesting that the effective injection site did not encroach on the right TBd. There is a concentration of labeled neurons in the caudolateral third of the tectum, particularly apparent in sections C and D.

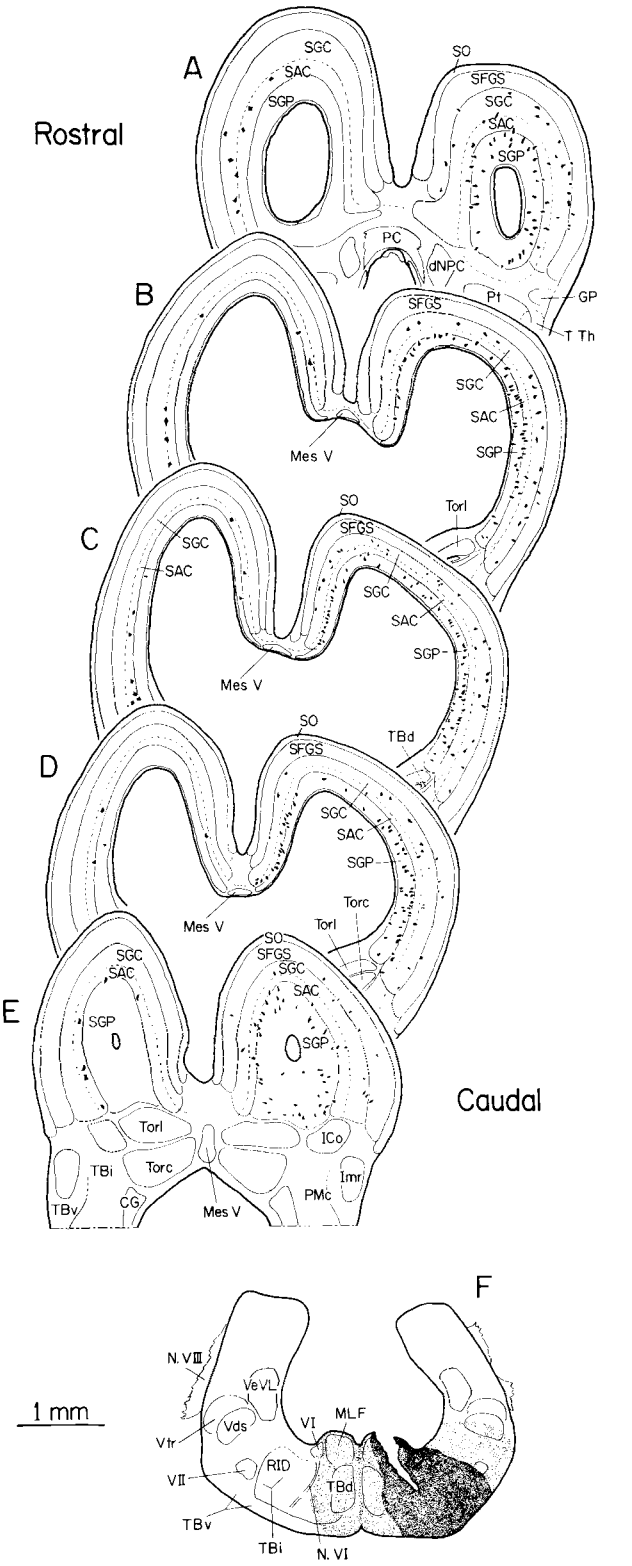


Fig. 2. Neurons labeled in the tectum after a combined intermediate (TBi) and ventral (TBv) pathway injection in the lateral tegmentum. The somata of most of the solid-filled and granular-filled neurons are small to medium-sized and are located ipsilateral to the injection. They are found in the stratum griseum periventriculare (SGP), the upper part of the stratum griseum centrale (SGC), and occasionally in the stratum fibrosum et griseum superficiale (SFGS). A few large granularly filled neurons appear contralaterally, probably as a result of the spread of the injection into the right TBd. No large neurons appear ipsilaterally, suggesting that the injection did not encroach on the left TBd.

small and medium-sized neurons in the ipsilateral (right) tectum. A few large cells showed light granular label contralaterally because the central uptake zone encroached slightly into the right TBd. Since no large cells appeared ipsilaterally, there was probably no uptake by the left TBd. Therefore, it is likely that solid-filled cells reconstructed from the right tectum all have axons in the TBi or TBv. Injections into the TBi and TBv labeled neurons in more tectal laminae than did TBd injections. Many small cells were labeled in the SGP. Larger cells appeared at the upper and lower borders of the SAC and were common in the upper half of the SGC. A few small cells were regularly labeled in the lower two-thirds of the SFGS. There tended to be a higher overall density of labeled cells around the periphery of the tectal hemisphere. The axons of a number of small cells labeled in the SGP and in the SFGS were traced through serial sections until they unequivocally entered the TBv. In addition, the small caliber axons (1 μm or less) of these cells were similar in size to the small caliber component of the TBv identified in the previous paper (Sereno, '85). This component contained the smallest axons of any of the tectobulbar pathways.

Thus, we conclude that the small cells in both the SGP and SFGS illustrated in Figure 2, which have the smallest axons of any of the labeled cell types, project into the small caliber bundle of the TBv. There remains some ambiguity, however, about the cells of origin of the intermediate pathway and the medium caliber component of the ventral pathway because only a few axons from ipsilaterally labeled cells could be traced far enough into these pathways to be sure of which they finally entered. Since the axons in these pathways have partially overlapping size distributions, we could unequivocally conclude only that, as a group, they originate from one or another of the labeled neurons with medium caliber axons that are located at the upper and lower boundaries of the SAC and in the upper half of the SGC.

Morphology of tectoreticular neurons

The morphology of tectal neurons that project into each of the pathways was determined by reconstructing neurons densely filled with HRP. Such Golgi-like filling occurred in 10–30% of the labeled neurons. The remaining 70–90% of labeled cells were granularly or diffusely filled so that only the soma and proximal dendrites could be seen. The solid-filled neurons were placed into six classes based on the morphology of their axons and dendrites. One of the classes sends axons into the contralaterally projecting dorsal pathway (TBd). Two others contribute to the small caliber component of the ipsilaterally projecting ventral pathway (TBv). With each of the remaining three ipsilaterally projecting classes, the small number of neurons whose output pathway could be positively identified made firm conclusions inappropriate. Our preliminary observations suggest that two classes enter the medium caliber component of the ventral pathway (TBv), and that the last class enters the intermediate pathway (TBi).

Dorsal pathway (TBd) neurons. Tectal neurons that give rise to an axon leaving the tectum in the dorsal pathway and crossing the midline to run in the contralateral predorsal bundle form a homogeneous class of large multipolar neurons. Figures 3 and 4 are drawings of such neurons made from transverse sections. Figure 5 is a reconstruction from sections through the caudal face of the tectum that provides a surface view of a dorsal pathway neuron. Figure 6B and C are photomicrographs of dorsal pathway neurons.

TBd neurons are larger than any other class of tectal neurons with cell bodies ranging from 20 to 40 μm in diameter located in the SGC and the SAC. Their sparsely distributed, polygonal somata are easily recognized in Nissl sections. Some are almost round while others are vertically or horizontally elongated. More superficially placed somata tend to be horizontally elongated. Three to six primary dendrites radiate into a hemisphere above the soma while one or two dendrites extend ventrally. The dendrites conspicuously cut across the overall vertical organization of the turtle tectum. This is especially apparent when a dorsal pathway neuron is seen against a background of vertically oriented dendritic bundles near a small tectal injection. The shape of the dendritic field is somewhat irregular when viewed from the tectal surface (Fig. 5). No systematic bias in orientation was seen in the dendritic fields of neurons recovered from sections parallel to the tectal surface (Fig. 5) or in en face reconstructions made for transversely sections cells (Figs. 3,4). The dendritic fields range from 900 to 1,200 μm in diameter. The dendrites of an individual neuron, therefore, sample activity from about 5% of the roughly 15 mm^2 of one tectal lobe.

Dendrites are not extensively ramified and commonly travel 200–500 μm without branching. They extend into the SFGS and occasionally reach the stratum opticum (SO). Ascending dendrites usually arborize to some extent in the lower half of the SFGS. Ventrally directed dendrites commonly enter the SGP. Dendrites bear many very fine spicules in well-filled cells (see the close-up in Fig. 4), but never emit the long, filamentous appendages characteristic of several classes of ipsilaterally projecting cells. Distal dendrites are commonly somewhat beaded. In cases with small tectal injections, boutons from incidentally labeled axons were observed to make intimate contacts suggestive of synapses on both the dendritic shafts and on the beads (Fig. 4).

An axon originates from the soma or the base of a dendrite and is always constricted to one-third or less of its final diameter for the first 30–40 μm of its length. Axons course directly toward the stratum album centrale and usually make an almost 90° turn at the surface of the periventricular cell layers to run laterally in the lowest layers of the stratum album centrale. In no case were local axon collaterals observed within the tectum. A marked lightening of staining just past the initial constricted segment and the appearance at periodic intervals of constricted, very darkly stained short segments suggest that dorsal pathway axons become myelinated after about 40 μm. In other species, the nodes of thick axons often show constrictions at the ultrastructural level as the myelin wrapping terminates in small "pillows" (Peters et al., '76, p. 215). The nodes are more intensely stained here, probably as a result of easier access of the staining solutions.

The previous paper showed that the dorsal pathway contains large (4–6 μm) and small diameter (1–2 μm) components with virtually identical branching patterns. Retrograde solid-filling occurred less often through smaller axons. The dendrites of small-axon cells tended to be less robust and the soma and dendritic field diameters were slightly smaller than the large-axon neurons.

Ventral pathway (TBv) neurons. The ventral tectobulbar pathway contains small and medium caliber components. Two classes of neurons give rise to axons in the small caliber component: (1) *small radial cells* in the SGP, and (2)

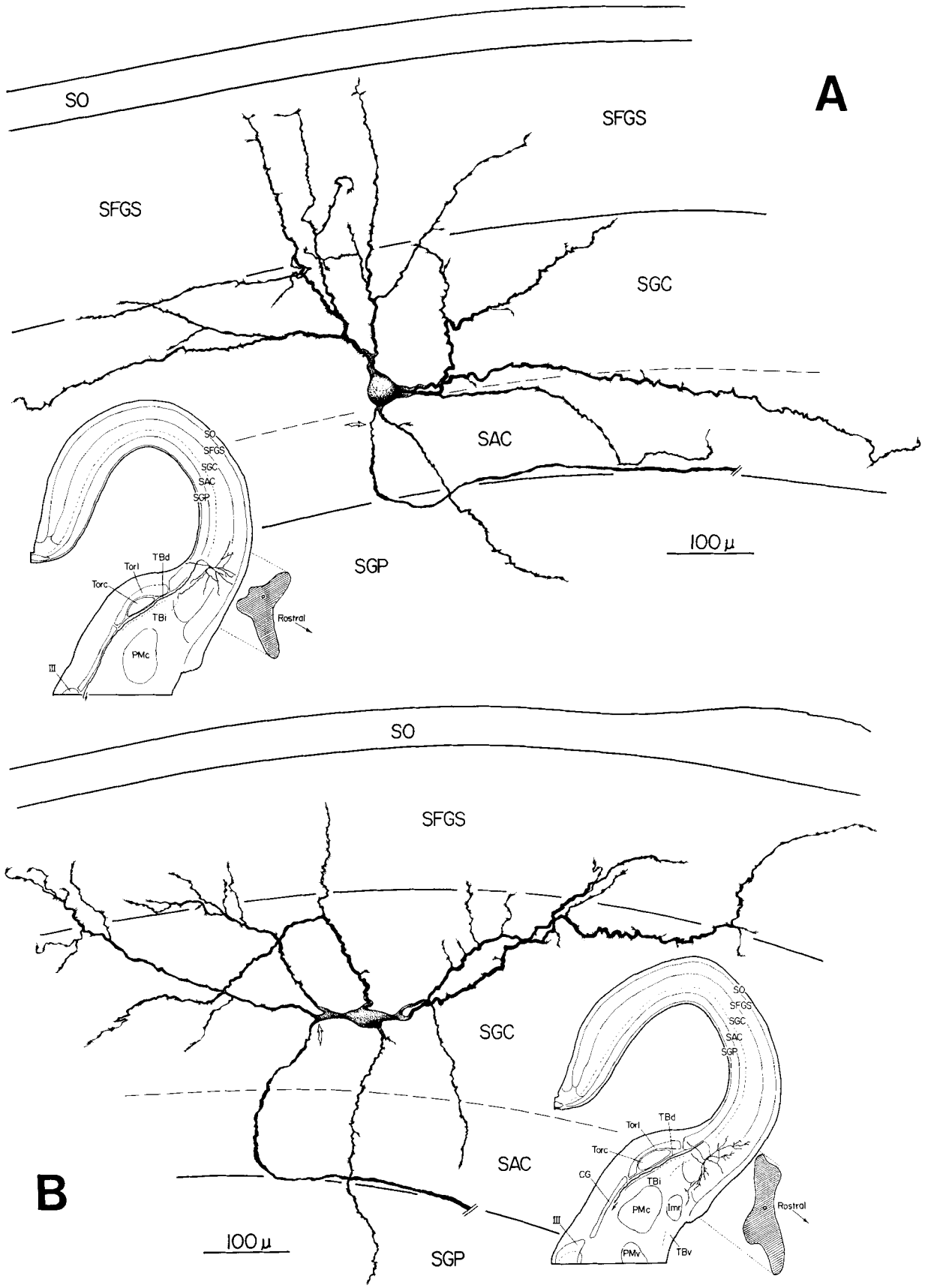


Fig. 3. Dorsal pathway (TBd) cells. The neurons in A and B were filled by a contralateral paramedian injection and then reconstructed from a number of adjacent sections. Their large caliber (5–6 μm) axons arise (open arrows) near the cell body and enter the large caliber component of the dorsal pathway. Dendrites are covered with fine spicules and have a tendency (made less apparent in these views by the curvature of the tectum) to arborize in the lower third of the stratum fibrosum et griseum superficiale (SFGS). Schematic en face views are given alongside the low-power drawings in the insets.

