

Ulinski, P.S., D.M. Dacey, and M.I. Sereno (1992) Organization of the optic tectum. In C. Gans and P.S. Ulinski (eds.), *Sensorimotor Integration, Biology of the Reptilia*, Vol. 17, Neurology C. University of Chicago Press, pp. 241-366.

Biology of the Reptilia

Edited by
Carl Gans

Volume 17, Neurology C
**Sensorimotor
Integration**

Coeditor for this volume
Philip S. Ulinski

The University of Chicago Press
Chicago and London

Optic Tectum

PHILIP S. ULINSKI, DENNIS M. DACEY, AND MARTIN I. SERENO

CONTENTS

| | |
|---|-----|
| I. Introduction | 242 |
| II. General Anatomy | 244 |
| A. General | 244 |
| B. Tectal Lamination | 244 |
| C. Neuronal Populations | 249 |
| III. Efferent Projections | 254 |
| A. General Pattern of Tectal Efferent Projections | 254 |
| B. Tectobulbar Neurons | 257 |
| C. Tectoisthmi Neurons | 273 |
| D. Tectorotundal Neurons | 273 |
| E. Tectogeniculate Neurons | 281 |
| F. Summary | 286 |
| IV. Intrinsic Neurons | 286 |
| A. General | 286 |
| B. Horizontal Cells (Type A Cell) | 288 |
| C. Small Cells with Descending Axons (Type B Cells) | 288 |
| D. Stellate Cells (Type C Cells) | 290 |
| E. Type D Cells | 293 |
| F. Summary | 293 |
| V. Afferents | 293 |
| A. General | 293 |
| B. Visual Afferents | 296 |
| C. Somatosensory Afferents | 323 |
| D. Auditory Information | 325 |
| E. Reticular Afferents | 325 |
| F. Afferents Related to the Striatum | 328 |
| G. Monoaminergic Projections | 328 |
| H. Summary | 329 |
| VI. General Concepts of Tectal Organization | 329 |
| A. Overview | 329 |
| B. Position of the Tectum in the Organization of the Nervous System | 330 |

| | |
|--|-----|
| C. Sensorimotor Transformation | 332 |
| D. Internal Organization of the Tectum | 335 |
| VII. Summary | 345 |
| Acknowledgments | 346 |
| Appendix: Reptilian Species Discussed | 346 |
| References | 348 |

I. INTRODUCTION

The optic tectum is made up of a pair of dome-shaped lobes that lie on the dorsal surface of the mesencephalon (Fig. 4.1A). All vertebrates have a tectum, but the term *optic tectum* is generally reserved for nonmammalian vertebrates, whereas the term *superior colliculus* is used for the homologous structure in mammals. The older term *optic lobes* is no longer in general usage. The size and shape of the optic tectum differs among species, being particularly large in birds. There is some correlation between the size of the tectum and the size of the eyes; within reptiles the tectum is relatively largest in diurnal lizards and crocodylians and smallest in burrowing forms with reduced eyes.

Some clue to the function of the tectum can be gleaned from a simple dissection of the brain, which shows that the optic tracts wind over the lateral surface of the brainstem and cover the dorsal aspect of the tectum (Fig. 4.1B). More sophisticated anatomical and physiological tracing techniques confirm that retinal ganglion cells carry visual information to the tectum and demonstrate that other sensory modalities are also represented in the tectum. They also demonstrate the existence of descending projections from the tectum to the brainstem reticular formation and spinal cord; by the early decades of this century (e.g., Huber and Crosby, 1943), studies using this technique led to the conclusion that the tectum is an important sensorimotor correlation center.

Functional observations on a variety of species have supported this conclusion. Experiments in which electrical currents are used to stimulate tectal neurons produce coordinated movements of the animal (Schapiro and Goodman, 1969; Distel, 1978). Lesions of the tectum produce defects or errors in visual tasks (Bass et al., 1973). The tectum thus appears to be important in the orientation of the animal to visual stimuli in the environment, as well as a wide range of orienting movements that include the turning of the pinnae toward sounds in cats (Stein and Clamann, 1981), snapping toward prey in frogs (Ingle, 1982; Grobstein, 1988), and eye movements in primates (e.g., Wurtz and Albano, 1980; Sparks, 1986; Sparks and Nelson, 1987).

The importance of orienting movements in behavior has prompted a number of anatomical and physiological studies of the optic tectum.

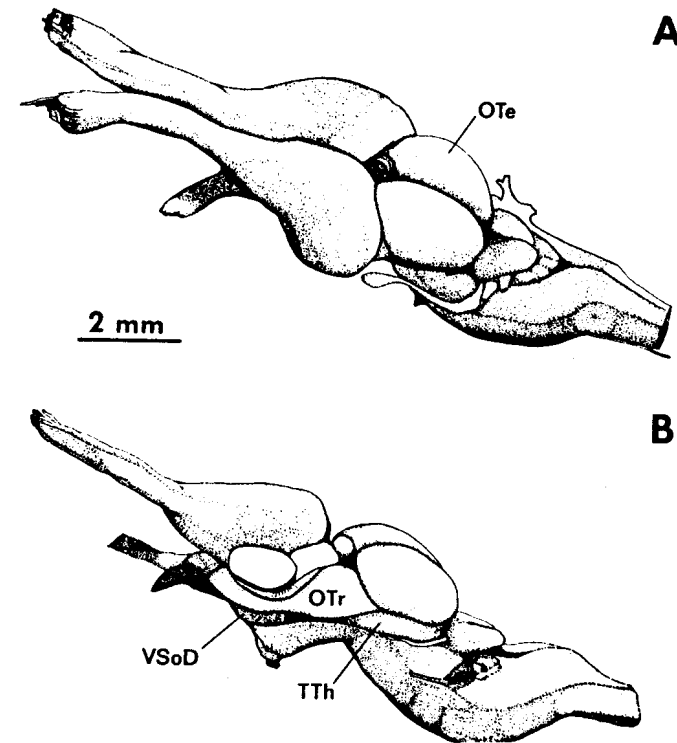


Fig. 4.1. *Thamnophis sirtalis*. (A) A dorsolateral view of the brain showing the optic tectum (OTe). (B) Removal of the telencephalon by cutting the cerebral peduncle reveals the relation of the optic tectum to the optic tract (OTr), tectothalamic tract (TTh), and ventral supraoptic decussation (VSoD).

The earliest studies used cell body stains to characterize the distribution of somata (e.g., Huber and Crosby, 1933); they showed that the tectum is a laminated structure composed of alternating layers of somata and axons. Application of the Golgi technique, notably by Santiago Ramón y Cajal (1911) and his brother Pedro Ramón (1896), to the tectum of lizards revealed that the tectum contains several morphologically distinct classes of neurons. Electrophysiological recording techniques showed that the retinal surface is mapped in a point-to-point or topological fashion onto the tectal surface (e.g., Kruger, 1969). Nauta and Fink-Heimer axon tracing techniques showed that the tectum gives rise to a large set of efferent projections, including some that ascend to the thalamus (e.g., Altman and Carpenter, 1961; Butler and Northcutt, 1971a; Ebbesson and Vanegas, 1976; Martin, 1969; Rubinson, 1968; Ulinski, 1977). Electron microscopic techniques provided an overall impression of the synaptic organization of the tectum and demonstrated the presence of complex forms of interactions between neurons (e.g., Ito, 1970; Lund, 1969, 1972; Sterling,

1971; Szekely et al., 1973; Tigges et al., 1973; Valverde, 1973; Graham and Casagrande, 1980). Recently, electrophysiological and behavioral studies have been combined to obtain information on the roles that individual neurons play in naturally occurring behaviors (e.g., Ewert, 1976; Ingle, 1976; Wurtz and Albano, 1980).

The introduction of horseradish peroxidase (HRP) and other intracellular markers as neuronal tracing and marking agents during the past few years (e.g., Mesulam, 1982) has permitted major advances. It is now possible to use these markers to correlate the morphology of neurons with the destinations of their axons and to visualize neurons that have been physiologically characterized (e.g., Gilbert, 1983). HRP procedures have recently been applied to the optic tectum in several taxa of reptiles to produce an overall picture of tectal organization that identifies the major populations of tectal neurons and outlines the ways in which tectal neurons are related to the fiber systems afferent to the tectum. This chapter will review the organization of the optic tectum in reptiles, emphasizing this new information and its impact on concepts of tectal organization.

The earliest studies of the tectum are summarized in Ramón y Cajal's 1911 monograph. The period up to 1936 is treated in the handbook by Ariëns-Kappers, Huber, and Crosby (1936). The role of the tectum in sensorimotor integration is reviewed by Ingle and Sprague (1975). The tectum in fishes (Vanegas, 1975), amphibians (Szekely and Lazar, 1976), reptiles (Northcutt, 1984), and mammals (Goldberg and Robinson, 1978; Wurtz and Albano, 1980; Huerta and Harting, 1984; Sparks, 1986) has been recently reviewed. The development of the tectum in reptiles has been reviewed by Senn (1979), and its neurophysiology has been reviewed by Belekova (1979) and Hartline (1984). Ulinski (1983) has discussed the relationship of the tectum to the forebrain in reptiles and birds.

II. GENERAL ANATOMY

A. General

The following three sections will consider in some detail the morphology of the neurons that are efferent from the tectum (Section III), of those neurons that appear to be intrinsic to the tectum (Section IV), and of the fiber systems that are afferent to the tectum (Section V). However, it will be useful to provide a general survey of tectal structure, including the nomenclature of tectal layers and neuronal populations, before turning to more extensive treatments.

B. Tectal Lamination

Routine histological procedures such as cell body and fiber stains give the impression that the tectum consists of alternating layers of neuronal somata and axons (Fig. 4.2). This is illustrated in Figs. 4.3 and

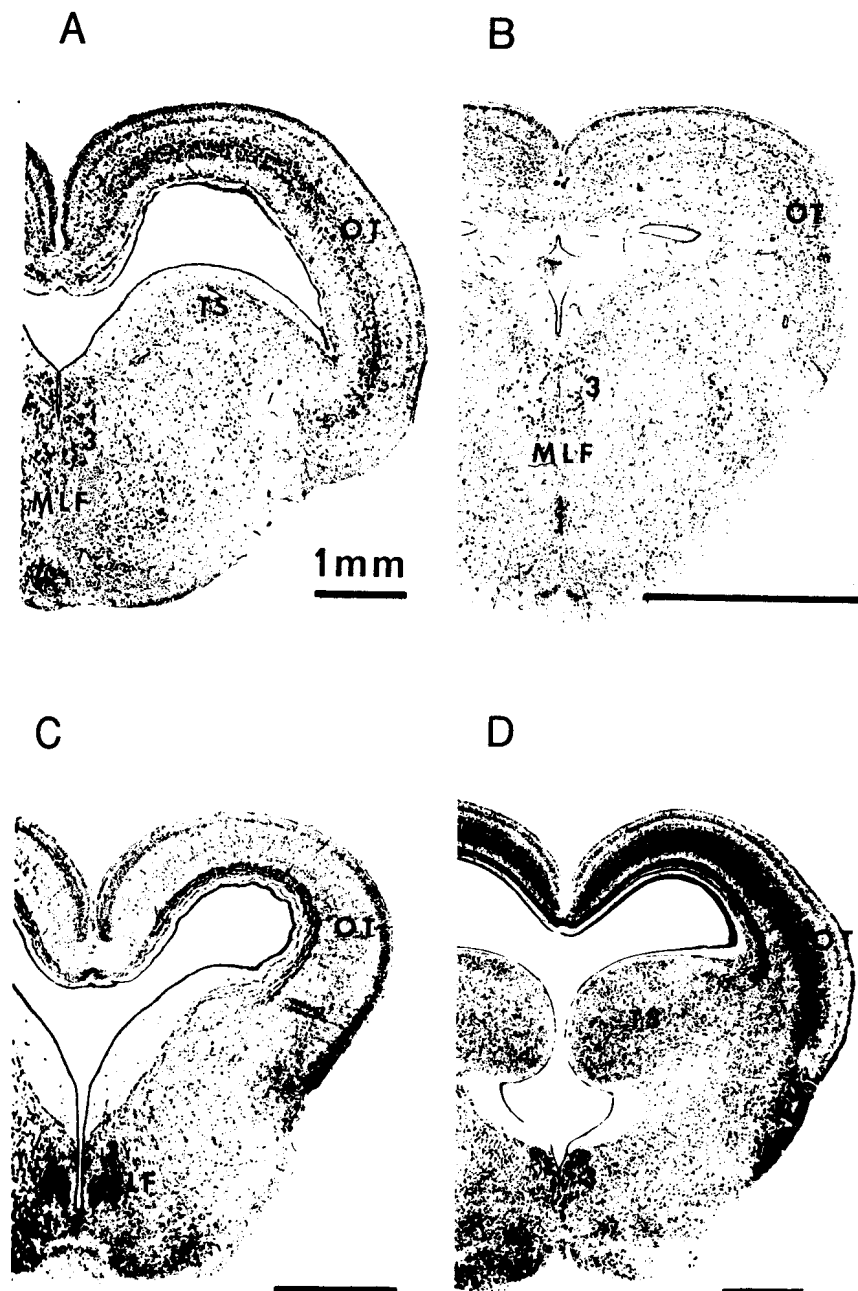


Fig. 4.2. Optic tectum. The general anatomy of the optic tectum is shown in transverse sections of the midbrain through the brains of representatives of each major taxon. (A) *Tupinambis tequixin*. Tegú lizard. (B) *Nerodia sipedon*. Water snake. (C) *Pseudemys scripta*. Red-eared turtle. (D) *Alligator mississippiensis*. American Alligator.

4.4, which show cross-sections through the midbrains of a turtle (Fig. 4.3) and a snake (Fig. 4.4). The cell body stain demonstrates the tendency for layers of densely packed neuronal somata to be separated by clear spaces that are composed largely of myelinated and unmyelinated fiber systems.

Several nomenclatorial systems have been applied to these layers in reptiles. The first stems from the work of Pedro Ramón (1896) on the lizard *Lacerta* and recognizes 14 layers (see Fig. 4.5). Layer 1 consists of the cell bodies of tanycytes, the processes of which extend throughout the depth of the tectum to end as subpial endfeet. The remaining layers consist of alternating bands of somata and fibers. Although this system proved entirely adequate for *Lacerta*, it has led to some confusion when applied to other species because there is enough interspecific variation in lamination patterns to make the identification of some of Ramón's layers difficult in other species. There is also some potential confusion with other, numerically based, nomenclatures. For example, Santiago Ramón y Cajal (1911) recognized 14 layers in the optic tectum of birds but numbered them in the opposite order (so that the ependymal cell bodies were situated in Layer 14). Huber and Crosby (1933) sought to allay confusion by proposing an alternate nomenclature in which the various layers were given Latin names. This nomenclature has the virtue of being more or less applicable to all vertebrates; however, it is generally necessary to subdivide some of the layers in a particular species. More recently, Serin (1968, 1979) recognized periventricular, central, and superficial groups of cells. The pros and cons of various schemes for naming the tectal layers have been discussed by Northcutt (1983).

The nature and clarity of layers among orders of reptiles and among species within orders vary substantially (see Fig. 4.2). In lizards, tectal cytoarchitecture has been described in most detail in the tegu, *Tupinambis teguixin* (Butler and Ebbesson, 1975) and the desert iguana, *Dipsosaurus dorsalis* (Peterson, 1981). In addition, Senn (1968a, 1968b), Senn and Northcutt (1973), and Northcutt (1978, 1983) have surveyed patterns of tectal organization in a large number of lizards. The tectum in lizards usually contains clearly defined laminae (see Fig. 4.3). There are generally several thin periventricular layers and as many as seven sharply defined layers of somata and fibers in the superficial tectum. Two major variants of this general pattern have been recognized in lizards (Northcutt, 1978). The first is seen in agamids, chamaeleonids, iguanids, teiids, and varanids and is called the iguanid pattern. In this variant, Ramón's lamina 14 is always the major layer that contains the axons of retinal ganglion cells. Lamina 12 is at least half the thickness of lamina 14. Laminae 8 and 10 contain many densely packed cells. Lamina 7 is also subdivided into inner and outer

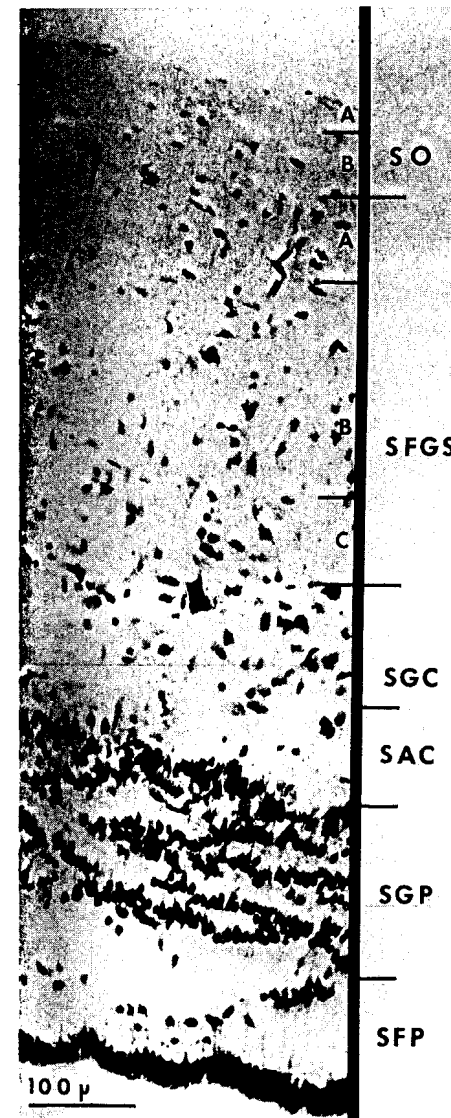


Fig. 4.3. *Pseudemys scripta*. Tectal cytoarchitecture. The lamination pattern of the tectum is shown in a transverse section through the brain of a red-eared turtle. (From Schechter and Ulinski, 1979.)

subdivisions with the neurons of the inner subdivision scattered within lamina 6. The periventricular layers are relatively reduced. The second pattern is seen in anguids, cordylids, gekkonids, gerrhosaurids, helodermatids, lanthanotids, lacertids, pygopodids, scincids, xantusiids, and xenosaurids and is called the lacertid pattern. In this variant, the superficial layers are relatively poorly developed. Lamina 12 is the principal optic layer and is always better developed than lamina 14. Laminae 8 and 10 are not nearly as well developed as in other

Fig. 4.4. *Thamnophis*. Tectal cytoarchitecture. The lamination pattern of the tectum is shown in a transverse section through the brain of a garter snake. (From Dacey and Ulinski, 1986a.)



lizards, and lamina 7 consists of single groups of cells with little if any overlap with lamina 6. By contrast, the periventricular laminae are well developed, with lamina 5 being twice the thickness of the comparable lamina in the iguanid pattern. The tectum in amphisbaenians and several groups of lizards with relatively reduced eyes (anelytropids, *Anniella*, dibamids, feyliniids, some microteids, and some scincids) fits neither the iguanid nor the lacertid pattern. Instead, the tectum in these groups shows a reduction or even loss of the superficial layers and the periventricular layers are diffuse.

In addition to these interspecific differences, Peterson (1981) has pointed out that the lamination pattern of any given species also

shows regional variations. She describes five areas within the optic tectum of the desert iguana, *Dipsosaurus dorsalis*, based on variations in the development and clarity of the various layers. She correlates this regional variation in lamination pattern to the pattern of retinal afferents as demonstrated in Fink-Heimer and autoradiographic cases.

Huber and Crosby (1933) have described the tectum in a crocodilian, *Alligator mississippiensis*. Its lamination pattern generally resembles that of lizards with the lacertid pattern. Lamina 5 is poorly developed and, by contrast, lamina 7 is relatively thick. Whereas all the superficial layers are present, they are poorly defined.

Northcutt (1978, 1983) has described the tectum in *Sphenodon*. Its periventricular layers are clearly laminated and well developed, lamina 7 is reduced, and the superficial layers are moderately well developed. As in lizards with the lacertid pattern, lamina 12 is the principal optic layer.

The tectum in turtles has been described by Huber and Crosby (1933) and Schechter and Ulinski (1979). It contains several distinct periventricular layers. Both the intermediate layers 6 and 7, and the superficial layers are relatively poorly developed.

The tectum of snakes has been described by Huber and Crosby (1933), Senn (1969), Senn and Northcutt (1973), Halpern and Frumin (1973), Schroeder (1981b), and Dacey and Ulinski (1986a). As a group, the snakes show relatively poorly developed tectal laminae. Their periventricular layers are poorly developed. The intermediate layers contain a relatively large number of cells, especially in the crotalid snakes and those boids that have infrared systems (Schroeder, 1981a; Auen, 1976). The basic pattern of superficial layers is present, but these are relatively difficult to discern. Snakes are unique among the reptiles in that the layer carrying retinal ganglion cell axons, the stratum opticum, is separated from the pia. Senn (1979) studied the development of the optic tectum in the grass snake, *Natrix natrix*, and discovered that the lamination pattern is more distinct in embryonic snakes than in adults. The periventricular layer in adults, for example, represents a fusion of several distinct embryonic layers.

C. Neuronal Populations

Until the recent development of the HRP technology, essentially all of our information on the morphology of tectal neurons was derived from the use of Golgi preparations. These studies all report the existence of several classes of neurons in the tectum as distinguished by the morphology of their somata and dendrites. Figs. 4.5 to 4.7 illustrate the major types of tectal neurons, which derive from Pedro Ramón's work on lizards.

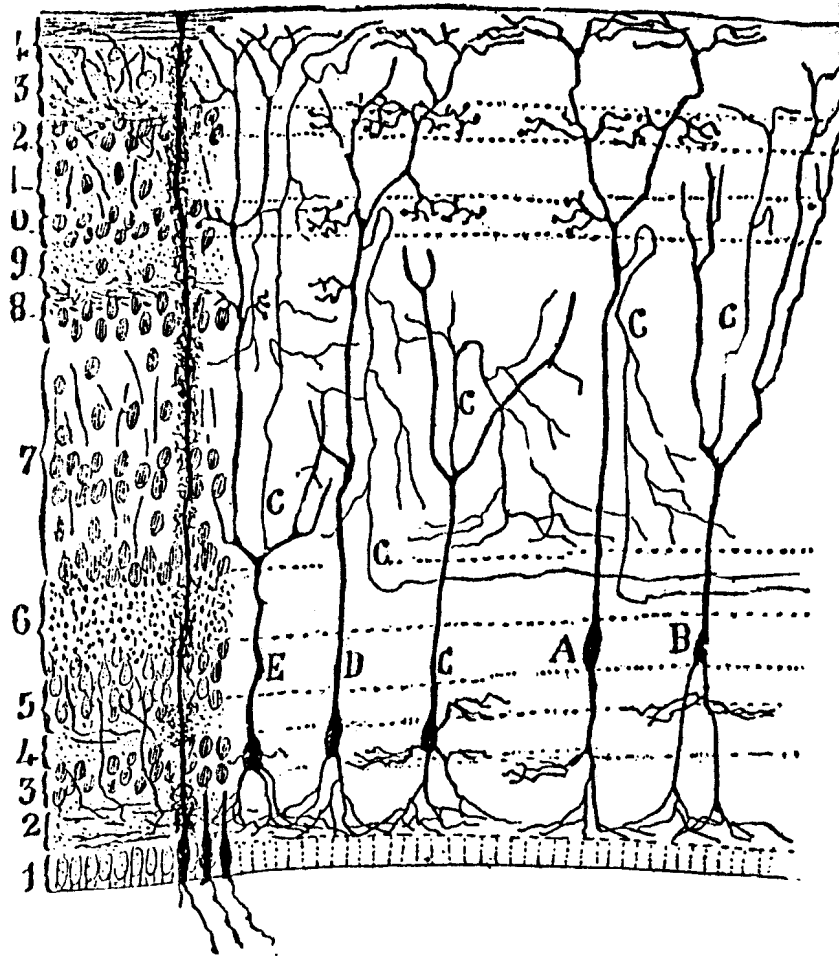


Fig. 4.5. Radial neurons. This and the following four illustrations are taken from Pedro Ramón's 1896 study of the tectum in the lizards *Lacerta* and *Chamaeleo*. They are all drawings done from Golgi preparations. This drawing illustrates Ramón's nomenclature (layers 1 through 14) for the tectal layers. Ependymal cells (not labeled) and radial neurons (A through E) are shown.

The most obvious tectal neurons are those with dendrites that extend radially across the tectal laminae (Figs. 4.5 to 4.7). These neurons have been called pyramidal, piriform, fusiform, or radial cells. They are found in all layers of the tectum but are most common in the strata griseum centrale and the griseum periventriculare. Superficially located radial neurons (Figs. 4.6 and 4.7) have smaller somata, shorter apical dendrites, and more extensive basal dendritic trees. More deeply situated radial neurons (Fig. 4.5) have larger somata, longer apical dendrites—often extending into the stratum opticum—and

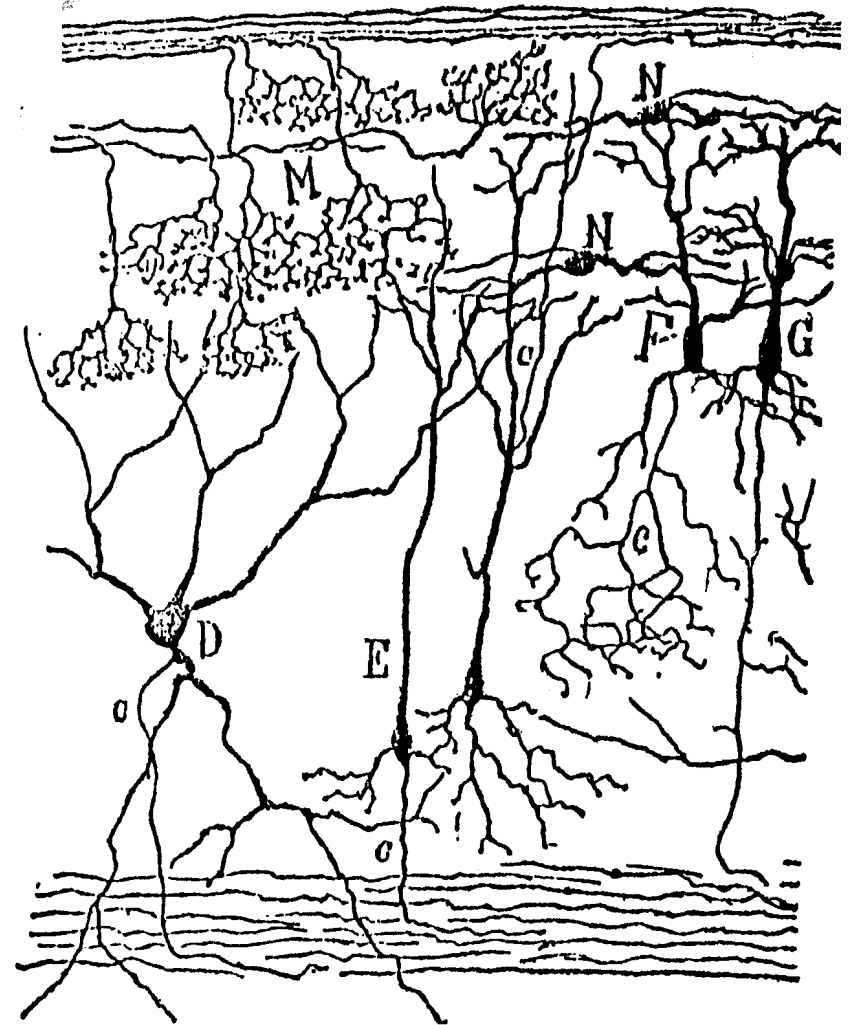


Fig. 4.6. *Lacerta*. Tectal neurons. A ganglion cell (D), radial neurons (E, F, and G), horizontal cells (N), and putative retinotectal arbors (M). (From Ramón, 1896.)

basal dendritic trees that are reduced or absent. The axons of radial neurons originate from their somata, from proximal dendrites, or occasionally from positions on the apical dendrites quite remote from the somata. In the last case, the radial neurons are sometimes called shepherd's crook cells.

A second type of tectal neuron is the ganglion cell. These are neurons with large somata that are often triangular and with extensive dendrites that extend toward the pial surface in a cone-shaped configuration (Figs. 4.6 and 4.7). The axon typically originates from the

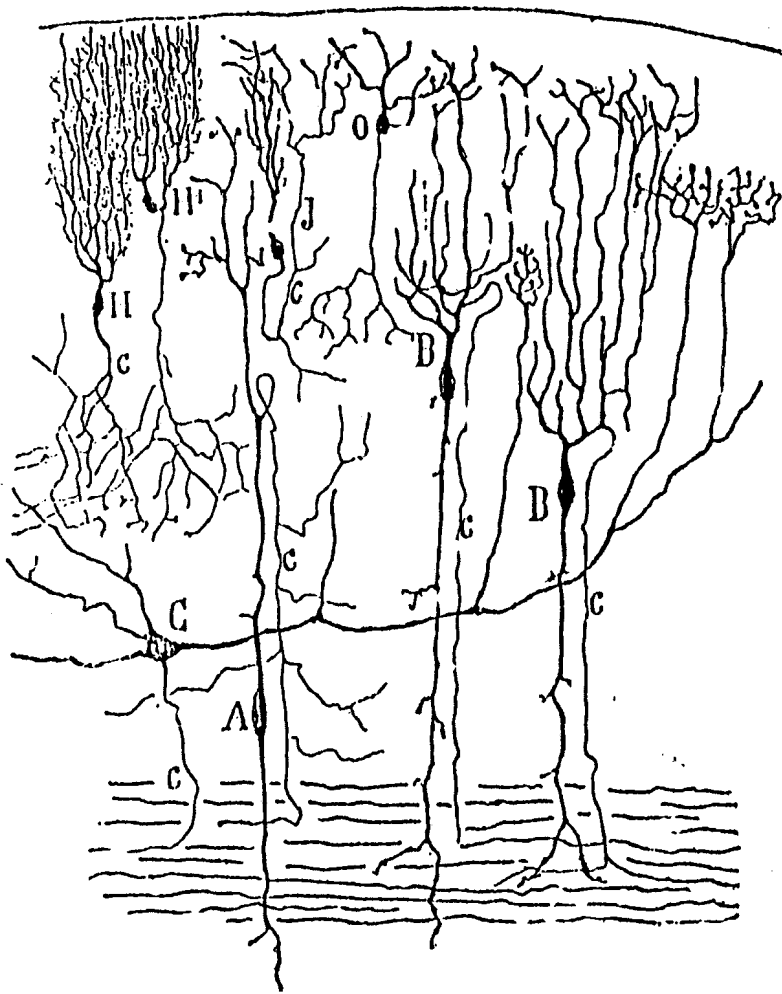


Fig. 4.7. *Lacerta*. Tectal neurons. A ganglion cell (C), several types of radial neurons (A, B, H, and J), and a small neuron with descending axon (O). (From Ramón, 1896.)

soma. Ganglion cells can be identified in Nissl preparations because of their size and shape. Such preparations suggest that they are relatively rare.

Stellate cells are a relatively frequent and variable population of tectal neurons (Fig. 4.8). They have small somata located in the superficial layers of the tectum. Their dendrites extend out in a star-shaped pattern, often bearing elaborate appendages. The axons may either ascend or descend within the tectum, but typically arborize extensively.

A further type of tectal neuron is the horizontal cell, which is usually found in the superficial layers (Fig. 4.9). These neurons have dendrites that extend relatively long distances concentric with the curva-

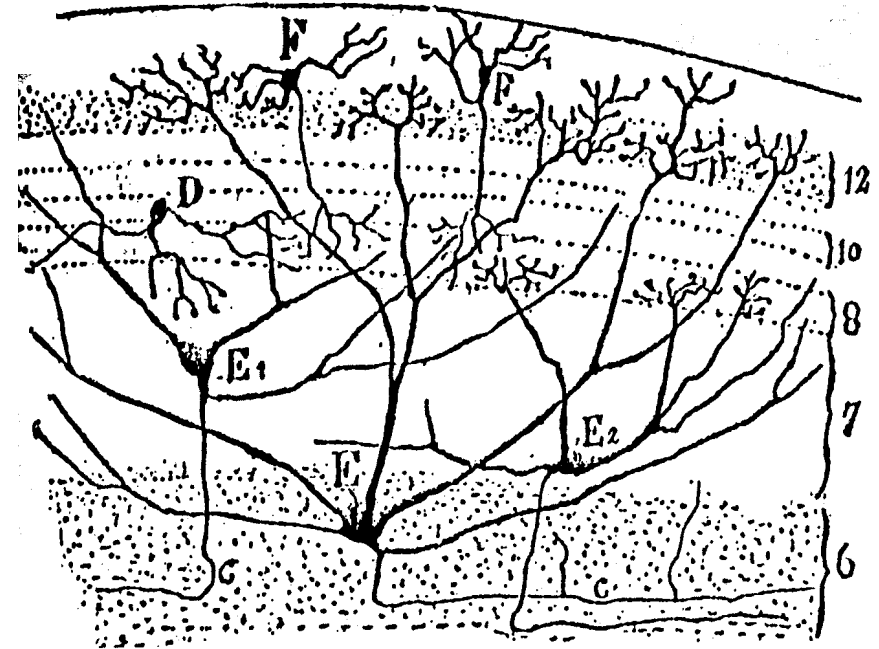


Fig. 4.8. *Lacerta*. Tectal neurons. Ganglion cells (E, E₁, and E₂) and small neurons with descending axons (F). (From Ramón, 1896.)

ture of the tectum. The primary dendrites are smooth, whereas the secondary dendrites may have dendritic specializations. The axons usually originate from the somata and travel relatively long distances.

Classification of tectal neurons into such general groups provides a convenient vocabulary with which to describe morphological results obtained by a variety of techniques. However, it can be misleading in that it greatly obscures the extent to which tectal neurons vary in morphology. Schechter and Ulinski (1979), for example, attempted to deal with the variation in dendritic morphology that is seen in radial neurons in *Pseudemys* by arranging the apical dendrites of radial neurons along two continua, one in the extent of branching and a second in the density of dendritic specializations and excrescences. Similarly, most authors (e.g., Butler and Ebesson, 1975; Ramón, 1886; Northcutt, 1984) have recognized several types of radial neurons based on variations in the shape of their soma and the arborization patterns of their dendrites and axons. The central issue here is whether radial neurons, for example, should be viewed as a single population of neurons that vary in morphology, or whether the variation reflects the existence of several types of radial neurons that should be explicitly recognized. This is a general problem, which arises in describing the morphology of any group of neurons and has been discussed extensively in the case of retinal ganglion cells (e.g., Rowe and Stone,

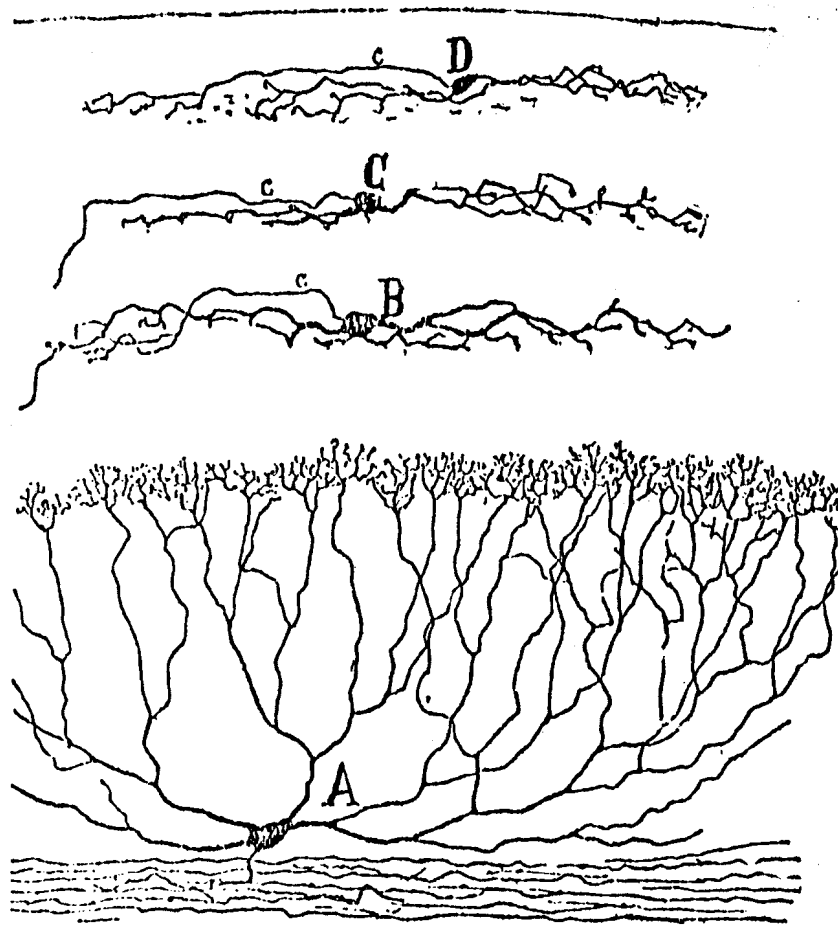


Fig. 4.9. *Lacerta*. Tectal neurons. A ganglion cell (A) and horizontal cells (B, C, and D). (From Ramón, 1896.)

1977). Although the best approach remains a matter of controversy, most authors agree that a classification should be based upon as many criteria as is possible. The ideal is to relate the different populations of tectal neurons just discussed to the pattern of their projections either within or out of the tectum. It is now possible to do this using HRP techniques, and in the following sections tectal neurons will be divided into several distinct subclasses based upon their intrinsic and extrinsic connections.

III. EFFERENT PROJECTIONS

A. General Pattern of Tectal Efferent Projections

The first studies of the efferent projections of the reptilian tectum were based on careful observations of serial sections stained to visu-

alize myelinated axons (e.g., Huber and Crosby, 1933). These studies show that both ipsilateral and contralateral pathways connect the tectum with the brainstem reticular formation. It was suspected that these pathways include tectal axons that descend to the brainstem and ascend to the diencephalon, but the difficulty in determining the polarity of axons in myelin preparations left the issue open. The ambiguity has been resolved with the application of Nauta and Fink-Heimer techniques to the study of tectal efferents (turtles: Foster and Hall, 1975; lizards: Butler and Northcutt, 1971b; snakes: Ulinski, 1977; crocodilians: Braford, 1972). More recently, the reptilian tectum has been studied with tracing techniques based on the anterograde transport of tritiated amino acids (Schroeder, 1981b) and HRP (Auen, 1976; Kass et al., 1978; Dacey and Ulinski, 1986a; Sereno, 1985).

All of the experimental studies, regardless of species, demonstrate a single pattern of efferent projections. This pattern is illustrated by HRP investigation (Sereno, 1985) of tectal efferents in *Pseudemys scripta* (Fig. 4.10). The HRP injection site is seen as a region of stipple in sections F through K. The pathways issuing from the injection site are charted onto sections spaced through the brainstem and diencephalon. The chartings show that several fascicles of axons course laterally from the injection site and leave the tectum. These can be divided into descending and ascending projections.

The first of the descending projections consists of axons that course ventrally and terminate in the mesencephalic tegmentum within the nucleus mesencephalicus profundus (PMr) and the nucleus of the medial longitudinal fasciculus (mlf). As the fibers are traced caudally (sections I and H), they sort out into four fascicles. The most dorsal fascicle terminates just caudal to the tectum in the magnocellular part of nucleus isthmi (lmc). The second is formed by fibers that cross the midline in the mesencephalic tegmentum and turn to descend in the contralateral tegmentum as the predorsal bundle or dorsal tectobulbar tract (Tbd). These axons reach a variety of cell groups in the caudal brainstem. The third fascicle is composed of fibers that descend in the ipsilateral tegmentum as the intermediate tectobulbar path (Tbi). Finally, a contingent of fibers course along the ventrolateral surface of the ipsilateral brainstem as the ventral tectobulbar path (Tbv). These latter two paths reach several cell groups in the caudal brainstem. The particular chartings shown in Fig. 4.10 do not include the spinal cord; however, tectal axons have been traced in the predorsal bundle as far as the cervical levels of the spinal cord in turtles (Foster and Hall, 1975), lizards (Foster and Hall, 1975), and snakes (Gruberg et al., 1979; Dacey and Ulinski, 1986a).