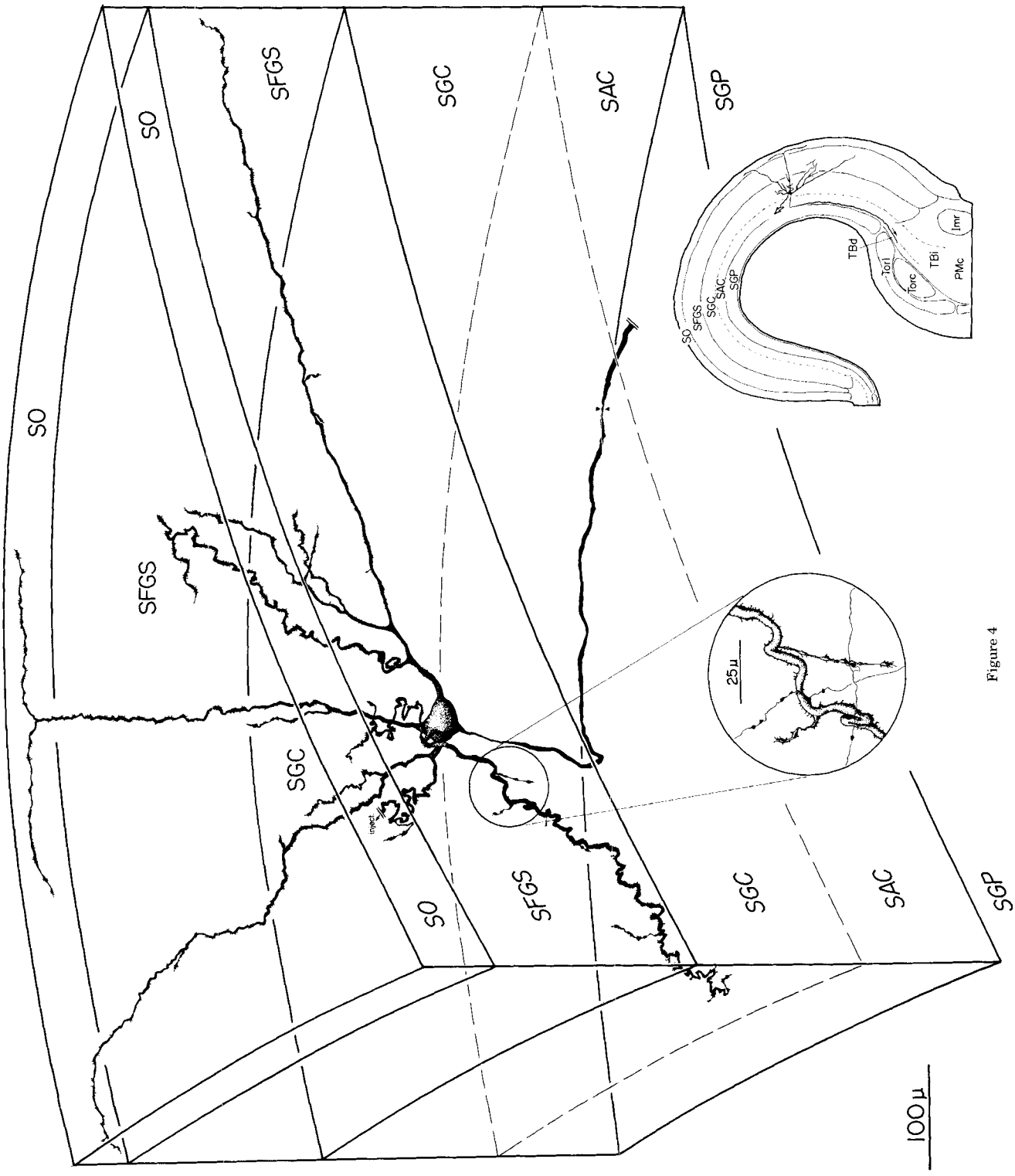


Figure 4

small bitufted cells in the SFGS. Examples of radial cells are illustrated in Figure 7; Figure 8 shows two bitufted cells.

Small radial cells in the SGP (Fig. 7). These are among the smallest cells in the tectum. Their 8–12 μm wide pyriform cell bodies are found at various depths in the SGP, which contains many similar but unlabeled somata tightly packed into several thin laminae. Typical radial cells have a single, radially oriented primary dendrite that extends to the tectal surface and usually, a small, branching, basal dendrite. In a few small ventral pathway cells in the medial tectum, the primary dendrite branches almost immediately (Fig. 7B). More typical TBv radial cells also occurred medially (Fig. 7A). Filamentous dendritic appendages usually arise from the main radial dendrites in the SGC and are rarely seen in the lower half of the SFGS. Most of the cells have dendritic fields restricted to cylinders 50–100 μm in diameter. The few cells with a branched primary dendrite spanned 300–500 μm and had rather expansive, branched basal dendrites giving them a multipolar appearance. The dendrites of these last cells stopped short of entering the retinal-recipient SFGS, in contrast to every other tectobulbar neuron seen in this study.

An axon commonly originates from the primary dendrite in the SGC and could be traced in some cases into the ventral pathway. The axon is constricted for the first 25–35 μm of its length and then expands to a final diameter of 1 μm or less. In cases where it could be followed, the axon looped toward the tectal surface to form a so-called "shepard's crook" (Fig. 7C) before continuing laterally in the SAC or lower SGC. No collaterals were observed in the tectum, although varicosities were sometimes seen in the proximal, constricted segment of the axon (Fig. 7B). These small axons usually stained evenly past the initial constriction and did not appear to be myelinated.

Small bitufted cells in the SFGS (Fig. 8). These neurons have bipolar somata, ranging from 10 to 15 μm in diameter, that can be located anywhere within the lower half of the SFGS. The soma give rise to ascending and descending primary dendrites, each bearing a tuft of filamentous dendritic appendages. The ascending dendrite usually branches into two or three main trunks upon entering the upper half of the SFGS. The location of this branch point is much less variable than is the laminar position of the soma (see Fig. 8A versus B). Each of the branches bear many fine, filamentous appendages with en passant varicosities. The appendages are mostly confined to the upper third of the SFGS. The varicosities are smaller, more transparent, and have less regular shapes than do varicosities on the axon collaterals of the same neurons. The SFGS appendages occupy a field about 100 μm in diameter. The descending primary dendrite can sometimes be traced into the SAC (Fig. 8A) but may branch repeatedly in other cases so that no main trunk can be identified in the lower SGC. Many filamentous, varicosity-laden dendritic appendages also arise from the descending trunk in the upper half of the SGC. They spread ventrally and laterally and occupy an area similar in size to that occupied by the appendages on the ascending dendrite.

A small caliber axon originates from the descending dendrite in the upper third of the SGC. As with the small radial cells, the initial constricted portion of the axon is often almost invisible and usually forms a dorsal loop. The axon then expands to a final diameter of approximately 1 μm and turns to run laterally within a cell-poor zone just below the SFGS that lies between cellular layers 7 and 8 of Ramón (1896). These axons usually had intratectal collaterals that distributed boutons to the SGC, SAC, and sometimes the SGP (see Sereno, '85). The collateral field ends at the lateral edge of the tectum. The axon continues ventrally through the rostral magnocellular nucleus isthmi (Imr), at which point a 90° bend brings the axon caudally into the fine caliber component of the ventral pathway just ventrolateral to the caudal magnocellular nucleus isthmi (Imc).

Other ipsilaterally projecting neurons. Three remaining classes of tectobulbar neurons contribute axons to either the medium caliber component of the ventral pathway, TBv(med), or to the intermediate pathway, TBi, or to both: (1) SGC cells with stratified dendrites, (2) SGC cells with horizontal dendrites, and (3) SAC/SGP cells with multiple radial dendrites bearing no appendages. Preliminary evidence suggests that 1 and 2 have axons in TBv(med), while 3 contributes to TBi.

Medium-sized SGC cells with stratified dendrites (Figs. 9–11). These neurons have a medium-sized cell body (15–22 μm) located in the upper half of the stratum griseum centrale. They can be subdivided into large- and small-field types with somata of similar size. Small-field types have rounded somata; large-field types have irregularly shaped somata that appear distorted by robust primary dendrites. Figure 9 is a transverse view and Figure 10 an oblique view of large-field types. Figure 11 is an oblique view of a small-field type. The tectal laminae in Figures 10 and 11 have been drawn as planes to emphasize their oblique orientation relative to the viewer. These neurons all have a dense dendritic plexus at the top of the SFGS and a less dense field of dendritic appendages in the SGC. The photomicrograph in Figure 12 shows an example of these specializations.

In large-field types, two or sometimes three robust ascending dendrites bear a proximal tuft of filamentous appendages in the upper SGC. Upon entering the SFGS, these dendrites branch into three to six radial stalks that course through the bottom two-thirds of the SFGS without giving off appendages. As these stalks enter the top third of the SFGS, they each branch two or three times and then turn horizontally, forming a dense, stratified plexus of varicosity-laden strands that occupies an almost ciruclar field about 300 μm in diameter (Figs. 9,10). Small-field cells usually have a single, thinner ascending dendrite that forms a smaller plexus of branches, similar in size to that of the small, bitufted SFGS cells described previously. Cells near the lateral edge of the tectum occasionally have an aberrant branch that travels horizontally for some distance toward the midbrain reticular formation (Fig. 10), sometimes entering it.

The large-field cells have a robust, vertically oriented descending dendrite that makes an acute angle bend in

Fig. 4. Three-quarter view of a dorsal pathway cell. This neuron was filled by a small HRP injection into a distal dendrite (labeled "inject.") Its 6 μm diameter axon (node indicated by paired triangles) entered the large caliber component of the dorsal pathway and was traced through serial sections until it crossed the midline to run in the predorsal bundle. Tectal laminae have been drawn as planes to emphasize this cell's oblique orientation. The circular inset shows the characteristic dendritic spicules on this type of neuron as well as incidentally labeled terminal boutons in apparent contact with dendritic shafts and beads. In the inset to the right, the cell is drawn to scale on one of the sections used for the reconstruction.

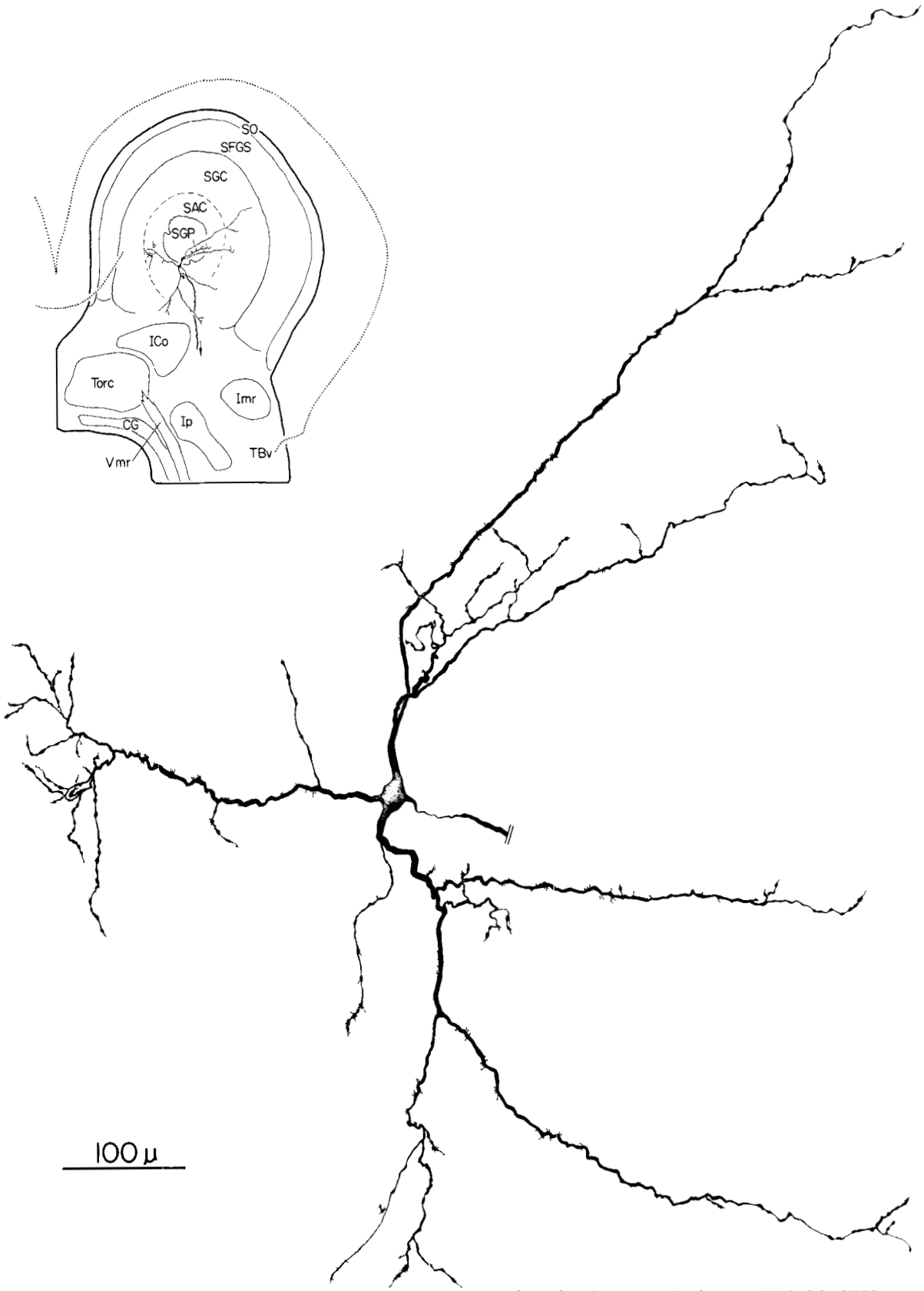


Fig. 5. Surface view of a dorsal pathway cell. This neuron was recovered from the caudal face of the tectum after a contralateral paramedian injection into the tegmentum. Its soma is in the stratum griseum centrale (SGC) and most of the dendrites travel upward (out of the page) into the stratum fibrosum et griseum superficiale (SFGS). As before, the dendrites bear fine spicules and tend to arborize in the lower third of the SFGS (e.g., arbor at the extreme left). The inset shows the cell drawn to scale on one of the caudal tectal sections used in the reconstruction; in addition, the silhouette of a mid-tectal section (dotted outline) is superimposed for size reference.

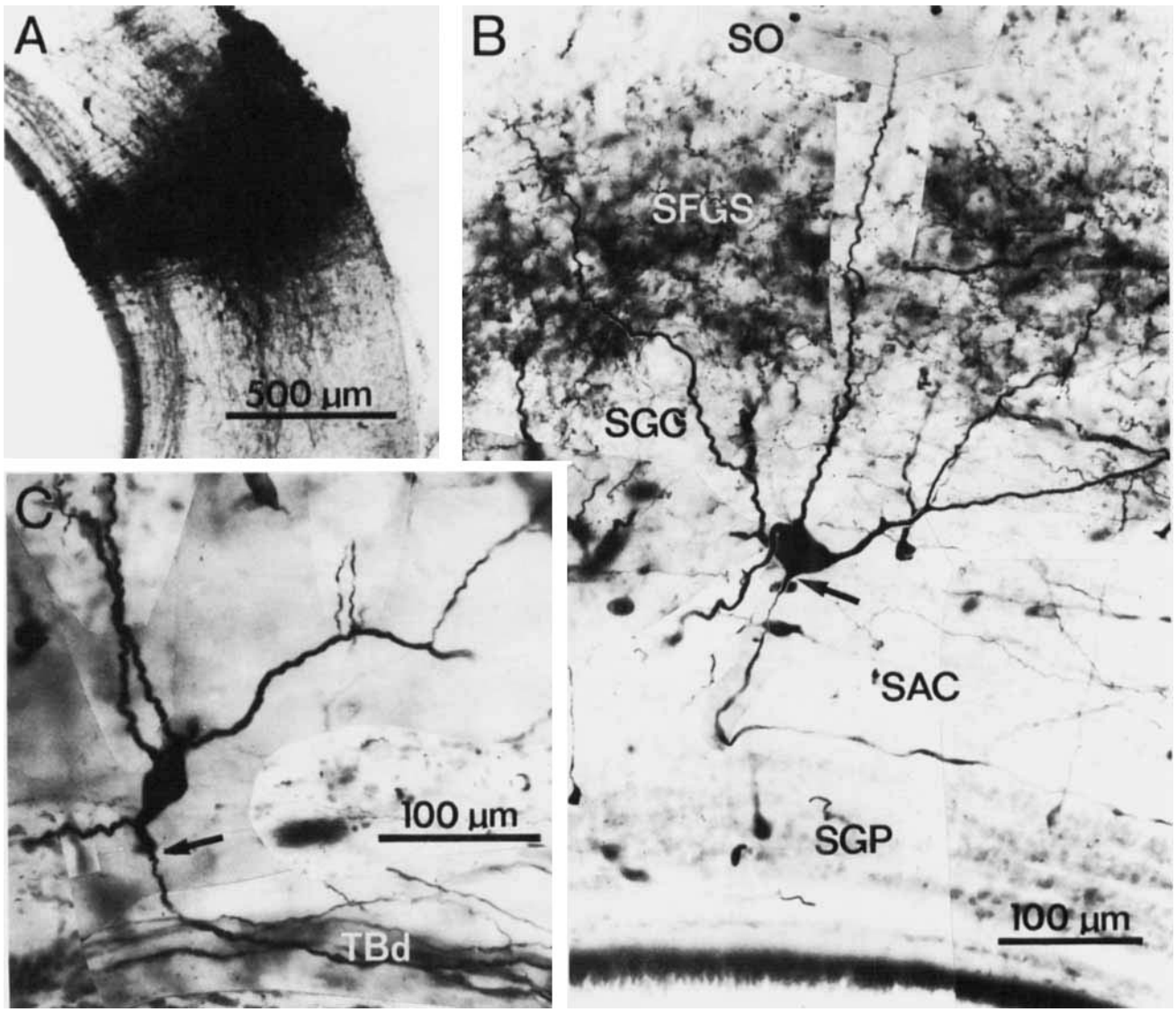
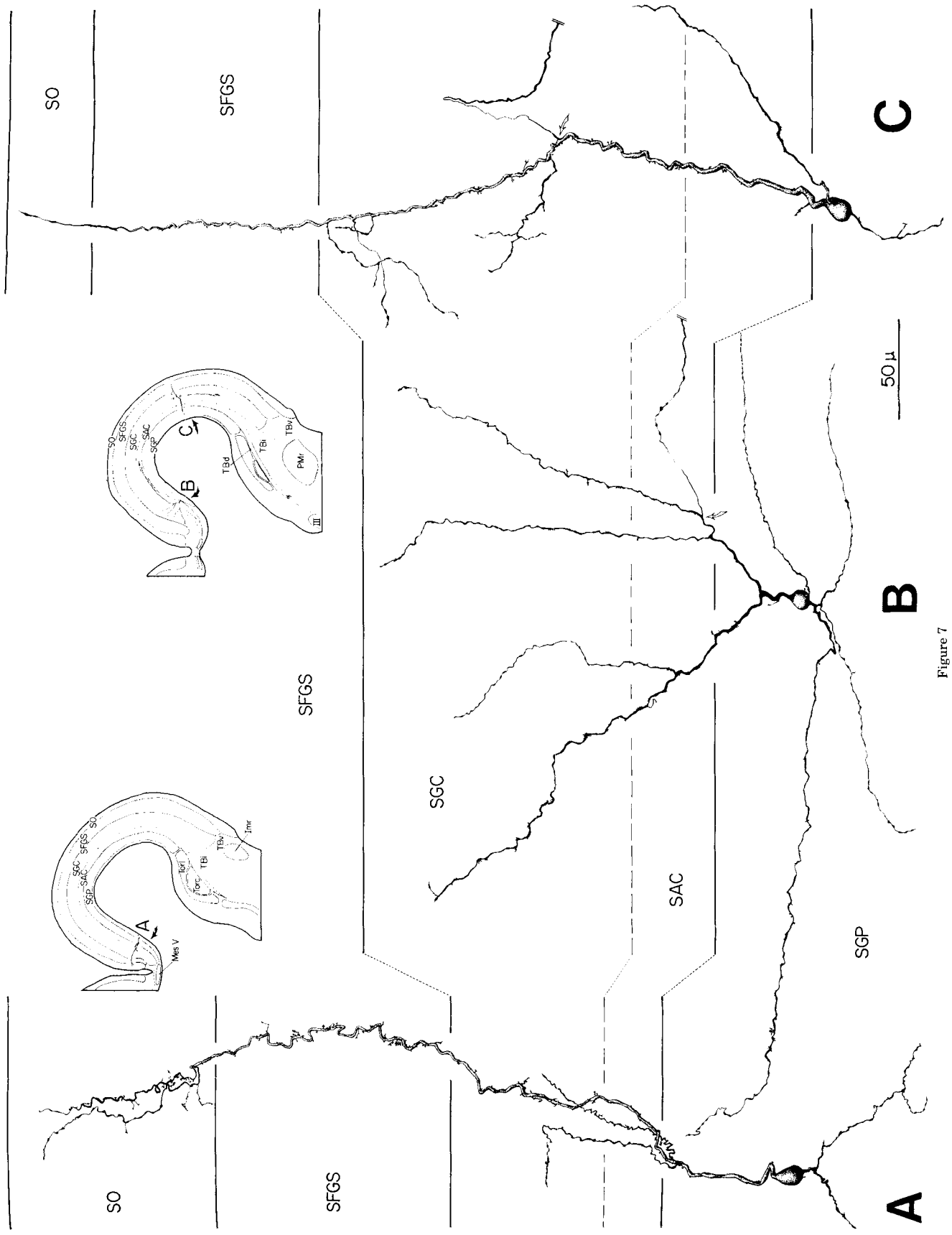


Fig. 6. Photomicrographs of an injection site and HRP-filled dorsal pathway neurons. A. An example of a small tectal injection. B. Dorsal pathway (TBd) cell filled through a distal dendrite by the injection in A. This cell is reconstructed fully in Figure 4. Its axon emerges (arrow) from the cell body and runs out of the tectum in the deepest layer of the stratum album centrale (SAC) just above the stratum griseum periventriculare (SGP). C. Dorsal pathway cell filled after a contralateral paramedian injection in the tegmentum. A 5 μm diameter axon arises from the base of a dendrite (arrow).

the SGC at the point of origin of the axon. Its main trunk continues upward in some cases (Fig. 9), but recurves and descends into the SAC in others (Fig. 10). A series of varicosity-laden filamentous appendages arises from the descending dendrite near the axon and overlaps the appendages arising from the proximal portion of the ascending dendrites. The appendages occupy a field in the SGC with about the same lateral dimensions as the plexus just below the stratum opticum. The small-field cells usually lack a primary descending dendrite and their appendages arise directly from the soma or from thin, laterally directed stalks (Fig. 11).

A medium caliber axon (2.5–3 μm), with an initial 30 μm long constriction, originates either from a kink in the descending dendrite as described above in large-field cells or from the soma, or very near to it, in small-field cells. The axon descends directly to the SAC where it makes a 90° bend to run laterally in the middle layers of the SAC. In a number of cases, (e.g., Fig. 9) small caliber axon collaterals are emitted in the SAC bearing local groupings of synaptic boutons. The collateral illustrated in Figure 9 continued medially in the SAC without any additional varicosities until it was lost entering the tectal commissure. In most cases, the laterally directed main axon trunk of these cells could not be reliably traced out of the tectum through the tangle of stained axons in the SAC. The appearance of short, darkly stained segments (putative nodes) suggests that the laterally directed trunk is myelinated. In a few


SO
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TBd
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TBv
PMr
III

Figure 7

instances, axons were traced far enough to suggest that they entered the TBv(med) rather that the more medially coursing TBi.

Medium-sized SGC cells with horizontal dendrites (Figs. 13,14). A second type of ipsilaterally projecting cell in the upper half of the SGC has horizontally oriented primary dendrites. These neurons have a medium-sized (15–23 μm) fusiform soma, a horizontally elongate dendritic field, and dendritic appendages in the SGC. Two robust dendrites emerge from opposite ends of the soma and travel horizontally, sometimes for several hundred microns. One or two main branches arise from each dendrite and course vertically. The parent shafts then turn upward as well and usually define the lateral borders of the dendritic field. Many filamentous, varicosity-laden dendritic appendages extend laterally and vertically, but remain strictly confined to the SGC. Most of the varicosities are small, translucent, and irregularly shaped, but a few at the ends of the filaments (e.g., swellings at extreme right of Fig. 13) are larger, darker staining, and smoother than most and are virtually indistinguishable from HRP-filled axonal boutons in the same material. The four to six vertically oriented shafts course through most of the superficial gray without branching or emitting appendages. The thinner shafts usually end without branching, just before penetrating the SO while the thicker shafts are sometimes capped by a small dendritic arbor just below the SO. None of these dendrites are as thick as the vertical shafts of the cells in the SGC that support a dense plexus under the SO. Viewed from the tectal surface, SGC neurons with horizontal dendrites have elongated dendritic fields, four to five times as long as they are wide, that contrast with the almost circular fields of the stratified cells. The long axis commonly measures 500–600 μm and was always oriented mediolaterally in a small sample.

A medium caliber (2–3 μm) axon with a 20–30 μm long constricted segment originates from a kink in one of the horizontal dendrites. The axon descends to the SAC, turns sharply laterally, and runs in the middle to upper layers of the SAC emitting collaterals in the tectum in a number of cases. It appears to become myelinated and most of the time could only be traced far enough to suggest that it entered the ventral pathway.

SAC/SGP cells with multiple radial dendrites (Figs. 15,16). These cells have fusiform- to pyriform-shaped somata, 15–25 μm in diameter, located at the top or bottom of the SAC, or in the upper layers of the SGP. Their larger, sparsely distributed somata stand out among numerous, tightly packed small neurons in Nissl-stained material.