Ascending projections from the tectum are illustrated in sections K through M. Some fibers course ventrorostrally from the tectum and terminate bilaterally in the pretectum in nuclei such as the nucleus

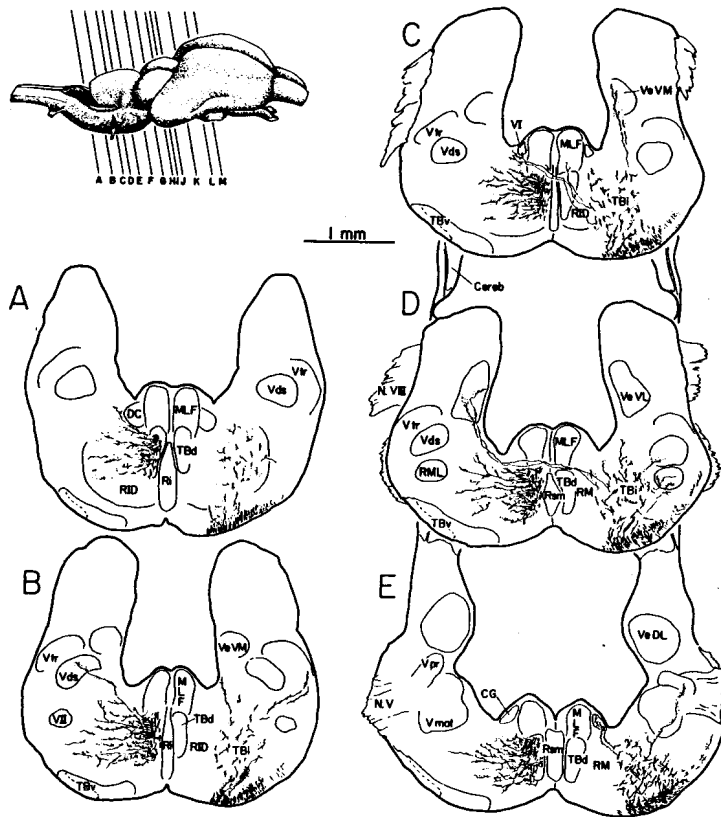


Fig. 4.10. *Pseudemys scripta*. Drawings of fibers labeled by a large unilateral tectal injection of HRP. Retrogradely labeled tracts are marked with an asterisk. The planes of sections A through M are indicated on the brain in the inset. (From Sereno, 1985.)

lentiformis mesencephali and the pretectal nucleus. Other fibers turn and run rostrally in the tectothalamic tract (TTh). These terminate in nucleus rotundus in the dorsal thalamus, in several ventral thalamic nuclei (e.g., the suprapeduncular nucleus, SP), and in the hypothalamus. The projections tend to be bilateral. They reach the contralateral diencephalon principally through the ventral supraoptic decussation, but some fibers cross through the posterior and habenular commissures.

Tracing experiments of this sort adequately display the overall pattern of tectal efferents but provide little or no information on which types of tectal neurons contribute to the various pathways. Does each set of efferent projections originate from a different population of neurons? Can an individual neuron contribute to more than one efferent pathway or terminate in multiple regions within a given pathway? These questions have been addressed directly by intracellular injection

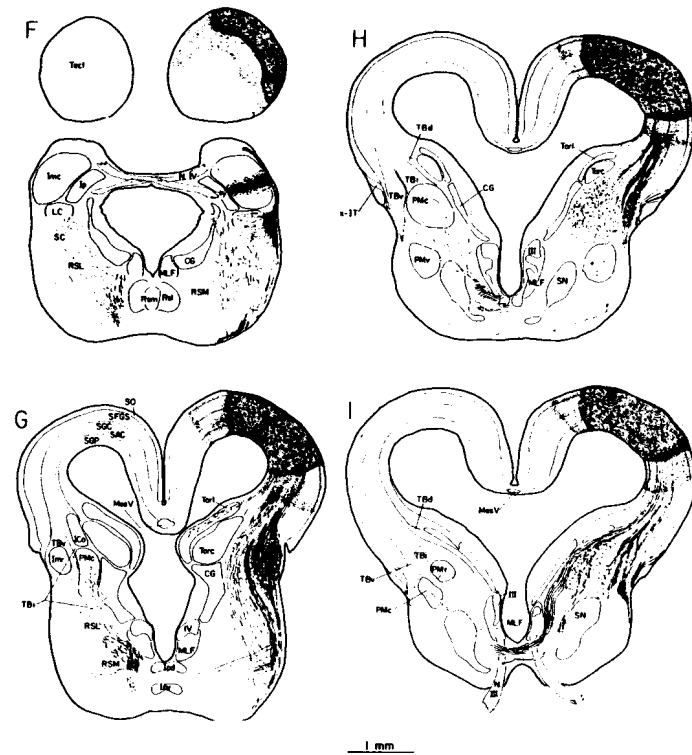


Fig. 4.10. (cont.)

techniques to demonstrate the complete morphology of individual neurons (e.g., May et al., 1982; Berson and Hartline, 1988; Rhoades et al. 1989). The limitation of these experiments is the technical one of successfully injecting a large number of relatively small neurons. However, some progress has also been made by combining two types of experiments. The first is to inject HRP into the ascending and descending pathways and then look for retrogradely labeled neurons in the tectum so as to demonstrate which populations of tectal neurons contribute to each pathway. The second type of experiment is to trace individual axons from small injections of HRP in the tectum in order to show the morphology of axons in each tectal pathway. In combination, these experiments can provide a relatively complete account of the organization of tectal efferents. Results from procedures of this sort have been obtained in snakes (Dacey and Ulinski, 1986a, 1986b) and turtles (Sereno, 1985; Sereno and Ulinski, 1985).

B. Tectobulbar Neurons

1. GENERAL Tectobulbar neurons are those tectal neurons whose primary terminations are in the brainstem reticular formation. They

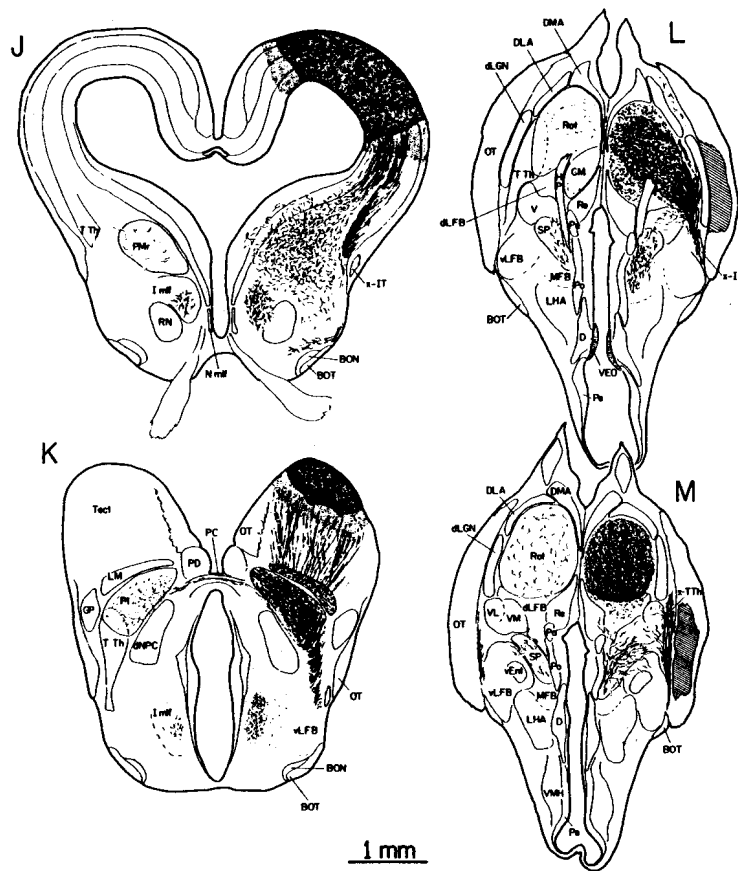


Fig. 4.10. (cont.)

can be identified by injecting HRP into one of the three tectobulbar paths. Experiments of this sort show that tectobulbar neurons are distributed throughout the central and periventricular layers of the tectum both in turtles (Sereno and Ulinski, 1985) and snakes (Dacey and Ulinski, 1986b), but the distribution and morphology of the tectobulbar neurons that project contralaterally and ipsilaterally vary.

2. CONTRALATERAL TECTOBULAR NEURONS

Tectobulbar neurons that have axons crossing the midline generally resemble the ganglion cells seen in Golgi preparations. Their somata generally lie in the central layers of the tectum. They have large, multipolar somata and four to six thick spiny dendrites. Some of the dendrites descend into the stratum album centrale, whereas most extend toward the pial surface. The extent of the ascending dendrites differs between snakes and turtles. The ascending dendrites stop quite abruptly at the upper boundary of the stratum griseum centrale of snakes (Fig. 4.11) but extend well into the stratum fibrosum et gri-

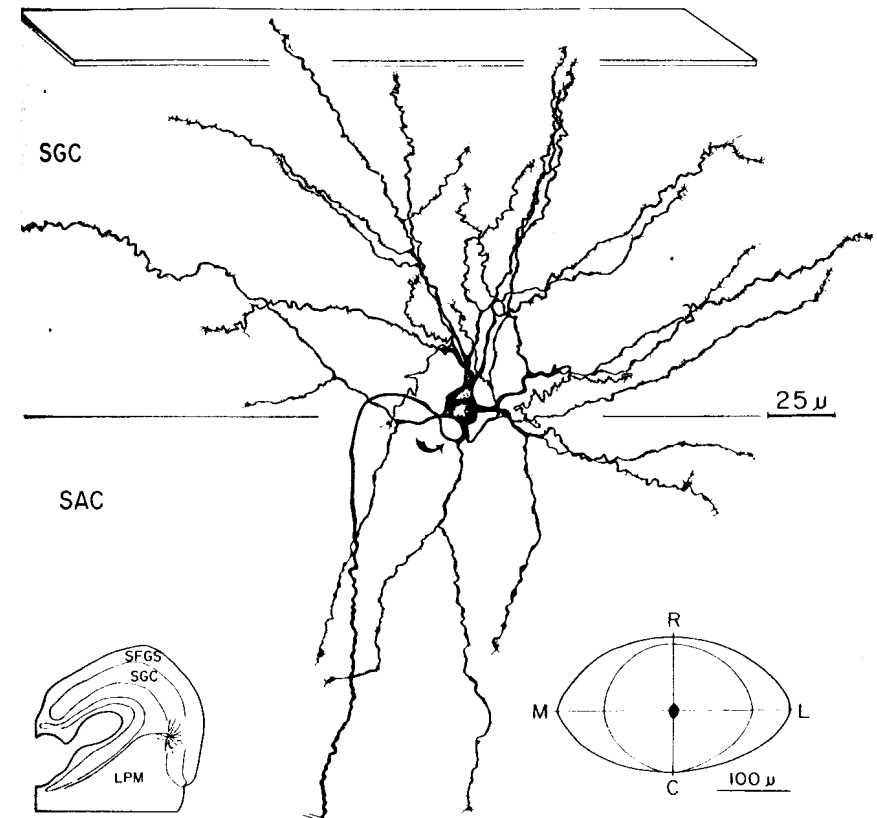


Fig. 4.11. *Thamnophis sirtalis*. Crossed tectobulbar cell. The axon of this neuron (arrow) descends vertically through the central white without branching or collateralizing and makes a sharp lateral turn at the border of the central white with the periventricular gray. The position of this cell and its axon in the tectum is shown in the inset at the lower left. The soma of this cell is situated at the border of the central gray and central white. The dendritic field spread is $320 \times 180 \mu\text{m}$. (From Dacey and Ulinski, 1986b.)

seum superficiale in turtles (Fig. 4.12). This difference is significant because it makes it unlikely that the crossed tectobulbar neurons of snakes can receive direct retinal input. However, the dendritic fields are extensive in both cases, ranging up to $400 \mu\text{m}$ in diameter in *Thamnophis* and $700 \mu\text{m}$ in diameter in *Pseudemys*.

The axons of the crossed tectobulbar neurons are relatively thick, measuring from 2.5 to $3.0 \mu\text{m}$ in diameter. They course laterally following the ventral border of the stratum album centrale and leave the tectum at its ventrolateral border. The overall configuration of the crossed axons and their collaterals are illustrated in diagrammatic form in Fig. 4.13, which shows a sketch of a crossed tectobulbar cell in *Pseudemys* reconstructed through serial sections. The axons give

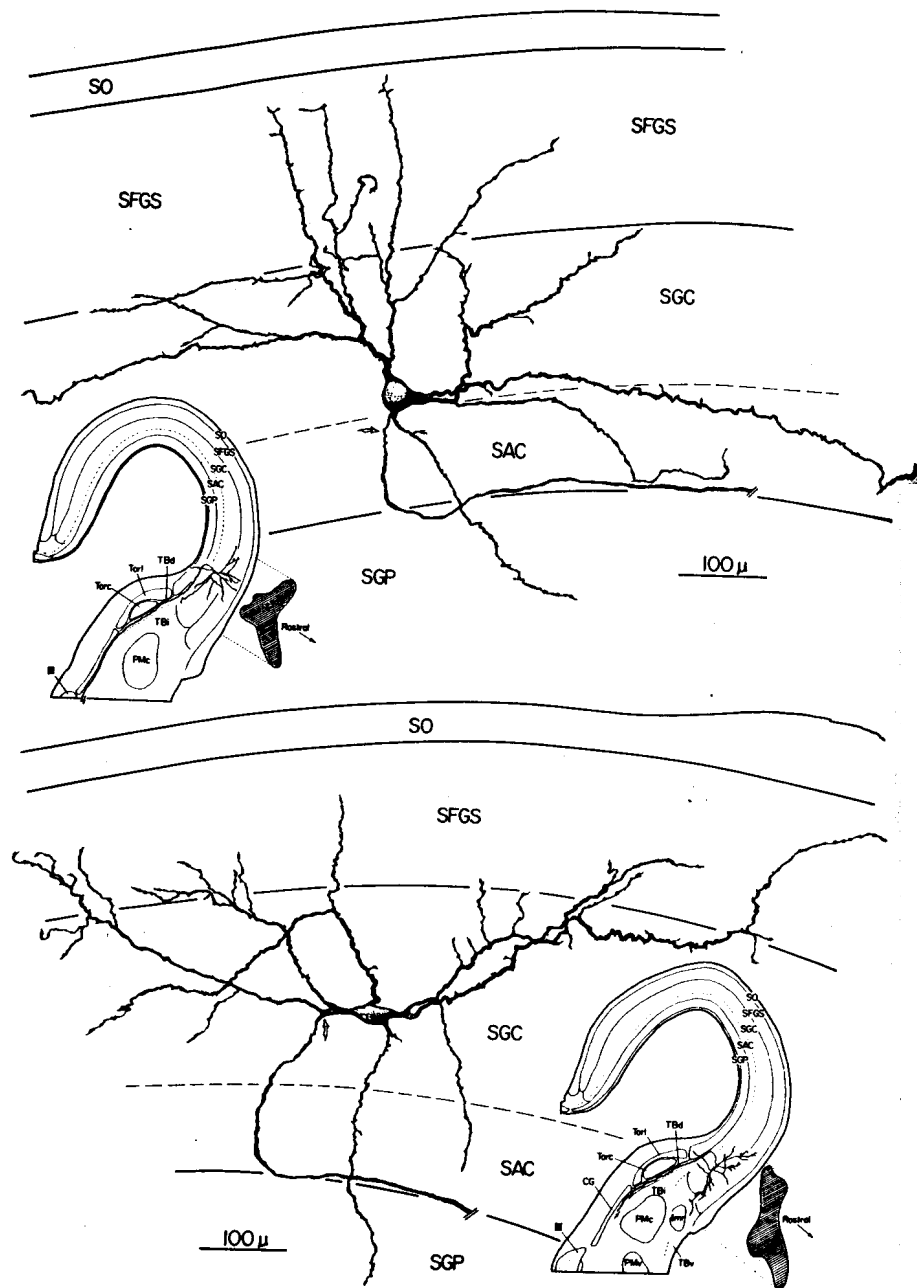


Fig. 4.12. *Pseudemys scripta*. Crossed tectobulbar cells. Reconstruction of two large dorsal tectobulbar pathway (Tbd) neurons. They were labeled after an HRP injection into the contralateral medial reticular formation. The open arrows indicate the axon origins. A schematic *en face* view is given alongside each low-power drawing. The dendrites of these neurons were covered with very fine spicules. (From Sereno and Ulinski, 1985.)

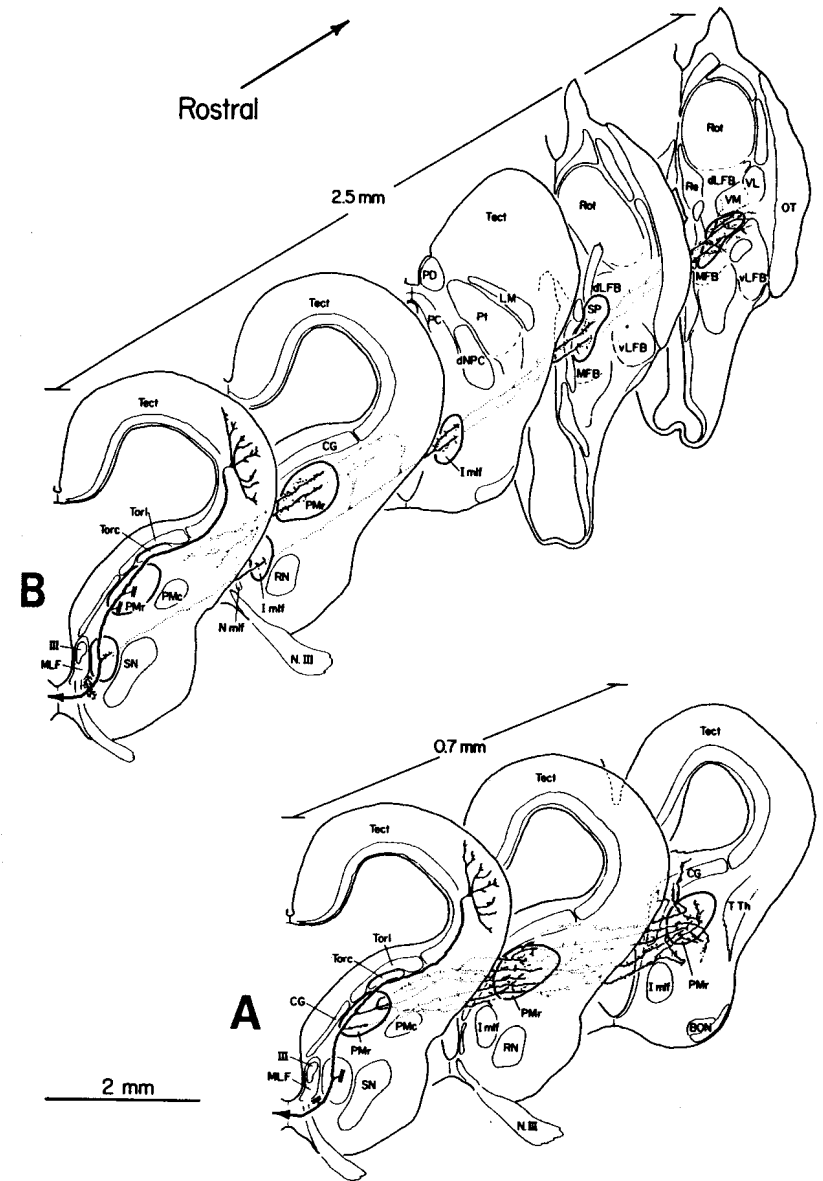


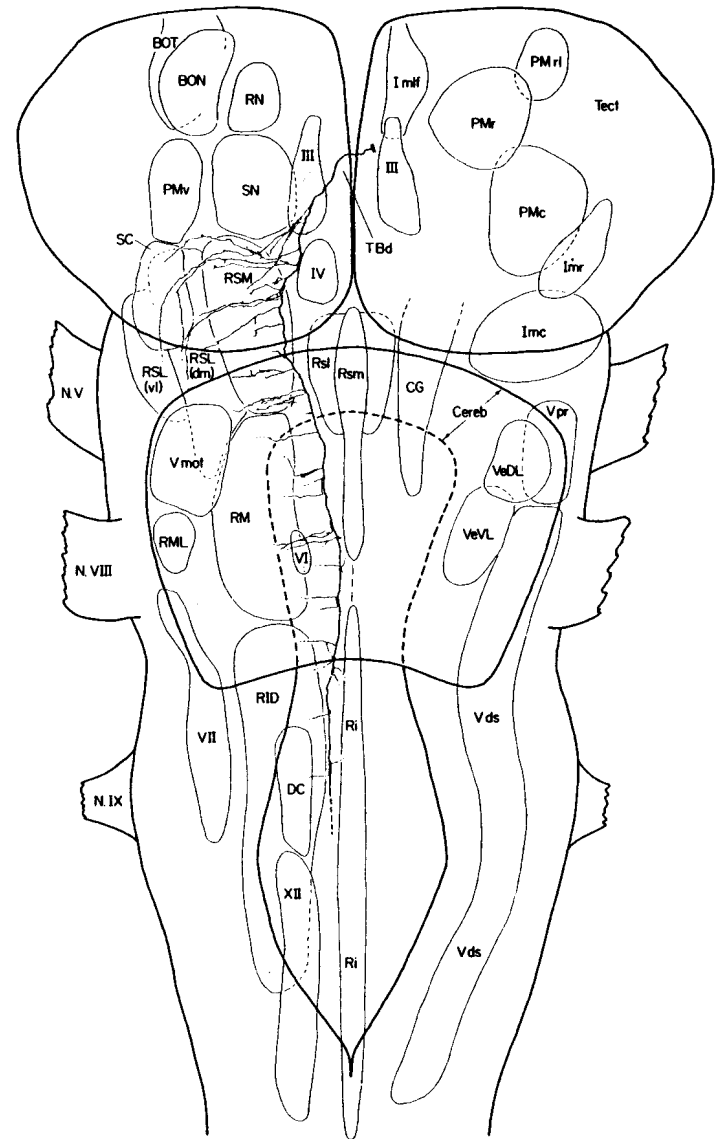
Fig. 4.13. *Pseudemys scripta*. Tectobulbar axon. Schematic diagram of the ipsilateral collaterals of a dorsal pathway (TBd) axon. (A) The first branches arborize in the mid-brain reticular nucleus profundus mesencephali rostralis (PMr). (B) The PMr branches have been removed here to better illustrate a robust collateral that courses under PMr, eventually arborizing in the ventral thalamic suprapeduncular nucleus (SP). It gives off terminals throughout its course through the interstitial nucleus of the medial longitudinal fasciculus (Imlf) as well as several branches that reach PMr from below. The main trunk of this axon crosses the midline to run in the contralateral predorsal bundle. (From Sereno and Ulinski, 1985.)

rise to ipsilateral collaterals that run rostrally into the midbrain tegmentum and the diencephalon. The collateral reconstructed in Fig. 4.13A extends principally into the nucleus mesencephali profundus. It consists of several branches that run parallel to each other through the rostrocaudal extent of the nucleus. Other ascending branches are shown in Fig. 4.13B. They run rostrad through the midbrain and terminate in the ventral thalamus.

The main branch of the axon continues ventromedially through the tegmentum, crosses the midline ventral to the medial longitudinal fasciculus, and enters the contralateral predorsal bundle. Its caudal trajectory is best illustrated in horizontal sections. Fig. 4.14 shows a diagram of the major branches of a crossed tectobulbar axon as it courses caudally through the brainstem. They run in the predorsal bundle and issue collaterals at regular intervals. These extend into the medial components of the brainstem reticular formation. The anatomy of one such collateral, from the mesencephalic reticular formation, is illustrated in Fig. 4.15 from an experiment in which a predorsal axon was filled by a tectal injection in *Thamnophis*. It is typical in that the stem branch is relatively thick and gives rise to a larger number of thin collaterals that fan out into the reticular formation. Each collateral bears many varicosities that presumably correspond to synaptic boutons. It has not been possible to label completely crossed tectobulbar axons in turtles, but axons in the predorsal bundle in *Thamnophis* continue caudally into the spinal cord (Fig. 4.16). They run in the ventral funiculus and have axons that turn dorsally into the gray matter of the cervical cord.

3. IPSILATERAL TECTOBULBAR NEURONS

Tectobulbar neurons, the axons of which do not cross the midline, resemble the ganglion cells, radial cells, and "plumed cells" (see Fig. 4.9) of Golgi preparations. They have somata positioned in the stratum griseum centrale, stratum album centrale, and stratum griseum periventriculare. They are rather uniform in morphology in *Thamnophis* (Fig. 4.17). Their fusiform somata are 12 to 20 μm long and fusiform in shape. Several dendrites originate from each soma, but the neuron is dominated by a stout primary dendrite that arises from its pole and ascends radial to the pial surface so that it can be classified as a radial cell. These dendrites issue several thin branches that bear a moderate density of short spicules or hairlike protrusions and end abruptly at the interface of the stratum griseum centrale and the stratum fibrosum et griseum superficiale. The morphology of ipsilateral tectobulbar neurons in *Pseudemys scripta* is more variable. Some, like those in *Thamnophis*, have a generally radial cell configuration (Fig.



4.14. *Pseudemys scripta*. Tectobulbar axon. Reconstruction from horizontal serial sections of the contralateral course of a dorsal pathway (Tbd) axon traveling in the dorsal bundle. This axon was labeled after a small HRP injection into the right eye. It had ipsilateral collaterals similar to those schematically illustrated in Fig. 4.13. Most of the several thousand synaptic boutons supported by this axon were located in the medial half of the reticular formation. A few branches also entered the spinal cord caudally. The axon was not completely filled past the level of the trigeminal ganglion or nucleus.

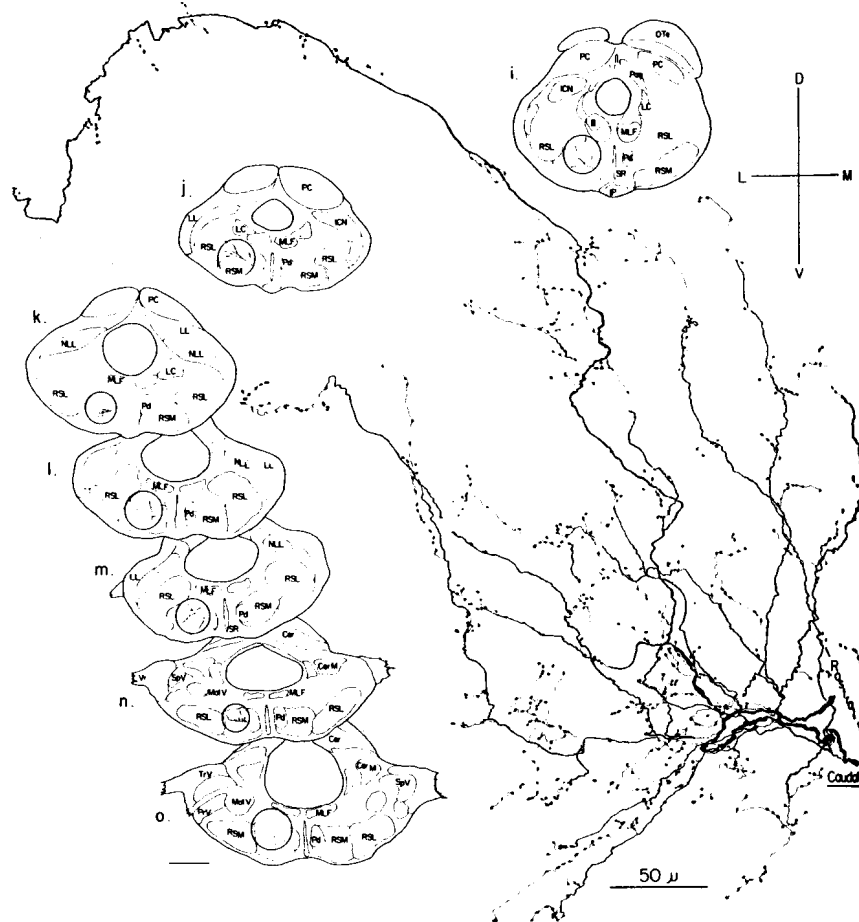


Fig. 4.15. *Thamnophis sirtalis*. Crossed tectobulbar axon. This large-caliber axon (3 μm in diameter) was reconstructed through 25 serial sections from the rostral mid-brain to the caudal medulla. This figure shows the seven most caudal sections (i through o) and the part of the axon that terminates in section j. It forms a rostrocaudally elongated cylindrical zone of termination in reticularis medialis and reticularis inferior pars dorsalis. (From Dacey and Ulinski, 1986a.)

4.18), whereas others (Figs. 4.19 and 4.20) have more widespread dendritic fields. The major difference between the two species, however, is that the dendrites of the ipsilateral cells in *P. scripta* extend well into the stratum fibrosum et griseum superficiale, whereas those in *Thamnophis* do not reach the superficial layer.

Axons of ipsilateral cells course dorsally or ventrally in the tectum, depending on the positions of their somata, and enter the stratum album centrale. They may collateralize in this layer (Fig. 4.21) but eventually exit the ventrolateral border of the tectum. Descending col-

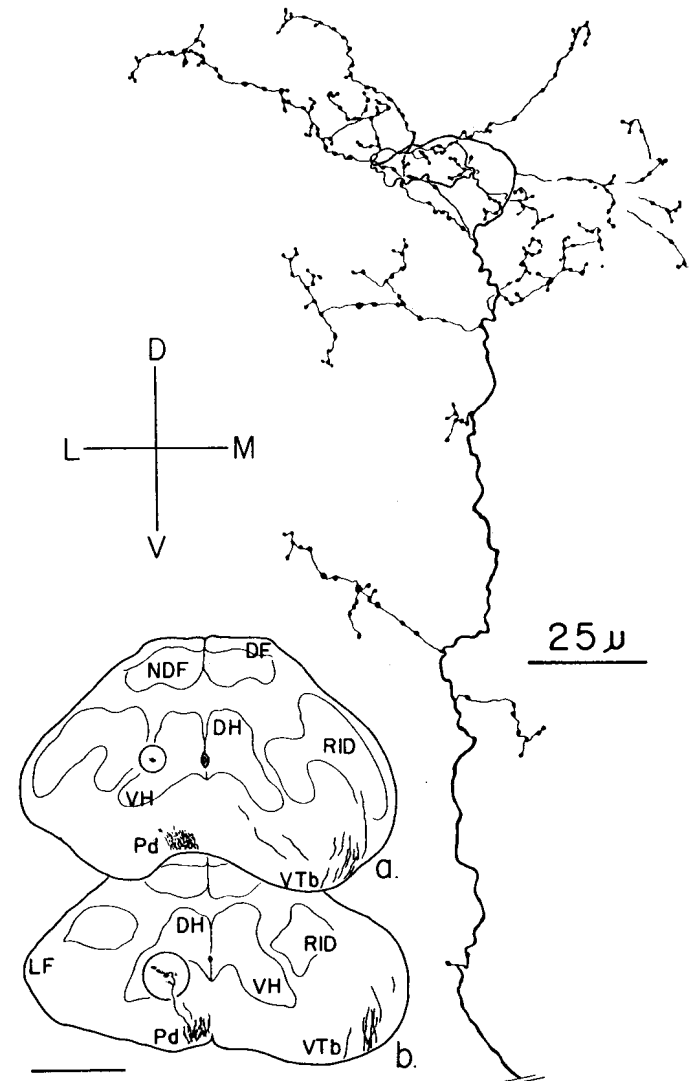


Fig. 4.16. *Thamnophis sirtalis*. Tectospinal terminals. Crossed tectobulbar axons were traced to the cervical spinal cord, where they ascended vertically from the predorsal bundle to terminate in the ventral horn of the spinal cord. These axons ended in a single terminal arbor just dorsal to the region of the motoneuron somata. (From Dacey and Ulinski, 1986a.)

laterals run caudally in the brainstem tegmentum in two tracts. An intermediate tract runs through the central region of the tegmentum, and a ventral tract runs along the ventrolateral surface of the brainstem. The main branches of the axons give off collaterals at regular intervals throughout their trajectory. The collaterals arborize in the lateral regions of the brainstem. Fig. 4.22 shows one such collateral

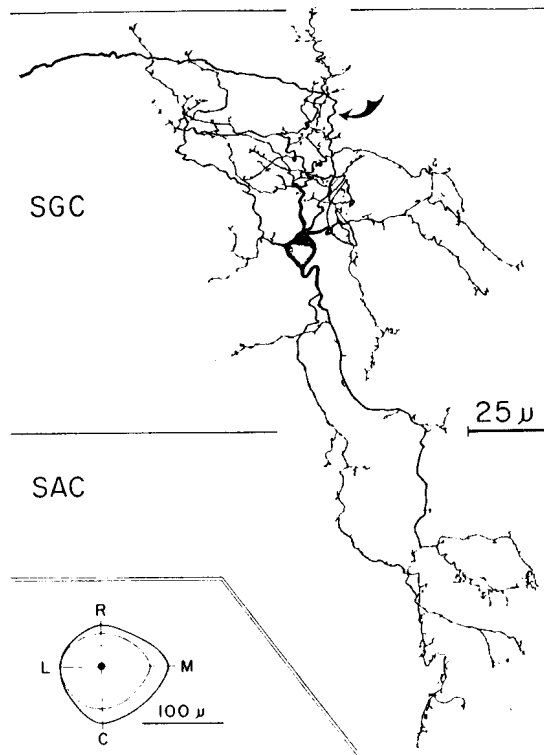


Fig. 4.17. *Thamnophis sirtalis*. Ipsilateral tectobulbar cells. Tectobulbar neurons are multipolar but radially elongate. Their dendritic fields occupy the central gray and extend into the central white but never enter the superficial gray. The inset at the bottom of this figure is an approximate projection of the cell's dendritic field spread the horizontal plane. The black dot represents the position of the soma. The inner circular profile represents a primary dendritic zone, encompassing the bulk of the dendritic arborization, whereas the outer circle outlines the extension of this primary zone by a few tertiary dendrites. (From Dacey and Ulinski, 1986b.)

filled by an injection of ipsilateral axons running in the intermedia tract in *Thamnophis*. These collaterals bear a general resemblance the collaterals on contralateral tectobulbar axons in that several th branches, bearing varicosities, radiate into the reticular formatio. Because of their relative positions in the brainstem, the contralateral and two ipsilateral pathways terminate in somewhat separate b overlapping territories throughout the reticular formation caudal the brainstem.

4. GENERAL FEATURES

Each tectobulbar cell has an extensive axonal system that includ both ascending and descending branches. Each individual cell the fore projects to several nuclei in the brainstem, and the projection each individual target structure involves a highly collateralized p

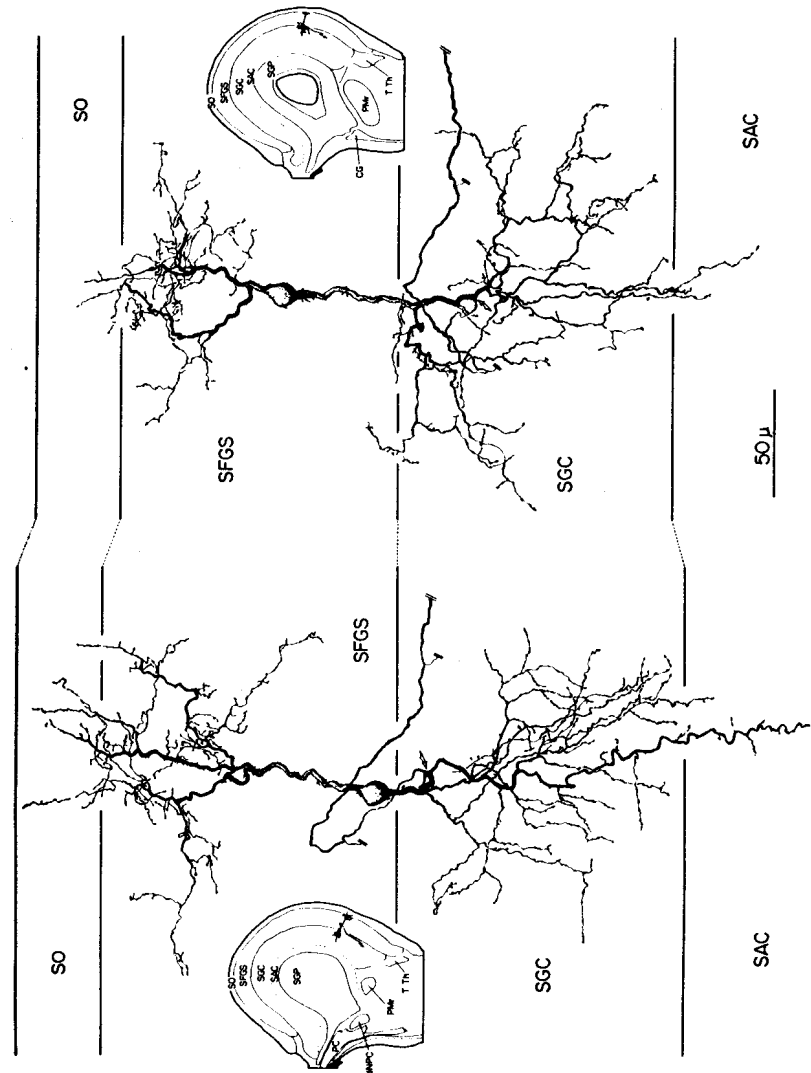


Fig. 4.18. *Pseudemys scripta*. Ipsilateral tectobulbar cells. Reconstruction of two small ventral pathway neurons in the SFGS. They were labeled after ipsilateral HRP injections into the lateral reticular formation. Both have a radially oriented ascending dendrite that gives rise to a plexus of filamentous dendritic appendages just beneath the SO as well as a radial descending dendrite that emits appendages in the SGC. Their thin axons (origins at open arrows) emit "local" collaterals into the SGC (see Fig. 4.23) before leaving the tectum to enter the smaller caliber (1 μ m) component of the ventral tectobulbar pathway, TBV(sm). (From Sereno and Ulinski, 1985.)