Two or three ascending dendrites emerge from the soma and may travel a short distance horizontally before turning upward. They sometimes branch once or twice, giving rise to three to six radially oriented dendrites. In other neurons, one primary dendrite travels a short distance vertically before dividing into branches. The radial branches initially diverge in the SGC and then follow parallel courses through the SFGS to the surface without branching. Dendritic fields range from 200 to 300 μm across. These neurons lack the filamentous dendritic appendages in the central gray observed on the other four classes of ipsilaterally projecting neurons. Instead, their dendrites bear many fine spicules similar to those seen on the contralaterally projecting TBd neurons. Neurons with somata located near the top of the stratum album centrale may have one or two descending dendrites bearing spicules, but those whose somata border the SGP lack basal dendrites. One or two filamentous strands occasionally arise from a descending dendrite in the SAC (Fig. 15B) or SGP and course downward.

A medium axon (1.5–2.5 μm) arises from the proximal portion of an ascending or descending dendrite in the SAC or from the soma, and courses laterally in the deeper parts of this layer without giving off collaterals. Axons apparently become myelinated after an initial constriction. In several instances, collaterals were observed in profundus mesencephali caudalis (PMc) after the axon had emerged from the tectum, but these could not be traced completely because of the large numbers of stained axons in that region. Axons were running just ventral to the location of the unlabeled dorsal pathway (TBd) when they were lost, suggesting that they entered the intermediate pathway (TBi). It was not possible in most cases to rule out a ventrolaterally directed turn into the contiguous medium caliber ventral pathway past the point where the axons were lost. A second suggestion that these neurons contribute to the intermediate pathway comes from comparing axon diameters. The axons of these neurons and the axons anterogradely labeled in the intermediate pathway have a smaller average diameter (about 2 μm) than do the axons of the two remaining cell types and axons in the medium caliber ventral pathway (about 3 μm).

DISCUSSION

The present study identified six classes of tectal neurons in *Pseudemys* that send axons into the three tectobulbar pathways characterized in the previous paper (Sereno, '85). An example of each type is schematically illustrated in Figure 17 at a uniform magnification. In this section the morphology of these neurons will be summarized and compared with findings in other vertebrates. Some of the possible functional implications of the data from both papers are then considered.

Anatomy of tectobulbar cells

In turtles, large multipolar neurons in the central gray with sparsely branched dendritic fields spanning up to 1,200 μm give rise to the contralaterally projecting TBd. Medium-sized neurons with deeper lying somata and more vertically oriented dendrites probably give rise to the ipsilaterally projecting TBi. The dendrites of both types of neurons bear short hair-like spicules and both extend well into the retinorecipient superficial layers. Dorsal pathway neurons exhibit a particular tendency to arborize in the bottom third

Fig. 7. Small radial ventral pathway (TBv) cells in the SGP. These neurons were filled by ipsilateral injections into the lateral tegmentum. The axons of cells B and C (origins at open arrows) were traced directly into the small caliber component (1 μm or less) of the TBv. The insets show the location of the reconstructed neurons. C is a typical periventricular TBv radial cell. The axon characteristically loops upward before coursing laterally, forming a "shepherds crook." The medially located periventricular cell in B is unusual; its branched ascending dendrite and extensive basal dendrites give it a multipolar appearance. Furthermore, its dendrites clearly end before entering the stratum fibrosum et griseum superficiale (SFGS), unlike any other class of tectobulbar neuron. The cell in A demonstrates that more typical periventricular TBv neurons occur in the medial tectum as well.

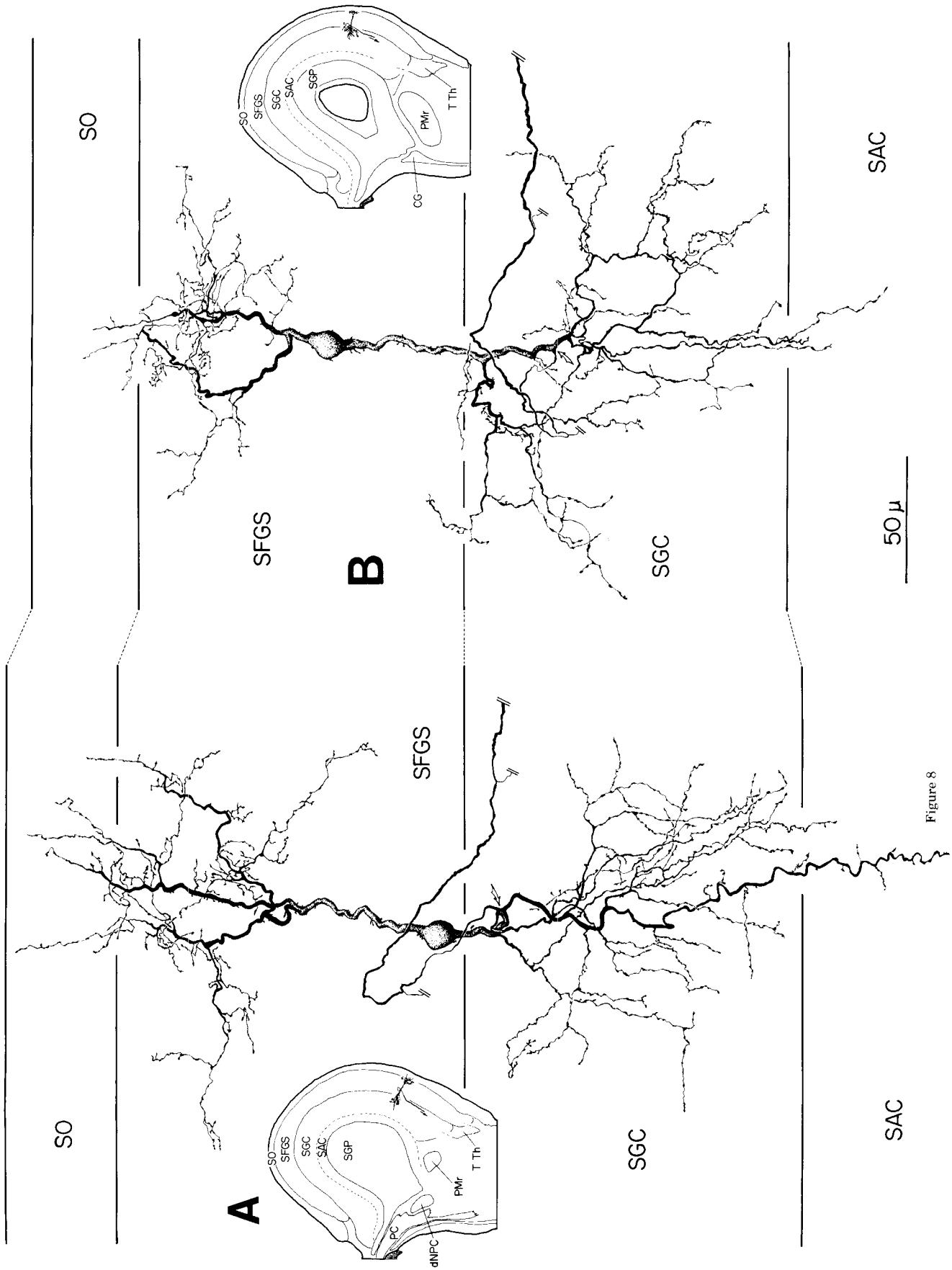

Figure 8

of the superficial gray. The axons of both cell types lack intratectal branches but emit an extensive series of collaterals in their long, descending course through the brainstem. In most cases, a main rostral branch can also be identified. Each dorsal and intermediate pathway neuron thus gives rise to a widespread, low-density, non-topographic terminal field distributed throughout reticular structures at diencephalic, mesencephalic, pontine, and medullary levels.

The four remaining classes of tectobulbar neurons probably send axons into the ipsilateral TBv. In two of these types—small periventricular radial cells and small bitufted radial cells in the superficial gray—axons were directly traced into the small caliber component of the ventral pathway. In two others—medium-sized central gray cells with stratified dendrites and central gray cells with horizontal dendrites—axons could only be traced far enough in most cases to suggest that they entered the medium caliber component of the ventral pathway rather than the adjacent intermediate pathway. In contrast to dorsal and intermediate pathway neurons, these last four classes give off a spray of long filamentous dendritic appendages in the central gray. Most of them also arborize extensively in the superficial gray, just below the stratum opticum. Except for the small periventricular cells, the somata of these neurons are located above the relatively well-defined layer of large dorsal pathway neurons. Their axons, too, are distinct. In many cases, collaterals arise from the main axon trunk before it leaves the tectum, and the larger types sometimes have commissural branches. Outside of the tectum, ventral pathway axons apparently have no main rostral branch and are somewhat less extensively collateralized in the tegmentum than their dorsal and intermediate pathway counterparts.

Comparable data at the single-cell level exist for the garter snake *Thamnophis* (Dacey, '82) and for cats (Moschovakis and Karabelas, '82; Grantyn et al., '83). In the garter snake, as in *Pseudemys*, large multipolar central gray neurons give rise to dorsal pathway axons. The smaller intermediate pathway neurons, however, are also multipolar and their somata are more intermixed vertically with those of dorsal pathway neurons than is the case in turtles. Nevertheless, as in turtles, both types have dendrites covered with hair-like spicules and give rise to axons without intratectal collaterals. The most striking difference is that the dendritic fields of dorsal and intermediate pathway neurons in the snake are restricted to the central gray and deep tectal layers, which presumably prevents them from receiving significant direct retinal input. The ventral pathway seems to be much less differentiated in snakes than in turtles. In snakes, it consists of a single, fine-caliber component that arises from a uniform class of small neurons in the superficial gray. Like the small bitufted ventral pathway neurons in the superficial gray of turtles, these radially oriented neurons have somata lying above those of dorsal and intermediate pathway neurons as well as dendritic arbors just under the stratum opticum. However, they lack central gray dendritic appendages and intratectal collaterals, and have a compact, apparently topographic collateral to nucleus isthmi not seen in turtles.

In cats, intracellular injections of antidromically identified dorsal pathway axons revealed large, rather profusely branched, multipolar neurons located in the intermediate gray lacking obvious dendritic specializations (Grantyn and Grantyn, '82; Grantyn et al., '83). These authors did not illustrate the laminar location of their reconstructed cells, but their depth measurements and dendritic field dimensions, as well as earlier Golgi studies of large intermediate gray ganglionic neurons (Victorov, '68; Norita, '80), suggest that the dendrites of dorsal pathway neurons extend into the deepest-lying retinal terminal zone in the SO. In support of this last conjecture, Berson and McIlwain ('82) found that almost 40% of the dorsal pathway neurons (that is, cells that could be driven antidromically from the predorsal bundle) encountered in the intermediate and deep layers responded with monosynaptic spikes to optic disc or optic tract stimulation. Less single-cell information is available on the morphology of ipsilaterally projecting neurons in cats. Grantyn and Grantyn ('82) and Moschovakis and Karabelas ('82) filled a number of smaller tectobulbar neurons in the upper intermediate gray with vertically elongated dendritic fields and intratectal as well as commissural collaterals that suggest a comparison with certain ventral pathway neurons in turtles and snakes. A number of these had ipsilaterally projecting caudal trunks, but it is unclear exactly which pathway they eventually entered.

Lazár et al. ('83) obtained Golgi-like back-filling of tectobulbar neurons after tegmental injections of cobaltic-lysine in frogs. They did not serially reconstruct any of the labeled neurons in their 60–80 μm sections. Nevertheless, several differences in laminar distribution are readily apparent. Contralaterally projecting dorsal pathway axons arise from large multipolar ganglionic cells located not in the central gray, but at the surface of the periventricular layers (layer 6), which otherwise consist mostly of tightly-packed small pyriform neurons. The widespread dendrites of dorsal pathway neurons arborize in lamina B, the most superficial retinal terminal layer, unlike either turtles or snakes. Multipolar ipsilaterally projecting neurons are mostly situated in the central gray (layer 7), above the dorsal pathway neurons. Although their widespread and sparsely branched dendrites sometimes ascend to the tectal surface, they only arborize profusely in lamina F, one of the deepest retinal terminal layers, again in contrast to intermediate (and ventral) pathway neurons in turtles and snakes. There is also a small population of ipsilaterally projecting neurons in the superficial retinal-recipient layers 8 and 9 with small somata and vertically oriented dendrites. These last neurons suggest that there might be a ventral pathway in frogs.

A pattern of laminar origins of tectobulbar pathways similar to that in turtles can be discerned from retrograde experiments in mammals and birds (Hashikawa and Kawamura, '77; Kawamura and Hashikawa, '78; Murray and Coulter, '78; Holcombe and Hall, '81a,b; Reiner and Karten, '82). The *dorsal pathway* arises almost exclusively from the

Fig. 8. Small bitufted ventral pathway (TBv) cells in the SFGS. Cells A and B were labeled after ipsilateral injections into the lateral tegmentum. These cells have a radially oriented ascending dendrite that gives rise to a plexus of filamentous, varicosity-laden dendritic appendages just below the stratum opticum (SO) as well as a radial descending dendrite that emits similar appendages in the stratum griseum centrale (SGC). Their thin axons (origins at open arrows) loop dorsomedially and then turn laterally and emit "local" collaterals into the SGC before leaving the tectum to enter the small caliber component (1 μm or less) of the ventral pathway. The insets show the location of the reconstructed neurons.

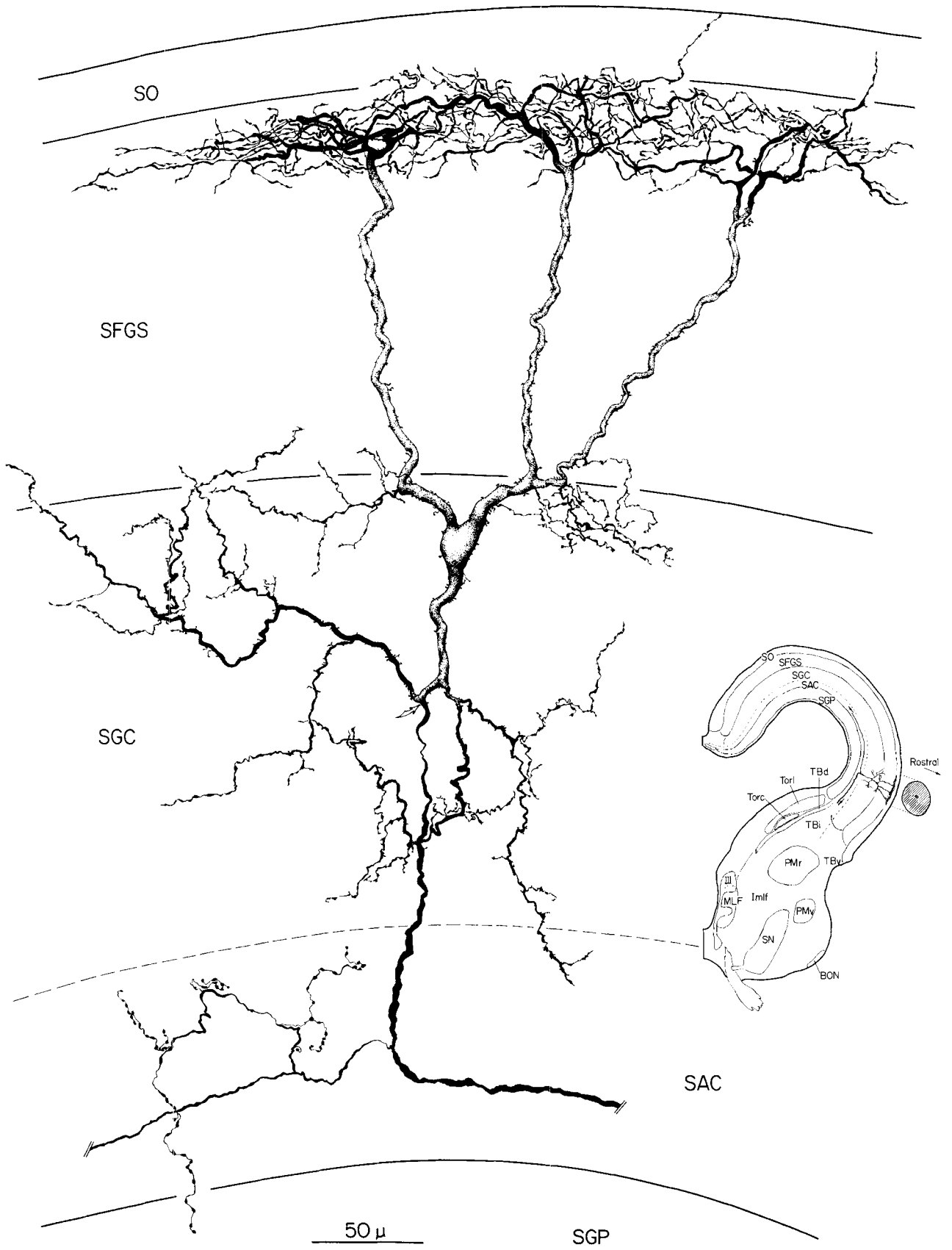

Fig. 9. Medium-sized ventral pathway (TBv) cell in the SGC with stratified dendrites. This neuron was labeled by an ipsilateral injection into the lateral tegmentum. Robust ascending dendrites give rise to a stratified plexus of appendages just beneath the stratum opticum (SO) that looks almost circular when viewed from the surface (see inset). The descending dendrite emits a second series of appendages in the stratum griseum centrale (SGC). A medium caliber myelinated axon (3 μm diameter) arises from a kink in the descending dendrite (open arrow) and emits a small local collateral and a thin commissural branch before turning laterally to leave the tectum. It was traced into the medium caliber component of the ventral pathway. The inset shows the neuron's location.

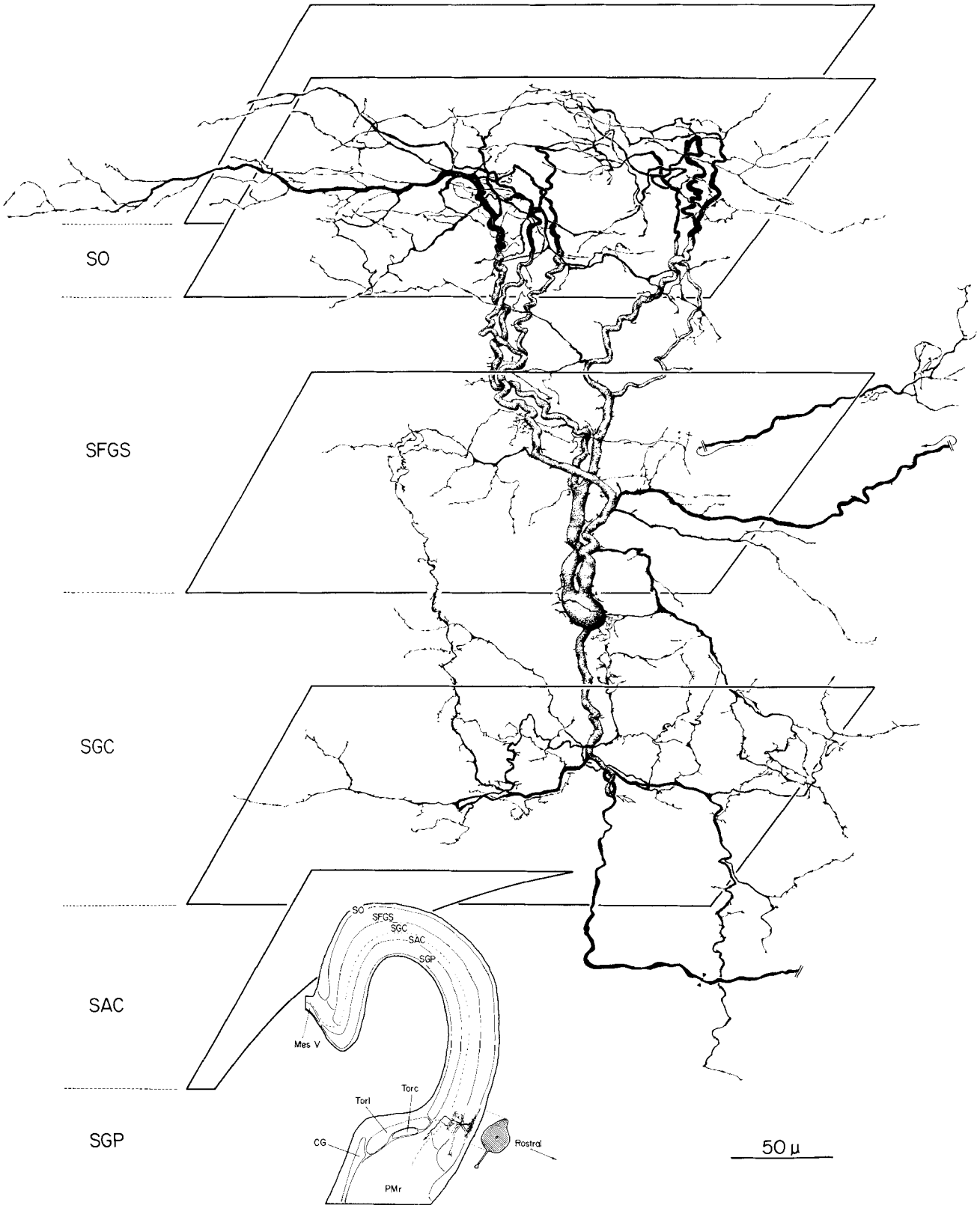

Fig. 10. Oblique view of a probable ventral pathway (TBv) cell in the SGC with stratified dendrites. This neuron was labeled by an ipsilateral injection into the lateral tegmentum. It is quite similar in form to the neurons in Figure 9; however, the top of its main radial axis is tilted into the picture. The tectal laminae have consequently been drawn as planes to emphasize the tilt which gives the impression that the viewer is looking up at the neuron from below. This orientation better shows how the ascending dendrites splay out at the bottom of the stratum opticum (SO). As in the previous example, a second series of appendages arise in the SGC, and a medium caliber axon is given off at a kink in the descending dendrite (open arrow). This neuron has an aberrant dendritic branch that travels for some distance toward the reticular formation, away from the main dendritic field, eventually ending in the stratum fibrosum et griseum superficiale (SGFS; see inset).

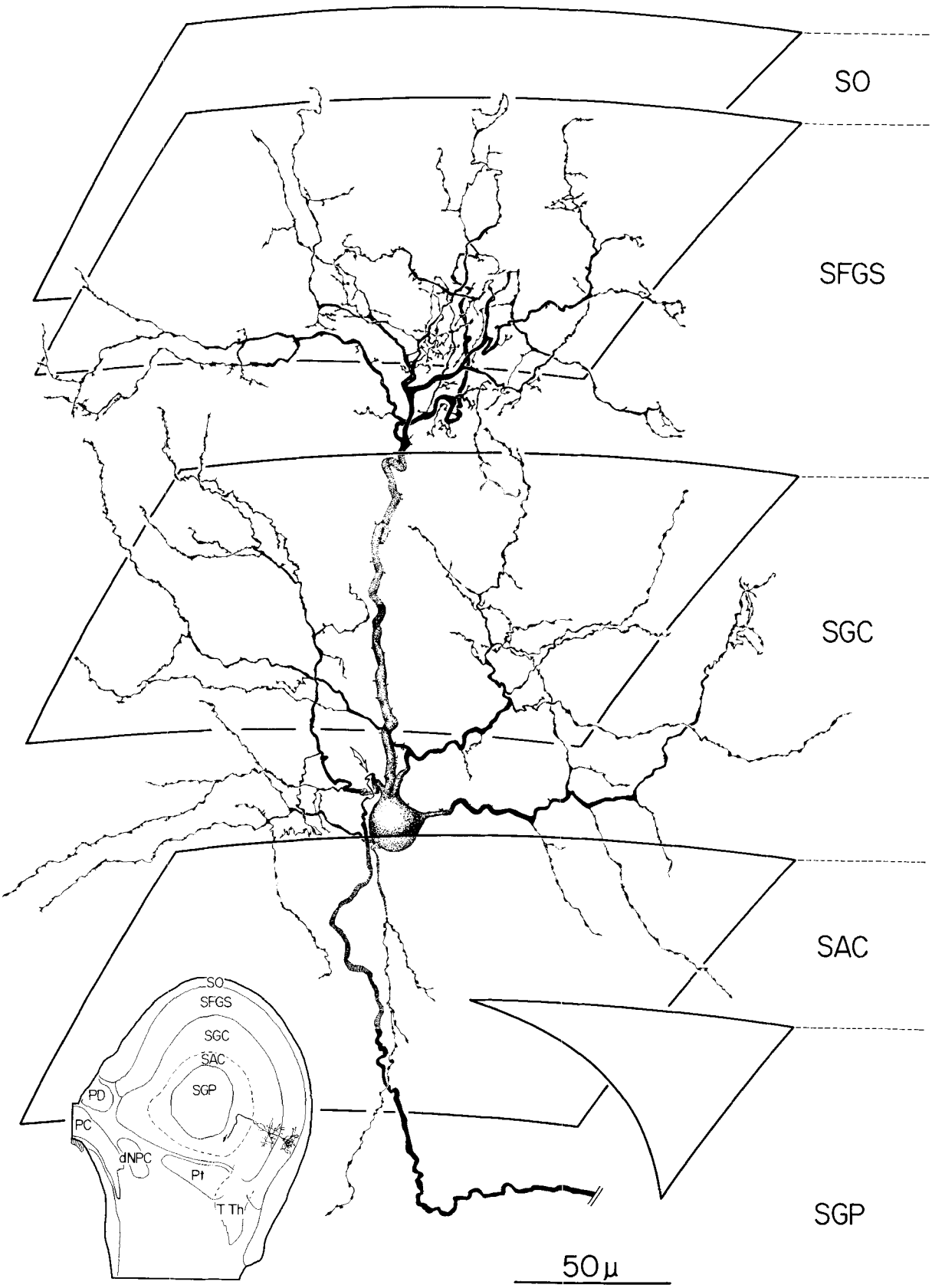

Fig. 11. Oblique view of a probable ventral pathway (TBv) cell in the SGC. This neuron is a small-field version of the neurons illustrated in Figures 9 and 10. Its soma and axon is similar in size to those of the large-field types, but its primary dendrites are much less robust and the sprays of dendritic appendages just below the stratum opticum (SO) and in the SGC are confined to proportionately smaller areas. Furthermore, the axon is emitted (open arrow) near the soma, rather than from a descending dendrite. The inset shows the location of the neuron.