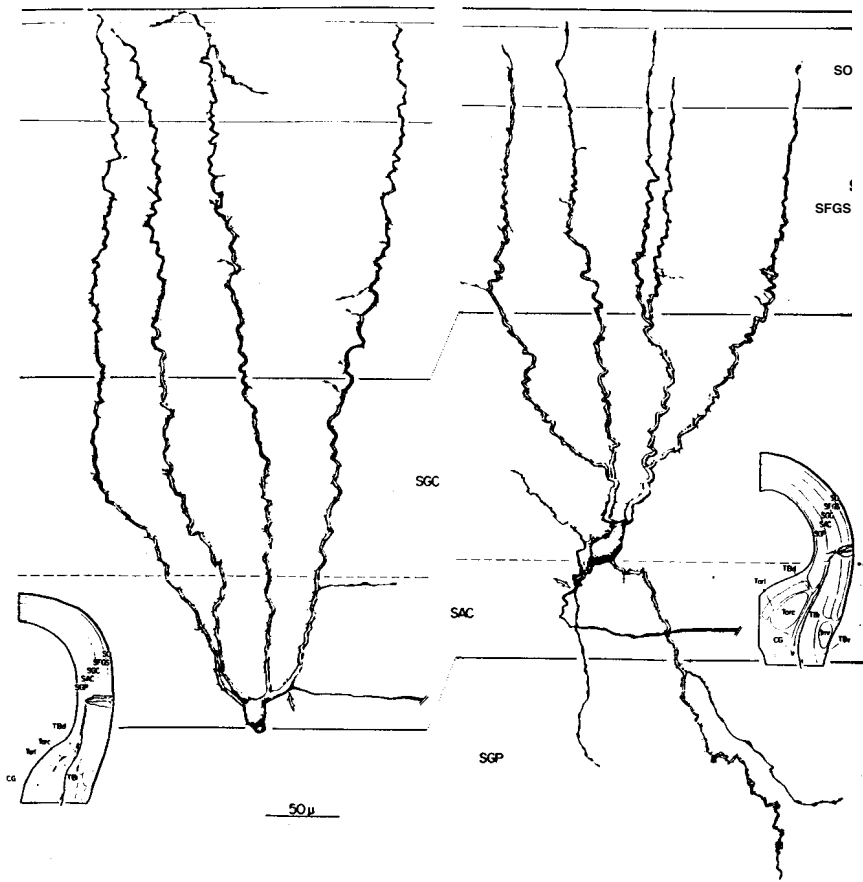


Fig. 4.19. *Pseudemys scripta*. Ipsilateral tectobulbar cells. Reconstruction of two probable intermediate pathway (TBI) neurons. They were labeled after an ipsilateral HRP injection into the lateral reticular formation. Both have radial ascending dendrites covered with very fine spicules similar to those on TBd neurons. Their medium-caliber axons (open arrows) could be traced far enough out of the tectum to suggest that they entered the TBI (rather than the TBv). No collaterals were observed in the tectum. (From Sereno and Ulinski, 1985.)

jection that effectively fills the target. This implies that there may be a convergence of information from many tectal neurons to a single region of the brainstem. This premise has been investigated explicitly in experiments (Fig. 4.23) in which two disjunct HRP injections were made in the tectum in *Pseudemys scripta* (Sereno, 1985). Labeled axons could then be followed from the two injection sites into the brainstem. Although the fascicles were initially separate, the individual axons eventually intermingled in the brainstem so that two adjacent axons may originate from disjunct tectal loci. Morphologically similar tectobulbar cells have recently been described in squirrel monkeys

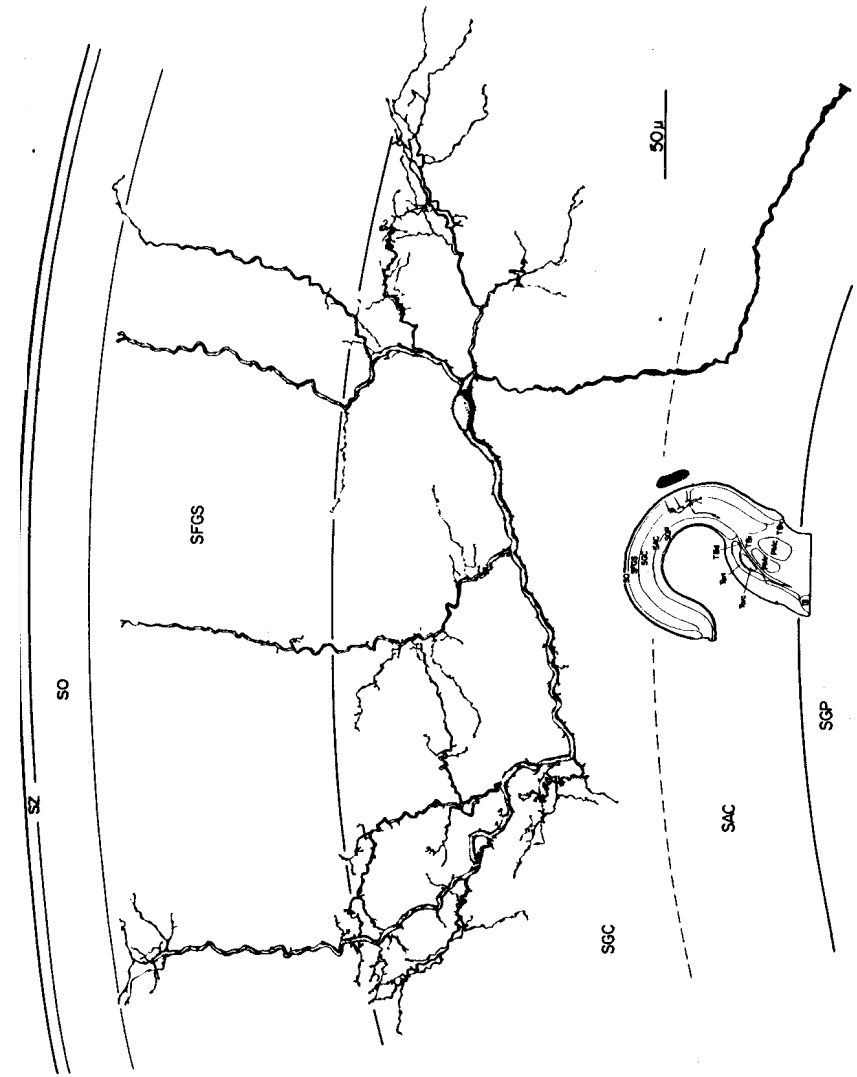


Fig. 4.20. *Pseudemys scripta*. Ipsilateral tectobulbar cell. Reconstruction of a probable ventral pathway (TBv) neuron. It was labeled after an ipsilateral HRP injection into the lateral reticular formation. The primary dendrites initially travel horizontally before turning upward, generating a mediolaterally elongated dendritic field (see *en face* view in low-power drawing). Many filamentous dendritic appendages are given off in the central gray (SGC). (From Sereno and Ulinski, 1985.)

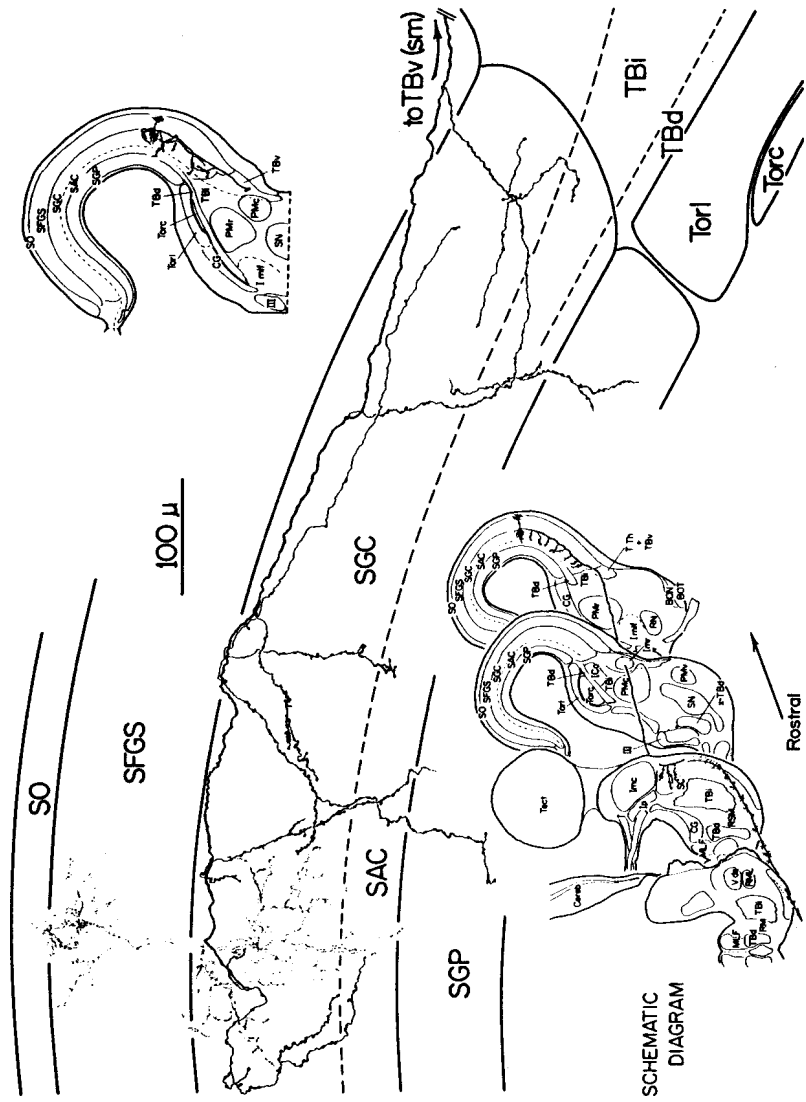


Fig. 4.21. *Pseudemys scripta*. Reconstruction of the intratectal collaterals of one of the TBv (sm) neurons illustrated in Fig. 4.20. The axon arises from the descending radial dendrite and immediately begins emitting strings of synaptic boutons downward into the SGC. Some penetrate the SGP. The main trunk then leaves the tectum (see schematic diagram) to enter the small-caliber component of the TBv. It passes through lmr without branching, emits several long collaterals into a small-celled nucleus ventral to lmc, and finally turns ventrally to run along the ventrolateral surface of the brainstem, where many short branches arise. (From Sereno and Ulinski, 1985.)

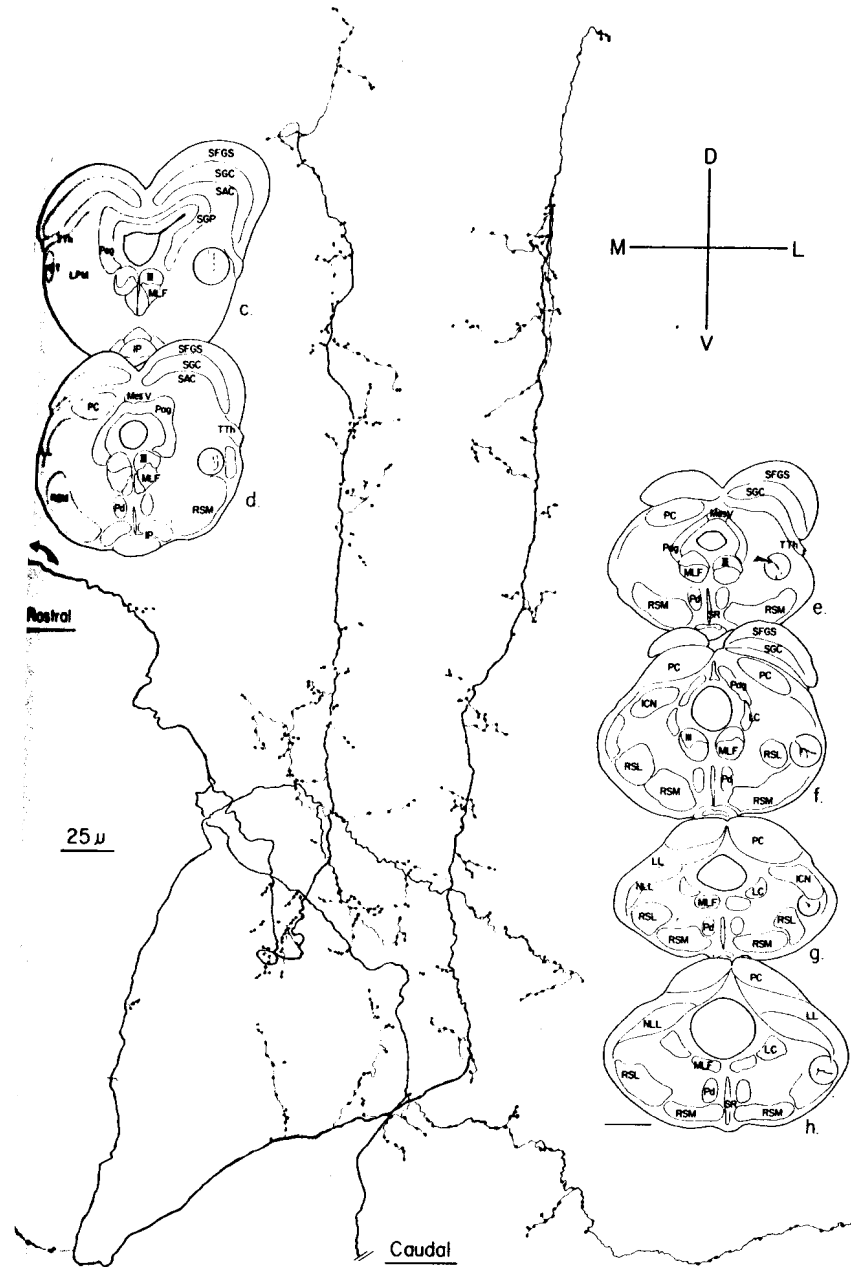


Fig. 4.22. *Thamnopis sirtalis*. Ipsilateral tectobulbar axon. This axon was reconstructed through 16 serial sections from an HRP injection site in the tectum. The figure shows six middle sections from the series. It illustrates a series of terminal collaterals in reticular superior pars lateralis (RSL) and reticular medialis (RM) (B and C). Circled areas in the 80- μ m coronal sections show the portion of the axon as it descends through the brainstem. Axons from two adjacent sections were collapsed in sections a, h, and i for illustrative purposes. (From Dacey and Ulinski, 1986a.)

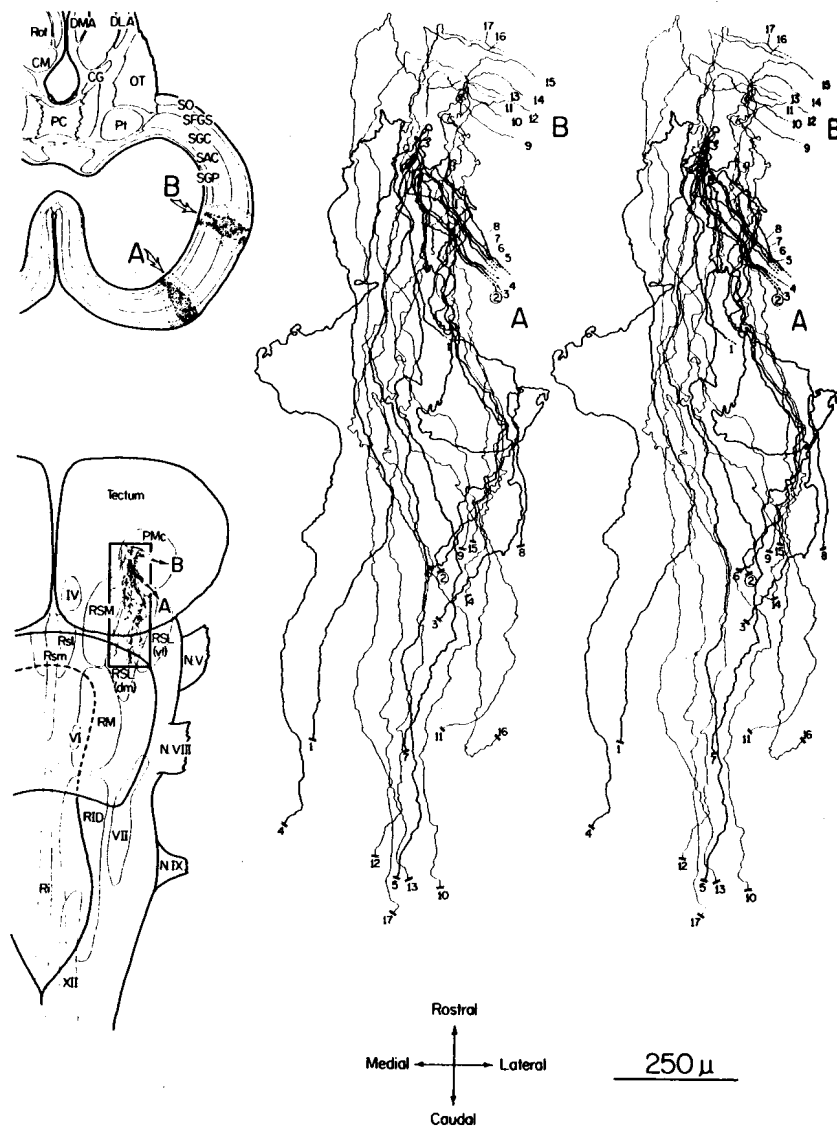


Fig. 4.23. *Pseudemys scripta*. Stereoscopic view of the main trunks of 17 TBi axons emerging from two punctate injection sites and coursing into the lateral pontine reticular formation. Two small HRP injections at A and B labeled eight and nine TBi axons, respectively. They were traced through 17 110- μ m serial horizontal sections into the dorsomedial segment of reticularis superioris lateralis, RSL (dm), where they formed two spatially distinct clumps, each, however, containing a mixture of axons from the two injection sites. The axons emerging from site A are drawn thicker to distinguish them from site B axons. The stereodiagram was made by hand as described by Glenn and Burke (1981) and can be viewed by ocular deviation or by using a stereoviewer. (From Sereno, 1985.)

(Moschovakis et al., 1988a, 1988b) and cats (Grantyn and Grantyn, 1982; Grantyn et al., 1984).

C. Tectoisthmi Neurons

The nucleus isthmi is situated in the isthmus region of the brainstem, immediately caudal and ventral to the optic tectum. Tectoisthmi projections have been demonstrated by experimental procedures in the green iguana *Iguana iguana* (Foster and Hall, 1975), the red-eared turtle *Pseudemys scripta* (Foster and Hall, 1975; Sereno, 1983), and garter snakes *Thamnophis sirtalis* (Dacey and Ulinski, 1986a).

The tectoisthmi neurons in *Thamnophis* have been identified following small HRP injections in nucleus isthmi (Fig. 4.24). They fall in the general class of radial cells and have small somata distributed throughout the superficial and central gray layers. Each spherical or pear-shaped soma bears a single, relatively thick radial dendrite that ascends into the superficial gray layers. The overall shape of the dendritic tree is roughly cylindrical and 60 to 80 μ m in diameter. The individual dendrites bear thin branchlets and arborize profusely in the stratum zonale, forming nests of horizontally flattened appendages that bear a variety of complex swellings. Many of the somata also bear thin descending dendrites that arborize sparsely.

The axons of tectoisthmi neurons originate from a thin basal dendrite or from the lower pole of a soma. They bear varicose collaterals in the superficial layers. The parent axons exit the tectum in the ventral tectobulbar tract and terminate in the ipsilateral nucleus isthmi (Fig. 4.25). They are of fine caliber, about 0.5 μ m in diameter, and descend vertically into the isthmi cell plate to terminate as single arbors. Each arbor is spherical or oval in shape and 10 to 30 μ m in diameter. A few tectoisthmi neurons have axons that continue past nucleus isthmi into the brainstem reticular formation after issuing a collateral that terminates in nucleus isthmi. The axons of these tectoisthmi-bulbar neurons continue in the ventral tectobulbar pathway and issue thin collaterals at irregular intervals.

Like the other tectobulbar axons, the reticular components of the tectoisthmi-bulbar axons appear to lack any obvious topography in their organization. However, the small terminals of the tectoisthmi collaterals appear to embody a retinotopic, or topographic, map between the tectum and nucleus isthmi. Since nucleus isthmi projects bilaterally to the tectum, the tectoisthmi projections are one limb of a reciprocal set of connections that interconnects the two tectal lobes. This point will be considered in more detail in Section V.B.3.

D. Tectorotundal Neurons

The nucleus rotundus is a large and prominent structure in the dorsal thalamus of reptiles (Rainey, 1979). There are bilateral projections from the tectum to nucleus rotundus in lizards (Butler and Northcutt,

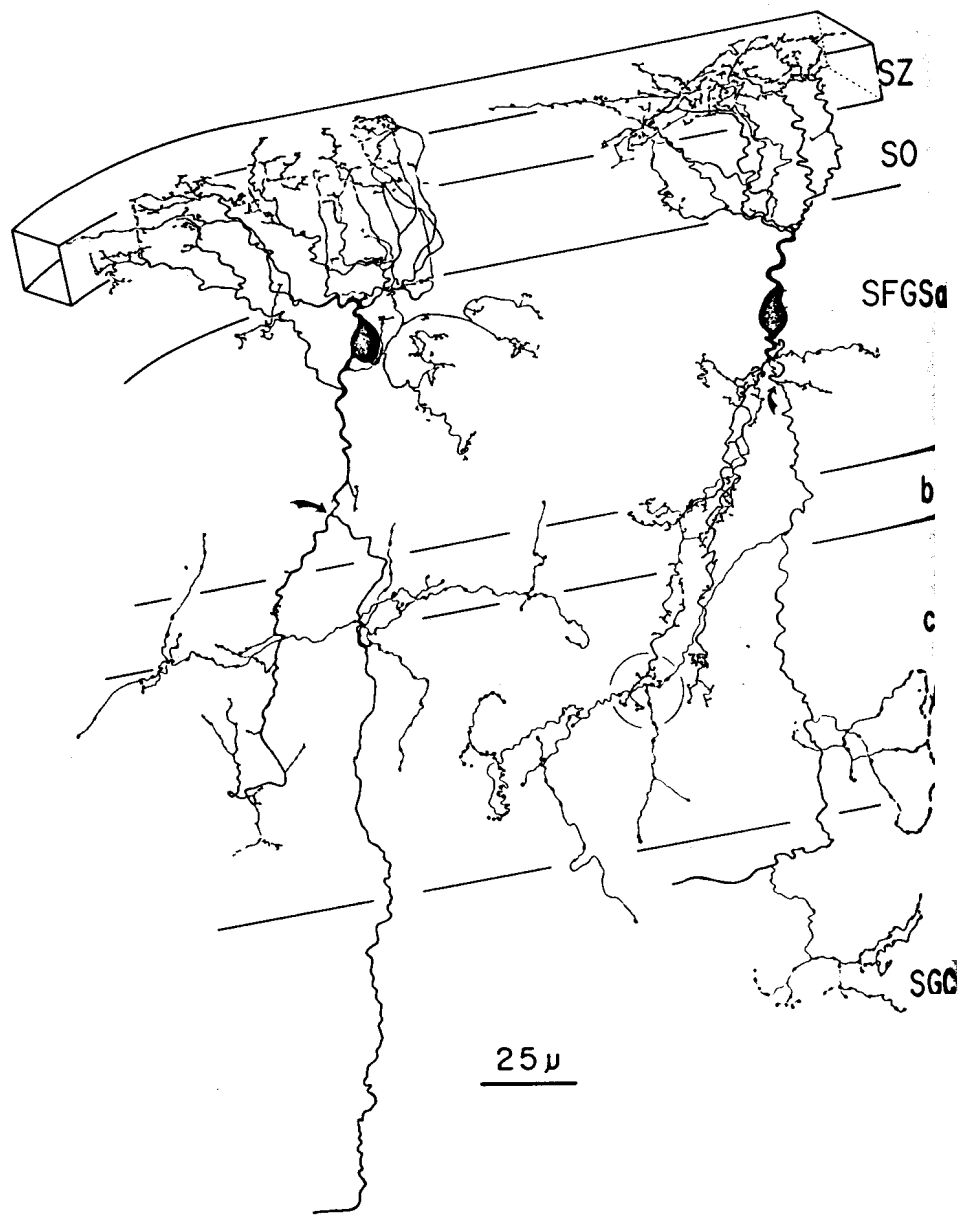


Fig. 4.24. *Thamnophis sirtalis*. Tectothalamic cells. This figure illustrates the morphology and laminar distribution of some cells that could be backfilled from injections of HRP into the ventral tectobulbar tract rostral but not caudal to nucleus isthmi. Somata in the upper part of the superficial gray have short radial dendrites that ascend through the optic fascicles in the stratum opticum and arborize in the stratum zonale. Thin descending dendrites extend for a variable distance into the SFGS. The axons (arrow) issue local collaterals in the superficial and central gray. (From Dacey and Ulinski, 1986a.)

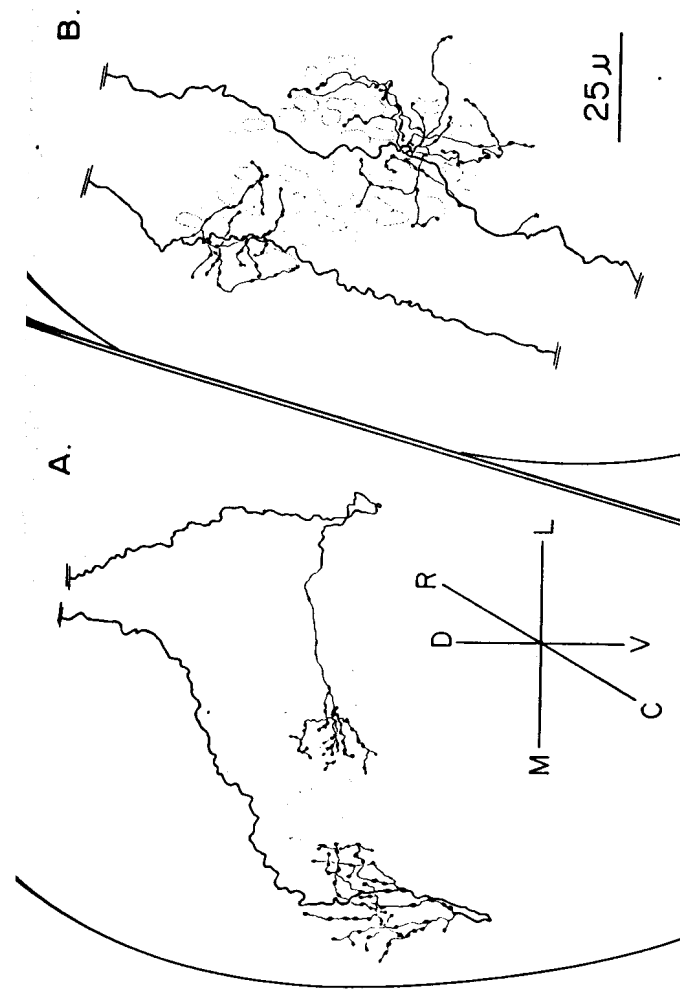


Fig. 4.25. *Thamnophis sirtalis*. Tectothalamic axons. Fine-caliber axons descend vertically into the nucleus isthmi (1st) and terminate in extremely small, spherical arborizations 10 to 30 μm in diameter (A) or course through the nucleus giving rise to a similarly shaped arbor (B). The somata of a few counterstained isthmic cells are outlined by the dotted lines. (From Dacey and Ulinski, 1986a.)

1971b; Butler, 1978; Hoogland, 1982), turtles (Hall and Ebner, 1970a; Rainey and Ulinski, 1982a), and crocodylians (Braford, 1972). The situation in snakes is less clear. Early cytoarchitectural (Warner, 1947) and Fink-Heimer (Northcutt and Butler, 1974b; Ulinski, 1977) studies failed to unequivocally demonstrate tectorecipient nucleus in the central thalamus of water snakes, *Nerodia sipedon*. Autoradiographic studies (Schroeder, 1981b) were similarly unable to demonstrate a nucleus rotundus in a rattlesnake, *Crotalus*. However, Dacey and Ulinski (1983) identified nucleus rotundus in garter snakes, *Thamnophis sirtalis*, using the orthograde transport of HRP following tectal injections. Nucleus rotundus projects to the ipsilateral anterior dorsal ventricular ridge in each group of reptiles (snakes: Dacey and Ulinski, 1983; Berson and Hartline, 1988; lizards: Distel and Ebbesson, 1975; Butler, 1976; Lohman and van Woerden-Verkley, 1978; Butler and Ebner, 1972; Bruce and Butler, 1979; Bruce, 1982; turtles: Hall and Ebner, 1970b; Kosareva, 1974; Balaban and Ulinski, 1981a, 1981b; crocodylians: Pritz, 1975).

Tectorotundal neurons have been identified in *Thamnophis* following injections of HRP into nucleus rotundus (Fig. 4.26). They belong in the general class of radial neurons. Their somata are positioned throughout the central and superficial gray layers but show a slight tendency to concentrate in the middle of the stratum griseum centrale. They are fusiform, with long axes of 15 to 20 μm . The upper and lower poles of the somata give rise to stout, primary dendrites, and thin branchlets arise from the somata and dendrites. The upper dendrites ascend into the superficial layers and reach the ventral border of the stratum zonale. The lower dendrites descend through the central gray to the upper border of the stratum album centrale. The overall dendritic field is hourglass in shape with a maximum diameter of 75 to 100 μm .

The thick axons of tectorotundal neurons arise from somata or dendrites and turn ventrally to descend to the lower half of the stratum griseum centrale (Fig. 4.27). They form a cluster of collaterals and terminal boutons just adjacent to the lower dendritic tree of the cell. The parent axon emerges from this tangle, descends obliquely into the stratum griseum centrale, and courses laterally into the stratum album centrale. The axons turn into the ipsilateral nucleus rotundus when they reach the thalamus, but at least some have collaterals that continue rostrally to cross the midline in the ventral supraoptic decussation and recurve to terminate in the contralateral nucleus rotundus. Butler (1978) showed that the distribution of terminal degeneration produced in nucleus rotundus in the tokay gecko, *Gekko gekko*, is not uniform. Unilateral tectal lesions produce rod-shaped patches of degeneration. The degeneration is bilateral, with the ipsilateral projection being densest. Bilateral lesions produce evenly distributed de-

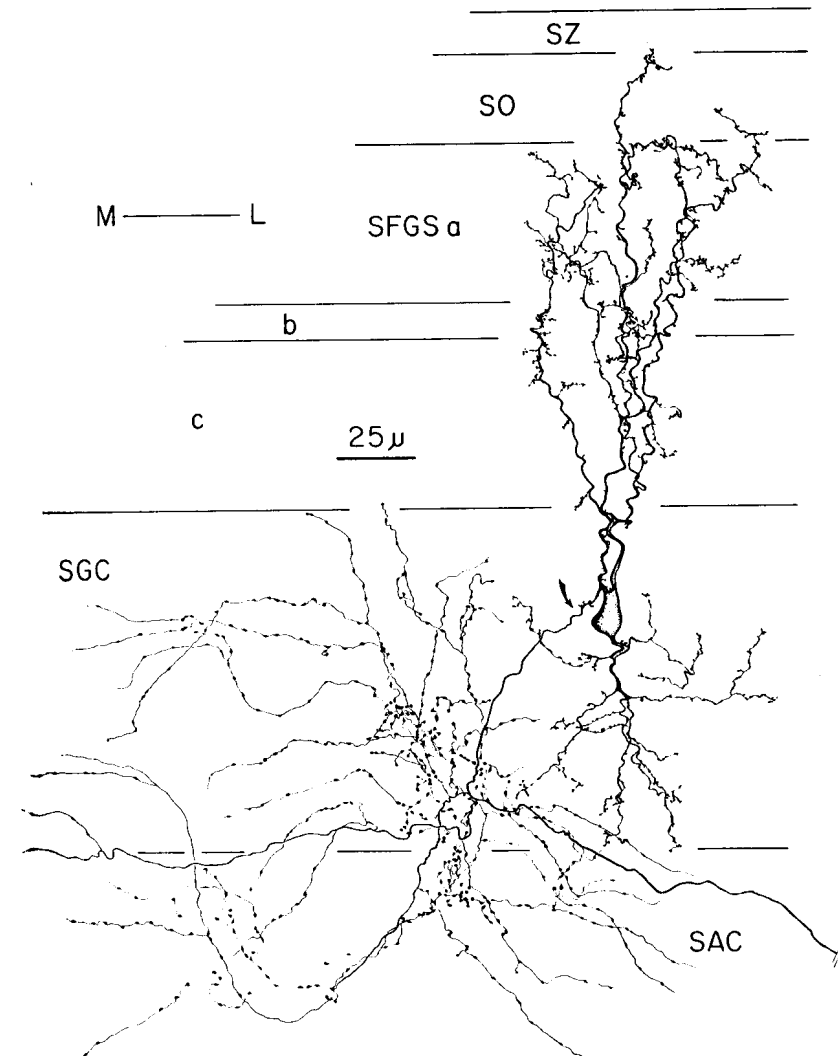


Fig. 4.26. *Thamnophis sirtalis*. Tectorotundal cell. This neuron has its soma positioned in the middle of the central gray. Dendrites bear threadlike, elongate appendages laden with clusters of complexly indented swellings. The axon forms a dense terminal plexus in the vicinity of the cell's lower dendrites and then gives rise to a large number of terminal collaterals that extend away from the cell's dendritic domain in the horizontal plane. The origin of the axon is indicated by the arrow. M-L, Medial-lateral. (From Dacey and Ulinski, 1986b.)

generation bilaterally in rotundus. Degeneration techniques do not provide an unambiguous interpretation of these experiments; however, experiments in which the morphology of tectorotundal axons is demonstrated using the orthograde transport of HRP clarify the organization of the tectorotundal projection. These axons course rostrally in the tectothalamic tract in both *Pseudemys* (Rainey and Ulinski,

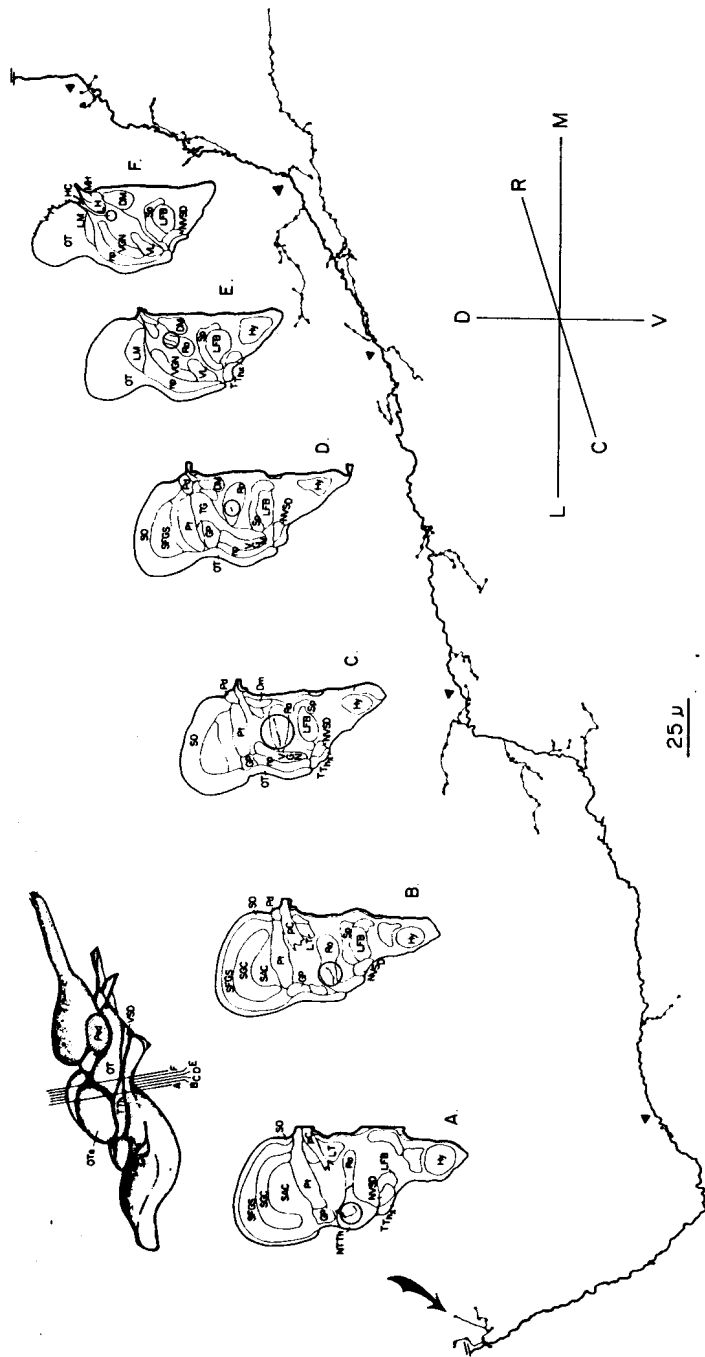


Fig. 4.27. *Thamnophis sirtalis*. The tectorotundal axon. This axon was reconstructed through seven serial sections from the nucleus of the tectothalamic tract (A) to the rostral pole of rotundus (F). After issuing small-terminal collaterals as the nucleus of the tectothalamic tract (NTTh), the axon courses in a straight line from the caudolateral to the dorsal pole of rotundus. The axon gives rise to several fine-caliber collaterals, forming a sheetlike terminal field that extends mediolaterally across the nucleus but is flattened in the dorsoventral axis. (From Dacey and Uliniski, 1983.)

1982b) and *Thamnophis* (Dacey and Uliniski, 1983). As they approach the ipsilateral rotundus, collaterals leave the parent axons and fan into the nucleus. These enter rotundus from its ventrolateral aspect in *Pseudemys* and from its caudal pole in *Thamnophis*. The experiments in *Thamnophis* show explicitly that each parent axon and its collaterals form a sheetlike distribution of terminals that extends rostrocaudally through the nucleus. It is likely that a similar organization obtains in *Pseudemys*. There is no apparent order to the manner in which the axons enter the nucleus, so that each particular region in rotundus is likely to contain collaterals of axons originating from neurons located in several different regions of the tectum. Detailed examination of the terminal collaterals of tectorotundal axons in *Pseudemys* suggests that several individual axons converge to form fascicles of varicose terminals. It seems likely that the rodlike terminal degeneration seen in *Gekko* reflects these fascicles.

The morphology of rotundal neurons is quite constant across species (Rainey, 1979). The central core of rotundus is occupied by multipolar neurons, the dendrites of which extend away from somata in an isodendritic pattern (Fig. 4.28). Neurons situated around the periph-

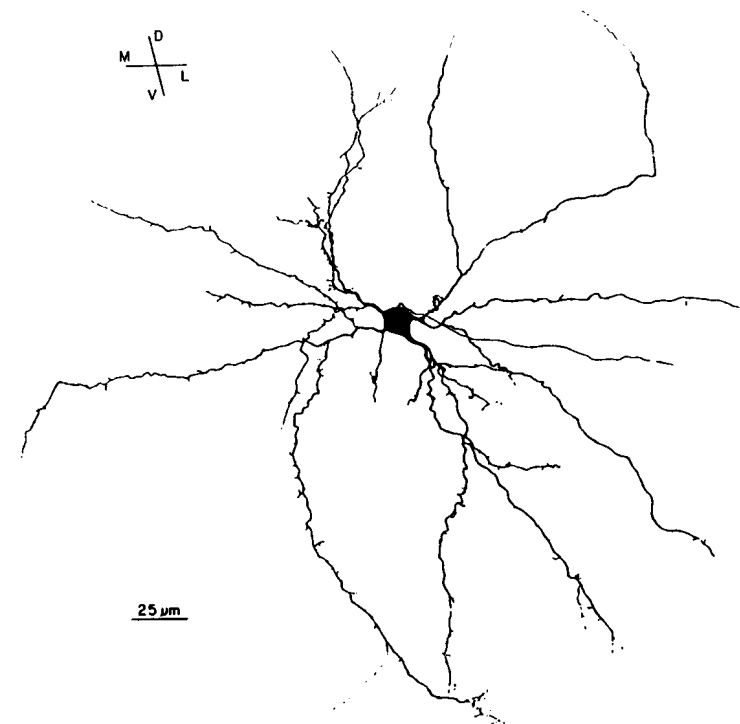


Fig. 4.28. *Thamnophis sirtalis*. Rotundal neuron. This neuron in nucleus rotundus was retrogradely labeled following an injection of HRP in the lateral forebrain bundle. (From Dacey and Uliniski, 1983.)

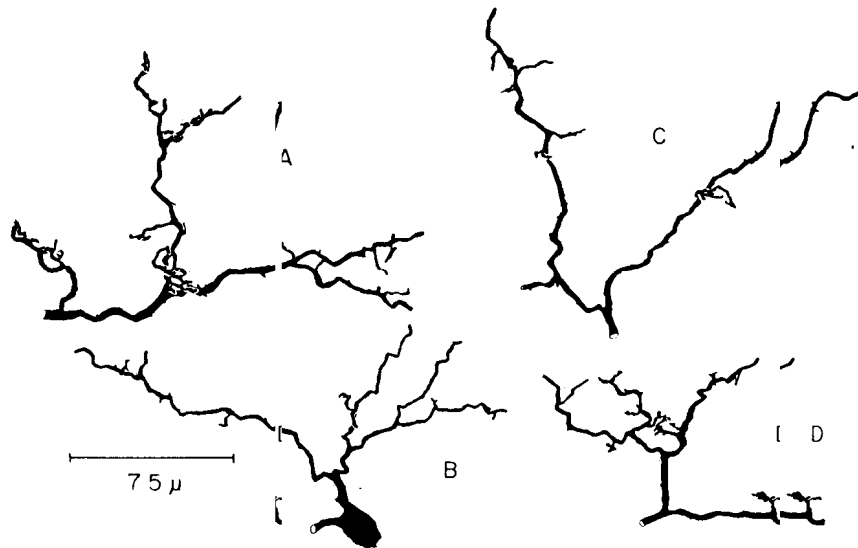


Fig. 4.29. *Pseudemys scriptae*. Dendrites of rotundal neurons. These are examples of the dendrites of rotundal neurons, which show complex appendages. They are drawn from neurons that were retrogradely labeled with HRP following an injection in the forebrain bundle. (From Rainey and Ulinski, 1982a.)

ery of the nucleus have dendrites that extend into the core. The diameters of the dendritic fields of rotundal neurons are quite large, so that an individual neuron can span as much as two thirds the diameter of the nucleus. Electron microscopic experiments show that the synapses of tectorotundal axons preferentially contact the distal dendrites of rotundal neurons. They occur on the shafts of the dendrites as well as on complex appendages that are situated on the distal dendrites (Fig. 4.29). The appendages are surrounded by nests of synapses suggesting that each appendage is embedded in a fasciculus of terminal axons, each of which contains axons from several tectorotundal neurons (Fig. 4.30).