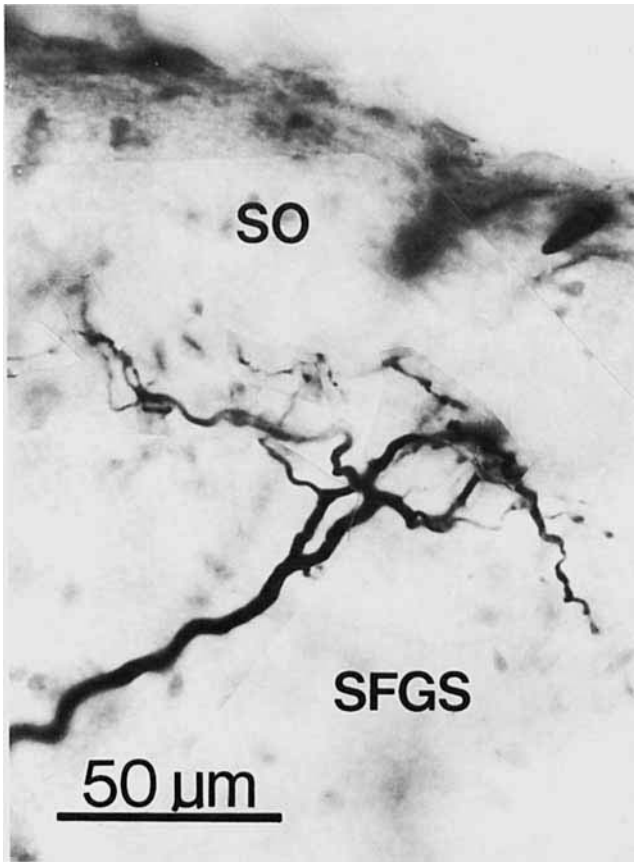

Fig. 12. High-power photomicrograph of a portion of the superficial dendritic plexus of a stratified SGC cell. The varicose dendritic strands are confined to a rather thin layer just below the SO.

central (intermediate) gray, the *intermediate pathway* mostly from the periventricular (deep) gray and the deeper parts of the central gray, and the *ventral pathway* mostly from the lower parts of the superficial gray and the upper parts of the central gray. Dorsal and intermediate pathway neurons are more intimately intermixed in the avian tectum than they are in mammals, and the periventricular cell layers are quite reduced as well.

Parallel tectoreticular channels

The available information thus indicates that several populations of tectal neurons send axons into three tectoreticular pathways in each of the species that have been studied to date. The tectoreticular projection can then be viewed as several parallel channels, each formed by a particular population of tectal neurons. This and the previous paper (Sereno, '85) provide the most complete picture of the organization of the tectoreticular projection obtained to date and it is now possible to comment on several features of the organization of the tectoreticular channels.

First, although virtually all of the neurons that project to the reticular formation in turtles have dendrites extending into the retinal-recipient layers of the superficial gray, the various populations differ in their pattern of sublaminar specialization. Dorsal pathway neurons arborize in the bottom third of the superficial gray, ventral pathway neurons at the very top, and intermediate pathway neurons have dendrites that traverse the layer without branching. The experiments necessary to confirm that the tectoreticular neurons receive direct retinal input have not been done, but the position in the tectum of the tectoreticular neurons relative to retinotectal axon terminals makes this likely and raises the possibility that the different populations of tectoreticular neurons receive different combinations of inputs. It is known, for example, that retinal ganglion cells in *Pseudemys* vary in their soma size, dendritic morphology, and physiological properties (e.g., Peterson and Ulinski, '82; Kolb, '82; Marchiafava, '83). Since ganglion cells of all sizes project to the tectum (Peterson, '78), it is likely that several classes of ganglion cells participate in the retinotectal projection. Our results on the morphology of tectoreticular neurons lead to the testable hypothesis that the various classes of tectoreticular neurons receive particular mixes of inputs from the various classes of retinal ganglion cells.

A second feature of the organization of the tectoreticular projections is that the dendritic fields of different classes of tectoreticular neurons as viewed from the tectal surface range over two orders of magnitude. Large dorsal pathway neurons have access to 1/20 of the tectal surface, intermediate pathway neurons cover only 1/200, and small ventral pathway neurons, 1/2,000 of one tectal lobe. This is consistent with reports of large differences in the receptive field sizes of tectal units in different laminae (e.g., Stein and Gaither, '83) and suggests that the several channels of tectoreticular neurons differ greatly in the amount of visual space sampled by individual component neurons.

Third, the pathways differ in their brainstem targets. The dorsal pathway projects to the medial part of the reticular core while the intermediate pathway projects to its lateral parts and the ventral pathway to its ventrolateral parts. A complex picture emerges when these results are put together with information on the dendritic morphology and the spinal cord connections of the turtle reticular neurons (ten Donkelaar, '76; ten Donkelaar et al., '80; Newman and Cruce, '82; Newman et al., '83; see Fig. 12 from Sereno ('85) for a horizontal view of the nuclei in the turtle reticular formation). The *dorsal pathway* has (1) an ipsilateral projection to the ipsilateral interstitial nucleus of the medial longitudinal fasciculus, which projects ipsilaterally to the spinal cord, and crossed projections to (2) reticularis superioris medialis, which projects bilaterally to the cord, (3) reticularis medius, which projects ipsilaterally, and (4) reticularis inferioris dorsalis, which projects bilaterally with an ipsilateral preference. The *intermediate pathway* has ipsilateral projections to (1) the dorsomedial segment of reticularis superioris lateralis, which projects bilaterally to the cord, (2) reticularis medius lateralis, which projects contralaterally, and (3) reticularis inferioris dorsalis, which has an ipsilateral preference. Finally, the *ventral pathway* projects ipsilaterally to (1) the ventrolateral segment of reticularis superioris lateralis and (2) reticularis superioris medialis, which both project bilaterally to the cord, (3) reticularis medius, which projects ipsilaterally, (4) reticularis medius lateralis, which projects contralaterally, and (5) reticularis inferioris dorsalis, which has an ipsilateral preference. All of the reticulospinal pathways terminate in the medial half of the ventral horn (ten Donkelaar, '76). Each tectoreticular pathway, thus, appears to have equally direct access to motoneurons on the two sides of the spinal cord, but the pattern and weighting of the connections is different in each case.

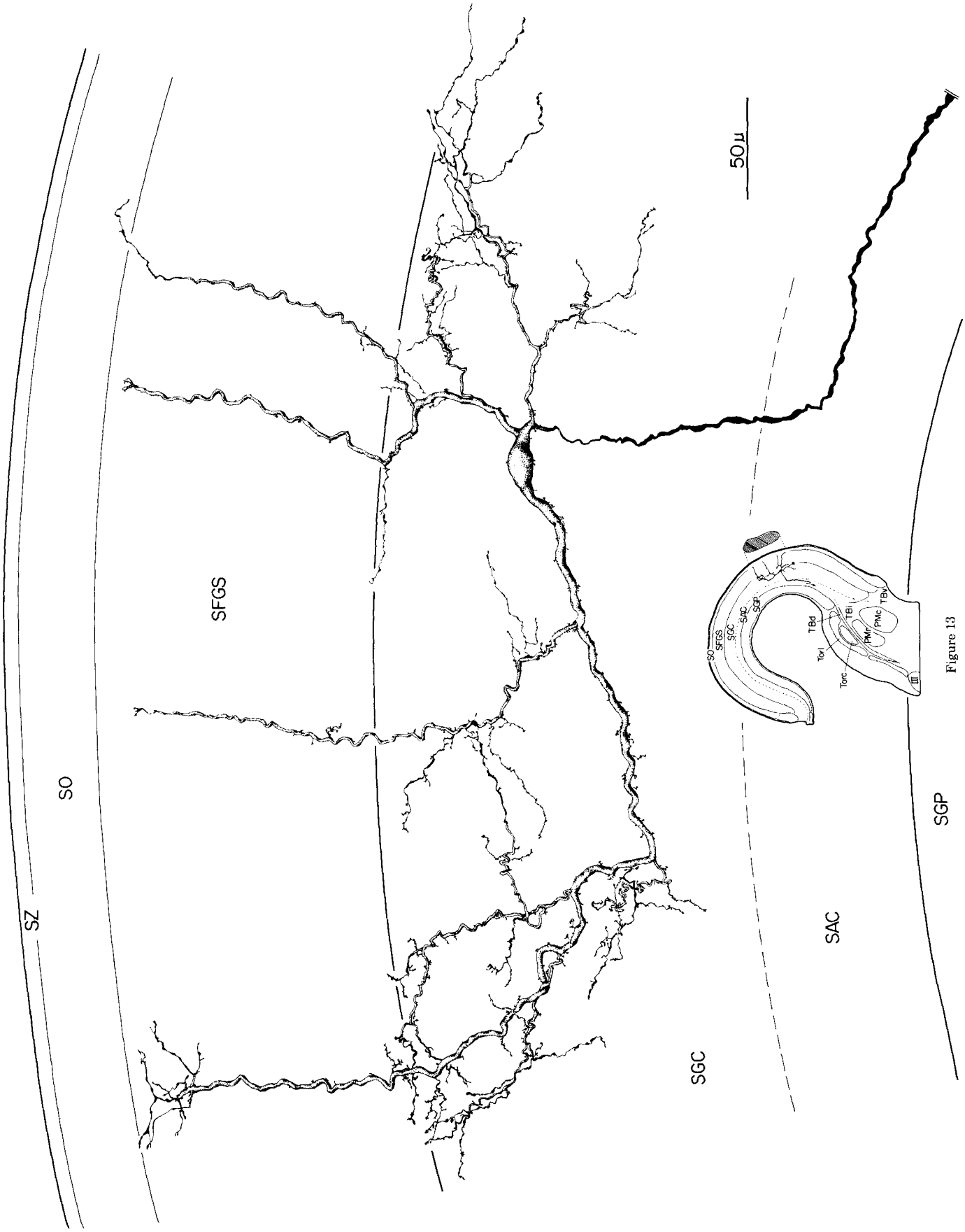
SZ
SO
SFGS
SGC
SAC
SGP
50 µ
SO
SFGS
SGC
SAC
SGP
TBd
TBl
TBv
Torl
Torc
PMr
PMc
III

Figure 13

In summary, it is now clear that the tectoreticular pathway should not be viewed as a single entity. Rather, it is composed of as many as six separate, parallel channels in turtles, each of which (1) probably receives a distinctive mix of inputs from retinal ganglion cells, (2) differs in the amount of visual space sampled by constituent neurons, and (3) projects to its own set of targets in the brainstem reticular formation. How these multiple channels contribute to the generation and control of orientation movements can only be surmised at this point, but Ingle and Fraser ('84) have preliminary evidence in frogs suggesting that a particular class of tectoreticular neurons receives inputs from a distinct class of retinal ganglion cells and is involved in a particular set of behaviors.

Non-topographic nature of the projections

One factor that must be considered when beginning to think about the behavioral roles of the tectoreticular channels is that the projections are apparently non-topographic. That is, there is no systematic relation between the spatial distribution of terminal boutons from a single tectoreticular axon and the location of its dendritic field in the tectum. Rather, axons branch and terminate at many rostrocaudal levels. The projection is not completely divergent at the level of single axons, since the boutons of one axon do not occupy all parts of the overall terminal field as defined by large injections. In the intermediate pathway, for example, a single axon terminates in a dorsoventrally restricted portion of the lateral reticular formation; however, even injections occupying well under 1% of the tectal surface reproduce the overall pattern of the projection. This type of organization contrasts sharply with the topological or point-to-point mappings in other projections where single axons have spatially restricted arbors (Ferster and LeVay, '78; Bowling and Michael, '80; Sereno, '83), and where adjacent cells in the source map project to adjacent regions of the target map.

In addition, the number of synaptic contacts effected by tectoreticular neurons in any given region of the reticular formation appears small and variable. One axon commonly gives rise to thousands of boutons distributed throughout a considerable volume in small irregular clumps or strings. It is not yet certain that these boutons are presynaptic elements, but in several cases where the target cells (in profundus mesencephali rostralis) of a tectoreticular axon have a reciprocal projection back to the tectum (and were thus sometimes simultaneously back-filled), more direct observations (Sereno, '85) indicate that a reticular cell might receive anywhere from a few to 15 to 20 contacts from one tectoreticular axon. There is also significant variability between different axons at a regional level. For example, the axon in Figures 12–15 from Sereno ('85) has one-third as many boutons in the region of the reticular formation ventral to the trochlear nucleus as does the axon in Figure 16 from Sereno ('85).

Fig. 13. Medium-sized probable ventral pathway (TBv) cell with horizontal dendrites. This neuron was labeled by an ipsilateral injection into the lateral tegmentum. The soma emits robust, horizontally directed dendrites that give off vertical branches, and eventually turn upward themselves. As with other ventral pathway neurons, is given off in the SGC. The 3 μm diameter axon was traced far enough out of the tectum to suggest that it entered the medium caliber component of the ventral pathway. The inset shows the location of the neuron and gives a surface view of the dendritic field, which is quite elongated mediolaterally.

Rough estimates of the strength of these sparse connections can be derived from recent work combining intracellular recordings with pre- and post-synaptic HRP-filling (Ia/motoneuron contacts—Jack et al., '81; Redman and Walmsley, '81; inhibitory Mauthner neuron inputs—Korn et al., '82; dorsal root ganglion/spinal cord cell co-cultures—Nelson et al., '83; Neale et al., '83). The maximum number of quanta released at a connection comes quite close to, but never exceeds, the number of boutons in the terminal arbor that contact the recorded cell at the light microscopic level, suggesting that each bouton either produces one quantum or nothing. The average unitary post-synaptic potential in these studies ranged from 100 to 350 μV. Assuming a somewhat non-linear summation (see, e.g., Langmoen and Anderson, '83), a minimum of 50–150 simultaneously active boutons at a connection would therefore be necessary for a pre-synaptic spike to overcome threshold and produce a spike in the post-synaptic cell. The implication in the present context is that the concerted activity of a sizable number of tectoreticular neurons is probably required to activate a reticular target cell. By contrast, one axon in a topographically organized projection usually emits hundreds or thousands of boutons in a small volume of tissue and is probably capable of causing a post-synaptic spike by itself.

The organization of tectoreticular axons might, at first, seem to preclude the transmission of specific information about how far the eyes, head, or body should be moved. Grantyn and Grantyn et al. ('82) in fact suggest that the large caliber dorsal pathway neurons convey only a "coarse movement image" upon which other signals from classes of as yet undiscovered axons with less widespread connections could be superimposed to specify the actual parameters of the movement. The present survey of all the tectoreticular pathways did not uncover any axons with restricted, dense terminations. Small axons often had as widespread and non-topographic terminals fields as did larger axons (see, e.g., large versus small caliber axons in the dorsal pathway). There are, however, several plausible ways in which a sparse, divergent projection could encode the locus of tectal activity (cf. Keller, '81; McIlwain, '82).

First, the size of the movement could be coded by the number of active tectoreticular neurons, assuming functionally indistinguishable termination patterns. This weighing could be the result of a higher density of tectoreticular cells at tectal loci that evoke larger movements. There is some evidence in frogs (Weerasuriya and Ewert, '78), snakes (Dacey, '82), turtles (this paper), and cats (Edwards and Henkel, '78; Kawamura and Hashikawa, '78) that tectal loci corresponding to peripheral visual field locations (roughly, large movement loci) contain more tectoreticular neurons than do central visual field loci. An obvious problem is that a single output frequency is one-dimensional, while several independent vectors (e.g., up, down, and lateral for eye movements) must be specified by each tectum. One way to obtain independent outputs would be to have several tectal cell classes with different spatial density gradients (e.g., see Edwards and Henkel, '78; McIlwain, '82) each project to a movement generator for a different direction. However, the presence of collaterals to presumptive brainstem centers both for horizontal (paramedian pontine reticular formation) as well as for vertical movements (rostroventral mesencephalic reticular formation) in all dorsal pathway neurons examined by Grantyn and Grantyn ('82) and in all dorsal pathway neurons and

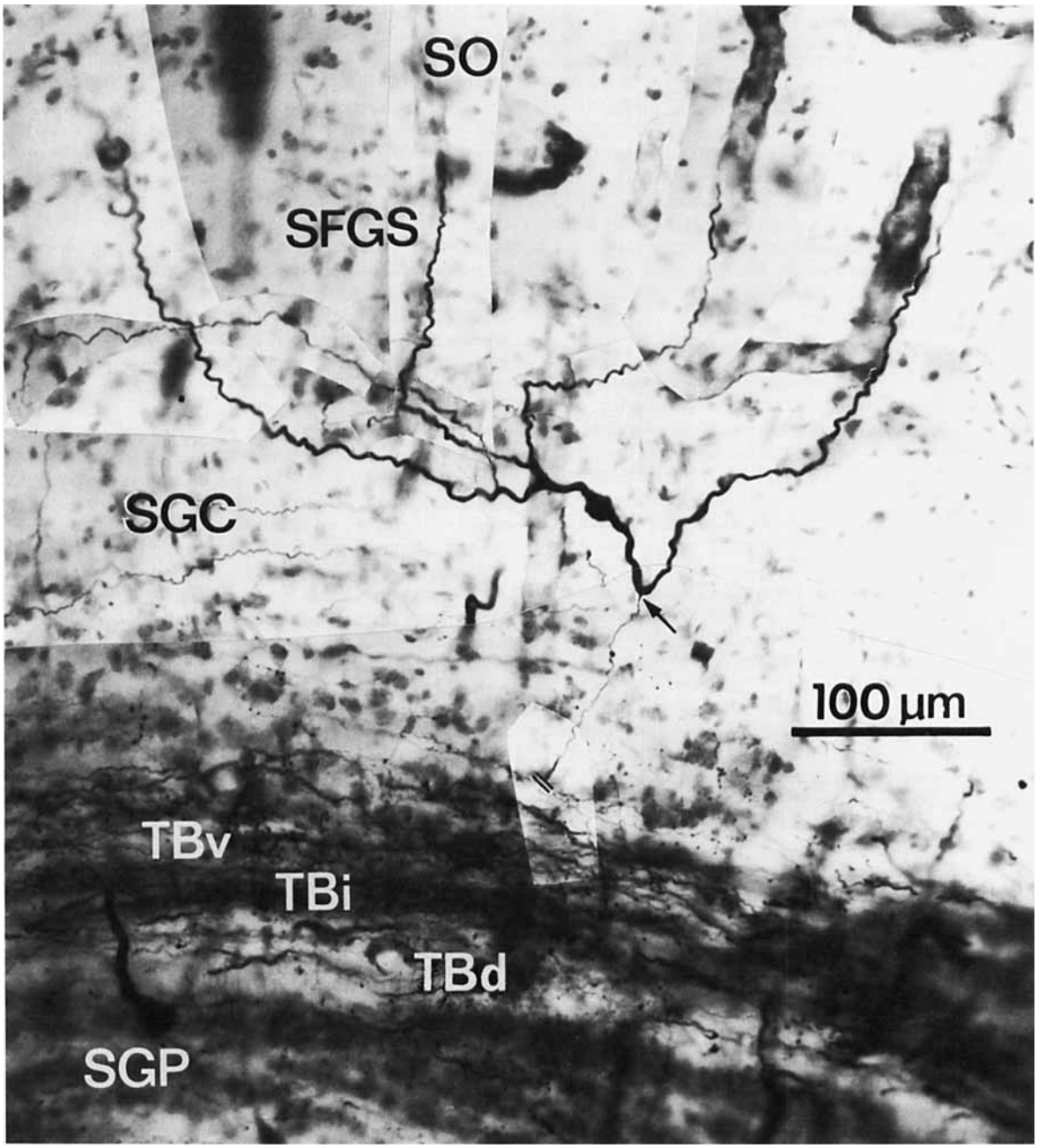

Fig. 14. Photomontage of an SGC cell with horizontal dendrites. This neuron is similar to the one in Figure 13 but has a smaller soma and a smaller diameter axon (origin at arrow). The spray of filamentous dendritic appendages in SGC is not visible at this magnification. The axon was traced far enough out of the tectum to suggest that it entered the medium caliber component of the ventral pathway. The neuron was labeled by an ipsilateral injection into the lateral tegmentum that left the deepest lying contralaterally projecting dorsal pathway (TBd) unlabeled.

even some intermediate pathway neurons in the present study seems to argue against this last conjecture.

Alternatively, the size of the movement could be signalled by termination density. Neurons in a tectal locus generating large movements would terminate more densely in a premotor region than would small movement loci neurons. The number of activated tectal neurons would remain about the same, regardless of the magnitude of the movement. Such a mechanism is consistent with the observed variability in termination density, but it remains to be tested explicitly. In contrast to the first scheme, this model generalizes naturally to several dimensions, since the termination densities of a single neuron in vertical and horizontal movement centers could vary independently. Thus, neurons in a line across the tectum from which one can elicit movements with a given horizontal component would all terminate with equal density in a horizontal movement center but with systematically varying densities in a verti-

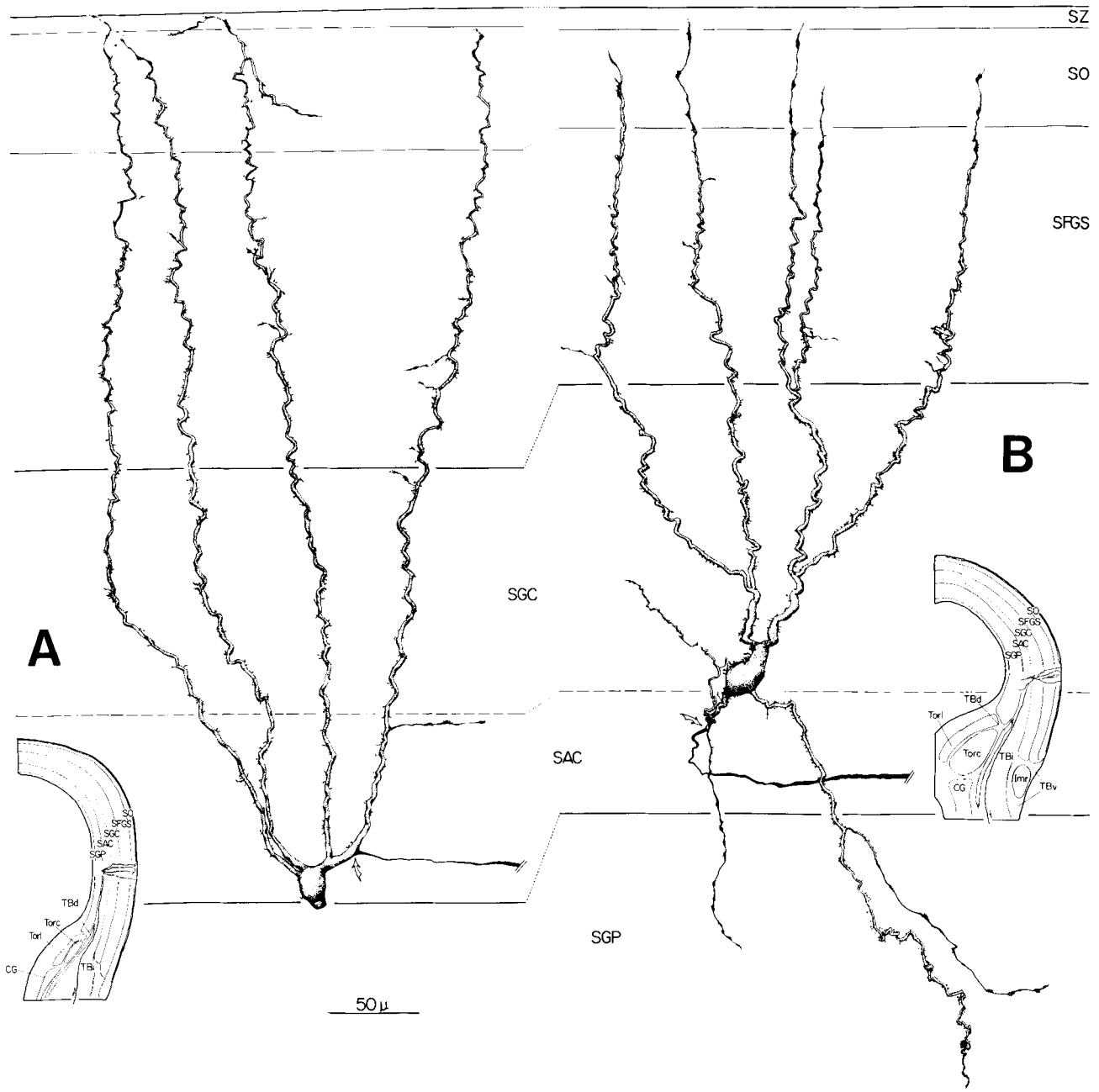

Fig. 15. Intermediate pathway (TBi) cells with multiple radial dendrites. These neurons were labeled by an ipsilateral injection into the lateral tegmentum. Their dendrites, like those of dorsal pathway neurons, are covered with fine spicules. In contrast to the three previously illustrated classes of ipsilaterally projecting ventral pathway neurons, these neurons lack filamentous dendritic appendages in the stratum griseum centrale and under the stratum opticum. Medium caliber (2–3 μm) axons arise (open arrows) from the base of a dendrite and were traced far enough out of the tectum to suggest that they entered the intermediate tectobulbar pathway. The insets show the location of the neurons.

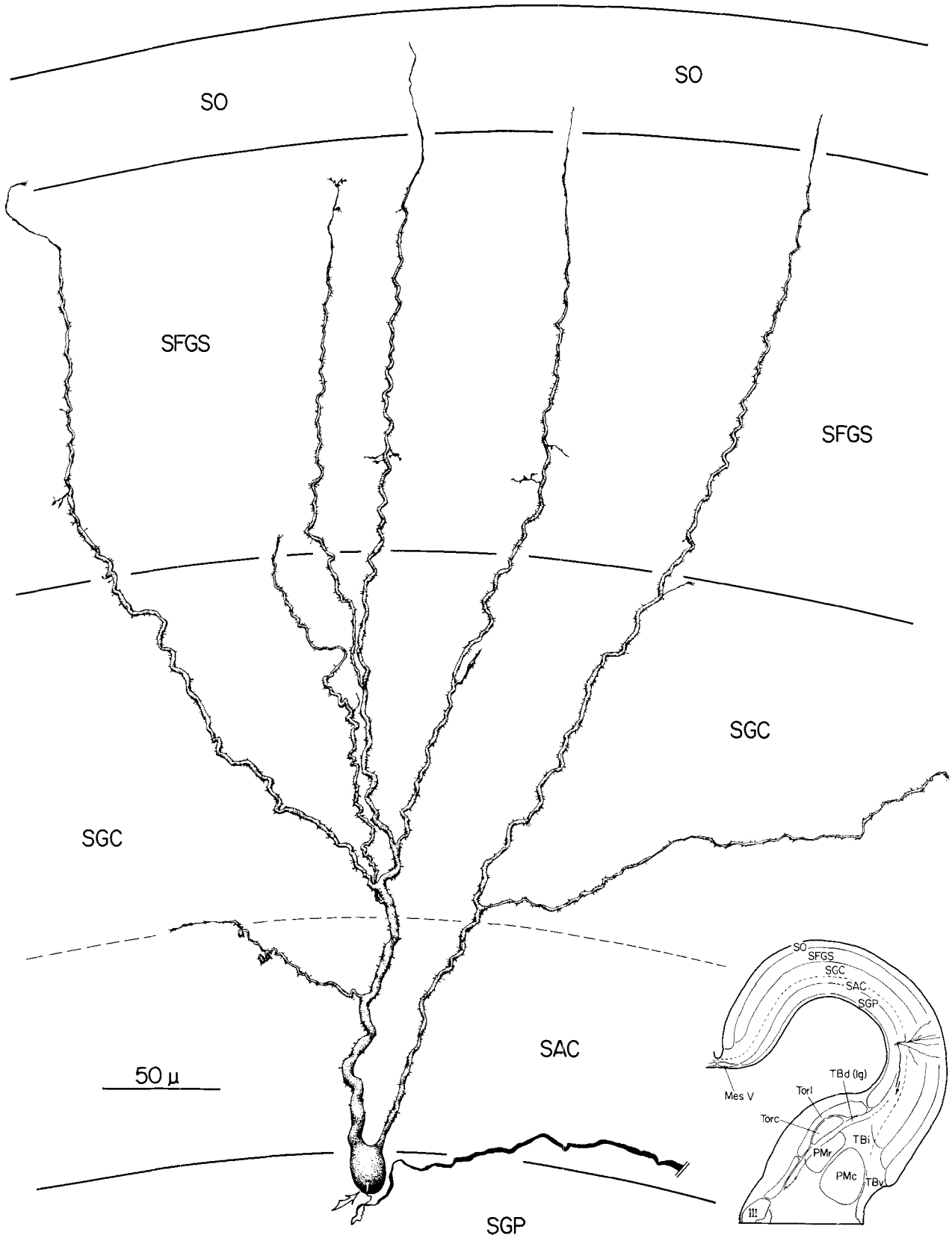

Fig. 16. Intermediate pathway (TBi) cell with multiple radial dendrites. This neuron was labeled by an ipsilateral injection into the lateral tegmentum. It is quite similar to the neurons in Figure 15; its spicule-covered radial dendrites, however, are more spread out and the axon arises directly from the soma (open arrow). The axon was traced well into the intermediate pathway.