The available anatomy thus suggests that the tectorotundal projection lacks a simple point-to-point relationship between the tectal surface and nucleus rotundus. Each tectorotundal neuron will potentially synapse on neurons throughout much of the volume of nucleus rotundus. Conversely, any neuron in rotundus is likely to receive input from neurons in many regions of the tectal surface. The results of electrophysiological investigations of the properties of rotundal units in turtles (Morenko and Pivavarov, 1973, 1975) and pigeons (De Britto et al., 1975; Revzin, 1970, 1979; Granda and Yazulla, 1971; Crossland, 1972; Maxwell and Granda, 1979) are consistent with the anatomy. Rotundal units typically have wide-field receptive fields

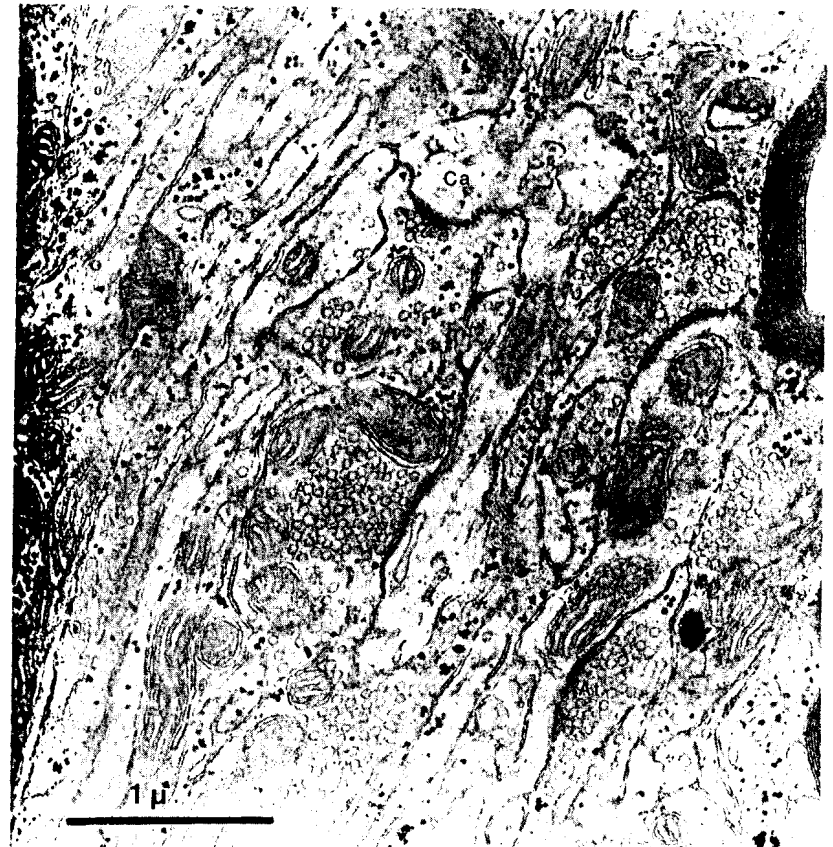


Fig. 4.30. *Pseudemys*. Rotundal synaptic nest. This electron micrograph shows a detail of the neuropil in nucleus rotundus. The irregular shaped and electron-lucent profiles (Ca) are probably the complex appendages of rotundal neurons. Degeneration experiments suggest that the presynaptic elements (At) are the terminals of tectorotundal neurons. (From Rainey and Ulinski, 1981b.)

that respond to stimuli placed throughout much of the contralateral visual field and often through the entire bilateral visual field. They respond well to small, moving stimuli, sometimes with preferred directions, velocities, or colors.

E. Tectogeniculate Neurons

The geniculate complex occupies the lateral diencephalon in all reptiles. It consists of several cytoarchitecturally delineated nuclei that have in common the receipt of direct projections from retinal ganglion cells. The diencephalic structures that receive direct retinal projections have been determined in snakes (Armstrong, 1951; Halpern and Frumin, 1973; Repérant, 1973; Repérant and Rio, 1976; Northcutt and

Butler, 1974b), lizards (Armstrong, 1950; Butler and Northcutt, 1971a; Butler, 1974; Northcutt and Butler, 1974a; Cruce and Cruce, 1975, 1978); turtles (Kosareva, 1967; Knapp and Kang, 1968a, 1968b; Hall and Ebner, 1970a; Belekhova and Kosareva, 1971; Bass and Northcutt, 1981a, 1981b), crocodylians (Burns and Goodman, 1967; Braford, 1973; Repérant, 1975) and *Sphenodon* (Northcutt et al., 1974). The organization of the geniculate complex is still poorly understood, but it is usually possible to recognize a ventral lateral geniculate nucleus that has reciprocal connections with the optic tectum and a dorsal thalamic nucleus that projects to the telencephalon. The latter structure is sometimes called the dorsal lateral geniculate nucleus. It has been claimed that the tectum projects to the dorsal lateral geniculate nucleus (see Ulinski, 1977), but recent work (Ulinski et al., 1983) reaches the conclusion that there is at present no evidence for a tectal projection to the components of the geniculate complex that project to the telencephalon.

Tectogeniculate projections have been best studied in *Thamnophis*. In this species, the geniculate complex is divided into a neuropil that lies internal to the optic tract and contains loosely packed neurons and a cell plate that contains densely packed neurons. The cell plate is divided into a rostrally placed nucleus ovalis and dorsal, dorsomedial, and ventral parts. The tectum projects to the ipsilateral ventral and dorsal parts of the cell plate (Fig. 4.31). The tectal neurons that give rise to this projection have been identified following small HRP injections in the geniculate (Fig. 4.32). They fall in the general class of radial cells. The somata of the tectogeniculate neurons are present in moderate numbers in the central gray and the lower half of the superficial gray, with the largest number occurring at the border between the two layers. Their somata are spherical or pear shaped in diameter and slightly smaller than the somata of the tectorotundal neurons. Each soma gives rise to a single thick dendrite that ascends into the superficial gray layers and one or two extremely thin basal dendrites that descend into the deeper tectal layers. The ascending dendrites occupy a narrow cylindrical space, 60 to 80 μm in diameter, extending from the border of the central and superficial gray layers to the stratum opticum. Many thin and complex branchlets issue from both the primary and secondary ascending dendrites.

Axons of tectogeniculate neurons ascend vertically into sublamina c of the superficial gray. They bifurcate into branches of unequal thickness at about the middle of this sublayer. The thinner branch remains in sublayer c and gives rise to a collateral arbor that overlaps the dendritic field of the neuron. These collaterals have several branches laden with varicosities that form nearly spherical arbors. The thicker branch ascends from sublamina c and turns rostrad as it

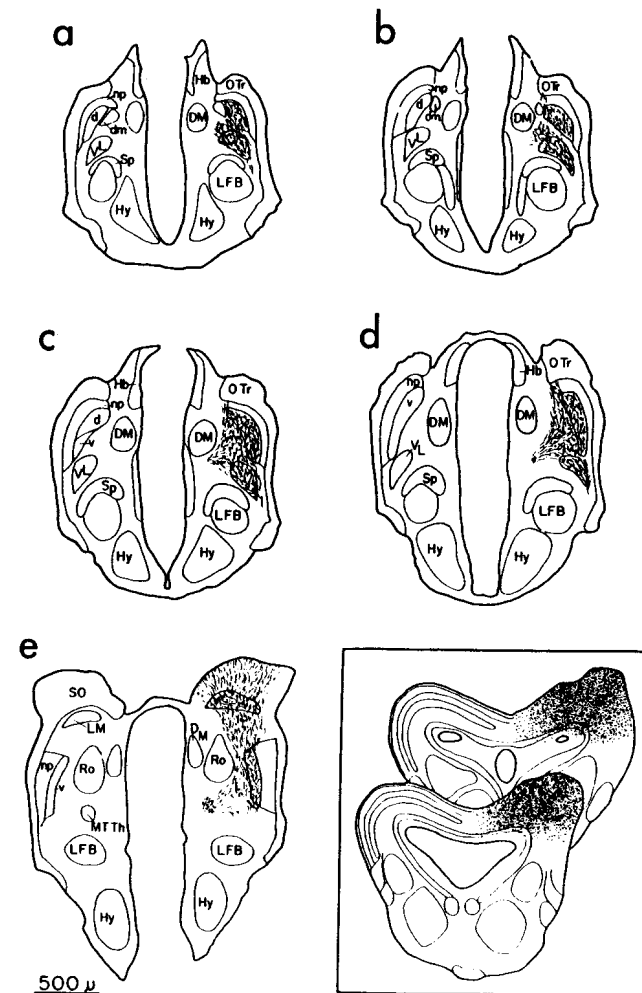


Fig. 4.31. *Thamnophis sirtalis*. Tectogeniculate projections. The inset shows the locus of a tectal HRP injection. The main part of the figure (a-e) shows the pattern of orthograde labeling in the geniculate. Labeled fibers distribute to the dorsal (d) and ventral (v) parts of the geniculate complex and to the ventrolateral nucleus (VL). (From Dacey and Ulinski, 1986a.)

reaches the lower border of the stratum opticum. As it passes ventro-rostrally into the pretectal nucleus, it issues collaterals that terminate within the pretectal and geniculate pretectal nuclei of the pretectal complex (Fig. 4.33). The parent axon descends through the pretectum medial to the ventral part of the geniculate cell plate within a region of low cell density that is designated as the tectogeniculate pathway. A collateral extends laterally into the cell plate, forming a highly

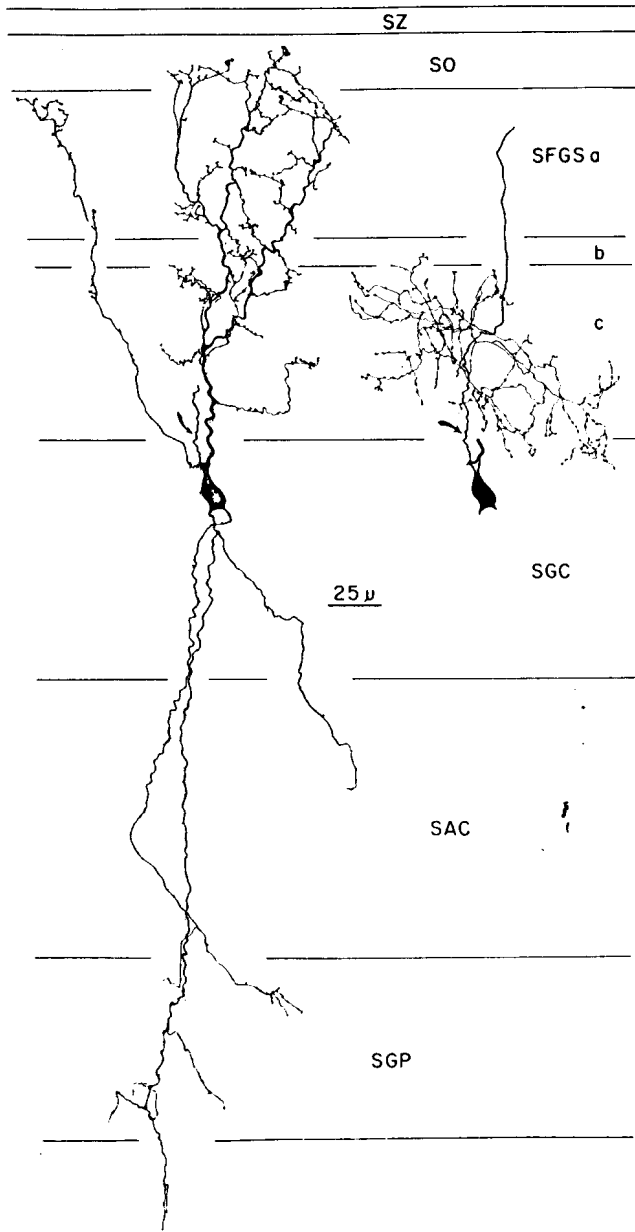


Fig. 4.32. *Thamnophis sirtalis*. Tectogeniculate cell. This figure illustrates the morphology of neurons whose axons could be traced into the tectogeniculate pathway. The axon collateral system and dendritic trees of this cell were traced separately; the same position in each tracing is indicated by arrows. Tectogeniculate neurons are characterized by a radial dendritic arbor in the superficial gray layers, by extremely thin, unarborized descending dendrites that can often be traced to the deep tectal layers, and by an axon that forms a collateral projection restricted to sublamina c of the SFGC and then ascends to the upper border of SFGSa, where it courses rostrally below the stratum opticum. (From Dacey and Ulinski, 1986b.)

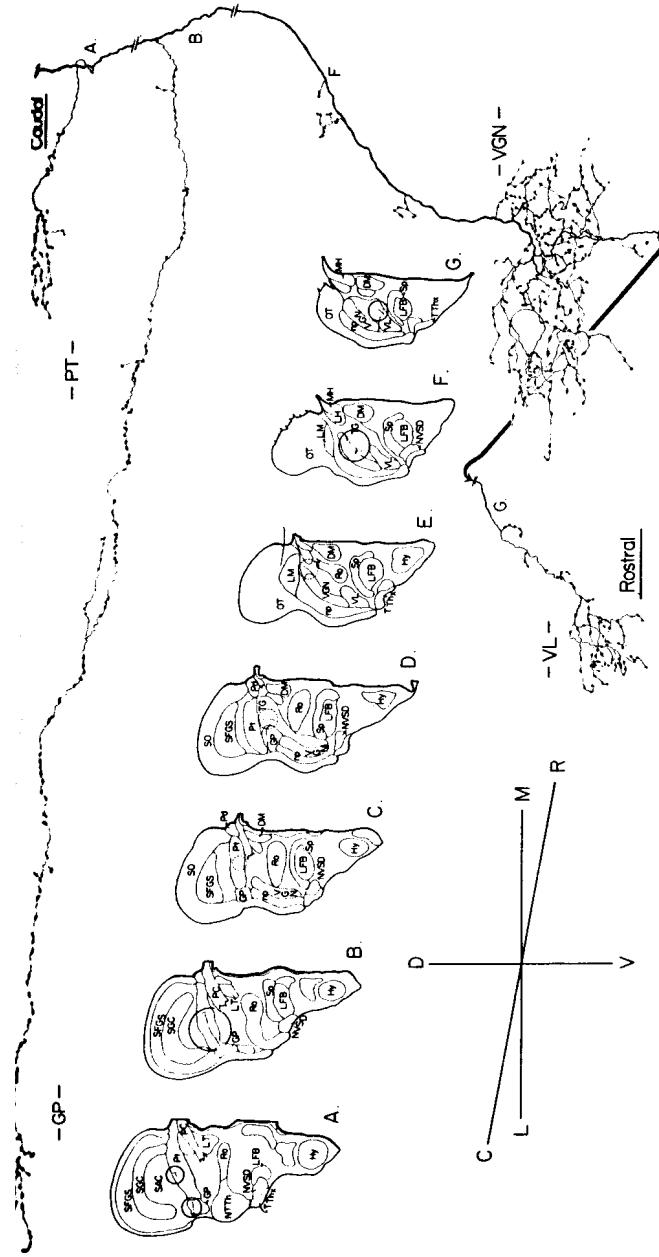


Fig. 4.33. *Thamnophis sirtalis*. The tectogeniculate axon. This axon was followed through eight serial sections (circled areas in A through G). Only the parts of the axon bearing collaterals (circles A, B, E, F, and G) are illustrated at higher magnification. Single, topographically organized terminal arbors are formed in the geniculate pretectal nucleus (GP), the pretectal nucleus (Pt), the cell plate of the ventral geniculate nucleus (VGN), and the ventrolateral nucleus of the thalamus (VL). The geniculate pretectal, the pretectal, and the ventral geniculate nuclei all receive a topographic retinal input. (From Dacey and Ulinski, 1986a.)

branched arbor that is shaped like a flattened cylinder 50 to 70 μm in diameter. Some geniculate axons extend into the ventrolateral nucleus of the ventral thalamus. Small injections indicate that the projections to the pretectal complex, the ventral part of the geniculate complex, and the ventrolateral nucleus are topologically organized and in register with the direct retinal input to these structures.

F. Summary

All of the studies of the optic tectum based on Golgi preparations recognized that several types of neurons in the tectum have axons that can be traced out of the tectum. The problem has been that it is generally not possible to trace the axons to their ultimate destination in Golgi preparations because single axons have to be followed through serial sections. However, the use of HRP as a neuronal marker in *Thamnophis* and in *Pseudemys* has permitted the correlation of the morphology of various populations of tectal neurons with the ultimate target of their axons. The results for *Thamnophis* are the most complete and are summarized in Fig. 4.34. Each class of tectal neuron, defined on the basis of its connections, has a characteristic morphology and is localized within a specific lamina or set of laminae. The HRP fills show that several of the efferent neurons also have extensive collateral systems within the tectum; beyond the intrinsic interactions within the tectum, they give rise to extrinsic projections. Many of the earlier Golgi studies show these collateral systems, but their extent has been generally underestimated. Most of the efferent neurons in *Pseudemys*, and probably all in *Thamnophis*, have dendrites that extend into the superficial layers and are therefore in potential receipt of retinal inputs. All of the efferent cells have axons that terminate in more than one target structure. Thus, the tectogeniulate neurons have collaterals in the pretectum, some tectoissthmi neurons have collaterals that continue to the reticular formation, and apparently all tectoreticular neurons have widely ranging axonal systems that include both ascending and descending branches.

IV. INTRINSIC NEURONS

A. General

Intrinsic tectal neurons are those that have synaptic interactions only with other tectal neurons. In practice, it is difficult to unequivocally recognize them because of the difficulty in assuring that a neuron with axon collaterals within the tectum really lacks efferent projections. Golgi preparations often impregnate only a fraction of the axon system of an individual neuron and lead to the false impression that a neuron forms only intrinsic connections. Also, intracellular injections of HRP may only partially fill an axon system. Thus, neurons in

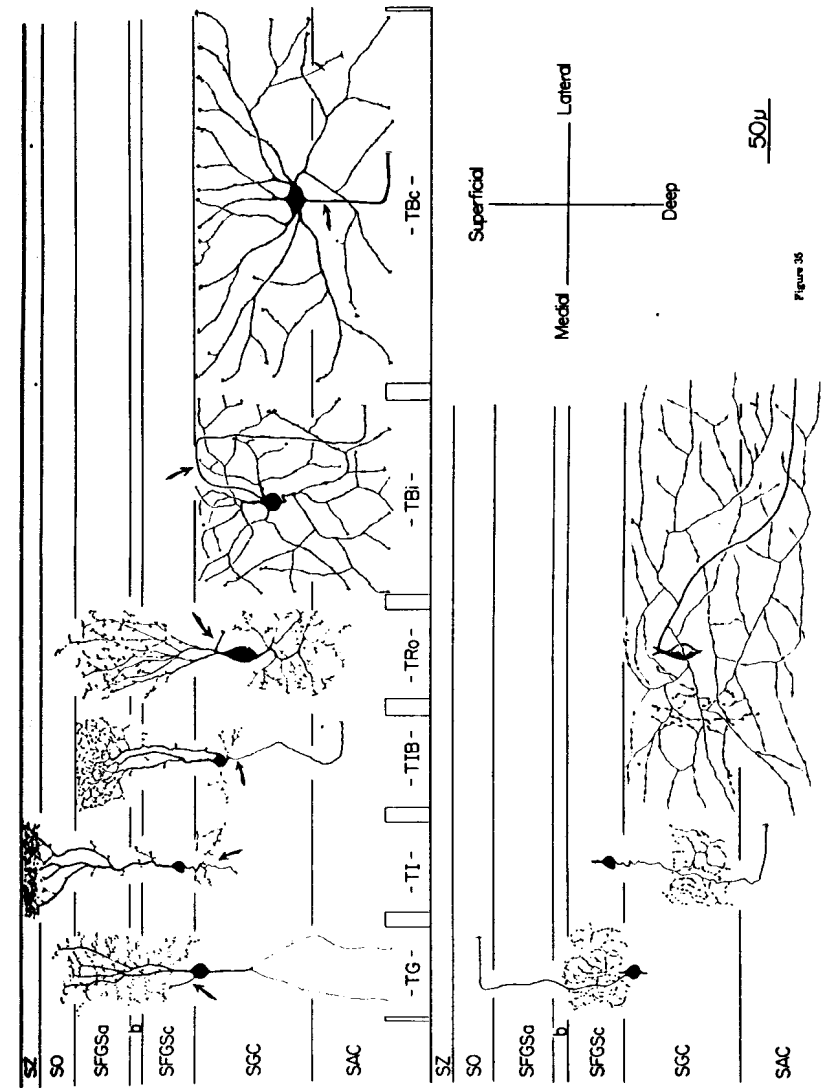


Fig. 4.34. *Thamnophis sirtalis*. Summary of efferent tectal neurons. This figure provides an overall summary of the classes of tectal neurons described in this study. Neurons are all drawn to about the same scale to facilitate comparison. The upper figure shows the morphology of the somata, dendrites, and the principal efferent tectal branch of the axon. Tectogeniulate (TG), tectoissthmi (TI), tectoissthmiulbar (TIB), tectoreticular (TRO), ipsilateral tectobulbar (TBI), and contralateral tectobulbar (Tbc) neurons are shown. The layers of the tectum are indicated by horizontal lines. The lower figure shows the somata of the tectogeniulate, tectoissthmi, and the tectoreticular neurons with their intrinsic axon collaterals drawn. The origins of the axons are indicated by arrows. (From Dacey and Ulinski, 1986b.)

the dorsolateral geniculate complex of cats (e.g., Friedlander et al., 1981) that were classically designated as *interneurons* are now known to be efferent neurons. Intrinsic tectal neurons must, therefore, be defined by negative evidence, but several classes of tectal neurons are potential candidates.

B. Horizontal Cells (Type A Cell)

Horizontal cells are neurons with dendrites that extend for considerable distances concentric to the pial surface of the tectum. They have been identified in Golgi preparations of the tectum in lizards (Ramón, 1896; Leghissa, 1962; Butler and Ebbesson, 1975) and turtles (Peterson, 1978b). The most detailed accounts of the morphology are obtained from experiments (Dacey and Ulinski, 1986c) in which horizontal cells were filled with HRP by means of injections in the tectum (Fig. 4.35). The somata of horizontal cells in these preparations are distributed throughout the superficial gray layer but are most frequent just above or below the stratum opticum. They tend to be horizontally fusiform and have thick primary dendrites that taper from the pole of the soma. Each dendrite issues several thinner dendrites that fan out in the horizontal plane for as much as 500 μm , following the curvature of the tectum. They extend further mediolaterally than rostrocaudally so that the overall shape of the dendritic field is elliptical in the horizontal plane. The secondary dendrites bear spines and large varicosities at irregular intervals. The axons of horizontal cells collateralize heavily within their dendritic fields and then extend horizontally in parallel with the dendritic field. Detailed electron microscopic studies have not been conducted on reptiles, but several authors have suggested that the dendritic appendages of horizontal cells in other groups are presynaptic in dendrodendritic synapses (Hayes and Webster, 1975; Angaut and Repérant, 1976) and may use γ -aminobutyric acid (GABA) as a transmitter (Streit et al., 1978). Such synapses raise the possibility that various portions of each horizontal cell function as independent units. Inputs to the distal dendrites will produce relatively large excitatory postsynaptic potentials (EPSPs) due to the large input resistance of the thin dendrites, whereas inputs to the soma will produce relatively small EPSPs. Different regions of the neuron might then differ in their function and participate primarily in local interactions.

C. Small Cells with Descending Axons (Type B Cells)

In contrast with horizontal cells, Type B cells are small, vertically oriented and have an axon that projects to deeper tectal layers. They may correspond to the "pequeños corpusculos de cilindre-eje descendante" of Pedro Ramón (1896). The somata of these neurons are

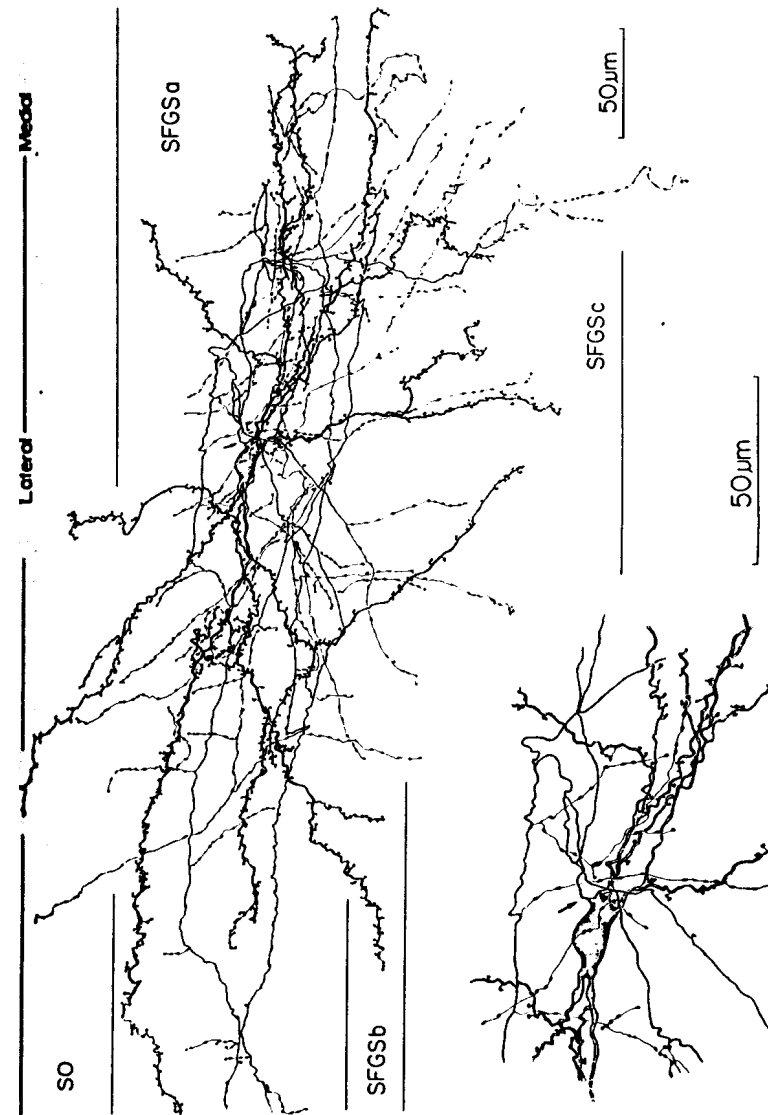


Fig. 4.35. *Thamnophis sirtalis*. Horizontal cell. The dendrites of horizontal cells are extended in the mediolateral axis and fan out from their point of origin. They are thick and varicose and bear numerous appendages in the form of single lollipoplike protrusions or long beaded strands and clusters. The dendritic field of this cell is relatively planar and is restricted to the stratum zonale. The axon is shown in a separate tracing for clarity; the same point in each tracing is indicated by the arrow. (From Dacey and Ulinski, 1986c.)

always positioned within or very close to the cell dense lamina b of the stratum fibrosum et griseum superficiale and seem to participate in clusters of neurons with apposed somata (Fig. 4.36). The dendrites ascend into sublamina a of the stratum fibrosum et griseum superficiale, branching into thin, varicose secondary dendrites. They often recurve at their ends, sometimes forming grapelike clusters or lobulated masses of swellings. The result is a compact bushy arbor that forms a cylindrical field 50 to 80 μm in diameter and extending 40 to 65 μm above the soma. The axons of these neurons originate from the bases of their somata and descend vertically into sublamina c of the stratum fibrosum et griseum superficiale. They recurve and terminate in a spray of collateral branches in sublamina c and bear collaterals that ascend through sublamina c or descend into the upper central gray. The axon system is a vertically aligned field and has dimensions similar to those of the dendritic field, so that the neuron as a whole occupies a cylindrical space 50 to 80 μm in diameter that extends through the superficial gray.

An electron microscopic study of the superficial layers of the asp viper (Repérant et al., 1981) has demonstrated varicose, radially oriented dendrites containing flattened synaptic vesicles that are pre-synaptic to other dendrites and postsynaptic to retinal ganglion cell terminals. Serial section analysis shows that these profiles arise from small, vertically oriented neurons in the stratum fibrosum et griseum superficiale that may, therefore, correspond to the dendrites of these neurons. It is possible that these neurons are similar to horizontal cells and participate in triadic relations with retinal afferents and the dendrites of other neurons. A study of the optic tectum of the pigeon suggests that these cells accumulate tritiated GABA and may mediate inhibition in the superficial gray (Hunt and Kunzle, 1976).

D. Stellate Cells (Type C Cells)

A third group of intrinsic neurons corresponds to the stellate cells of Golgi preparations but may also be viewed as a form of small radial cells. Similar neurons have been illustrated for the lizard *Pentadactylus* (Quiroga, 1978). Their somata are small and spherical and lie in the middle third of the central gray layer (Fig. 4.37). Their dendritic arbors are spherical or cylindrical with diameters of 60 to 80 μm . One to three primary dendrites arise from each soma and extend radially. The thin and wavy secondary dendrites are laden with complex, varicose appendages. The axons extend laterally in a wavy and often re-coiled path, issuing primary collaterals near the dendritic tree of the cell. The primary branches extend vertically through the central gray and form a distinct plexus displaced laterally from the soma. The plexus occupies a cylindrical space 40 to 80 μm in diameter and lies in the central gray.

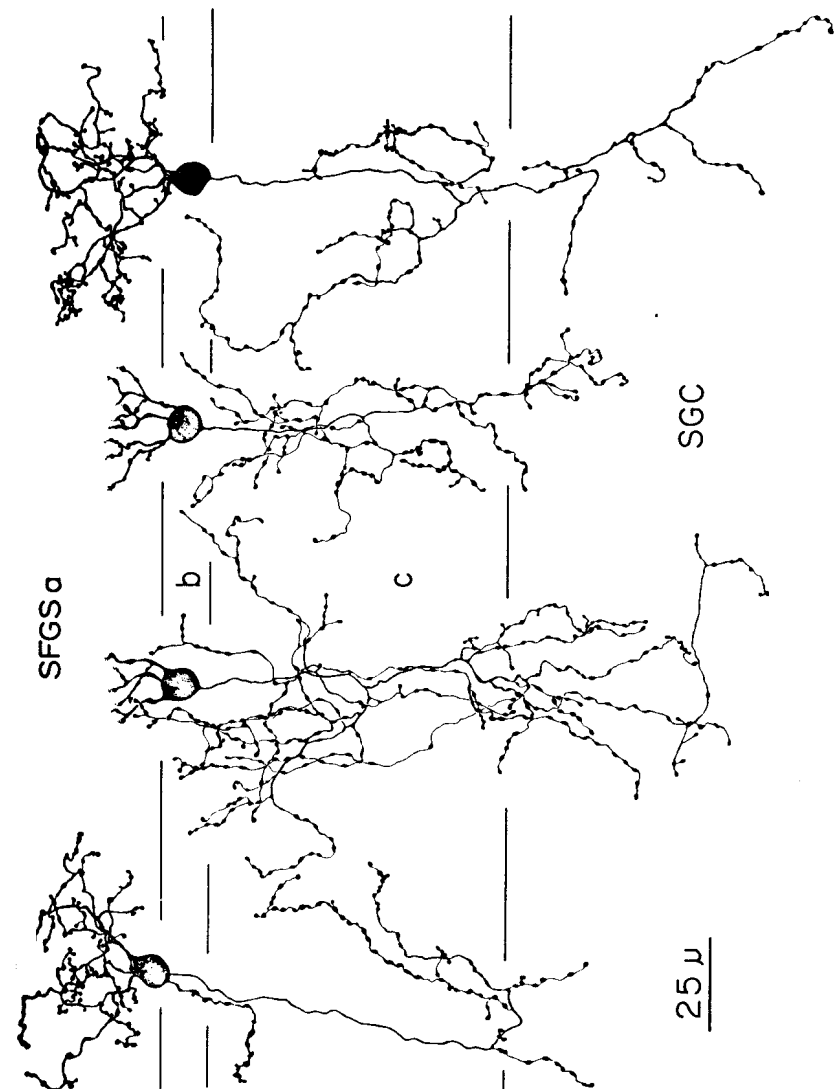


Fig. 4.36. *Thomomys striatalis*. Small cells with descending axons. The axons of these cells descend from the base of the soma and arborize in vertical alignment with the cell's dendritic field in sublamina c of the stratum fibrosum et griseum centrale. The axon collaterals are often thick and bear large varicosities (1 to 2 μm in diameter). (From Dacey and Ulinski, 1986c.)

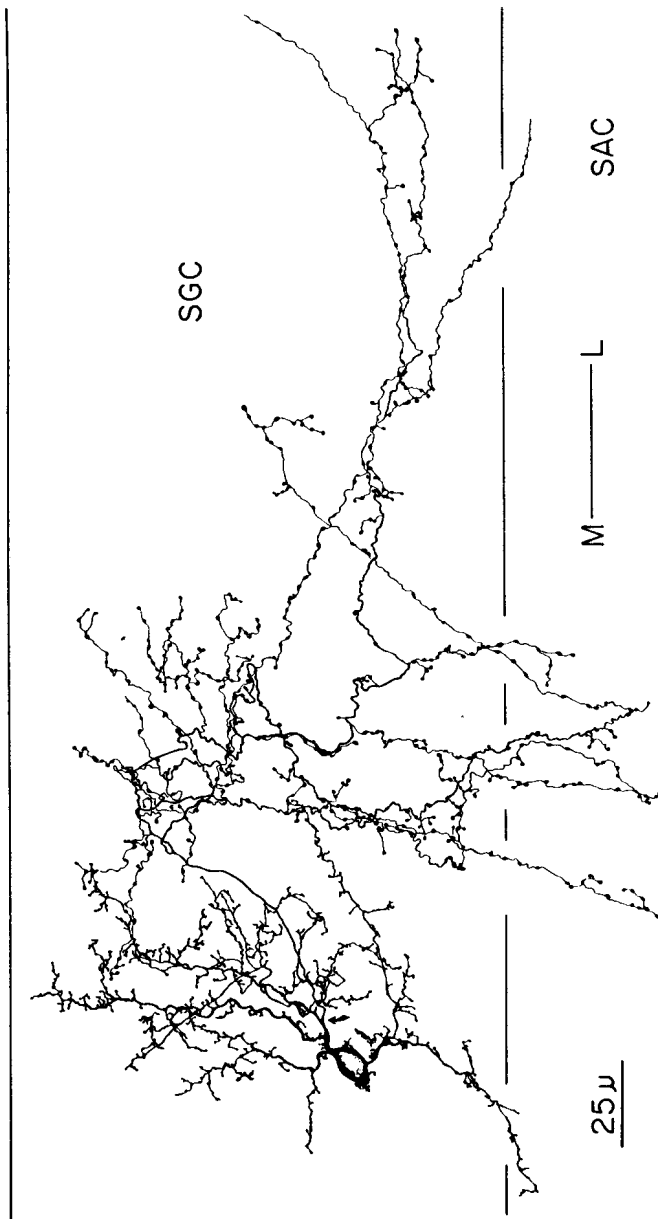


Fig. 4.37. *Thamnophis sirtalis*. Stellate cell. The fine appendage-laden dendrites of this cell type are restricted to the stratum griseum centrale. The axon forms a dense terminal plexus laterally displaced from the cell's dendritic field. Single terminal collaterals may extend laterally for a few hundred micrometers. The origin of the axon from a primary dendrite is indicated by the arrow. M-L, medial-lateral. The soma of this cell is positioned at the border of the central white and periventricular gray. The dendritic field spread is $450 \times 260 \mu\text{m}$. (From Dacey and Uliniski, 1986c.)

E. Type D Cells

A final group of intrinsic neurons has vertically fusiform somata; most of them lie at the interface of the central and superficial gray layers (Fig. 4.38). The two poles of the somata each issue a single primary dendrite. The ascending dendrites bifurcate within $25 \mu\text{m}$ of the soma into branches that ascend at slightly oblique angles, forming a conical dendritic field 60 to $80 \mu\text{m}$ in diameter. The descending dendrites extend to the lower border of the stratum griseum centrale. Both sets of dendrites bear fine terminal branchlets, varicose appendages, and single spinelike protrusions. Axons arise from somata or primary dendrites and extend medially 10 to $50 \mu\text{m}$ without branching before descending vertically or obliquely into the middle of the central gray, where they issue fine, varicose collaterals. Single collaterals participate in a loose terminal plexus that occupies the central white layer. The cylindrical plexus is cylindrical, 50 to $70 \mu\text{m}$ in diameter and displaced up to $100 \mu\text{m}$ medial to the dendritic field of the cell.

F. Summary

Like the efferent neurons, each particular class of putative intrinsic neurons is associated with particular tectal laminae (Fig. 4.39). The horizontal (Type A) neurons and small neurons with descending axons are most superficially located. The radial neurons (types B and D) are located at the border of the superficial and central layers and the stellate cells (type C) lie within the central gray. There is presently no clear evidence for purely intrinsic neurons within the deeper layers. Each set of intrinsic neurons will, therefore, be embedded in its own set of afferents, but all are in potential receipt of retinal input to the superficial layers. The presence of varicosities and appendages on the dendrites of all four types of intrinsic neurons suggests that they are involved in dendrodendritic synapses with other tectal neurons and are likely to participate in triadic relationships with retinal afferents. There is limited direct evidence in reptiles, but studies in frogs (Szekely et al., 1973), pigeons (Hayes and Webster, 1975), and several species of mammals (e.g., Sterling, 1971; Graham and Casagrande, 1980) suggest that intrinsic neurons are involved in relationships of this type. All intrinsic neurons also have axonal systems, but nothing is known about the nature of their synaptic contacts with other neurons.

V. AFFERENTS

A. General

The axons of retinal ganglion cells are the most obvious source of afferents to the optic tectum. They can be traced from the optic nerves, through the optic tracts, and into the substance of the tectum. However, large injections of HRP into the tectum reveal that an over-

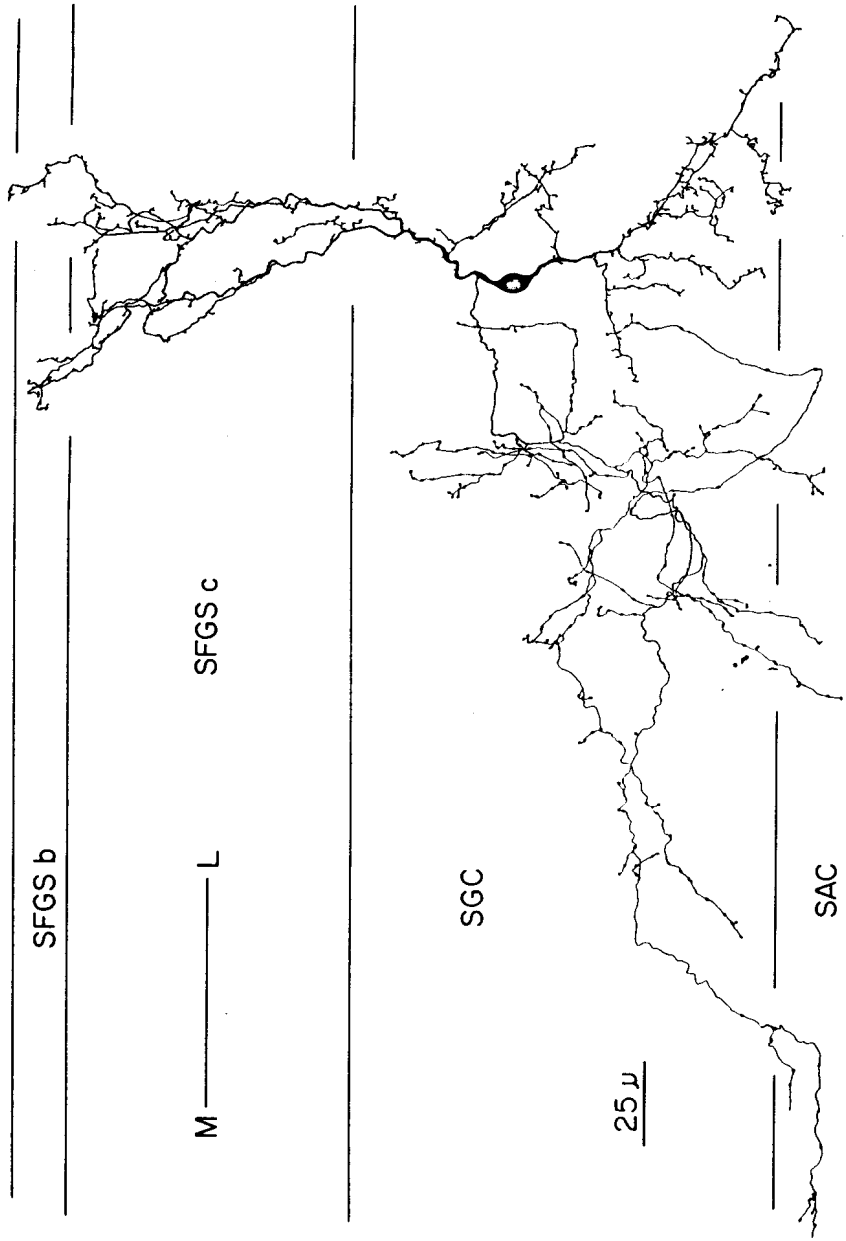


Fig. 4.38. *Thamnophis sirtalis*. Radial cell. The dendrites are thin and radially aligned. They give rise to a moderate density of complex appendages. The appendages may be long and varicose and bear knobby and lobulated protrusions. The dendritic field occupies a narrow cylindrical zone 60 to 80 μm in diameter. (From Dacey and Ulnski, 1986c.)

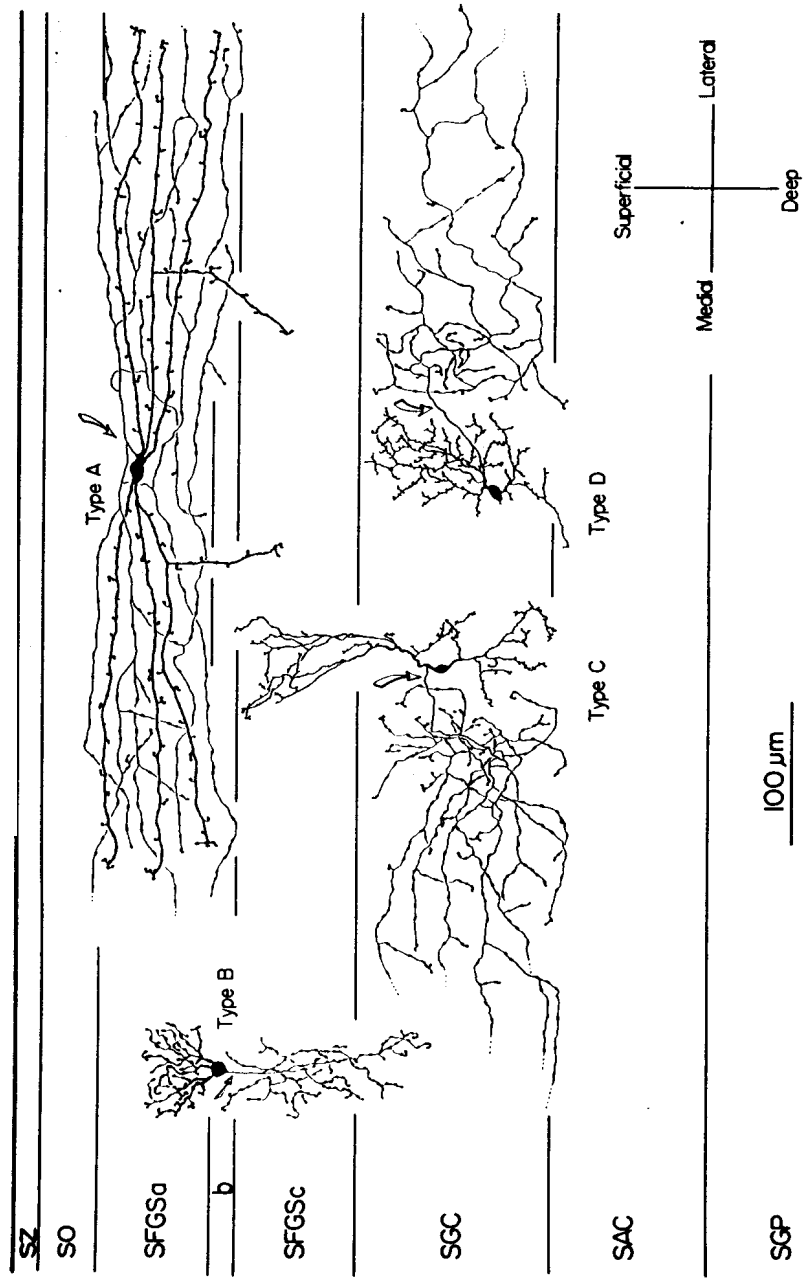


Fig. 4.39. *Thamnophis sirtalis*. Summary of intrinsic neurons. This figure shows examples of each of the four types of intrinsic neurons described here. They are drawn schematically and to the same scale to facilitate comparison. Arrows indicate origins of the axons. (From Dacey and Ulnski, 1986c.)

whelming number of other structures also terminates in the tectum. Fig. 4.40 illustrates the results of such an experiment in *Thamnophis*. No telencephalic afferents to the tectum have been reported in snakes and none are shown, but turtles show projections from the visual cortex to the tectum (Hall et al., 1977). Within the diencephalon of *Thamnophis*, neurons in the geniculate complex, ventral thalamus, and hypothalamus project bilaterally to the tectum. All of the major pretectal structures project bilaterally to the tectum. Several nuclei in the mesencephalic tegmentum and in the torus semicircularis (which is called the posterior colliculi in snakes; Senn, 1969) project to the tectum. The trigeminal nuclei and reticular formation of the rhombencephalon project to the optic tectum. Finally, the spinal cord has a direct projection to the optic tectum.

As far as is possible, afferents to the tectum are here grouped into functional categories for discussion.

B. Visual Afferents

1. VISUAL REPRESENTATION The representation of visual information in the optic tectum can be studied by recording with microelectrodes in anesthetized animals while presenting visual stimuli to one or both eyes. This procedure has been carried out on a wide range of vertebrates (see Kruger, 1969), including snakes (Terashima and Goris, 1975; Hartline et al., 1978), lizards (Stein and Gaither, 1981), turtles (Gusel'nikov et al., 1970), and a crocodilian (Heric and Kruger, 1966). Several general properties have emerged.

There is universally a topological representation of the retinal surface within the optic tectum. The temporal edge of the retina is usually represented rostrally in the tectum with the representation of the nasotemporal axis extending from rostromedial to caudolateral on the tectum. This orientation has been reported for snakes (Terashima and Goris, 1975; Hartline et al., 1978), turtles (Gusel'nikov et al., 1970), and a crocodilian (Heric and Kruger, 1966). A slightly different orientation has been reported in the iguana, *Iguana iguana* (Stein and Gaither, 1981). It is not clear if this difference reflects differences in the shape and orientation of the tectum as a whole or possibly technical difficulties such as the incomplete compensation for the rotation of the eye that often occurs during anesthesia.

Although the complete retinal surface is represented, some regions of the retina may occupy a disproportionate percentage of the total tectal map. Such differences can be quantified by calculating a magnification factor that indicates the number degrees of visual space represented per millimeter of tectal surface. The most accurate estimates of relative magnification have been carried out on *Alligator* (Heric and Kruger, 1966). The magnification factor is fairly constant in

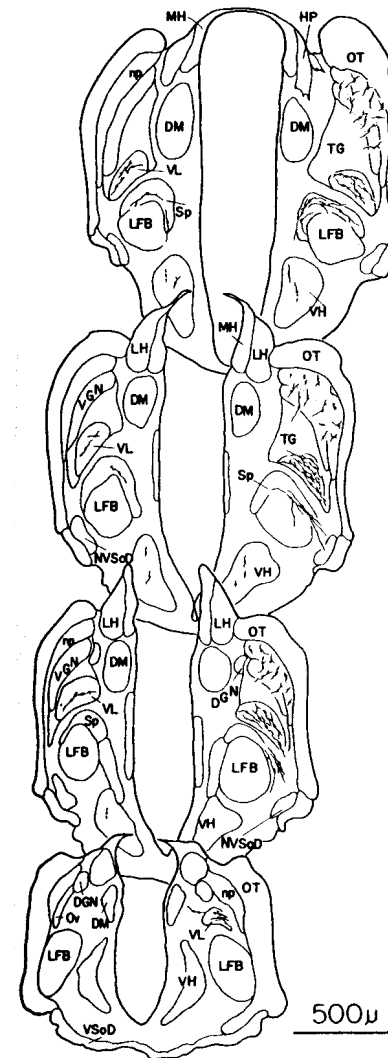
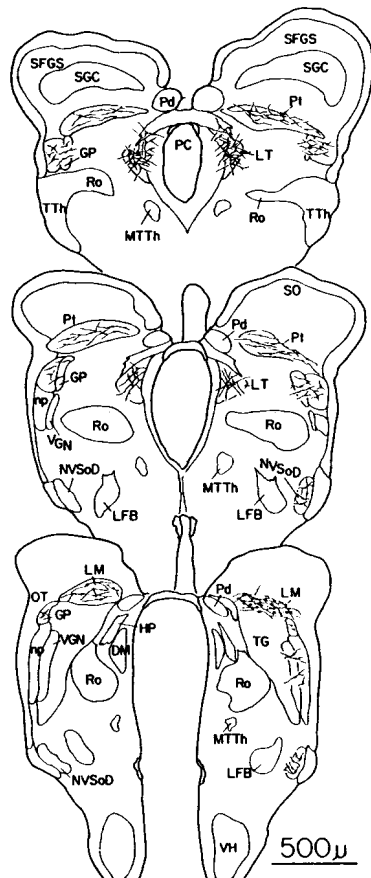


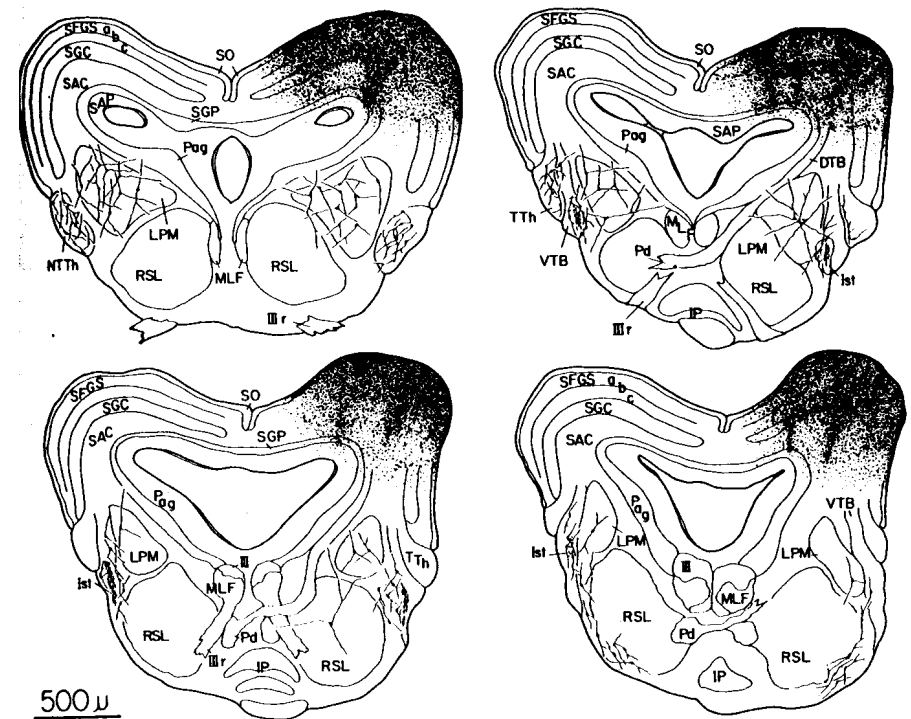
Fig. 4.40. *Thamnophis sirtalis*. Tectal afferents. This figure illustrates the pattern of retrograde cell labeling in the brainstem after a large injection of HRP into the tectum. Diencephalic projections arise from the ventral geniculate nucleus (VGN) ipsilaterally and the ventrolateral nucleus (VL), suprapeduncular nucleus (Sp), and ventral hypothalamus (VH) bilaterally. 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). 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. Projections arise from the posterior colliculus (PC), nucleus of the lateral lemniscus (NLL), and the spinal nucleus of the trigeminal (SpV) bilaterally and a small cluster of neurons associated with the vestibular complex (VeVm) contralaterally. Filled neurons are also embedded in the ventral tectobulbar tract (VTB) ipsilaterally and the predorsal bundle contralaterally. Chartings were traced from 80- μ m coronal sections. They are presented as a series of 15 consecutive sections on this and the following three pages. (From Dacey and Ulinski, 1986e.)

this species, and there is only a slight exaggeration of the portion of the retina that sees the central visual fields. Comparable results have been obtained in snakes in a less detailed study. Inferences drawn about the retinal map of *Pseudemys scripta* from such experiments on the red-eared turtle suggest that much of the tectal surface is occupied by a highly magnified representation of the retinal visual streak, which is a linear area of high density of photoreceptors and ganglion cells that extends across the nasotemporal axis of the retina (Brown, 1969; Peterson and Ulinski, 1979).

Experiments in which a microelectrode is systematically advanced into the tectum indicate that most visual units occur in the superficial



layers of the tectum. The properties of visual units have been studied in turtles (Robbins, 1972; Boyko and Goncharova, 1976; Davydova et al., 1982), snakes (Hartline et al., 1978; Kass et al., 1978), and the iguana, *Iguana iguana* (Stein and Gaither, 1983). Visual units are found throughout the depth of the tectum, but units in the superficial layers typically have smaller receptive fields than those in the deeper layers. Boyko and Goncharova (1976) report receptive field sizes are 5° to 10° in the superficial layers of turtles. In *Iguana*, the receptive field sizes are 0.5° within the central 5° of visual field representation but increase to as large as 40° more peripherally (Stein and Gaither, 1981, 1983). Receptive fields in the deeper layers range from 31° to 110° (Boyko and Goncharova, 1976). Units with small field sizes tend to be elliptical, with the long axis parallel to the horizontal meridian (Boyko and Goncharova, 1976). Tectal units respond with either on, off, or on-off responses to the presentation of visual stimuli (Robbins, 1972; Stein



and Gaither, 1983). Stimuli of different sizes show that tectal receptive fields in *Iguana* have an internal structure, including a suppressive surround region (Stein and Gaither, 1983). Units in the superficial layers, at least of turtles (Robbins, 1972; Granda and O'Shea, 1972) and *Alligator* (Heric and Kruger, 1966), are color sensitive. Spectral sensitivity curves in turtles vary in shape but usually peak between 600 and 700 μm . Spectral plots for on and off responses indicate antagonistic inputs from spectrally different receptor processes (Robbins, 1972). Tectal units in the superficial layers of *Pseudemys* lack spontaneous activity, whereas those in the stratum griseum periventriculare show high spontaneous rates of discharge (Robbins, 1972). Both directionally selective (Boyko and Goncharova, 1976; Robbins, 1972; Stein and Gaither, 1983) and velocity-selective (Stein and Gaither, 1983) units have been reported. These units tend to be a minority (10% to 33%) of units encountered. Some units will respond to stationary stimuli, but most units respond best to moving ones. Units in the superficial layers respond only to visual stimuli; units in the deeper layers may be multimodal and respond to somatosensory, infrared, or auditory stimuli as well as visual stimuli (Hartline et al., 1978; Stein and Gaither, 1981, 1983).

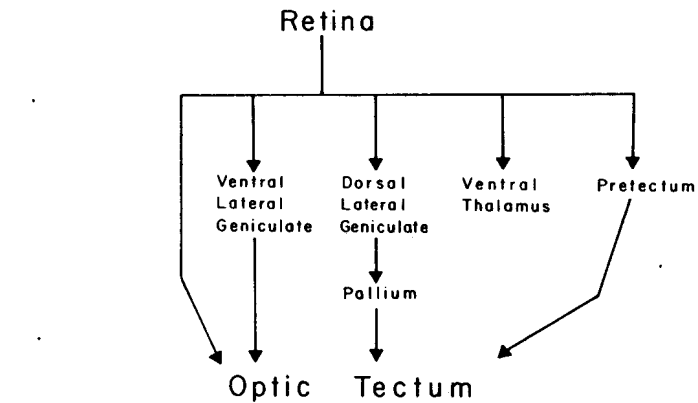
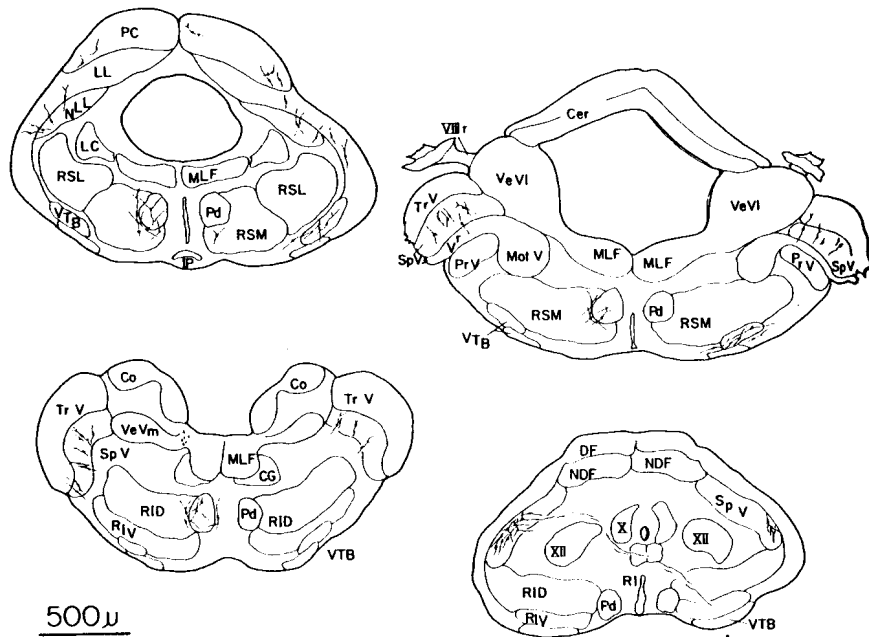


Fig. 4.41. Visual routes to the optic tectum. This diagram summarizes the major routes by which information from the retina can reach the optic tectum. Each route is discussed in detail in the text.

majority of retinal ganglion cell axons cross in the optic chiasm and reach the contralateral tectal lobe through the marginal optic tract, which divides into lateral and medial branches at the rostral pole of the tectal lobe. Some of the axons continue caudally over the tectal surface from the rostral pole, whereas others continue some distance in the two divisions of the marginal optic tract before turning into the tectum, where they terminate.

A minority of retinal ganglion cell axons continue uncrossed to the ipsilateral optic tectum. Evidence for ipsilateral retinotectal projections has been reported in some turtles, crocodylians, lizards, and snakes, but not in *Sphenodon*. The extent of ipsilateral projections is important in understanding the representation of the binocular visual field within the tectum, and we will return to this issue in Section V.B.3. However, it is worth noting here that the ipsilateral projection is fairly difficult to demonstrate with either degeneration or autoradiographic techniques, so that statements about the presence or absence of an ipsilateral projection in any given species should be regarded with caution.

Once the axons of retinal ganglion cells reach the tectum, they can run in the stratum zonale, stratum opticum, or in the stratum fibrosum et griseum superficiale. The stratum opticum contains distinct fascicles of rostrocaudally oriented axons; in transverse sections they appear as vertically elongate columns interposed between the dendritic bundles formed by radial cells. Electron microscopic observations of these fascicles show that they contain very few axon terminals. The overwhelming majority of terminals is present on axons after they have turned out of the fascicles.

2. SOURCES OF VISUAL INFORMATION

a. GENERAL Fig. 4.41 summarizes various routes by which visual information can reach the optic tectum. The most familiar involves direct projections from retinal ganglion cells to the optic tectum. However, there are several more complex routes involving one or more relays in other structures. Except for the cortical projection to the tectum, all other routes terminate in the superficial layers. Some of the routes involve topological representations of the retinal surface; others do not.

b. RETINAL AFFERENTS

The overall pattern of the retinotectal projection has been studied by degeneration or autoradiographic techniques in turtles (Kosareva, 1967; Knapp and Kang, 1968a, 1968b; Hall and Ebner, 1970a; Belkova and Kosareva, 1971; Bass and Northcutt, 1981a, 1981b), crocodylians (Burns and Goodman, 1967; Braford, 1973; Repérant, 1975), *Sphenodon* (Northcutt et al., 1974), snakes (Armstrong, 1951; Halpern and Frumin, 1973; Repérant, 1973; Repérant and Rio, 1976; Northcutt and Butler, 1974a), and lizards (Armstrong, 1950; Butler and Northcutt, 1971a; Butler, 1974; Northcutt and Butler, 1974b; Cruce and Cruce, 1975). The pattern is similar in all of the species studied. The

The overall distribution of retinal ganglion cell terminal boutons can be studied to a first approximation in Fink-Heimer preparations following retinal lesions or in autoradiographic preparations following intraocular injections of tritiated materials. Such experiments indicate that most of the retinal ganglion cells terminate in the superficial layers of the tectum. Fig. 4.42 is an example of an autoradiogram from the optic tectum of *Pseudemys* following an injection of tritiated proline in the contralateral eye and shows the general pattern of silver grains. Notice that silver grains occur densely over sublayers a and c of the stratum fibrosum et griseum superficiale. In the stratum opticum, regions devoid of grains are bundles of retinal axons. The band of low grain density in sublayer b of the stratum fibrosum et griseum superficiale is a consequence of the densely packed somata. Notice that the density of grains decreases markedly at the upper border of the stratum griseum centrale. This pattern is shown quantitatively in Fig. 4.43, which shows the density of silver grains as a function of tectal depth in a transect through the tectum of *Pseudemys*.

In addition to the retinal projection to the superficial layers, there may be minor retinal projections to the deeper tectal layers. Fig. 4.43, for example, shows grain counts that are above background over the stratum griseum periventriculare. There is some precedent for such projections; thus, Berson and McIlwain (1982) have confirmed direct projections from the Y class of retinal ganglion cells to the deep layers of the superior colliculus of cats. However, sparse projections are difficult to demonstrate convincingly with axonal tracing techniques. Fink-Heimer techniques generate artifact by undersuppression of normal fibers. Autoradiographic techniques can be confounded by the transsynaptic transport of labeled material. Thus, the existence of direct retinal projections to the deep layers requires confirmation with electron microscopy or HRP techniques.

It has been traditional to report that the retinal terminal field occupies three layers (layers 14, 12, and 10 of Pedro Ramón) in the superficial layers, which vary in thickness and density—both among species and between tectal areas within the same species. The most careful study is that of Peterson (1981) on the desert iguana, *Dipsosaurus dorsalis*. It utilizes both Fink-Heimer and autoradiographic techniques, with a range of survival times. The autoradiographic experiments show that the density of silver grains over layers 14, 12, and 10 varies for each of the five cytoarchitectonic areas of the tectum (see Section II.A), being quite high in the lateral wall, for example, but low in the dorsolateral area. The Fink-Heimer experiments are consistent with these results but add the additional information that the caliber of degenerating axons varies as a function of tectal locus.

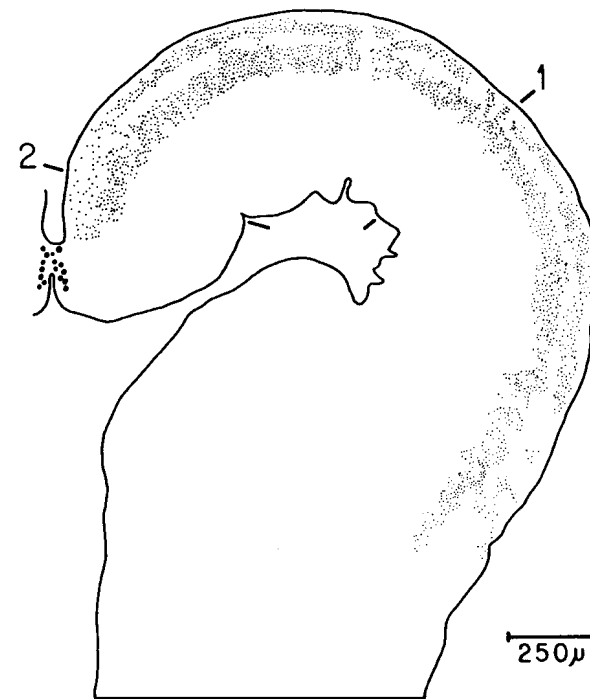


Fig. 4.42. *Pseudemys scripta*. Retinotectal projection. This is a charting made from an autoradiogram of the optic tectum contralateral to the intraocular injection of tritiated proline. The fine dots indicate the distribution of silver grains. The numbered lines indicate the transects used for the grain counts shown in Fig. 4.43.

These experiments give a good impression of the overall structure of the retinotectal projection but do not allow a direct visualization of the terminal arbors of the retinal ganglion cell axons themselves. It is possible to visualize ganglion cell axons in Golgi preparations, but it is often difficult to completely visualize individual terminals because the superficial tectal layers are usually heavily impregnated in Golgi preparations and obfuscate the relations of individual elements. This difficulty can be circumvented by using very small injections of HRP that will only fill small numbers of retinal ganglion cell axons. The labeled arbors can then be carefully studied.

Golgi or HRP preparations show that retinal arbors fall into two groups. The first are flat and form brush-shaped arbors that extend horizontally in the stratum fibrosum et griseum superficiale. These arbors have been described in Golgi preparations of *Pentodactylus schreiberii* (Quiroga, 1978). The second group of retinotectal arbors turn down into the tectum from axons running rostrocaudally in the

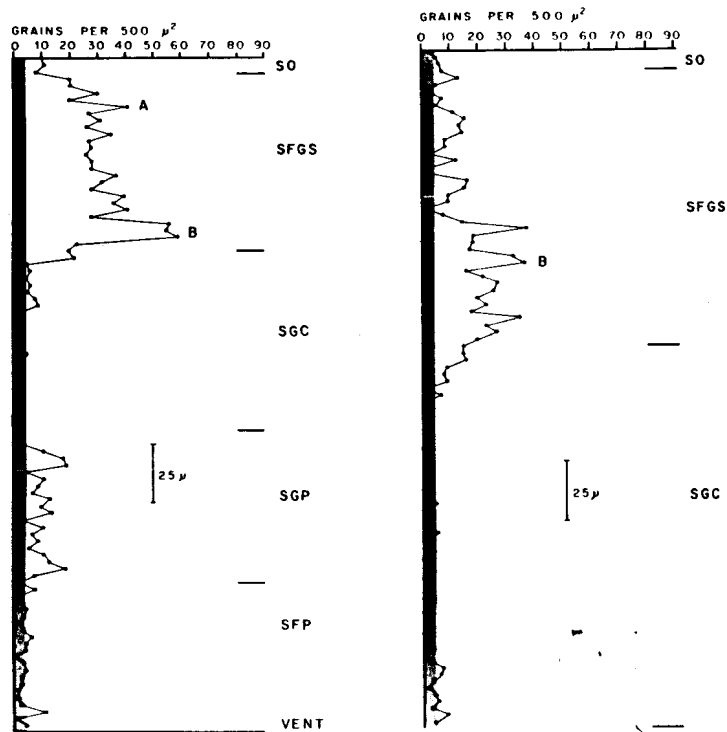


Fig. 4.43. *Pseudemys scripta*. Retinotectal projection. These are grain counts performed on the transects shown in Fig. 4.42. The graph on the left is for transect 1; the graph on the right is for transect 2.

stratum opticum (Fig. 4.44). These form vertically elongate masses of collaterals that bear many varicosities. They have been studied in HRP preparations of *Thamnophis sirtalis* (Dacey and Ulinski, 1986d). Almost all arbors originate from axons that turn down into the stratum fibrosum et griseum superficiale (Fig. 4.44). The parent axons typically branch into several, varicosity-laden collaterals that form a rectangular-shaped mass, about 65 by 65 by 100 μm , regardless of the locus of the terminal in the tectum. Most of the arbors are confined to either sublayer a or sublayer c of the stratum fibrosum et griseum superficiale, although there are a few bilaminar arbors. The arbors can be placed into three groups based on the diameter of their parent axons and the size of their varicosities. Type 1 arbors have parent axons with diameters of 3.0 to 3.5 μm and varicosities about 3.5 μm long (Fig. 4.45). Type 2 arbors have parent axons 1.5 to 2.5 μm in diameter and varicosities about 2.5 μm long (Fig. 4.46). Type 3 arbors have axons 0.5 to 1.0 μm in diameter and varicosities about 0.5 to 1.0 μm in diameter (Fig. 4.47). All tectal loci contain all three types of arbors, but their relative proportions may vary. The size spectrum histograms

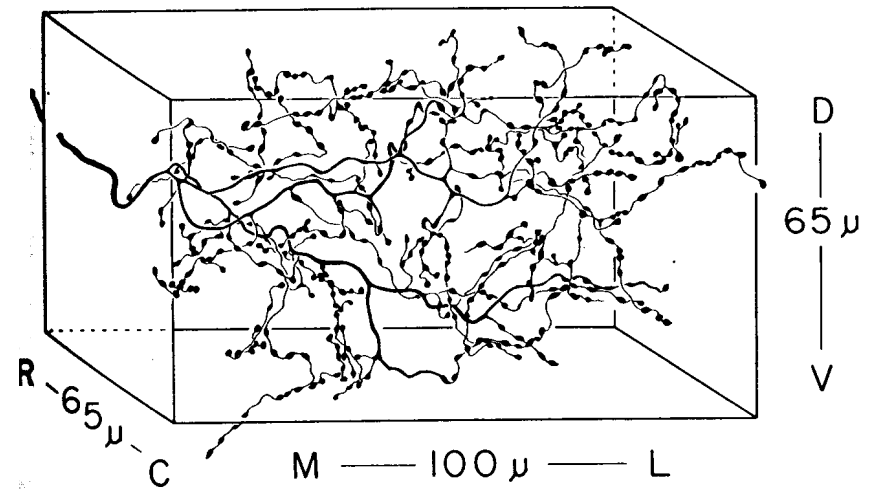


Fig. 4.44. *Thamnophis sirtalis*. Retinotectal terminal arbor. Rapid Golgi impregnation of an axon terminal that was restricted to sublayer a of the SFGS. The primary axon descends into the SFGSa from the overlying optic fiber layer (stratum opticum), splitting into several preterminal branches that in turn issue highly branched, beaded collaterals. The approximate dimensions of the terminal field are shown. Abbreviations: R-C, rostromedial; M-L, mediolateral; D-V, dorsoventral. (From Dacey and Ulinski, 1986d.)

of parent axons in the HRP-filled samples may be compared to the histogram of axon diameters taken from electron micrographs of the fiber fascicles in the stratum fibrosum et griseum superficiale (Dacey and Ulinski, 1986d; Repérant et al., 1981). Comparison suggests that the HRP sample is biased in favor of large-caliber terminals. However, the caliber of axons varies as a function of tectal locus, so it appears that the variations in axon caliber seen in degeneration experiments reflect differences in the relative proportions of the several types of arbors seen in different regions of the tectum.

It is likely that many retinal ganglion cell axons branch, sending one collateral to the tectum and a second to other targets such as the lateral geniculate complex. This makes it difficult to directly correlate the diameters of tectal axons in the tectum to those in the optic nerve. However, it seems probable that there is a general correlation, so that the largest-caliber tectal collaterals originate from the largest-caliber axons in the optic nerve and, therefore, from retinal ganglion cells with the largest somata. Data on the size spectra of axons in the optic tract are limited to observations on several species of turtles (Geri et al., 1982; Davydova et al., 1982). These studies report histograms with a distinct peak in the small-diameter range and either a second peak or a tail toward large diameters. These observations are consistent with measurements of conduction velocities of optic nerve axons in

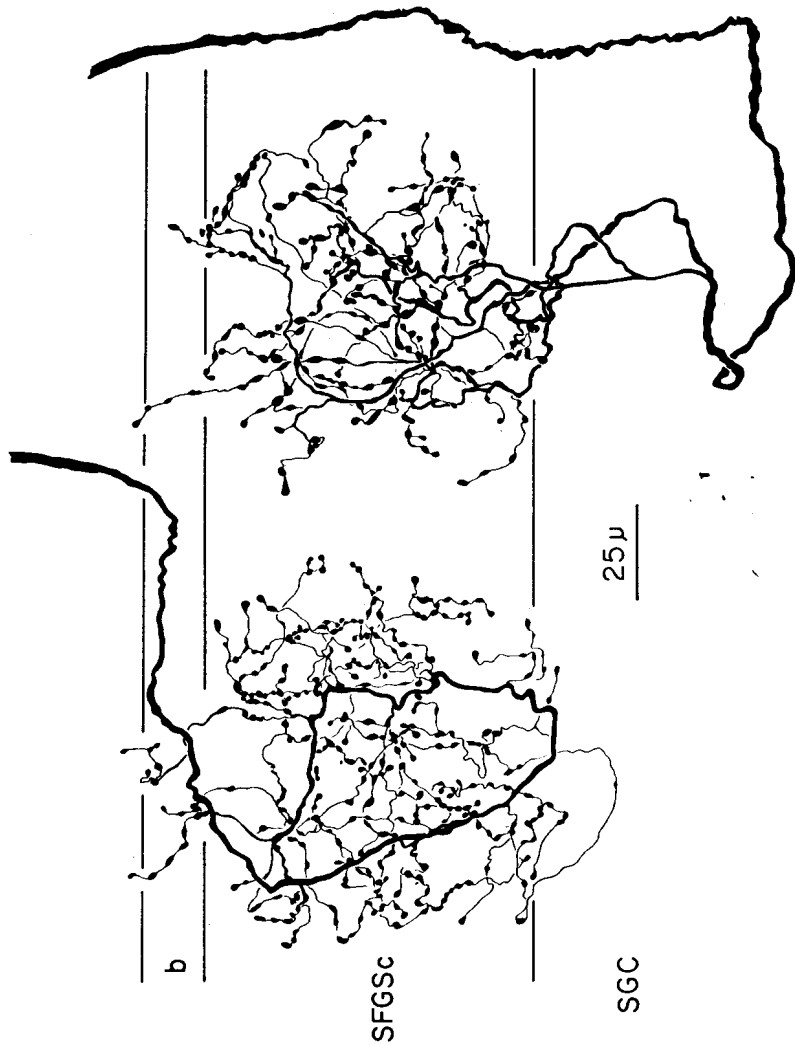


Fig. 4.45. *Thamnophis sirtalis*. Type 1 arbors. Two arbors restricted to the SFGSc are shown in the coronal plane. (From Dacey and Ullinski, 1986d.)

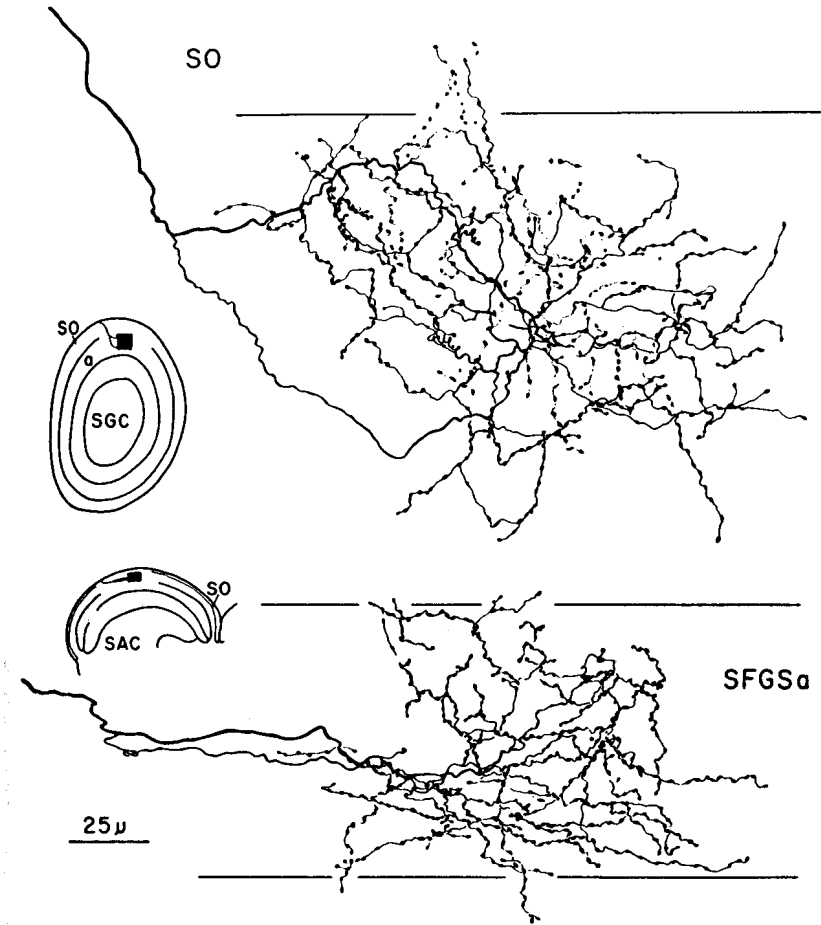


Fig. 4.46. *Thamnophis sirtalis*. Type 2 arbors. A horizontal and a coronal view of two terminals in SFGSa are compared. In the upper arbor, an elongation in the mediolateral axis can be seen. Axon diameter = 1.5 to 2.0 μm in all Type 2 arbors and most terminal boutons were 1.0 to 2.5 μm in diameter. As for the Type 1 arbors, the horizontal dimensions of all medium-caliber terminals = 100 to 110 μm in the mediolateral axis and 60 to 70 μm in the rostrocaudal axis. (From Dacey and Ullinski, 1986d.)

turtles (Davydova et al., 1982) that show the existence of at least two conduction velocity groups.

There are now abundant data from a number of mammalian species showing that conduction velocity groups within the optic nerve reflect the existence of morphologically and physiologically distinct classes of retinal ganglion cells (e.g., Rodieck, 1979; Lennie, 1980). Cells of each class have specific soma sizes, dendritic trees, physiological properties, and patterns of central terminations. There are fewer data on retinal ganglion cells in reptiles. Ramón y Cajal's drawings of

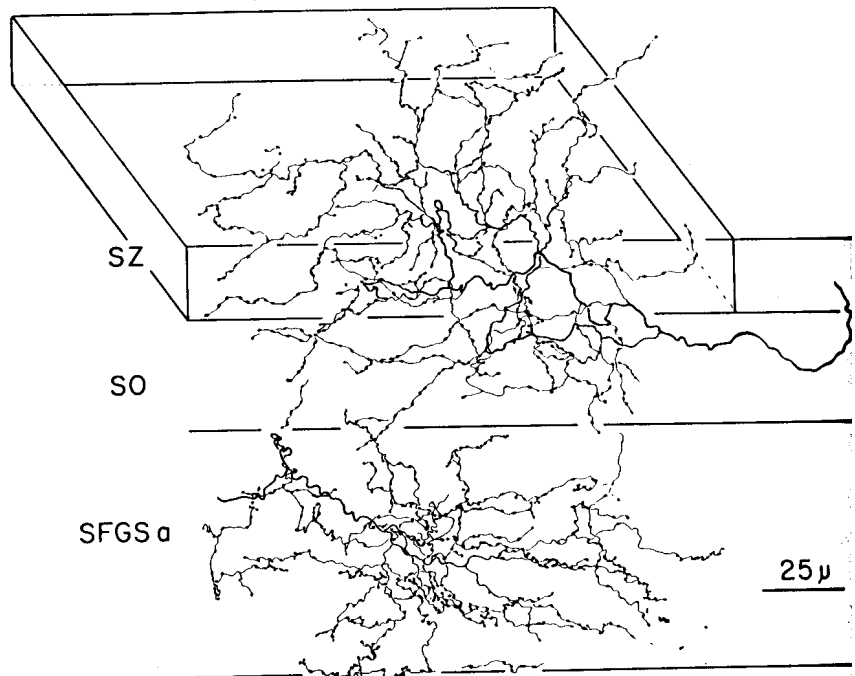


Fig. 4.47. *Thamnophis sirtalis*. Type 3 arbors. This figure shows an arbor with a small-diameter primary axon and small terminal boutons. The upper arbor is viewed in an oblique section. The part seen in the coronal plane extends ventrally into the stratum opticum (SO), and the part seen in the horizontal plane extends caudally in the stratum zonale (SZ). The lower arbor is restricted to the SFGS α and is viewed in the coronal plane; it has precisely the same rostrocaudal extension as the upper arbor. (From Dacey and Ulinski, 1986d.)

the retinal cells of the lizard *Lacerta* show several distinct types of ganglion cells. More recently, observations of ganglion cells in *Pseudemys scripta*, using both HRP-filled and Golgi-impregnated cells (Peterson, 1982; Kolb, 1982), show several morphologically distinct types of cells. At least two groups of ganglion cells can be recognized by physiological criteria (Marchiafava and Weiler, 1980; Marchiafava and Wagner, 1981). Filling of physiologically categorized cells with procion yellow shows that the Type A and Type B ganglion cells are morphologically distinct and have different conduction velocities.