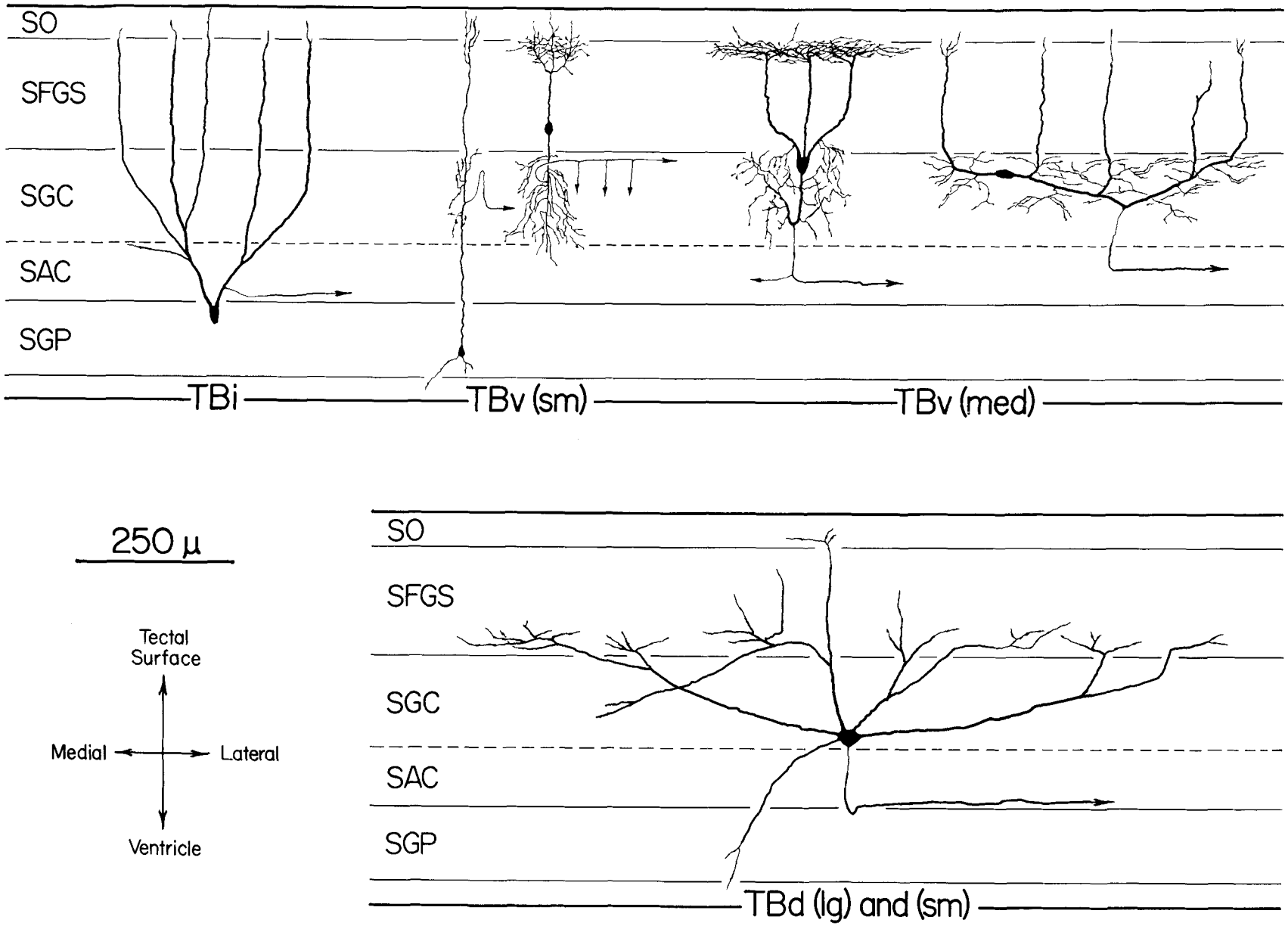

Fig. 17. Summary of tectoreticular neuron types. Six classes of tectoreticular neurons are schematically drawn at a uniform magnification. The top row illustrates ipsilaterally projecting classes and the bottom row, the contralaterally projecting class.

cal movement center (or centers) as a function of location along that line. In this case, the location of tectal activity is signalled by the firing frequencies of several different post-synaptic cell groups.

It should be noted that the two schemes are not incompatible. An explicit test for the second scheme could be carried out at the single-cell level in an animal (e.g., a snake or a frog) with a brain small enough to allow simultaneous complete filling of both the ascending and the descending branches of a dorsal (or intermediate) pathway tectobulbar axon. The ratios between termination densities in different regions could then be determined and correlated with the location of a neuron's dendritic field in the tectum.

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LITERATURE CITED

Berson, D.M., and J.T. McIlwain (1982) Retinal activation of deep-layer cells in superior colliculus of the cat. J. Neurophysiol. *47*:700–714.

Bowling, D.B., and C.R. Michael (1980) Projection patterns of single physiologically characterized optic tract fibers in cat. Nature *286*:899–902.

Dacey, D.M. (1982) Neural Organization of the Optic Tectum in the Eastern Garter Snake, *Thamnophis sirtalis*: Structural Analysis of a Sensorimotor Transformation. Ph.D. dissertation, University of Chicago.

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.

Ferster, D., and S. LeVay (1978) The axonal arborizations of lateral geniculate neurons in the striate cortex of the cat. J. Comp. Neurol. *182*:923–944.

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

Grantyn, R., A. Grantyn, and A. Schierwagen (1983) Passive membrane afterpotentials and repetitive firing of superior colliculus neurons studied in the anesthetized cat. Exp. Brain Res. *50*:377–391.

Hashikawa, T., and K. Kawamura (1978) Identification of cells of origin of tectopontine fibers in the cat superior colliculus: An experimental study with the horseradish perioxidase method. Brain Res. 130:65–79.

Holcombe, V., and W.C. Hall (1981a) Laminar origin of ipsilateral tectopontine pathways. Neuroscience *6*:255–260.

Holcombe, V., and W.C. Hall (1981b) The laminar origin and distribution of the crossed tectoreticular pathways. J. Neurosci. *1*:1103–1112.

Ingle, D.J., and J.M. Fraser (1984) Feeding by frogs in absence of class-2 retinal input to the tectum. Invest. Ophthalmol. Vis. Sci. [Suppl.] *25*:34.

Jack, J.J.B., S.J. Redman, and K. Wong (1981) The components of synaptic potentials evoked in cat spinal motoneurones by impulses in single group Ia afferents. J. Physiol. (Lond.) *321*:65–96.

Kawamura, K., and T. Hashikawa (1978) Cell bodies of origin of reticular projections from the superior colliculus of the cat: An experimental study with the use of horseradish perioxidase as a tracer. J. Comp. Neurol. *182*:1–16.

Keller, E.L. (1981) Brain stem mechanisms in saccadic control. In A.F. Fuchs and W. Becker (eds): Progress in Oculmotor Research. New York: Elsevier, pp. 57–62.

Kolb, H. (1982) The morphology if the bipolar cells, amacrine cells and ganglion cells in the retina of the turtle *Pseudemys scripta elegans*. Philos. Trans. R. Soc. Lond. [Biol.] *298*:355–393.

Korn, H., A. Mallet, A. Triller, and D.S. Faber (1982) Transmission at a central inhibitory synapse. II. Quantal description of release, with a physical correlate for binomial *n*. J. Neurophysiol. *48*:679–707.

Langmoen, I.A., and P. Andersen (1983) Summation of excitatory postsynaptic potentials in hippocampal pyramidal cells. J. Neurophysiol. *50*:1320–1329.

Lazár, G., P. Toth, G. Csank, and E. Kicliter (1983) Morphology and location of tectal projection neurons in frogs: A study of HRP and cobalt-filling. J. Comp. Neurol. *215*:108–120.

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.

Marchiafava, P.L. (1983) The organization of input establishes two functional and morphologically identifiable classes of ganglion cells in the retina of the turtle. Vision Res. *23*:325–338.

Moschovakis, A.K., and A.B. Karabelas (1982) Tectotectal interactions in the cat. Soc. Neurosci. Abstr. *8*:293.

Murray, E.A., and J.D. Coulter (1982) Organization of tectospinal neurons in the cat and rat superior colliculus. Brain Res. *243*:210–214.

Neale, E.A., P.G. Nelson, R.L. Macdonald, C.N. Christian, and L.M. Bowers (1983) Synaptic interactions between mammalian central neurons in cell culture. III. Morphological correlates of quantal synaptic transmission. J. Neurophysio. *49*:1459–1468.

Nelson, P.J., K.C. Marshall, R.Y.K. Pun, C.N. Christian, W.H. Sheriff, Jr., R.L. Macdonald, and E.A. Neale (1983) Synaptic interactions between mammalian central neurons in cell culture. II. Quantal analysis of EPSPs. J. Neurophysiol. *49*:1442–1458.

Newman, D.B., and W.L.R. Cruce (1982) The organization of the reptilian reticular formation: A comparative study using Nissl and Golgi techniques. J. Morphol. *173*:325–349.

Newman, D.B., and W.L.R. Cruce, and L.L. Bruce (1983) The sources of supraspinal afferents to the spinal cord in a variety of limbed reptiles. I. Reticulospinal systems. J. Comp. Neurol. *215*:17–32.

Norita, M. (1980) Neurons and synaptic patterns in the deep layers of the superior colliculus of the cat. A Golgi and electron microscopic study. J. Comp. Neurol. *190*:29–48.

Peters, A., S.L. Palay, and H. D. Webster (1976) The Fine Structure of the Nervous System: The Neurons and Supporting Cells. Philadelphia: Saunders.

Peterson, E.H. (1978) Size classes of ganglion cells which project to the optic tectum of the turtle, *Pseudemys scripta*. Anat. Rec. *190*:509–510.

Peterson, E.H., and P.S. Ulinski (1982) Quantitative studies of retinal ganglion cells in a turtle, *Pseudemys scripta elegans*. II. Size spectrum of ganglion cells and its regional variation. J. Comp. Neurol. *208*:157–168.

Ramón, P. (1896) Estructura de encefalo del camaleon. Rev. Trim. Micrograf. *1*:146–182.

Redman, S., and B. Walmsley (1981) The synaptic basis of the monosynaptic stretch reflex. Trends Neurosci. *4*:248–251.

Reiner, A., and H.J. Karten (1982) Laminar distribution of the cells of origin of the descending tectofugal pathways in the pigeon (*Columba livia*). J. Comp. Neurol. *201*:165–187.

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

Sereno, M.I. (1985) Tectoreticular pathways in turtles. I. Organization and morphology of tectoreticular axons. J. Comp. Neurol. *233*:48–90.

Stein, B.E., and N.S. Gaither (1983) Receptive-field properties in reptilian optic tectum: Some comparisons with mammals. J. Neurophysiol. *50*:102–124.

ten Donkelaar, H.J. (1976) Descending pathways from the brainstem to the spinal cord in some reptiles. II. Course and site of termination. J. Comp. Neuro. *167*:443–463.

ten Donkelaar, H.J., A. Kusuma, and R. DeBoer-van Huizen (1980) Cells of origin of pathways descending to the spinal cord in some quadrapedal reptiles. J. Comp. Neurol. *192*:827–851.

Victorov, I.V. (1968) Neuronal structure of copora quadregemina in the cat. Arkh. Anat. Gistol. Embriol. *54*:45–55 (in Russian with English summary).

Wang, R., J.L. Kubie, and M. Halpern (1977) Brevital Sodium: An effective anesthetic agent for performing surgery on small reptiles. Copeia *1977*:738–743.

Weerasuriya, A., and J.-P. Ewert (1981) Prey-selective neurons in the toad's optic tectum and sensorimotor interfacing: HRP studies and recording experiments. J. Comp. Physiol. *144*:429–434.