The distribution of ganglion cells in *Pseudemys* (Peterson and Ulinski, 1979, 1982) has been studied with retinal whole mount preparations (Stone, 1981). Ganglion cells are inhomogeneously distributed; they occur in high densities along the visual streak that is aligned along the nasotemporal axis of the retina. The distribution of cell sizes varies in an orderly fashion; cells with small somata are predominant

in the visual streak and a particularly large population of cells lies in the temporal-ventral retina. Comparisons to Marchiafava's results suggest that the visual streak consists largely of Type B cells, with Type A cells being spread more evenly over the retinal surface.

Tectal HRP injections have been used to establish the sizes of retinal ganglion cells that project to the tectum (Peterson, 1978a). Comparison of the cell size histograms of labeled and unlabeled ganglion cells indicates that ganglion cells of all sizes project to the tectum and that most cells within each size class project to the tectum. This, of course, does not eliminate the possibility that collaterals of these cells also project to the other targets.

The overall hypothesis, then, is that the nature of the retinotectal terminal zone in the superficial layers reflects retinal organization (Peterson, 1981). Retinal regions containing predominantly ganglion cells with small somata and axons project to tectal regions containing predominantly ganglion cell preterminal axons with small diameters. Conversely, retinal regions containing significant populations of large ganglion cells project to tectal regions of arbors with large diameter. The significance of these differences is presumably that the different regions of the tectum will receive functionally distinct types of information about the visual world.

The nature of the tectal elements that are postsynaptic to retinal arbors has been examined in turtles using electron microscopic preparations following retinal lesions (Davydova and Smirnov, 1973; Davyova et al., 1982) and with somewhat less certainty in normal electron microscopic preparations of the snake *Vipera aspis* (Repérant et al., 1981). Retinal terminals contact predominantly small dendritic profiles. Some of the profiles postsynaptic to retinal terminals contain synaptic vesicles. Some workers have regarded these as axoaxonic synapses, but it is likely that at least some of the vesicle-containing profiles represent presynaptic dendrites. This would be consistent with the presence of varicosities on the dendrites in the superficial layers of several classes of tectal neurons. The studies completed to date do not tell which classes of tectal neurons are postsynaptic to retinal terminals or whether the different types of ganglion cells preferentially contact different classes of neurons. It is now possible to approach these questions by using electron microscopy to examine identified neurons in Golgi or HRP material. However, no such time-consuming studies have yet been undertaken in reptiles.

C. AFFERENTS FROM THE VENTRAL LATERAL GENICULATE NUCLEUS

A second route whereby visual information can reach the optic tectum involves the ventral lateral geniculate nucleus. This is a plate-shaped structure that makes up the caudal part of the geniculate com-

plex. A geniculate occurs in all orders of reptiles and universally comprises a medial cell plate and a lateral neuropil (turtles: Bass and Northcutt, 1981a; snakes: Repérant, 1973; Halpern and Frumin, 1973; lizards: Cruce, 1974; Butler and Northcutt, 1973; crocodylians: Huber and Crosby, 1926).

The geniculotectal projections have been studied only in *Thamnophis*. Neurons in both the neuropil and the cell plate project to the tectum. Fig. 4.48 shows a neuropil cell that was filled by a small injection of HRP in the geniculate. The injection damaged the dendrites and demonstrates the complete morphology. These neurons have spherical somata 12 to 15 μm in diameter and dendritic arbors restricted to the retinorecipient part of the neuropil. The axon arises from the soma, gives off a single collateral in the neuropil, and then proceeds dorsocaudally in the tectogeniculate pathway. Collaterals with restricted arbors terminate en route in the nucleus lentiformis mesencephali of the pretectum. The axon continues in the stratum album centrale and ascends into sublamina a of the stratum fibrosum et griseum superficiale. It ends in a single, sparsely branched arbor with terminal boutons distributed into small clusters separated by bouton-free gaps. The overall spread of the arbor is about 200 to 250 μm in both the horizontal and sagittal planes.

Fig. 4.49 shows a cell plate neuron filled by an injection that impinged on the cell plate. Such neurons have narrow, fusiform dendritic fields that are oriented radial to the optic tract and have a diameter of about 75 μm . The axon (arrow) arises from a primary dendrite and passes dorsocaudally in the tectogeniculate path. Arbors attributable to cell plate neurons are characterized by a single cluster of boutons lying at the border of the superficial and central gray layers (Fig. 4.50). Some arbors occupy a horizontal area as small as 25 μm , whereas others form flattened sheets of boutons that measure 75 to 100 μm by 60 to 80 μm .

These experiments indicate that the ventral lateral geniculate is actually involved in two parallel paths to the optic tectum. The paths involve different populations of geniculate neurons and terminate in different sublayers of the tectum.

d. AFFERENTS FROM THE PALLIUM

A potential third route for transmission of visual information to the optic tectum involves the dorsal lateral geniculate nucleus. The dorsal lateral geniculate complex receives direct retinal projections and projects to the telencephalon. Evidence for this pathway has been assembled for lizards (Bruce, 1982) and turtles (Hall and Ebner, 1970b). Projections from the regions of the telencephalon that receive projec-

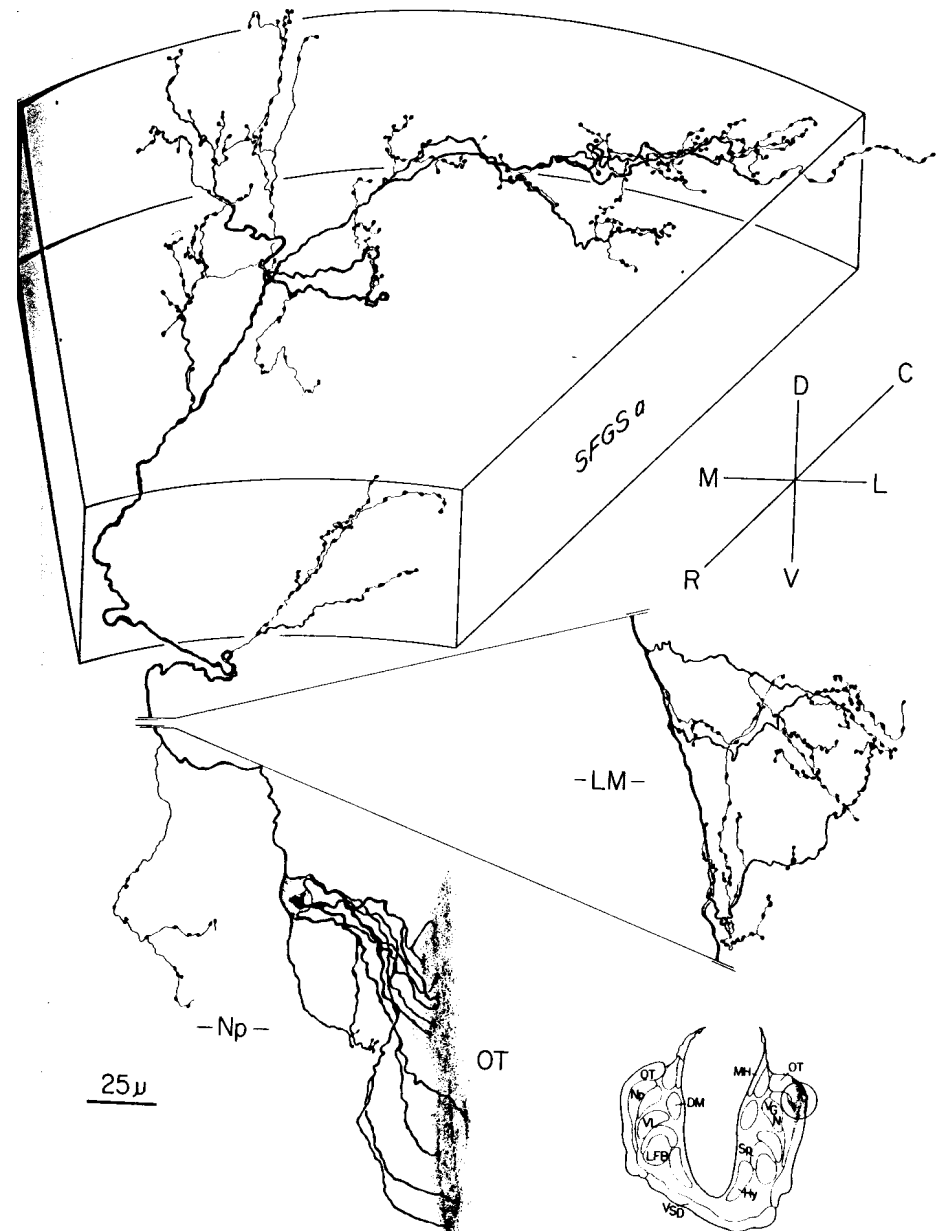


Fig. 4.48. *Thamnophis sirtalis*. Geniculate neuropil cell. Injections of HRP into the optic tract at the level of the ventral geniculate nucleus (circled area in the inset at the lower right) anterogradely filled the axon of this cell. It was traced through nine 80- μm serial sections to its terminus in the tectum. Terminal collaterals arise in the VGN neuropil (np), the lentiform mesencephalic nucleus (LM), and sublamina a of the stratum fibrosum et griseum superficiale (SFGSa). (From Dacey and Ulinski, 1986e.)

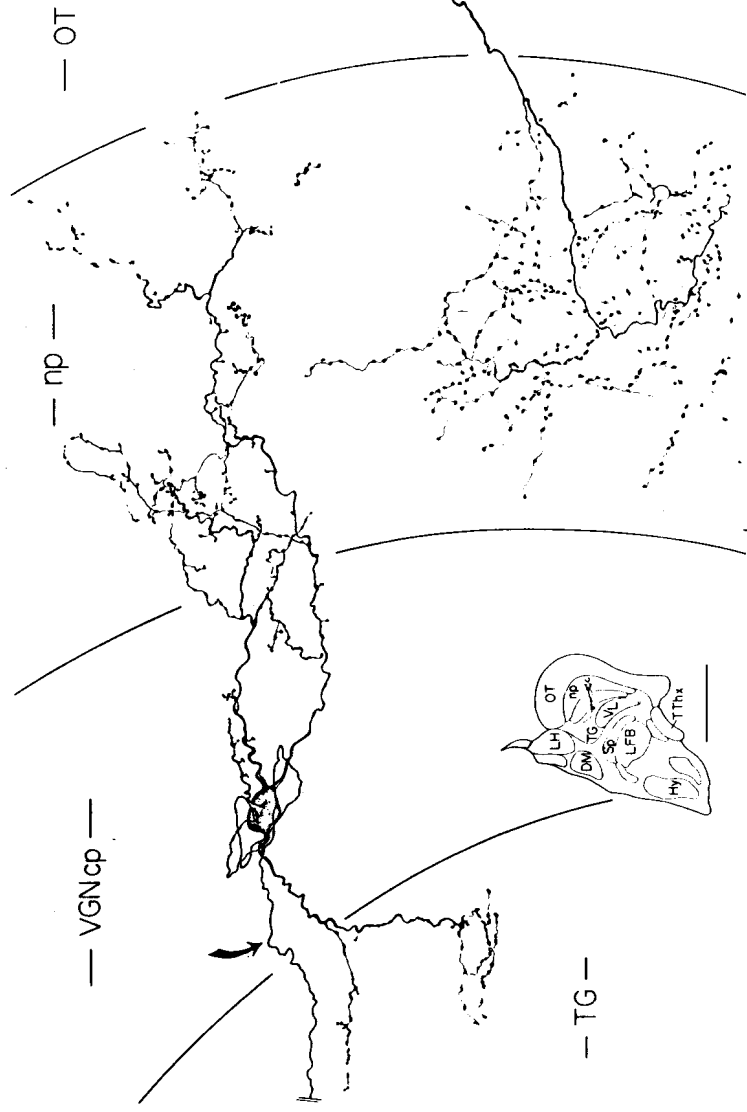


Fig. 4.49. *Thamnophis sirtalis*. Geniculate cell plate neuron. A neuron of the ventral lateral geniculate cell plate retrogradely filled from injections of HRP into the tectum. Laterally directed dendrites occupy a narrow, cylindrical space, approximately 75 μ m in diameter in the retinorecipient neuropil. Medially directed dendrites have similarly sized arborizations in the tectorecipient zone. An anterogradely filled optic tract axon and its collateral terminal arbor in the geniculate neuropil is also shown. The diameter of the dimensions of the arbor are closely matched to the dendritic field size of the geniculate cell. (From Dacey and Ulinaki, 1986e.)

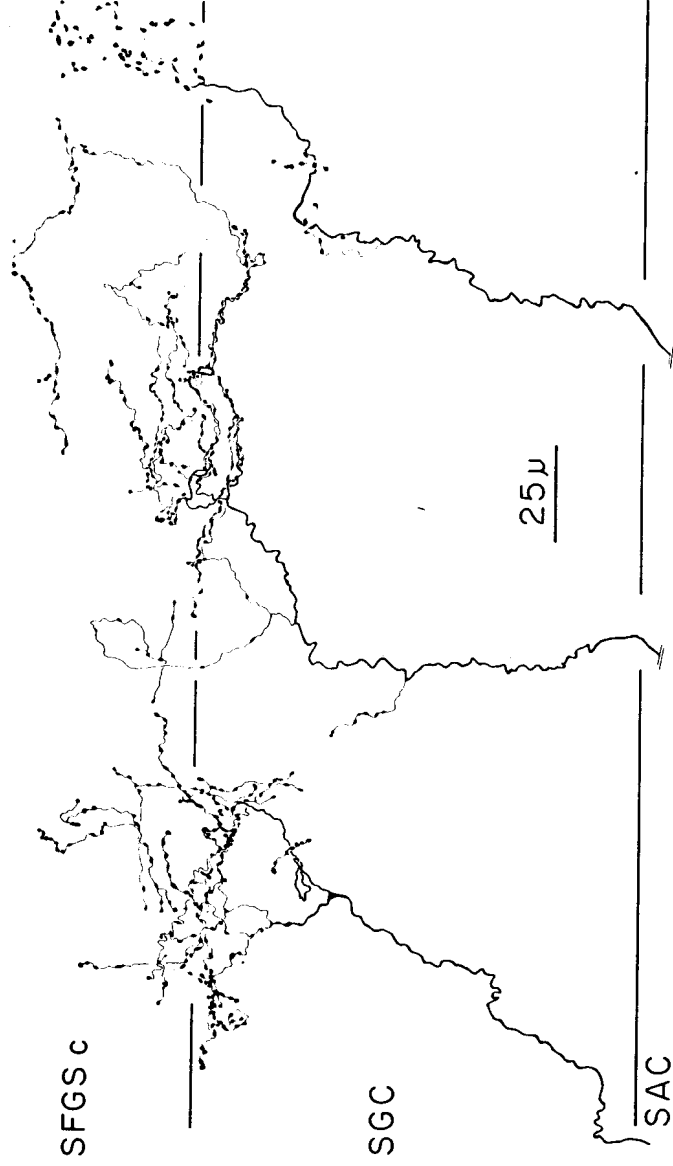


Fig. 4.50. *Thamnophis sirtalis*. Thalamic arbors. Putative terminal arbors of ventral geniculate cell plate neurons. The parent axon ascends through the central layers of the tectum and arborizes as a single cluster of terminal boutons at the border of the stratum griseum centrale (SGC) and the stratum fibrosum et griseum superficiale (SFGS). (From Dacey and Ulinaki, 1986e.)

tions from the dorsal lateral geniculate to the deep layers of the tectum have been reported in *Pseudemys*, but nothing is known of the organization of this projection. Another corticotectal projection has been reported in the lizard *Agama agama* (Elprana et al., 1980), but the projection originates from a region of cortex that probably does not receive visual input from the thalamus. It thus remains to be determined how widespread corticotectal projections are in reptiles and what might be their organization. Projections from the visual Wulst to the optic tectum have been well established by both anatomical and electrophysiological techniques for several species of birds (see Bagnoli and Burkhalter, 1983).

e. AFFERENTS FROM THE PRETECTUM

Visual information can also reach the optic tectum through the pretectum. This is a complex of nuclei that lies between the rostral pole of the tectum and the diencephalon. No uniform nomenclature has been established, but posterodorsal, mesencephalic lentiform, geniculate pretectal, and pretectal nuclei are usually recognized (e.g., Curwen and Miller, 1939; Cruce, 1974; Butler and Northcutt, 1973; Repérant, 1973). Each of these receives direct and generally bilateral projections from the retina.

The organization of the projection from the pretectum to the tectum has been studied in *Thamnophis* (Dacey and Ulinski, 1986a). Tectal HRP injections indicate that the pretectal, geniculate pretectal, and mesencephalic lentiform nuclei project to the tectum. The mesencephalic lentiform and pretectal nuclei in this species together contain a single, topographically organized projection from both the retina and the tectum (Dacey and Ulinski, 1986d). Soma sizes vary, but neurons in both nuclei issue stout dendrites that branch dichotomously and extend widely within the nuclear complex (Fig. 4.51). The axon arises from a dendrite close to the soma and courses to the contralateral tectum through the posterior commissure. The axon gives rise to a series of terminal branches as it passes caudally. Each branch is heavily studded with boutons and travels parallel to the tectal surface. Such terminal branches often give rise to small, tertiary branchlets that extend dorsoventrally within the stratum fibrosum et griseum superficiale (Fig. 4.52). The projection from a single axon therefore has collaterals that can terminate densely within wide areas of the tectum. Thus, in spite of a topography in the retinopretectal projection, the extensive size of pretectal dendritic fields and the widespread distribution of pretectal axons within the tectum make it unlikely that the retinopretectal-tectal path is carrying topographic information about retinal position.

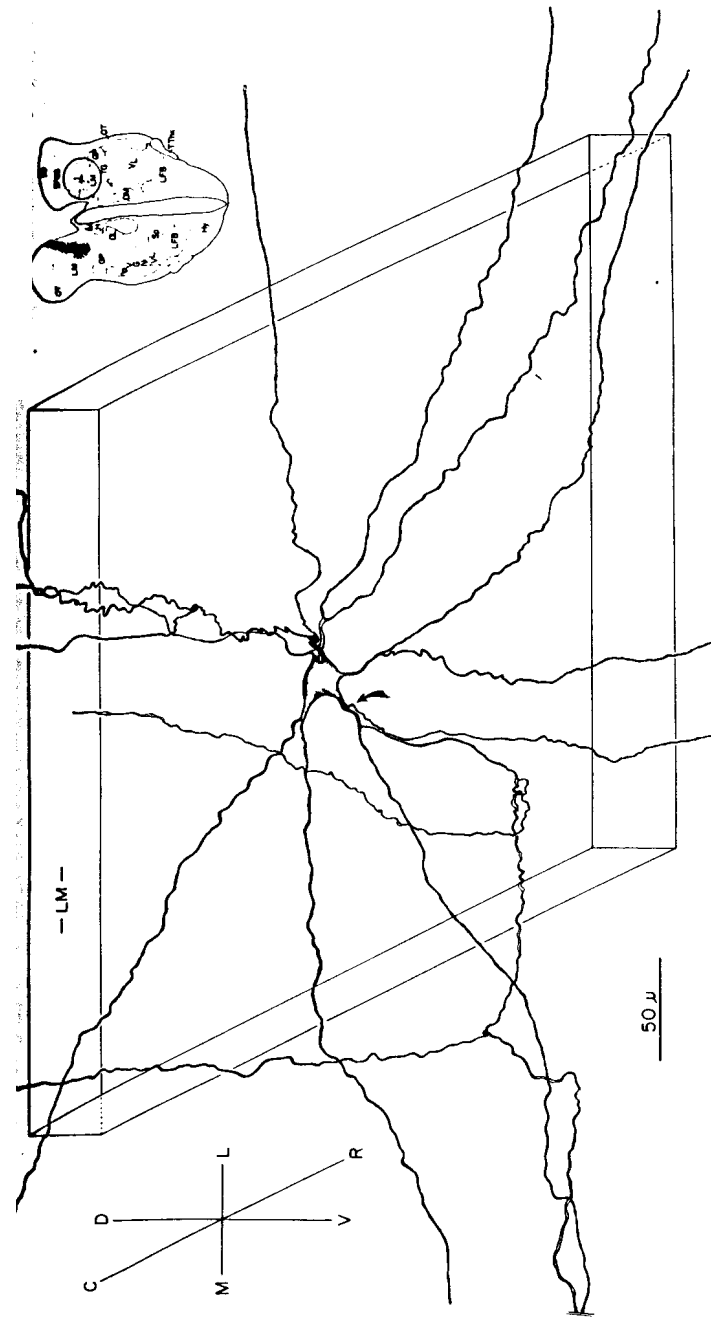


Fig. 4.51. *Thamnophis sirtalis*. Lentiform mesencephalic cell. These cells have long, unbranched dendrites. They are smooth and radiate for at least 250 μm from the soma and tend to be flattened in the horizontal plane. The axon (arrow) gives off primary collaterals that ascend into the superficial gray. The parent axon crossed 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 tectum (circled area). (From Dacey and Ulinski, 1986e.)

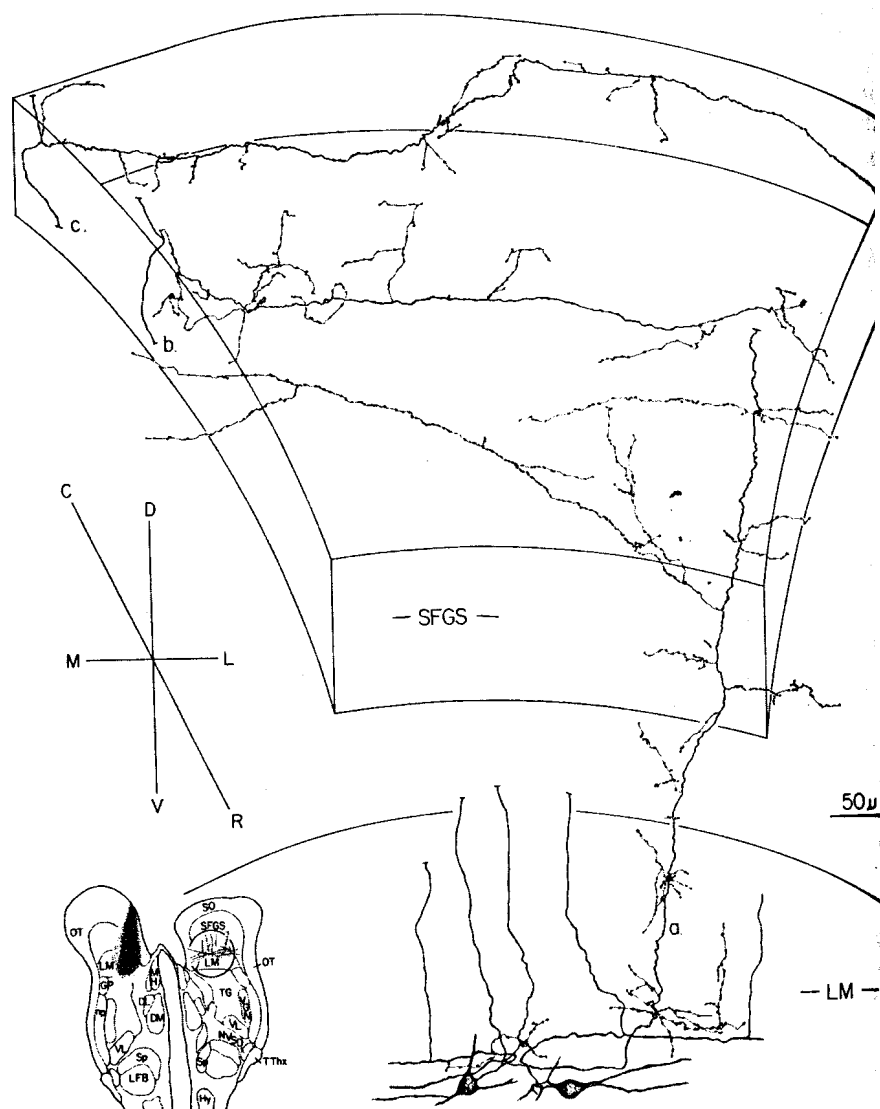


Fig. 4.52. *Thamnophis sirtalis*. Lentiform mesencephalic axons. Anterogradely filled tectal afferent terminals arising from cells of the lentiform mesencephalic nucleus (LM) after injections of HRP into the contralateral pretectal region. Primary collaterals that ascend into the tectum (a, b, and c) were traced for up to 600 μm rostrocaudally within the superficial gray. Collaterals give rise to terminal branches that course parallel to the tectal surface. These branches give rise to short branchlets that extend dorsoventrally within the superficial gray. The inset at the lower left indicates the injection site (stippling) and the position of the labelled cells (circled area). C-R, caudal-rostro; M-L, medial-lateral; D-V, dorsal-ventral. (From Dacey and Ulinski, 1986e.)

3. BINOCULAR VISUAL REPRESENTATION

a. GENERAL The discussion has so far considered the routes whereby visual information reaches the optic tectum without regard to the laterality of the projections. However, the issue of laterality is functionally important because certain parts of the visual world are seen by both eyes. It is generally agreed that binocular cues are an important (although not essential) source of information about the distance of objects in the visual world. Most discussions of the binocular visual field in reptiles have been dominated by considerations of the binocular field of humans, which lies principally in front of the individual. Walls (1942), for example, provides measurements of the frontal visual fields that range from 10° to 40° of binocular overlap for several species of reptiles. The general idea has been that the binocular field is relatively restricted in nonmammalian vertebrates and increases as one proceeds up the "phylogenetic scale" to primates. However, it is now clear that many nonmammals have extensive binocular fields that include visual space both above and behind the animal. This point has been demonstrated most clearly for ranid frogs (Grobstein et al., 1983), using both behavioral and electrophysiological mapping techniques to measure the binocular visual field. Many species, such as some arboreal snakes, have extensive frontal binocular fields, but most reptiles probably have significant binocular fields above their heads and behind their bodies.

The rest of this section considers the nature of binocular interactions in the optic tectum. However, two points should be made before becoming embroiled in details. The first is that binocular interactions are not necessary for depth perception. Chameleons (*Chamaeleo jacksoni*), for example, use accommodative cues to make depth discriminations used in catching insects with their prehensile tongues (Harkness, 1977; Collett and Harkness, 1982). The second point is that binocular integration does not necessarily involve the tectum. In birds, both the tectum and visual thalamus seem to receive information only from the contralateral eye, and binocular integration occurs at the telencephalic level, mediated by bilateral thalamotelencephalic projections (Karten et al., 1973; Miceli et al., 1975; Bagnoli and Burkhalter, 1983). Thus the degree of binocular interaction in the tectum is not necessarily a measure of an animal's ability to make depth discriminations.

b. RETINAL AFFERENTS

All reptiles have contralateral retinotectal projections (see Section V.B.3). The extent to which ipsilateral retinotectal projections are also present is not entirely certain for technical reasons. However, ipsilateral projections to the tectum from those parts of the two retinas that

see the binocular field would be expected a priori. Thus, ipsilateral projections to the rostral medial pole of the tectum (which receives information from the frontal binocular field), to the medial rim of the tectum (dorsal binocular field), and to the caudal pole of the tectum (caudal binocular field) would be expected. Autoradiographic tracing techniques have been used to examine retinotectal projections in the painted turtle, *Chrysemys picta* (Bass and Northcutt, 1981a). Silver grains were distributed in the ipsilateral tectum around the lateral and medial rims of the ipsilateral tectum. The projections to the medial edge of the tectum correspond to the tectal representation of the dorsal and caudal binocular fields. The projection to the lateral edge of the tectum is surprising at first glance because it would bring together information from disjunct points in visual space. However, examination of the retinotectal projection using both Fink-Heimer and the orthograde transport of HRP (Ulinski, unpublished observations) indicates that the fibers running around the lateral edge of the tectum are en route to the caudal pole of the ipsilateral tectum and represent fibers derived from the nasal retina, which sees the caudal binocular field.

c. NUCLEUS ISTHMI

In addition to bilateral retinal projections to the tectum, several brainstem projections potentially involve the tectum in binocular integration. The first of these is nucleus isthmi, which receives afferents from the ipsilateral tectum and projects bilaterally back to the tectum. The contralateral isthmotectal projections thus form a route whereby information from one tectal lobe reaches its opposite member. Comparable structures occur in frogs (Gruberg and Udin, 1978; Gruberg and Lettvin, 1980; Wang et al., 1981; Grobstein et al., 1978), birds (Hunt et al., 1977), and mammals (Sherk, 1979).

Projections from nucleus isthmi to the tectum have been demonstrated in turtles (Foster and Hall, 1975; Sereno, 1983), lizards (Foster and Hall, 1975), and snakes; details of the isthmotectal system have been investigated in *Thamnophis* (Dacey and Ulinski, 1986d) and *Pseudemys* (Sereno and Ulinski, 1987). Small injections of HRP into the tectum disclose topographically organized tectoisthmic and isthmotectal projections. A small patch of anterogradely labeled boutons lies in nucleus isthmi; here it precisely overlaps several retrogradely labeled isthmotectal neurons. The size and position of the label in isthmi varies with the size and position of the tectal injection site, but the details of the maps have not been determined. Isthmotectal neurons have small spherical or slightly larger fusiform somata (Fig. 4.53).

In *Thamnophis*, axons from ipsilaterally projecting neurons arise from a soma or primary dendrite and exit the nucleus dorsally to run

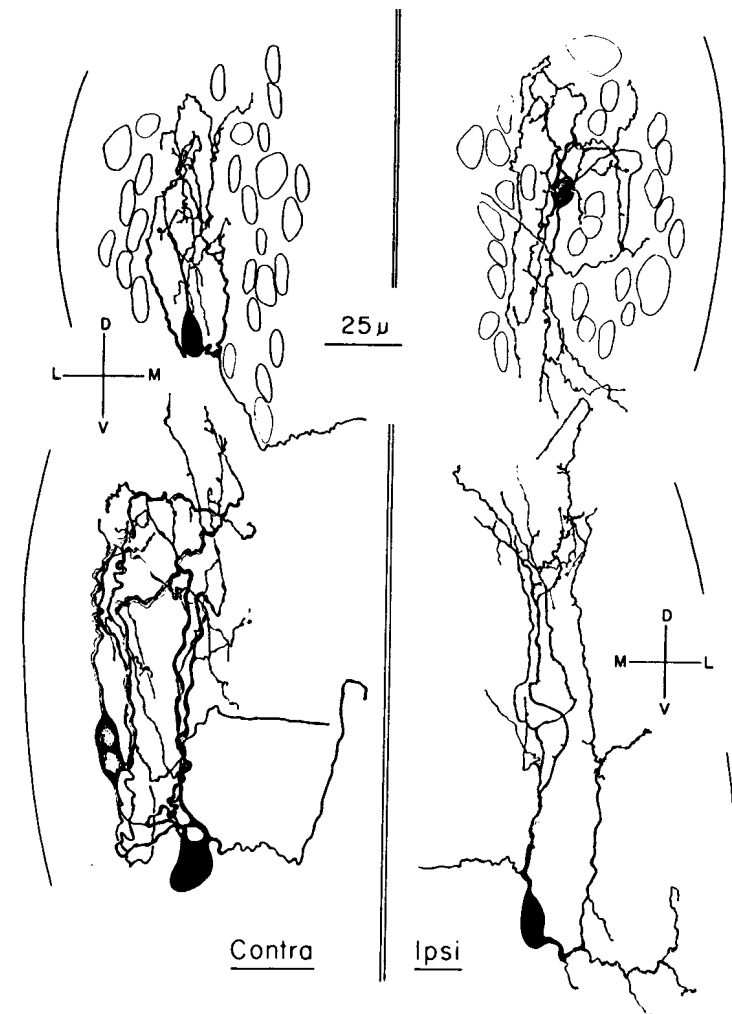


Fig. 4.53. *Thamnophis sirtalis*. Isthmotectal neurons. These cells were retrogradely filled from injections of HRP into the tectum. Neurons both contralateral and ipsilateral to the injection site range from small stellate to larger fusiform types. The dendrites of isthmotectal cells often recurve to form small, spherical dendritic nests around the soma. The axons are indicated by the arrows. The somata of a few counterstained isthmi neurons are included in the top tracings. The curved lines indicate the lateral margin of the brainstem. M-L, medial-lateral; D-V, dorsal-ventral. (From Dacey and Ulinski, 1986e.)

into the stratum album centrale without branching (Fig. 4.54). The axons then ascend through the central and superficial gray and arborize heavily in the stratum zonale and stratum opticum. There is some variation in the morphology of the isthmotectal arbors. Some form conical clusters of terminals that reach the pial surface and spread to

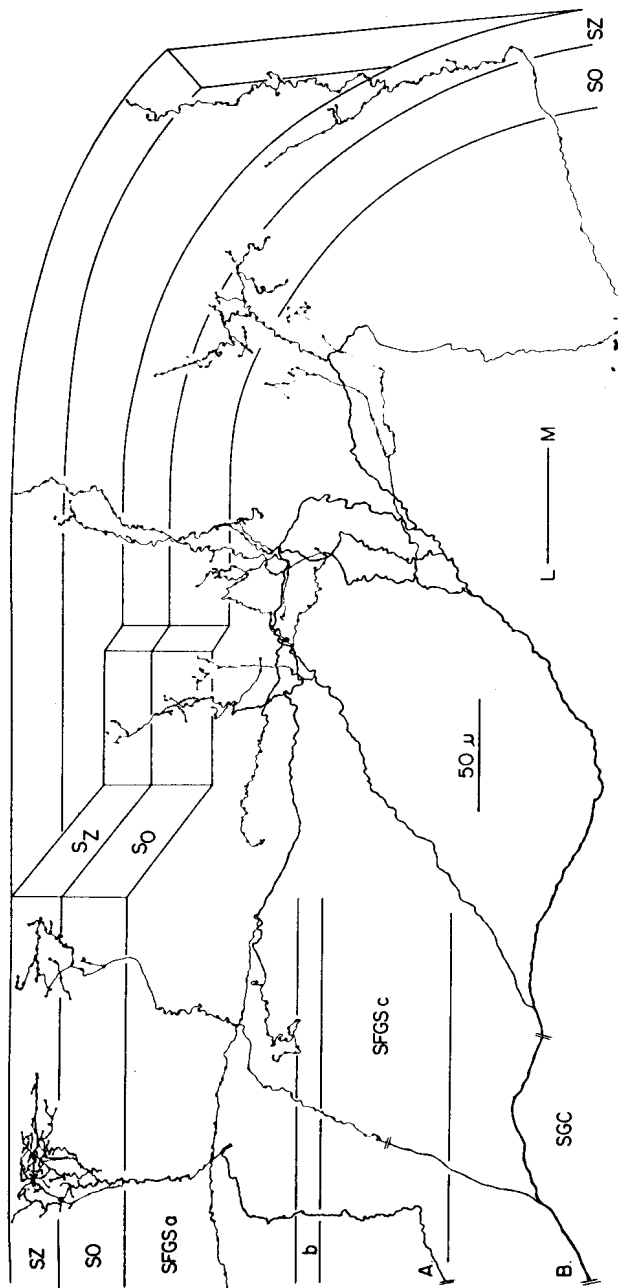


Fig. 4.54. *Thamnophis sirtalis*. Isthmotectal neurons. Tectal afferent axons anterogradely filled after injections of HRP into nucleus isthmi. These fine-caliber axons ascend through the superficial gray and arborize heavily in the stratum opticum (SO) and stratum zonale (SZ). One type of axon (A) forms a single arbor with a maximum diameter of 75 μm . Another type (B) arises from a slightly larger diameter axon that gives rise to multiple, thin collaterals. Terminal arbors issued from these collaterals are patchily distributed over a large area. (From Dacey and Ulinski, 1986e.)

a maximum diameter of 75 μm . Others ascend from the stratum album centrale and travel within the stratum griseum centrale, giving rise to a series of widely spaced, fine-caliber collaterals that eventually ascend to the pial surface, bearing boutons that arborize most heavily in the stratum zonale. The clusters of boutons on different collaterals of single axons are separated by gaps ranging from 20 to 100 μm . The total spread of the terminal field can extend over 500 μm in the mediolateral axis and 250 μm in the rostrocaudal axis. Axons of crossed isthmotectal neurons turn ventrally, join the ventral supraoptic decussation, and ascend dorsocaudally on the surface of the diencephalon just below the optic tract. The axons form a small bundle at the ventrolateral margin of the stratum opticum and course into the superficial layers of the tectum. They are of fine caliber and travel within these layers lateral to medial, parallel to the tectal surface (Fig. 4.55). The axons ascend into the stratum zonale in the interfascicular spaces present in the stratum opticum. They then give off tangentially oriented collaterals of fine caliber that form intertwined clusters of boutons, shaped like small cylinders, about 10 to 20 μm in length and 2 to 3 μm in diameter. The overall size of the arbors ranges from 70 to 100 μm in the mediolateral axis and from 40 to 80 μm in the rostrocaudal axis. Terminals from both the ipsilateral and contralateral nucleus isthmi thus converge in the superficial tectal layers and particularly in the stratum zonale. The topography of the projections has not been examined in reptiles; however, it seems likely that the contralateral isthmotectal projection will supplement the representation of the binocular visual field upon a given tectal lobe with information about corresponding points in the visual world as seen by the ipsilateral retina. It is noteworthy that the terminals of both the ipsi- and contralateral isthmotectal arbors overlap the dendrites of the tectoisthmi cells, which arborize in the stratum zonale.

In *Pseudemys*, nucleus isthmi is a complex of structures (Sereno and Ulinski, 1987). One component of the complex participates in reciprocal, topographically organized projections with the contralateral tectum, as is usually described in a wide range of vertebrates. However, a pair of components participates in connections with the ipsilateral tectum. The caudal nucleus isthmi contains neurons with flattened, bipolar dendritic fields that span only a few percent of the isthmi cell plate. These neurons project topographically to the ipsilateral tectum. The rostral nucleus isthmi contains neurons with large, sparsely branched dendritic fields. These neurons project nontopographically to the tectum by axonal arbors that cover large expanses of the tectum. The rostral nucleus, in turn, receives nontopographically organized projections from the tectum. Conjectures about the functional significance of the components of the nucleus isthmi complex are offered by Sereno and Ulinski (1987).

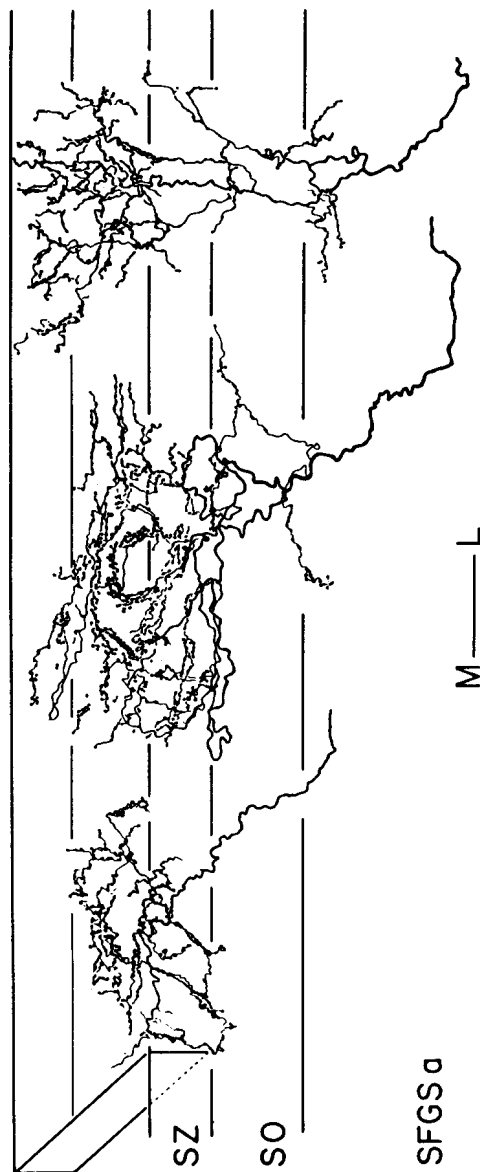


Fig. 4.55. *Thamnophis sirtalis*. Isthmotectal arbors. Tectal afferent axons anterogradely filled after injections of HRP into the ventral supraoptic decussation. These axons are believed to form the crossed isthmotectal projection. Single parent axons ascend through the superficial gray and form a single dense terminal arbor within the stratum zonale (SZ). The dimensions of these arbors in the horizontal plane range from 70 to 100 μm in the mediolateral axis and 10 to 80 μm in the rostrocaudal axis. (From Dacey and Ulinski, 1986e.)

d. PRETECTUM

The pretectum is also a possible route for binocular integration because it projects bilaterally to the tectum. The morphology of the pretectotectal axons in *Thamnophis* has been discussed in Section III.E. In contrast to the isthmotectal projections, pretectal projections to the tectum appear to be nontopologically organized and may therefore serve some function other than the integration of information from homotypic points in the two visual fields.

e. COMMISSURAL PROJECTIONS

The two tectal lobes are interconnected by a commissure running in the rostral face of the tectum. Several classic descriptions of tectal anatomy (e.g., Huber and Crosby, 1933) and studies of tectal efferents using degeneration techniques (e.g., Ulinski, 1977; Schroeder, 1981b) describe commissural connections that interconnect the two tectal lobes through the tectal commissure. Such projections could serve as a substrate for binocular interactions; however, these observations are ambiguous because of the potential difficulty posed by axons that originate from outside of the tectum and pass through the tectal commissure to the contralateral tectum. Orthograde tracing studies of reticular-tectal projections with HRP indicate that there are probably several axon systems that follow this trajectory (see Section V.E). Autoradiographic tracing techniques would presumably circumvent this fibers of passage problem, but there is no clear evidence at this time that reptiles have commissural connections. However, commissural interactions occur between the frontal binocular field representations in the superior colliculus of cats (Edwards, 1977).

C. Somatosensory Afferents

1. SOMATOSENSORY REPRESENTATIONS Two types of somatosensory information are represented in the optic tectum. The first is information derived from mechanoreceptors in the head or postcranial body surface (see von Düring and Miller [1979] for a summary of the mechanoreceptors of reptiles). Tectal responses to somatosensory stimuli have been recorded from the deeper tectal layers in turtles (Robbins, 1972), lizards (Stein and Gaither, 1981, 1983), and snakes (Hartline et al., 1978), but the only detailed studies are mapping studies in the iguana, *Iguana iguana* (Stein and Gaither, 1981, 1983). Units in the optic tectum will be activated by innocuous stimulation of the contralateral of the head or body. Units that respond only to tactile stimulation lie below layer 5 of Pedro Ramón, whereas units that respond to both tactile and visual stimuli occur in layers 5 to 7. Somatic units habituate rapidly and have definable receptive fields that vary systematically in size. The somatic representation is topographically

organized and in register with the overlying visual representation. For instance, the representation of the face is in register with the representation of the central and nasal visual field. Consistent with the orientation of the representations, somatic magnification factors vary, and the face representation occupies approximately 40% of the tectal surface.

Infrared thermosensitive units provide a second type of sensory information that can be represented in the optic tectum. Such units occur on the face and jaws of boid and crotaline snakes, either in specialized pit organs or in labial scales (Barrett, 1970). Because only these two phylogenetically separate lineages of snakes show infrared reception, it is generally assumed that this sensory modality has evolved independently. Details of the infrared system are discussed by Molenaar in Chapter 5 of this volume. It is sufficient for present purposes to note only that the infrared representation resembles general somatosensory information in being restricted to the intermediate and deep layers, being topographically organized, and being in register with the overlying visual representation (Hartline et al., 1978).

2. SOURCES OF SOMATOSENSORY INFORMATION

a. GENERAL Somatosensory information can reach the optic tectum through the spinal cord, trigeminal nuclei, and thalamus.

b. SPINAL AFFERENTS

Spinotectal projections have been described in the red-eared turtle *Pseudemys scripta* (Ebbesson, 1969), several pleurodiran turtles (Pedersen, 1973), the lizard, *Tupinambis* (Ebbesson, 1967), the boa constrictor, *Boa constrictor* (Ebbesson, 1969), and the caiman, *Caiman* (Ebbesson and Goodman, 1981) using Fink-Heimer techniques following spinal hemisections. These studies all indicate that spinal afferents terminate in a small region of the caudomedial tectum. This is consistent with the representation of the caudal visual field in this part of the tectum and with a relatively small representation of the caudal body surface within the tectum, as suggested by Stein and Gaither (1981) for *Iguana*. The neurons within the spinal gray matter that give rise to this projection are not known.

c. TRIGEMINAL AFFERENTS

Trigeminal projections have been reported in the early descriptive literature (Woodburne, 1936) and are the subject of several recent studies of the infrared system in snakes. Ganglion cells that innervate the infrared organs have central processes that terminate in the trigeminal nuclei (Molenaar, 1974; Schroeder and Loop, 1976). Informa-

tion from these nuclei reaches the contralateral tectum in both boid and crotaline snakes but does so by different routes. In boid snakes, direct projections from the trigeminal complex pass to the deep layers of the optic tectum (Molenaar and Fizaan-Oostveen, 1980; Newman et al., 1980). In crotaline snakes, the trigeminal projections involve a relay in reticular nucleus that has been named the nucleus caloris (Gruberg et al., 1979). These projections are discussed more extensively by Molenaar in Chapter 5.

d. THALAMUS

Direct projections from the spinal cord (Ebbesson and Goodman, 1981) and the trigeminal complex (Molenaar and Fizaan-Oostveen, 1980) reach a nucleus situated in the ventral thalamus just dorsal to the forebrain bundle system. It has been variously named the supra-peduncular nucleus or the ventral lateral nucleus, among others, and appears to receive both cranial and postcranial somatosensory information. Tectal HRP injections indicate that this nucleus projects bilaterally to the optic tectum (Dacey and Ulinski, 1986d). The axons of these neurons in the ventrolateral nucleus have been potentially identified in *Thamnophis* following diencephalic injections of HRP (Fig. 4.56). The axons travel caudally in the periventricular gray and white layers and then turn to extend vertically through the stratum album centrale, where they terminate as sparsely branched conical arbors. The axons or arbors branch and issue collaterals within the stratum album centrale and stratum griseum centrale. Single arbors range in diameter from 50 to 100 μm .

D. Auditory Information

Several reports note units in the deep tectal layers that are responsive to auditory stimuli in reptiles (Hartline, 1971; Stein and Gaither, 1981, 1983). HRP injections into the optic tectum retrogradely label a few neurons in the torus semicircularis of the midbrain, thereby indicating a potential route whereby auditory information could reach the optic tectum (Dacey and Ulinski, 1986d).

E. Reticular Afferents

Injections of HRP into the optic tectum indicate that several structures throughout the brainstem reticular formation project to the tectum. Because the tectoreticular neurons project bilaterally and extensively to these same structures, these reticulotectal projections are the return loop of a reciprocal interaction between the tectum and reticular formation.

Only the projections to the tectum from the nucleus lateralis profundus mesencephali of the midbrain reticular formation have been

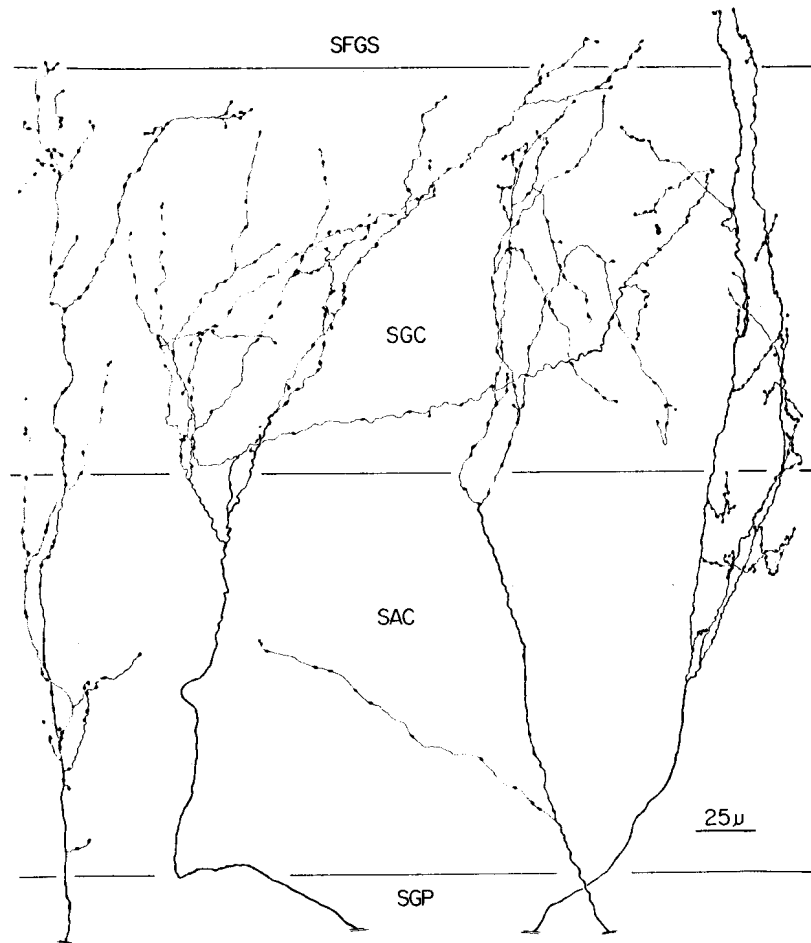


Fig. 4.56. *Thamnophis sirtalis*. Thalamic arbors. Putative terminal arbors of neurons of the ventrolateral nucleus. The parent axons ascend from the periventricular gray (SGP) and form vertically oriented arbors in the central white and gray layers. In comparison with the terminals shown in Figs. 4.8 to 4.10, these arbors have a sparse branching pattern that distributes boutons at a lower density over a more widespread area. (From Dacey and Ulinski, 1986e.)

studied in detail. Tectal HRP injections in *Thamnophis* retrogradely label neurons in the deep mesencephalic nucleus (Fig. 4.57). These neurons have large somata, about 30 μm in diameter, bearing several thick primary dendrites that radiate into the tegmental gray. The dendrites are smooth and bifurcate near the soma. They extend up to 400 μm and form a dendritic field that is relatively flat in the transverse plane. Axons arise from the somata, give off a small collateral within the dendritic field of the cell, and proceed dorsally into the stratum album centrale. The primary branches issue collaterals that terminate

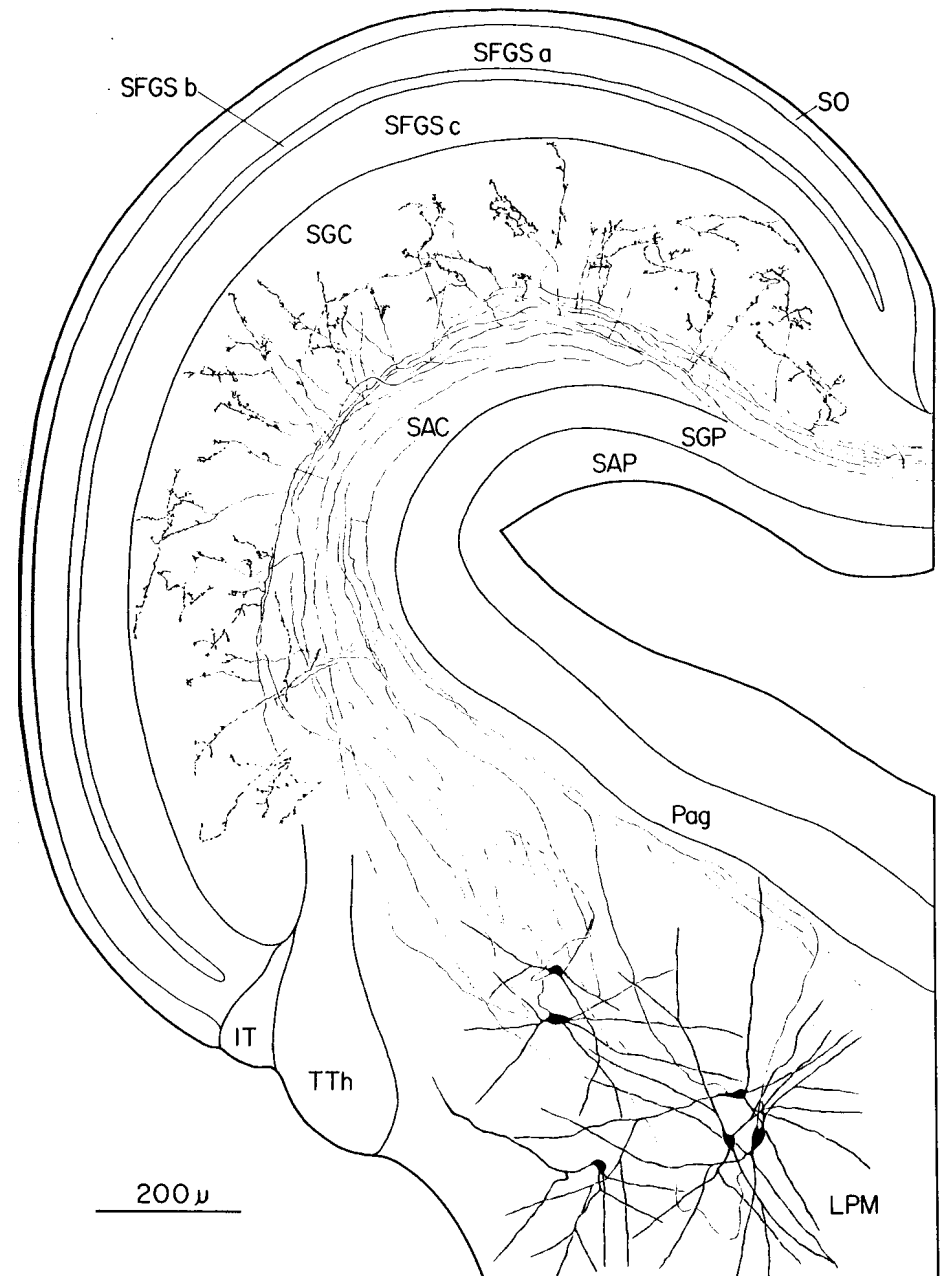


Fig. 4.57. *Thamnophis sirtalis*. Lateralis profundus axons. Tectal afferents from nucleus lateralis profundus mesencephali (LPM) retrogradely filled after an injection of HRP into the opposite tectal hemisphere. Large-caliber axons arising from the multipolar cells of LPM ascend into the stratum album centrale (SAC), course medially, and cross the midline in the tectal commissure. Terminal collaterals are restricted to the stratum griseum centrale (SGC). (From Dacey and Ulinski, 1986e.)

within the stratum griseum centrale, bearing numerous clusters of large boutons that are somewhat patchily distributed. Injections into the midbrain tegmentum anterogradely fill reticulotectal axons and retrogradely fill large tectoreticular neurons. These injections show that the deep mesencephalic terminals appose the somata and primary dendrites of the solid filled neurons, suggesting direct reciprocal relations between tectal and reticular neurons. The reticular axons can be traced through the tectal commissure and into the contralateral tectal lobe, where they terminate in the same fashion. Since the entire axon can often be traced in an individual section, it appears that the trajectories of the reticular axons are restricted to mediolateral planes.

F. Afferents Related to the Striatum

The striatum is a collection of structures in the ventral part of the telencephalon rostral to the anterior commissure. The anatomy of the striatum has been discussed at length (Ulinski, 1983). In brief, it receives afferents from the anterior dorsal ventricular ridge, which lies above it protruding into the lateral ventricle. The anterior dorsal ventricular ridge (ADVR) receives ascending sensory information from visual, auditory, and somatosensory nuclei in the thalamus, so that its projections to striatum presumably carry sensory information to the striatum. The striatum has reciprocal projections to ADVR, but the major striatal efferents run caudally into the brainstem and include two nuclei that project to the optic tectum.

The first of these nuclei lies in the ventrolateral midbrain tegmentum and contains dopaminergic neurons. It is called the substantia nigra in turtles (Parent, 1979) and lizards (Baumgarten and Braak, 1968) and the pedunculopontine nucleus in crocodylians (Brauth and Kitt, 1980). HRP injections into the optic tectum retrogradely label neurons in this nucleus in turtles (*Chrysemys*, Reiner et al., 1980), monitor lizards (*Varanus exanthematicus*, ten Donkelaar and DeBoer-van Huizen, 1981), and crocodylians (*Caiman*, Reiner et al., 1980).

The second link between the striatum and optic tectum lies at the transition between the caudal diencephalon and pretectum. It has been called the dorsal nucleus of the posterior commissure. Like the substantia nigra, it receives descending projections from the striatum (lizards: Hoogland, 1977; Voneida and Sligar, 1979; ten Donkelaar and DeBoer-van Huizen, 1981; Reiner et al., 1980). Nothing is known about the organization of these systems of tectal afferents in reptiles.

G. Monoaminergic Projections

The distribution of neurons and axon systems that contain either serotonin or catecholamines has been studied in turtles and lizards using histofluorescence techniques (reviewed by Parent, 1979). These stud-

ies indicate that the patterns of monoaminergic innervation in turtles and lizards are similar. Catecholaminergic terminals are distributed principally in the superficial layers of the tectum. These studies do not establish whether the terminals are noradrenergic or dopaminergic. They presumably derive from neurons with their somata in the locus coeruleus or the substantia nigra, or both, but this point has not been explicitly demonstrated with experimental techniques. Most serotonergic terminals lie in the deeper layers of the tectum and presumably derive from neurons with somata in the raphe nuclei.

H. Summary

The application of modern axonal tracing techniques has greatly increased the number of known afferent systems of the tectum. Investigations with the Golgi technique demonstrated that several morphologically distinct varieties of afferent axons are present in the tectum, but it was generally not possible to identify their sources. The use of the orthograde HRP tracing techniques has now permitted the identification of several of the major sets of axons afferent to the tectum and, when coupled with retrograde tracing techniques, has allowed the determination of the complete morphology of the cell. Orthograde tracing techniques have shown that most of the afferent systems of the tectum terminate preferentially within specific layers or sublayers. There must consequently be specific relationships between particular afferent systems and particular classes of efferent or intrinsic neurons. It has sometimes been possible to suggest relationships, such as the existence of a reciprocal loop between neurons in the reticular formation and the tectoreticular neurons. However, it is for the most part only possible to establish that specific classes of neurons lie within the domains of specific classes of afferents. The general rule seems to be that whenever reciprocal connections occur, the dendritic fields of neurons forming one limb of the loop lie within the terminal domains of the neurons forming the return limb. Like the efferent systems, some of the systems of afferents to the tectum are topologically organized, whereas others are not. The implications of topologically and nontopologically organized projections are considered in the next section.

VI. GENERAL CONCEPTS OF TECTAL ORGANIZATION

A. Overview

The preceding sections have considered the morphology of tectal neurons and afferents to the tectum in some detail. Much of the information reviewed was obtained by the application of contemporary neuroanatomical techniques, particularly those involving the use of HRP. It is inevitable that the accumulation of significant pieces of in-

formation on the anatomy of any neural structure will lead to some alteration in the prevailing concepts about its organization. This section will therefore discuss some general aspects of the relation of the optic tectum to the organization of the central nervous system as a whole and of the internal organization of the tectum itself.

B. Position of the Tectum in the Organization of the Nervous System

The concept prevailing up to the 1950s was that the optic tectum receives a variety of sensory inputs and projects to the brainstem reticular formation, thereby participating in the generation of relatively simple orienting movements in "lower" vertebrates. The tectum was held to be relatively unimportant in mammals, in which the cerebral cortex was thought to have taken over most important behavioral tasks through a process called encephalization. This view has been emended in two ways during the past three decades (Fig. 4.58). The first major change in our understanding of the way in which the tectum fits into the overall organization of the brain was the discovery of two circuits that link the optic tectum with the telencephalon in all vertebrates. In reptiles and birds, information from the optic tectum reaches the telencephalon through nucleus rotundus in the dorsal thalamus. Projections from the tectum to the nucleus rotundus were first established in pigeons (Karten, 1965) and then in red-eared turtles *Pseudemys scripta*, (Hall and Ebner, 1970b). They have since been demonstrated in representatives of all of the major groups of reptiles (see Section III.D). As the nucleus rotundus projects to the anterior part of the dorsal ventricular ridge (Section III.D; Ulinski, 1983), the tectorotundal projections are the first link in a pathway that carries information from the optic tectum to the dorsal or pallial component of the telencephalon. For our purposes, the anterior dorsal ventricular ridge has a principal efferent connection to the underlying striatum (Ulinski, 1983), which lies in the ventral or basal component of the telencephalon. The striatum influences the tectum through a pretectal structure (the dorsal nucleus of the posterior commissure) and through a nucleus in the midbrain tegmentum (substantia nigra or pedunculopontine nucleus). These projections thus constitute a feedback loop to the tectum. The sign of the loop—whether it is a negative or positive feedback loop—is not known in reptiles, but physiological studies (e.g., Hikosaka and Wurtz, 1983) on the nigro-tectal projections in mammals show they are inhibitory to collicular neurons.

A second loop between the tectum and the telencephalon has been demonstrated in some reptiles (see Section V.B.2.d) and more completely in birds. It involves a direct projection from the pallium to the

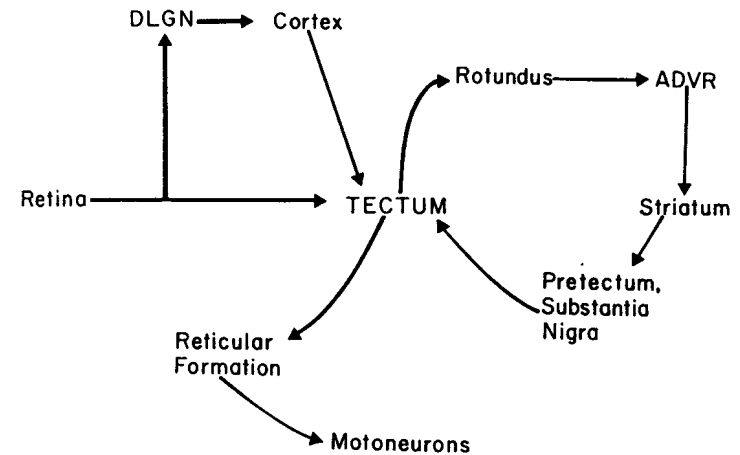


Fig. 4.58. Relation of tectum to other brain structures. This diagram summarizes the relation of some major structures to the optic tectum.

tectum. The regions of the pallium (i.e., pallial thickening or Wulst) that project to the tectum tend to receive visual information from the dorsal part of the geniculate complex (e.g., Hall and Ebner, 1970b; Karten et al., 1973; Miceli et al., 1975; Repérant et al., 1974). As many of the retinal ganglion cells that project to the tectum probably also project to the geniculate complex through collaterals, these pallial projections may represent a feedback to the tectum of part of its visual input. Electrophysiological studies in birds indicate that this loop exerts both an excitatory and an inhibitory effect on tectal units and plays a significant role in the construction of directionally selective units (e.g., Britto, 1978; Leresche et al., 1983).

Consequently, tectal output is a function not only of inputs from the major sensory systems, but also of at least two telencephalic feedback loops. The interaction of direct sensory and telencephalic inputs to modulate tectal output in reptiles is not well understood. There is, however, relevant information from studies on mammals. Both striatal (e.g., Rhoades et al., 1982) and pallial (e.g., Kawamura et al., 1974) projections to the tectum are also present in mammals. Anatomical (e.g., Mize and Sterling, 1976) and electrophysiological evidence indicates that retinal and cortical inputs can converge on the same collicular neuron. As is the case for tectal neurons in reptiles and birds, collicular neurons in mammals frequently show a preference for moving visual stimuli and are often directionally selective (e.g., Goldberg and Robinson, 1975). Experiments in which the visual cortex is either ablated or reversibly inactivated by cooling (e.g., Wickelgren and Sterling, 1969; Rosenquist and Palmer, 1971) suggest that directional selectivity can be conferred upon collicular neurons at least in part by

directionally selective neurons in layer V of the visual cortex. The contribution of the telencephalic loops to the behavior of the organism is not clear for either reptiles or mammals.

A second area in which there has been some change in our concept of how the tectum fits into the organization of the brain involves a gradual appreciation of the complexity of the pathways linking the tectum to motoneurons in the spinal cord and brainstem. It has been known for some time that the tectum sends both ipsilateral and contralateral projections from the brainstem reticular formation. Reticular neurons are premotor in the sense that their axons have a relatively direct influence on motoneurons, either in the brainstem or spinal cord. Recent work (e.g., Moschovakis et al., 1988a, 1988b) has shown that the tectoreticular pathways originate from several, morphologically heterogeneous groups of neurons and run in several fascicles distinguished by their position in the brainstem and the caliber of their axons (Section III.A). Each axon tends to collateralize rather extensively in the brainstem. Thus, the activation of any particular locus in the tectum will lead to a modulation of the activity of neurons spread throughout the brainstem and at least the cervical levels of the spinal cord.

The nature of the brainstem projections to the spinal cord has been studied in reptiles using both retrograde degeneration (Robinson, 1969; ten Donkelaar, 1976a, 1976b; Cruce and Newman, 1981) and HRP techniques (ten Donkelaar and De Boer-van Huizen, 1978; ten Donkelaar et al., 1980; Newman et al., 1982). These studies show that a large number of nuclei situated throughout the rostrocaudal extent of the neuroaxis project to the spinal cord ipsilaterally, contralaterally, and bilaterally. Thus, the tectum can modulate neuronal activity in the spinal cord through many parallel pathways in the hindbrain and midbrain reticular formations.

A further complexity in the tectal modulation of descending pathways involves the geniculate complex and the pretectum. Both of these structures receive topologically organized projections from the retina, have reciprocal connections with the tectum, and give rise to descending projections to either the spinal cord (Newman, personal communication) or brainstem (Ulinski et al., 1983). The tectogeniculate and tectopretectal projections thus provide the tectum access to additional, parallel routes to motoneurons.

C. Sensorimotor Transformations

From a functional viewpoint, the position of the tectum in the brain is that it modulates orienting movements of the organism through the brainstem reticular formation. In essence, the tectum participates in a transformation of information about the location of objects in extracorporeal space (which must be coded in spatial coordinates) to a set

of instructions to motoneurons (which must be coded in the firing frequencies of premotor neurons). Several types of models have been suggested for the mechanisms that underlie such sensorimotor transformations.

The first type of model for sensorimotor transformations—labeled line models—posits a series of direct connections from a locus on a sensory surface, to the tectum, and then through premotor structures (presumably the reticular formation) to those motoneurons that will, when activated, orient the animal toward the stimulus. One could imagine, for example, that stimulation of one region of the retina activates a particular tectal locus that projects, through the reticular formation, to a motoneuron pool, the activity of which causes the animal to orient toward the stimulus. Such connections would be sufficient, at least qualitatively, to account for orienting behaviors. There is evidence in cats, for example, that projections from the region of the tectum that receives a representation of the peripheral visual field (and peripheral auditory field) projects to the vicinity of the facial motoneurons that control pinna movement. These connections could account for orienting movements of the pinnae in response to sudden sounds (Stein and Clamann, 1981).

A drawback to the generality of labeled line models is that orienting behaviors are generally more complex than they imply. Animals do not orient to every stimulus in their environment, and, when they do respond, they have the capability of responding in a graded fashion. Thus, something more than a simple activation of a set of circuitry must be involved. There must be some evaluation of stimulus properties and of the relation between the stimulus and the total environmental context. Similarly, interactions occur when two or more stimuli are presented to the organism, so it is difficult to account for orienting movements in terms of circuitry that activates only restricted tectal loci. The labeled line models also face difficulty when the temporal aspect of orienting movements is considered, the problem being that the amount of time involved in direct activation of motoneurons through the tectum and reticular formation is much shorter than the time course of actual orientation movements.

A second type of model circumvents the first difficulty by suggesting that the efferent projections from the tectum form a distributed system. Distributed systems, in general, are those in which many of the system elements share in a given function (see Anderson and Hinton, 1981, for discussions of the concept of distributed systems). In the case of the tectum, the idea is that each tectoreticular neuron would project to many reticular neurons and influence more than a single pool of motoneurons. Information would be coded in a population of individual tectal neurons. Models of this type were proposed as early as 1947 by Pitts and McCulloch to account for the control of

eye movements by the superior colliculus. They suggest that a distributed system involving the superior colliculus and projections to motor pools controls vertical and horizontal eye movements. Data consistent with distributed system models are available in recent neurophysiological studies of the collicular control of eye movements in alert monkeys and cats. These experiments show, that neurons throughout a relatively widespread region of the tectum are active before a variety of eye movements occur (e.g., Wurtz and Albano, 1980), making it unlikely that a given cluster of collicular neurons codes particular eye movements. Rather, individual neurons appear to participate in a variety of different movements. Conversely, lesioning or inactivating a particular region of the colliculus appears to have relatively little specific effect on eye movements, suggesting again that the relationship between regions of the colliculus and the particular movements is not one to one (Lee et al., 1988). The little that is known about the anatomy of the tectoreticular projections is also consistent with distributed system models. Grantyn and Grantyn (1982) found that the tectoreticular axons in cats branch extensively throughout the brainstem reticular formation, so that each locus in the colliculus is likely to influence activity in many reticular neurons. Conversely, each region of the reticular formation will receive information from all collicular loci. The same picture emerges from studies in turtles and snakes (see Section III.A), which again emphasize the divergent character of tectoreticular projections.

Distributed system models are attractive because they help to explain how activity in several motoneuron pools is coordinated during a complex movement sequence. However, it is not entirely clear at this point how different movements are produced by the same system. One suggestion that has been explored attempts to explain how the amplitude of horizontal eye movements is coded. It is known that the superior colliculus projects to a center for horizontal gaze, presumably located in the paramedian pontine reticular formation. Neurons in this center drive motoneurons in the abducens nucleus (e.g., Wurtz and Albano, 1980; Robinson, 1981). The force generated by the lateral rectus muscle is a linear function of the firing frequency in abducens motoneurons. The execution of appropriate orienting movements requires the eye to move in the horizontal plane so as to fixate a stimulus located in a specific region of visual space. The problem is how the transformation from position coordinates in visual space to motoneuron firing frequencies is achieved. Orthograde HRP experiments indicate that reticular axons project diffusely within the abducens pool so that there is a divergent-convergent relationship. A simple solution can be achieved if there are differences in the number of neurons that issue from different tectal loci. Thus, the synaptic drive to abducens motoneurons would vary as a function of the tectal

locus. This could occur either due to density differences in the number of neurons as a function of tectal locus (see Section VI.D.4), to differences in the magnification factor as a function of position in visual space (McIlwain, 1982), or both.

A further difficulty with models of simple distributed systems is that they do not in themselves explain the temporal features of orientation movements. The relatively long time course of such movements suggests that some sort of computational process is taking place, involving either computations effected entirely within the tectum or feedback loops through the forebrain and brainstem. Behavioral support for more complex processes comes from experiments in which lesions of brainstem or telencephalic structures (e.g., Ewert, 1976; Ingle, 1973) are shown to influence the performance of tectally mediated orienting movements and from other experiments in which interaction effects are demonstrated between two or more simultaneously presented stimuli (Ingle, 1968). Based on their behavioral experiments, Ewert and von Seelen (1974) have produced models of the neural substrates of frog orientation movements that involve telencephalic and brainstem interactions with tectal neurons. Arbib and his colleagues (Lara et al., 1982) have explored a series of computational models involving interactions among tectal modules. They utilize horizontally aligned intratectal connections between neurons positioned throughout the tectum to produce specific tectal outputs. McIlwain (1982) has reported electrophysiological results consistent with extensive intratectal processing. He used microstimulation and recording techniques in cat superior colliculus to show that electrical stimuli that result in orienting movements of the eyes actually activate widespread neurons within the colliculus. The limitations inherent in earlier anatomical techniques led to an underestimation of the spatial extent of tectal axon collaterals. However, HRP techniques have now demonstrated widespread axonal systems within the tectum (see Sections III and IV). The axons of most tectal efferent and intrinsic neurons have extensive vertical components as well as, in many instances, axons that extend horizontally for relatively long distances. Many of these axons are asymmetric, spreading preferentially either laterally or medially. It is clear that such intratectal connections can form the substrate for intratectal processing, but the nature of the processing is not known.

D. Internal Organization of Tectum

1. GENERAL A major goal in neuroanatomy since the work of Ramón y Cajal has been to understand the patterns of neuronal organization that characterize major regions of the nervous system. Significant advances have been achieved in the case of the cerebellum (Eccles et al., 1967) and cerebral cortex of mammals (Lund, 1981), by using Golgi

and electron microscopic techniques in coordination. In contrast, most of the attention devoted to the optic tectum has focused on the organization of the retinorecipient layers, and we still lack any generally accepted idea of the overall organization of the tectum. However, several aspects of tectal organization merit consideration.

2. TECTAL LAMINATION

The concept that the tectum is a layered or laminated structure stems directly from cytoarchitectural observations that show a number of more or less distinct layers of somata in Nissl preparations. There is an ingrained tendency in neurobiology to assign specific functions to anatomically defined units (e.g., Kaas, 1982), and a subliminal thread that runs through much of the history of ideas of tectal function is an assignment of different functions to different tectal layers. The gradual establishment of relations between the pattern of afferent and efferent connections and that of tectal cytoarchitecture reinforced the concept that tectal layers constitute functional units and, combined with behavioral studies (e.g., Casagrande and Diamond, 1974), led to the general idea that the superficial layers are related through ascending projections to the forebrain with perceptual tasks, whereas the deep layers are related through their descending projections to motor tasks. The behavioral experiments consist of examining the effects of restricted tectal lesions on pattern discrimination versus motor tasks. More recently, studies using electrophysiological recordings from alert, unanesthetized animals have attempted to correlate the firing pattern of tectal neurons with motor activity; these studies found that neurons whose activity correlated with motor activity tend to be located in the intermediate or deep layers.

However, several considerations make it difficult to accept a strict assignment of "perceptual" or "motor" functions to tectal layers. First, it is now clear that auditory, tactile, and infrared information reaches the deeper layers of the tectum, so that no one set of layers can be regarded as "sensory" to the exclusion of others. Rather, there appears to be at least a partial laminar segregation of modalities within the tectum. Second, the idea that the superficial layers are involved in perceptual tasks, such as pattern vision, stems in large part from the demonstration of ascending projections from the superficial layers to the thalamus and ultimately to the telencephalon. It has subsequently been determined that the telencephalon has strong reciprocal projections back to the tectum through both the pallidum and striatum. Thus, the ascending projections to the forebrain can also be regarded as one limb in a feedback system to the deeper layers. Third, the idea that the tectal layers are functionally independent also requires some degree of anatomical independence. The apparent ab-

sence of interlaminar connections in mammals has been used in support of this notion (e.g., Edwards, 1980; Wurtz and Albano, 1980). However, there is good evidence for strong interactions between tectal layers in reptiles, and a good deal of neurophysiological evidence in primates and cats (e.g., Wurtz and Albano, 1980) indicates that there are short latency interactions between neurons in different layers involved in producing eye movements.

A correlate of the idea that tectal layers have functional significance is that the tectal layers should vary during evolution under the force of environmental selection pressures. Thus, several studies have shown that reptiles with large eyes and those that appear visually active have thicker superficial layers with more numerous and more clearly defined sublayers, whereas burrowing or other visually inactive forms have reduced superficial layers (Masai, 1973). Snakes as a group have relatively reduced superficial layers. Senn and Northcutt (1973) and Northcutt (1978) have discussed the tectum of snakes in relation to the theory of Walls (1942) that the snakes are derived from ancestral burrowing forms. (See Chapter 3 for a complete discussion of this theory.) Similarly, snakes with infrared systems tend to show a hypertrophy of those tectal layers that receive trigeminal input (e.g., Auen, 1976). Variations of this sort are clearly present, but the prominence of vertical interactions within the tectum of reptiles complicates their interpretation. For example, the dendrites of neurons with somata in the central and deep layers must constitute a large percentage of the postsynaptic targets in the superficial layers. Thus, hypertrophy of the superficial layers is likely to accompany major changes in neurons through the tectum and in the interaction of central and deep neurons within the superficial layers through interactions through dendritic bundles and axon collaterals.

Regardless of their functional or evolutionary significance, an immediate consequence of the presence of specific sets of connections with the various tectal layers is that each class of tectal efferent and intrinsic neurons is potentially in receipt of a specific pattern of afferent projections. Definitive demonstrations of the relationship between specific afferent systems and specific neuronal classes are for the most part lacking, but such experiments are now possible by combining orthograde tracing techniques with electronmicroscopic observations on individual neurons identified by HRP or Golgi procedures. These experiments are time consuming but are necessary to specify completely the network of connections involved in tectal function.

However, light microscopic information is sufficient to establish a major organizational difference between the tectum in mammals and that of most groups of nonmammalian vertebrates, including reptiles. The receptive surfaces of most types of neurons in mammalian tecta

are restricted principally, if not completely, to individual layers or groups of sublayers. Thus, afferent systems terminating in a given layer will make synaptic contacts principally with neurons whose somata are located in that layer. The laminar organization in the superior colliculus is then a relatively clear correlate to its afferent organization. By contrast, the optic tectum in reptiles contains several types of neurons whose dendrites extend across layers, so that an individual neuron can potentially integrate inputs across much, or sometimes the entire thickness, of the tectum. There are again specific relations among afferent systems and the receptive surfaces of the various types of neurons, but the relationship between the position of the soma of a neuron and the afferent organization of the tectum in reptiles is not straightforward.

3. COLUMNS, MODULES, AND BANDS

The radial organization of tectal neurons provides a first and most obvious line of evidence in support of the concept that the tectum has some radial or vertical mode of organization. This mode lies orthogonal to the horizontal organization provided by the tectal laminae and their associated connective specificities. The dendrites of radial cells form a vertical lattice work that is dramatically obvious in Golgi preparations. Retrograde HRP experiments (see Sections III and IV) reveal that radial neurons, as defined in Golgi preparations, actually include several classes of efferent neurons, each of which is morphologically distinct and has specific connections both within and without the tectum. Observations on light microscopic material suggest that there are interactions between some of these classes of neurons in that the deep and superficial populations of radial neurons have dendrites that come together in dendritic bundles within the superficial layers (Schechter and Ulinski, 1979). Electron microscopic observations indicate that chemical dendrodendritic synapses (Fig. 4.59) are prevalent in these layers (Schechter and Ulinski, 1979), but it is not known which of the various types of radial neurons are interrelated within the bundles.

Radial neurons could in principle serve to integrate inputs across tectal layers. The dendrites of radial neurons in pigeons are known to conduct dendritic spikes (Stone and Freeman, 1971) so that the output from a given radial cell could depend upon synaptic activity in the superficial layers. This activity is conducted to a site of impulse generation on the soma or on the dendritic shaft. The extent to which synaptic activity would be passively conducted to an impulse generation site depends upon the biophysical properties of the neuron. It is possible, for example, that the distal dendrites of radial neurons might serve as a unit that is relatively isolated from the rest of the



Fig. 4.59. *Pseudemys scripta*. Dendritic bundles. A low-power electron micrograph on the left shows the dendrites of several radial cells within a dendritic bundle. The electron micrograph on the right shows a chemical synapse between two dendrites.

neuron (e.g., Calvin and Graubard, 1979). In this case, the presynaptic dendrites in the superficial layers might serve as one output from a given radial neuron, whereas its axon in the deeper layers of the tectum would serve as a second output. The calculations necessary to determine the extent to which different regions of radial cells are coupled have not been carried out.

A second type of vertical organization within the tectum is provided by radially oriented collaterals of intrinsic and efferent tectal neurons. Some authors (e.g., Edwards, 1980) have denied the existence of interlaminar connections, at least in mammals. However, there is evidence for the existence of such collaterals from Golgi studies (e.g., Ramón, 1896; Ramón y Cajal, 1911), and Sterling (in Ingle and Sprague, 1975) reports radially organized connections within cat superior colliculus using orthograde degeneration techniques. Our HRP studies on tectal neurons in snakes and turtles lead us to believe that statements about the absence of interlaminar connections should be regarded with caution because HRP fills can apparently visualize collateral systems that are difficult to demonstrate with other existing techniques, and several laboratories have now demonstrated interlaminar connections in mammals (Rhoades et al., 1989; Grantyn et al., 1984).

A third type of vertical interaction is provided by the tendency of afferent axons to terminate in arbors that are restricted to domains, usually about 250 μm in diameter. This has been demonstrated directly in reptiles (Section V) with orthograde HRP techniques that explicitly show the morphology of terminal arbors. A similar organization is implied in mammals by autoradiographic tracing experiments that demonstrate several afferent systems terminate in patches or bands in autoradiographs. This was first reported for the retinal projection to the colliculus by Graybiel (1975) and Hubel et al. (1975), who showed that inputs from the two terminate within alternating "patches" and "puffs" within the superficial layers of the binocular zone. Reconstruction of these areas shows that they have the form of rostrocaudally aligned bands. Similar bands were subsequently reported for the nigrotectal (Graybiel, 1978), trigemintectal (Huerta et al., 1981), and several other systems afferent to the colliculus (Huerta and Harting, 1984). The implication of these findings is that these afferent systems would fit into vertically organized zones within the colliculus.

However, two sets of observations question the degree to which intratectal bands are of functional significance. First Killackey and Erzurumlu (1981) have argued that the banding is an artifact resulting from the way in which axon fascicles are arranged in the tectum. Axons participating in several fiber systems afferent to the tectum tend

to run in rostrocaudally oriented fascicles that appear as patches of axons in transverse sections of Fink-Heimer or autoradiographic preparations. Second, Constantine-Paton (e.g., 1981) has shown that intratectal banding of retinal afferents can be experimentally induced in frogs by surgically grafting a supernumerary eye at the tadpole stage. The banding appears to result from competitive effects between the retinotectal axons originating from a normal eye and the supernumerary eye. The banding may reflect developmental interactions that lack functional significance.

4. REGIONAL VARIATION

Compared to considerations of laminar and vertical organization, the concept of regional variation within the tectum has received relatively little attention. An initial clue to the regional organization of the tectum comes from cytoarchitectural observations. Studies of lizards (Peterson, 1981), and birds (Duff et al., 1981) reveal that although the same layers and sublayers occur throughout the tectum, the character and quantitative development of the layers often show significant regional variations at different tectal loci. The same types of neurons occur but appear to vary in the size, number, and packing density. The nature of this variation has been carefully documented in a study of the tectum in the desert iguana, *Dipsosaurus dorsalis* (Peterson, 1981). Tectal laminae are well developed in this species, as is generally the case in diurnal iguanid lizards, and correspond to Pedro Ramón's 14 layers in *Lacerta*. However, the tectum as a whole can be divided into five areas based on regional variation. Regional variation has also been documented in the red-eared turtle, *Pseudemys scripta* (Ulinski, 1978). The periventricular gray layers in this species consist of several well-demarcated sublayers, so it is possible to accurately calculate the density of somata in each sublayer. Using complete sets of serial sections, it was possible to determine the density of somata in the first or outer sublayer as a function of mediolateral position in the section. These data could be used to plot the density of somata onto the tectal surface as if the tectum had been flattened and to construct a series of isodensity lines (Fig. 4.60). The plots show that neurons in the outer sublayer are heterogeneously distributed throughout the tectum. The density of neurons is elevated in the central portion of the tectum and at its rostromedial pole but is low in a rim that extends around most of the tectal margin. There are only a few other studies on regional variation in other species. Regional variations in the synaptic organization of the superficial layers of the tectum in pigeons have been shown by Duff et al. (1981). It seems likely, though, that some degree of regional variation is a general feature of the tectum, at least in non-mammalian vertebrates.

STRATUM GRISEUM PERIVENTRICULARE
1st sublayer

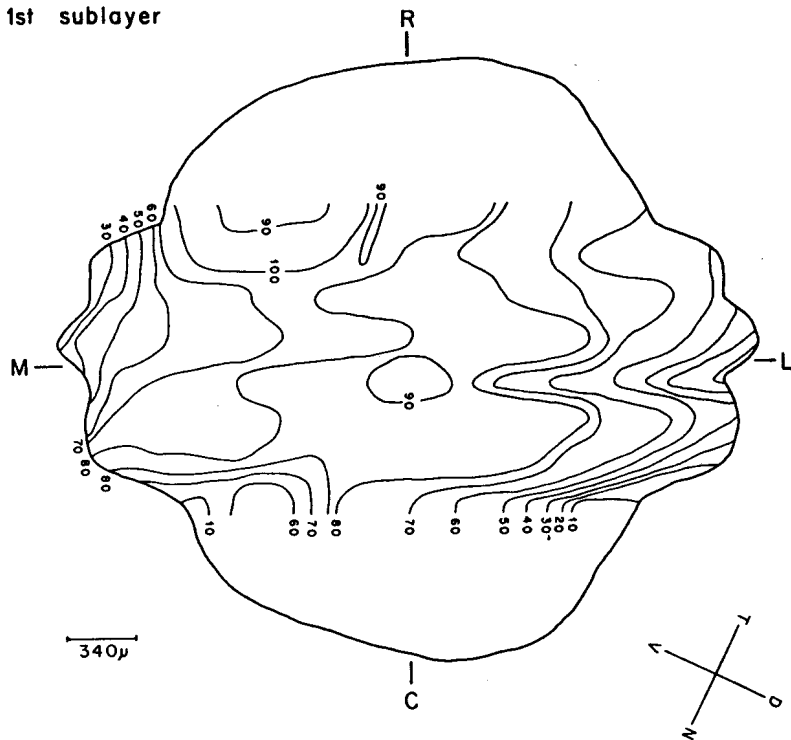


Fig. 4.60. *Pseudemys scripta*. Distribution of tectal neurons. This is an isodensity map for the somata in the outer sublayer of the stratum griseum periventriculare. The rostrocaudal and the medialateral axes are indicated. The inset shows the relation of the dorsoventral and nasotemporal axes of the retina to the tectal surface.

Such cytoarchitectural differences tend to be reflected in the afferent connections of the tectum. The nature of retinotectal input varies in concert with cytoarchitectural variations in lizards (Peterson, 1981), and the same type of variation appears to occur in pigeons (Duff et al. 1981). There also may be regional variations in the nature of somatosensory input (whether from the dorsal column nuclei and spinal cord or from the trigeminal complex). Where ipsilateral retinotectal projections are present, they are restricted to the binocular representation upon the tectal surface. Similarly, there is evidence in mammals that the tectal commissure distributes to one region within the superior colliculus and there appear to be regional variations in the extent of input from the retina and visual cortex, so that much of the representation of central visual fields reaches the colliculus through the visual cortex. It is likely that regional variation also reflects more subtle structures within the afferent projections to the tectum. As dif-

ferent types of ganglion cells are distributed unevenly over the retinal surface in many vertebrates, it follows that the nature of the input to different tectal loci must vary as a reflection of retinal organization. Peterson (1981) suggests that regional variation reflects regional specializations in the retina that include local variations in the number and types of photoreceptors and in the density and soma sizes of retinal ganglion cells. In *Dipsosaurus*, for example, the retina contains a horizontally elongate region of high ganglion cell density—or visual streak, a fovea, and a region in the temporal retina that contains ganglion cells with particularly large somata. It appears that the various areas of the tectum correspond to representations of retinal specializations upon the tectal surface. Similarly, the areas of increased soma density in *Pseudemys* seem to correspond to the representation of the visual streak (Peterson and Ulinski, 1979) and the temporal region of the retina that contains large ganglion cells (Peterson and Ulinski, 1982). Duff et al. (1981) suggest that the regional variation seen in the optic tectum of pigeons reflects the presence of the red and yellow fields of the retina (Galifret, 1968; Blough, 1979).

The extent to which the nature of tectal efferent projections shows regional variations has not been fully evaluated. Studies that place HRP injections in structures that receive input from the tectum and then plot the distribution of retrogradely labeled neurons in the tectum provide some evidence that there are regional variations in the origin of the tectum's efferent systems. Thus, the cells of origin of the tectoreticular (Holcombe and Hall, 1981a), tectopontine (Holcombe and Hall, 1981b), tectogeniculate (e.g., Albano et al., 1979; Harrell et al., 1982), tectotectal (e.g., Magalhaes-Castro et al., 1978), and tectospinal (Murray and Coulter, 1982; Huerta and Harting, 1982) projections each are distributed in particular regions of the superior colliculus.

The existence of such regional variation in cytoarchitecture, afferent connections, and efferent connections is consistent with labeled line models of tectal function in that different regions of the tectum have different relationships to the rest of the nervous system and presumably process information differently. Thus, activation of different tectal loci could possibly result in different behavioral responses. Although a certain degree of regional variation is well established, the ways in which this variation is exploited by the animal is not yet known.

5. MAPS

Each of the afferent and efferent projections of the tectum establishes a spatial relationship between neurons in the tectum and one or more other structures. From a mathematical point of view, the projections

therefore specify a series of maps between the tectum and either the retina or other brain regions. The most familiar of these are point-to-point or topological maps, such as that formed by the projections of the retina upon the tectal surface. Similarly, there are topological maps between the tectum and the geniculate complex, pretectum, nucleus isthmi, and so on. The presumed essential property of these maps is that they preserve information about spatial relationships. Thus, two adjacent loci on the retinal surface are represented by two adjacent loci on the tectal surface and vice versa.

The anatomical substrate for topological maps are axonal arbors with relatively restricted dimensions. For example, the arbors of retinal ganglion cells measure about 65 by 100 μm in *Thamnophis*, regardless of the location in the tectum. Thus, restricted lesions or injections of marker substances into the retina result in degeneration of transported label in a relatively restricted region of the tectum. Conversely, focal injections of HRP in the tectum retrogradely label focal patches of ganglion cells in the retina. The important point is that the size of these arbors is relatively small when compared to the total dimensions of the tectum so that the tectum can embody a relatively detailed representation of the retinal surface.

The existence of topological maps in the visual system is a familiar aspect of nervous system organization and tends to carry with it a certain degree of psychological comfort. However, the functional significance of such maps is not entirely certain. A topological representation of visual space is obviously useful in a variety of behaviorally important computations. It is also possible that topological representations play a role in the generation of complex receptive field properties such as contrast sensitivity and orientation selectivity by forming a substrate for local connections. On the other hand, it is possible that topological maps reflect the underlying developmental properties of the nervous system and have no direct functional significance.

The existence of nontopological maps in the nervous system is less widely appreciated. However, data obtained using the orthograde transport of HRP suggest that many of the tectal afferent and efferent systems consist of axons with widely branching terminals. These axons indicate the existence of maps that do not preserve spatial relationships. Nontopological maps apparently occur in the tectorotundal, tectoreticular, and pretectal-tectal projections. It is interesting to note that in some instances of reciprocal projections, one limb of the loop is topologically organized, whereas the other limb is not. It is possible that nontopological projections, like topological ones, serve to preserve information about spatial relationships. This is somewhat counterintuitive, but a distributed system can code information about spatial relationships. The difference is that spatial information would

be coded in the temporal domain, in terms of firing frequencies, in the case of nontopological projections, whereas it is coded in the spatial domain in the case of topological projections. A second possibility is that nontopological projections are involved in the formation of sets of neurons that code for stimulus parameters that are not coded on the receptor sheet. Thus, there is some evidence suggesting that neurons in nucleus rotundus code information about the velocity, or perhaps direction, of a stimulus moving anywhere in the visual field. This would be consistent with the existence of a nontopological projection from the tectum to nucleus rotundus (Dacey and Ulinski, 1983). Finally, nontopological projections can be involved in a transformation from the coding of information in the spatial domain to codes in the temporal domain. This idea has already been mentioned in the case of tectoreticular projections, which might be involved in a sensorimotor transformation (see Section VI.A).

VII. SUMMARY

This chapter has reviewed the anatomical organization of the optic tectum in reptiles. It has emphasized the impact of contemporary neuroanatomical techniques, particularly the use of HRP, upon our data base and other ideas of tectal organization. Until quite recently, information on the tectum was relatively fragmented because the available anatomical techniques only yielded information about parts of the various populations of neurons present in the tectum. However, newer methods, such as the HRP technology, are allowing initial glimpses of the various types of neurons in their entirety. It is often possible with either the intracellular or extracellular application of HRP to completely visualize the soma, dendrites, and axons of individual neurons in the tectum and in those neural structures that project to the tectum. The possession of such a picture serves to highlight areas that deserve future inquiry. The first is what might be called the *microcircuitry* (cf. Sterling, 1983; Gilbert, 1983) of the tectum. Although we now know something about the morphology of the classes of tectal neurons distinguished by their connections, almost nothing is known of the nature of their interactions within the tectum. Thus, we do not know the specific interconnections that obtain between different populations of tectal neurons, whether the synapses are chemical or electrical, excitatory or inhibitory. Many of the interactions that occur between tectal neurons can be determined by the coordinated use of electronmicroscopic techniques on individual neurons that have been studied electrophysiologically and then labeled with HRP. Recently developed neurophysiological techniques that permit the analyses of correlations among firing patterns in neuronal populations should also be useful in determining the physiological signifi-

cance of neuronal interactions, particularly if distributed representations figure heavily in tectal function.

A related area of investigation has to do with the geometric organization of the tectum. The dendrites of horizontal neurons in rat superior colliculus (Langer and Lund, 1974) and the optic tectum of turtles (Peterson, 1978b) have a local order. Specific patterns in the orientation of the axon systems of tectal intrinsic neurons occur in *Thamnophis* (Dacey and Ulinski, 1986c). It is likely that these are only first views of the patterning of neuronal elements within the tectum. Researchers have actively investigated the geometric arrangement of elements within the striate cortex of cats and monkeys in recent years. The motivation for this line of work is the assumption that the geometric arrangement of axons and dendrites within the striate cortex is important in determining the information-processing properties of the structure. The difficulty in the case of the striate cortex is that we still lack a precise, quantitative concept of what the striate cortex does. The situation is more sanguine in the case of the optic tectum because we have a better idea of the relation of the tectum to orienting movements and are reaching the point at which quantitative descriptions of the sensorimotor transformations seem possible.

Finally, the substantial enrichment of our pictures of tectal neuronal morphology that has resulted from the HRP technique is generating broader and more carefully considered ideas on the nature of topological and nontopological maps in the central nervous system. Ideas of tectal function have been dominated by the idea of a topologically organized retinotectal projection, but it is now apparent that only a minority of the afferent and efferent projections of the tectum are topologically organized. It will be necessary now to carefully rethink our ideas of neuronal information processing and seriously consider models involving distributed representations.

ACKNOWLEDGMENTS

The authors' work on the optic tectum has been supported by PHS Grant NS12518. Maryellen Kurek provided invaluable technical and photographic services. Debra Hawkins, Dorothy Crowder, and Roberta Mims typed the manuscript.

APPENDIX: REPTILIAN SPECIES DISCUSSED

TESTUDINES

| | |
|---|---|
| <i>Anomalepsis aspinosus</i> Senn, 1969 | <i>Chelonia mydas</i> Granda and O'Shea, 1972 |
| <i>Caretta caretta</i> Bass and Northcutt, 1981a | <i>Chelydra serpentina</i> Knapp and Kang, 1968a |

| |
|--|
| <i>Chrysemys picta</i> Bass and Northcutt, 1981a, 1981b Heller and Ulinski, 1987 Reiner et al., 1980 |
| <i>Emys orbicularis</i> Belekhova and Kosareva, 1971 Boyko, 1976 Boyko and Davydova, 1975 Davydova, 1971, 1973 Davydova et al., 1982 Davydova and Goncharova, 1970 Davydova and Mazurskaya, 1973 Davydova et al., 1976 Gusel'nikov et al., 1970 Kosareva, 1967 Morenkov and Pivovarov, 1975 |
| <i>Pelomedusa subrufa</i> Pedersen, 1973 |

| |
|--|
| <i>Pelusios subniger</i> Pedersen, 1973 |
| <i>Podocnemis unifilis</i> Bass et al., 1973 Knapp and Kang, 1968b Pedersen, 1973 |
| <i>Trachemys scripta</i> Balaban and Ulinski, 1981a, 1981b Brown, 1969 Curwen and Miller, 1939 Foster and Hall, 1975 Granda and Stirling, 1965 Hall et al., 1977 Hall and Ebner, 1970a, 1970b Heller and Ulinski, 1987 Kolb, 1982 Marchiafava and Wagner, 1981 Schechter and Ulinski, 1979 Serenio, 1983, 1985 |

CROCODILIA

| | |
|---|--|
| <i>Alligator mississippiensis</i> Heric and Kruger, 1965, 1966 Huber and Crosby, 1926 | Burns and Goodman, 1967 Ebbesson and Goodman, 1981 Reiner et al., 1980 Repérant, 1975 Schapiro and Goodman, 1969 |
| <i>Caiman crocodilus</i> Braford, 1972, 1973 Brauth and Kitt, 1980 | |

RHYNCHOCEPHALIA

| | |
|---|---|
| <i>Sphenodon punctatus</i> Cairney, 1926 | Northcutt, 1978, 1983 Northcutt et al., 1974 |
|---|---|

SAURIA

| | |
|--|--|
| <i>Agama agama</i> Elprana et al., 1980 | <i>Iguana iguana</i> Bruce, 1982 Bruce and Butler, 1979 Butler and Ebner, 1972 Butler and Northcutt, 1973 Butler and Northcutt, 1971a, 1971b Distel, 1978 Foster and Hall, 1975, 1978 Stein and Gaitner, 1981, 1983 |
| <i>Anniella pulchra</i> Senn, 1968a | <i>Lacerta viridis</i> Baumgarten and Braak, 1968 Robinson, 1969 |
| <i>Anolis carolinensis</i> Butler and Northcutt, 1971a | <i>Lacerta vivipara</i> Armstrong, 1950, 1951 |
| <i>Chamaeleo jacksoni</i> Collett and Harkness, 1982 Harkness, 1977 | |
| <i>Dipsosaurus dorsalis</i> Peterson, 1981 | |
| <i>Gekko gekko</i> Bruce, 1982 Butler, 1976, 1978 Northcutt and Butler, 1974b | |

Pentadactylus schreiberii
Quiroga, 1978
Podarcis muralis
Baumgarten and Braak, 1968
Podarcis sicula
Senn, 1968b
Tupinambis nigropunctatus
Butler and Ebbesson, 1975
Cruce, 1974
Cruce and Cruce, 1975, 1978
Cruce and Newman, 1981
Ebbesson, 1967, 1981
Ebbesson and Karten, 1981

Hoogland, 1977
Lohman and van Woerden-
Verkley, 1978
Voneida and Sligar, 1979
Varanus exanthematicus
Hoogland, 1982
ten Donkelaar and De Boer-van
Huizen, 1981
ten Donkelaar et al., 1981
Varanus sp.
Distel and Ebbesson, 1975
Xantusia vigilis
Butler, 1974

SERPENTES

Boa constrictor
Ebbesson, 1969
Crotalus atrox
Molenaar, 1974
Crotalus h. horridus
Auen, 1976
Crotalus sp.
Berson and Hartline, 1988
Hartline, 1971
Hartline et al., 1978
Newman and Hartline, 1981
Terashima and Goris, 1975
Crotalus viridis
Schroeder, 1981a, 1981b
Stanford et al., 1981
Liotyphlops albirostris
Senn, 1969
Natrix natrix
Senn, 1979
Nerodia sipedon
Northcutt and Butler, 1974a
Senn, 1970
Ulinski, 1977

Python
Molenaar and Fizaan-Oosteveen,
1980
Repérant and Rio, 1976
Repérant et al., 1981
Thamnophis sirtalis
Dacey and Ulinski, 1983, 1986a,
1986b, 1986c, 1986d, 1986e
Halpern and Frumin, 1973
Ulinski et al., 1983
Warner, 1947
Vipera sp.
Auen, 1978
Vipera aspis
Repérant, 1973
Marchiafava and Weiler, 1980
Peterson, 1978a, 1978b, 1982
Peterson and Ulinski, 1979, 1982
Rainey and Ulinski, 1982a, 1982b
Repérant et al., 1981
Robbins, 1972
Sereno, 1985
Sereno and Ulinski, 1985
Ulinski, 1978

REFERENCES

- Akert, K. (1945). Der visuelle Greifreflex. *Helv. Physiol. Acta* 7, 112-134.
Albano, J. E., Norton, T. T., and Hall, W. C. (1979). Laminar origin of projections from the superficial layers of the superior colliculus in the tree shrew, *Tupaia glis*. *Brain Res.* 173, 1-11.
Altman, J., and Carpenter, M. C. (1961). Fiber projections of the superior colliculus in the cat. *J. Comp. Neurol.* 116, 157-177.
Anderson, J. A., and Hinton, C. E. (1981). Models of information processing in the brain. In *Parallel Models of Associative Memory* (J. A. Anderson and C. E. Hinton, eds.). Erlbaum, Hillsdale, N.J., pp. 9-48.
Angaut, P., and Repérant, J. (1976). Fine structure of the optic fibre termination layers in the pigeon optic tectum: a Golgi and electron microscopic study. *Neuroscience* 1, 93-105.
Ariens Kappers, C. U., Huber, G. C., and Crosby, E. C. (1936). *The Comparative Anatomy of the Nervous System of Vertebrates, Including Man* (reprinted 1960). Hafner, New York.
Armstrong, J. A. (1950). An experimental study of the visual pathways in a reptile (*Lacerta vivipara*). *J. Anat.* (London) 84, 146-167.
Armstrong, J. A. (1951). An experimental study of the visual pathways in a snake (*Natrix natrix*). *J. Anat.* (London) 85, 275-287.
Auen, E. L. (1976). "A Study of the Optic Tectum of the Snake." Ph.D. dissertation, University of Wisconsin, Madison.
Auen, E. L. (1978). Axonal transport of HRP in descending tectal fibers of the pit viper. *Neurosci. Lett.* 9, 137-140.
Bagnoli, P., and Burkhalter, A. (1983). Organization of the afferent projections to the wulst in the pigeon. *J. Comp. Neurol.* 214, 103-113.
Bagnoli, P., and Magni, F. (1979). Interaction of optic tract and visual wulst impulses on single units of the pigeon's optic tectum. *Brain Behav. Evol.* 16, 19-37.
Balaban, C. D., and Ulinski, P. S. (1981a). Organization of thalamic afferents to anterior dorsal ventricular ridge in turtles. I. Projections of thalamic nuclei. *J. Comp. Neurol.* 200, 95-129.
Balaban, C. D., and Ulinski, P. S. (1981b). Organization of thalamic afferents to anterior dorsal ventricular ridge in turtles. II. Properties of the rotundo-dorsal map. *J. Comp. Neurol.* 200, 131-150.
Barrett, R. (1970). The pit organs of snakes. In *Biology of the Reptilia* (C. Gans and T. S. Parsons, eds.). Academic Press, London, Vol. 2, pp. 277-314.
Bass, A. H., and Northcutt, R. G. (1981a). Primary retinal targets in the Atlantic loggerhead sea turtle, *Caretta caretta*. *Cell Tissue Res.* 218, 253-264.
Bass, A. H., and Northcutt, R. G. (1981b). Retinal recipient nuclei in the painted turtle, *Chrysemys picta*: an autoradiographic and HRP study. *J. Comp. Neurol.* 199, 97-112.
Bass, A. H., Pritz, M. B., and Northcutt, R. G. (1973). Effects of telencephalic and tectal ablations on visual behavior in the side-necked turtle, *Podocnemis unifilis*. *Brain Res.* 55, 455-460.
Baumgarten, H. G., and Braak, H. (1968). Catecholamine im Gehirn der Eidechse (*Lacerta viridis* and *Lacerta muralis*). *Z. Zellforsch.* 86, 574-608.
Belekhova, M. G. (1979). Neurophysiology of the forebrain. In *Biology of the Reptilia* (C. Gans, R. G. Northcutt, and P. S. Ulinski, eds.). Academic Press, London, Vol. 10, pp. 287-359.
Belekhova, M. G., and Kosareva, A. A. (1971). Organization of the turtle thalamus: visual, somatic and tectal zones. *Brain Behav. Evol.* 4, 337-375.
Benevento, L. A., and Fallon, J. H. (1975). The ascending projections of the

- superior colliculus in the rhesus monkey (*Macaca mulatta*). *J. Comp. Neurol.* 160, 339–362.
- Benowitz, L. I., and Karten, H. J. (1976). Organization of the tectofugal visual pathway in the pigeon: a retrograde transport study. *J. Comp. Neurol.* 167, 503–520.
- Berson, D. M., and Hartline, P. H. (1988). A tecto-rotundal-telencephalic pathway in the rattlesnake: evidence for a forebrain representation of the infrared sense. *J. Neurosci.* 8, 1074–1088.
- Berson, D. M., and McIlwain, J. T. (1982). Retinal Y-cell activation of deep-layer cells in superior colliculus of the cat. *J. Neurophysiol.* 47, 700–714.
- Blough, P. M. (1979). Functional implications of the pigeon's peculiar retinal structure. In *Neural Mechanisms of Behavior in the Pigeon* (A. M. Grand and J. H. Maxwell, eds.). Plenum Press, New York, pp. 71–88.
- Boyko, V. P. (1976). Neuronal receptive fields in mesencephalic visual center of the tortoise *Emys orbicularis*. In *Comparative Neurophysiology and Neurochemistry* (E. M. Kreps, ed.). *Zh. Evol. Biokhim. Fiziol., Suppl.*, pp. 89–96.
- Boyko, V. P., and Davydova, T. V. (1975). Morphofunctional changes in the turtle mesencephalic visual centre after enucleation. *Neurofiziologia (Kiev)* 7, 172–177.
- Braford, M. R., Jr. (1972). Ascending efferent tectal projections in the South American spectacled caiman. *Anat. Rec.* 172, 275–276.
- Braford, M. R., Jr. (1973). Retinal projections in *Caiman crocodilus*. *Am. Zool.* 13, 1345.
- Brauth, S. E., and Kitt, C. A. (1980). The paleostriatal system of *Caiman crocodilus*. *J. Comp. Neurol.* 189, 437–465.
- Bravo, H., and Pettigrew, J. D. (1981). The distribution of neurons projecting from the retina and visual cortex to the thalamus and tectum opticum of the barn owl, *Tyto alba*, and the burrowing owl, *Speotyto cunicularia*. *J. Comp. Neurol.* 199, 419–441.
- Britto, L. R. G. (1978). Hyperstriatal projections to primary visual relays in pigeons: electrophysiological studies. *Brain Res.* 153, 382–386.
- Brown, K. T. (1969). A linear area centralis extending across the turtle retina and stabilized to the horizon by non-visual cues. *Vision Res.* 9, 1053–1062.
- Bruce, L. L. (1982). "Organization and Evolution of the Reptilian Forebrain: Experimental Studies of Forebrain Connections in Lizards." Ph.D. dissertation, Georgetown University, Washington, D.C.
- Bruce, L. L., and Butler, A. B. (1979). Afferent projections to the anterior dorsal ventricular ridge in the lizard *Iguana iguana*. *Neurosci. Abstr.* 5, 140.
- Burns, A. H., and Goodman, D. C. (1967). Retinofugal projections of *Caiman sklerops*. *Exp. Neurol.* 18, 105–115.
- Butler, A. B. (1974). Retinal projections in the night lizard, *Xantusia vigilis* Baird. *Brain Res.* 80, 116–121.
- Butler, A. B. (1976). Telencephalon of the lizard *Gekko gecko* (Linnaeus): some connections of the cortex and dorsal ventricular ridge. *Brain Behav. Evol.* 13, 396–417.
- Butler, A. B. (1978). Organization of ascending tectal projections in the lizard *Gekko gecko*: a new pattern of tectorotundal inputs. *Brain Res.* 147, 353–361.
- Butler, A. B., and Ebbesson, S. O. E. (1975). A Golgi study of the optic tectum of the tegu lizard, *Tupinambis nigropunctatus*. *J. Morphol.* 146, 215–228.
- Butler, A. B., and Ebner, F. F. (1972). Thalamo-telencephalic projections in the lizard *Iguana iguana*. *Anat. Rec.* 172, 282.
- Butler, A. B., and Northcutt, R. G. (1971a). Retinal projections in *Iguana iguana* and *Anolis carolinensis*. *Brain Res.* 26, 1–13.
- Butler, A. B., and Northcutt, R. G. (1971b). Ascending tectal efferent projections in the lizard *Iguana iguana*. *Brain Res.* 35, 597–601.
- Butler, A. B., and Northcutt, R. G. (1973). Architectonic studies of the diencephalon of *Iguana iguana* (Linnaeus). *J. Comp. Neurol.* 149, 439–462.
- Butler, A. B., and Northcutt, R. G. (1978). New thalamic visual nuclei in lizards. *Brain Res.* 149, 469–476.
- Cairney, J. (1926). A general survey of the forebrain of *Sphenodon punctatum*. *J. Comp. Neurol.* 42, 255–348.
- Caldwell, R. B., and Mize, R. R. (1981). Superior colliculus neurons which project to the cat lateral posterior nucleus have varying morphologies. *J. Comp. Neurol.* 203, 53–66.
- Calvin, W. H., and Graubard, K. (1979). Styles of neuronal computation. In *The Neurosciences: Fourth Study Program* (F. O. Schmitt and F. G. Worden, eds.). MIT Press, Cambridge, Mass., pp. 513–524.
- Casagrande, V. A., and Diamond, I. T. (1974). Ablation study of the superior colliculus in the tree shrew (*Tupaia glis*). *J. Comp. Neurol.* 156, 207–238.
- Collett, T. S., and Harkness, L. I. K. (1982). Depth vision in animals. In *Analysis of Visual Behavior* (D. J. Ingle, M. A. Goodale, and R. J. W. Mansfield, eds.). MIT Press, Cambridge, Mass., pp. 111–176.
- Constantine-Paton, M. (1981). Induced ocular-dominance zones in tectal cortex. In *The Organization of the Cerebral Cortex* (F. O. Schmitt, F. G. Worden, G. Adelman, and S. G. Dennis, eds.). MIT Press, Cambridge, Mass., pp. 47–68.
- Crossland, W. J. (1972). "Receptive Field Characteristics of Some Thalamic Visual Nuclei of the Pigeon (*Columba livia*)." Ph.D. dissertation, University of Illinois, Urbana.
- Cruce, J. A. F. (1974). A cytoarchitectonic study of the diencephalon of the tegu lizard, *Tupinambis nigropunctatus*. *J. Comp. Neurol.* 153, 215–238.
- Cruce, J. A. F., and Cruce, W. L. R. (1978). Analysis of the visual system in a lizard, *Tupinambis nigropunctatus*. In *Behavior and Neurology of Lizards* (N. Greenberg and P. D. MacLean, eds.). DHEW Publ. No. (ADM) 77-491, Rockville, Md., National Institutes of Health, pp. 79–90.
- Cruce, W. L. R., and Cruce, J. A. F. (1975). Projections from the retina to the lateral geniculate nucleus and mesencephalic tectum in a reptile, *Tupinambis nigropunctatus*: a comparison of anterograde transport and anterograde degeneration. *Brain Res.* 85, 221–228.
- Cruce, W. L. R., and Newman, D. B. (1981). Brain stem origins of spinal projections in the lizard *Tupinambis nigropunctatus*. *J. Comp. Neurol.* 198, 185–208.
- Curwen, A. O., and Miller, R. N. (1939). The pretectal region of the turtle, *Pseudemys scripta troostii*. *J. Comp. Neurol.* 71, 99–120.

- Dacey, D. M., and Ulinski, P. S. (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 Ulinski, P. S. (1986a). Optic tectum of the eastern garter snake, *Thamnophis sirtalis*. I. Efferent pathways. *J. Comp. Neurol.* 245, 1–28.
- Dacey, D. M., and Ulinski, P. S. (1986b). Optic tectum of the eastern garter snake, *Thamnophis sirtalis*. II. Morphology of efferent neurons. *J. Comp. Neurol.* 245, 198–237.
- Dacey, D. M., and Ulinski, P. S. (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 Ulinski, P. S. (1986d). Optic tectum of the eastern garter snake, *Thamnophis sirtalis*. IV. Morphology of retinal afferents. *J. Comp. Neurol.* 245, 301–318.
- Dacey, D. M., and Ulinski, P. S. (1986e). Optic tectum of the eastern garter snake, *Thamnophis sirtalis*. V. Morphology of brainstem afferents. *J. Comp. Neurol.* 245, 423–453.
- Davydova, T. V. (1971). The ultrastructure of nerve terminals in the tectum opticum of the turtle (*Emys orbicularis*). *Cytologia* 13, 433–440.
- Davydova, T. V. (1973). The ultrastructure of the midbrain in tectum visual fibers of *Emys orbicularis* L. in the norm and after degeneration. *Cytologia* 15, 150–155.
- Davydova, T. V., Boyko, V. P., and Goncharova, N. V. (1982). Correlations between the morpho-functional organization of some parts of visual analyzer and ecology in chelonia: II. Morpho-functional characteristics of the visual nerve and tectum after unilateral enucleation. *J. Hirnforsch.* 23, 433–446.
- Davydova, T. V., and Goncharova, N. V. (1970). Cytoarchitectonics and neuronal composition of midbrain tectum in the turtle (*Emys orbicularis*). *Arkh. Anat. Gistol. Embriol.* 59, 53–61.
- Davydova, T. V., Goncharova, N. V., and Boyko, V. P. (1976). Retinotectal system of the tortoise, *Testudo horsfieldi*, Gray (Morpho-functional study in the norm and after enucleation). *J. Hirnforsch.* 17, 463–488.
- Davydova, T. V., Goncharova, N. V., and Boyko, V. P. (1982). Correlation between the morpho-functional organization of some portions of visual analyzer of chelonia and their ecology: I. Normal morpho-functional characteristics of the optic nerve and the tectum opticum. *J. Hirnforsch.* 23, 271–286.
- Davydova, T. V., and Mazurskaya, P. Z. (1973). Ultrastructural features of the nerve terminal degeneration in the turtle tectum opticum after enucleation. *Cytologia* 15, 22–30.
- Davydova, T. V., and Smirnov, G. D. (1973). Retinotectal connections in the tortoise: an electron microscope study of degeneration in optic nerve and midbrain tectum. *J. Hirnforsch.* 14, 473–492.
- De Britto, L. R. G., Brunelli, M., Francesconi, W., and Magni, F. (1975). Visual response pattern of thalamic neurons in the pigeon. *Brain Res.* 97, 337–343.
- Distel, H. (1978). Behavior and electrical brain stimulation in the green iguana, *Iguana iguana*. II. Stimulation effects. *Exp. Brain Res.* 31, 353–367.
- Distel, H., and Ebbesson, S. O. E. (1975). Connections of the thalamus in the monitor lizard. *Soc. Neurosci. Abstr.* 1, 559.
- Duff, T. A., Scott, G., and Mai, R. (1981). Regional differences in pigeon optic tract, chiasm and retinoreceptive layers of optic tectum. *J. Comp. Neurol.* 198, 231–248.
- Ebbesson, S. O. E. (1967). Ascending axon degeneration following hemisection of the spinal cord in the tegu lizard (*Tupinambis nigropunctatus*). *Brain Res.* 5, 178–206.
- Ebbesson, S. O. E. (1969). Brain stem afferents from the spinal cord in a sample of reptilian and amphibian species. *Ann. N.Y. Acad. Sci.* 167, 80–101.
- Ebbesson, S. O. E. (1978). Somatosensory pathways in lizards: the identification of the medial lemniscus and related structures. In *Behavior and Neurology of Lizards* (N. Greenberg and P. D. MacLean, eds.), DHEW Publ. No. (ADM) 77-491, National Institutes of Health, Rockville, Md. pp. 91–104.
- Ebbesson, S. O. E. (1981). Projections of the optic tectum and the mesencephalic nucleus of the trigeminal nerve in the tegu lizard (*Tupinambis nigropunctatus*). *Cell Tiss. Res.* 216, 151–165.
- Ebbesson, S. O. E., and Goodman, D. C. (1981). Organization of ascending spinal projections in *Caiman crocodilus*. *Cell Tiss. Res.* 215, 383–396.
- Ebbesson, S. O. E., and Karten, H. J. (1981). Terminal distribution of retinal fibers in the tegu lizard (*Tupinambis nigropunctatus*). *Cell Tiss. Res.* 215, 591–606.
- Ebbesson, S. O. E., and Vanegas, H. (1976). Projections of the optic tectum in two teleost species. *J. Comp. Neurol.* 165, 161–180.
- Eccles, J. C., Ito, M., and Szentagothai, J. (1967). *The Cerebellum as a Neuronal Machine*. Springer-Verlag, New York.
- Edwards, S. B. (1977). The commissural projection of the superior colliculus in the cat. *J. Comp. Neurol.* 173, 23–40.
- Edwards, S. B. (1980). The deep cell layers of the superior colliculus: their reticular characteristics and structural organization. In *The Reticular Formation Revisited* (J. A. Thompson and M. A. Brazier, eds.). Raven Press, New York, pp. 193–209.
- Edwards, S. B., Ginsburgh, C. L., Henkel, C. K., and Stein, B. E. (1979). Sources of subcortical projections to the superior colliculus in the cat. *J. Comp. Neurol.* 184, 309–330.
- Elprana, D., Wouterlood, F. G., and Alones, V. (1980). A corticotectal projection in the lizard *Agama agama*. *Neurosci. Lett.* 18, 251–256.
- Ewert, J.-P. (1976). The visual system of the toad: behavioral and physiological studies on a pattern recognition system. In *The Amphibian Visual System* (K. V. Fite, ed.). Academic Press, New York, pp. 141–202.
- Ewert, J.-P. (1982). Neuronal basis of configurational prey selection in the common toad. In *Analysis of Visual Behavior* (D. J. Ingle, M. A. Goodale, and R. J. W. Mansfield, eds.). MIT Press, Cambridge, Mass., pp. 7–45.
- Ewert, J.-P., and von Seelen, W. (1974). Neurobiologie und Systemtheorie eines visuellen Muster-erkennungs Mechanismus bei Kröten. *Kybernetik* 14, 167–183.
- Fish, S. E., Goodman, D. K., Kuo, D. C., Polcer, J. D., and Rhoades, R. W. (1982). The intercollicular pathway in the golden hamster: an anatomical study. *J. Comp. Neurol.* 204, 6–20.
- Fite, K. V., and Scalia, F. (1976). Central visual pathways in the frog. In *The*

- Amphibian Visual System* (K. V. Fite, ed.). Academic Press, New York, pp. 87-118.
- Fitzpatrick, D., Carey, R. G., and Diamond, I. T. (1980). The projection of the superior colliculus upon the lateral geniculate body in *Tupaia glis* and *Galago senegalensis*. *Brain Res.* 194, 494-499.
- Foster, R. E., and Hall, W. C. (1975). The connections and laminar organization of the optic tectum in a reptile (*Iguana iguana*). *J. Comp. Neurol.* 163, 397-426.
- Foster, R. E., and Hall, W. C. (1978). The organization of central auditory pathways in a reptile, *Iguana iguana*. *J. Comp. Neurol.* 178, 783-832.
- Friedlander, M. J., Lin, C.-S., Stanford, L. R., and Sherman, S. M. (1981). Morphology of functionally identified neurons in the lateral geniculate nucleus of the cat. *J. Neurophysiol.* 46, 80-129.
- Galifret, Y. (1968). Les diverse aires fonctionnelles de la retine du pigeon. *Zeit. Zellforsch.* 86, 535-545.
- Geri, G. A., Kimsey, R. A., and Dvorak, C. A. (1982). Quantitative electron microscopic analysis of optic nerve of turtle, *Pseudemys*. *J. Comp. Neurol.* 207, 99-103.
- Gilbert, C. D. (1983). Microcircuitry of the visual cortex. *Ann. Rev. Neurosci.* 6, 217-248.
- Goldberg, M. E., and Robinson, D. L. (1978). Visual system: superior colliculus. In *Handbook of Behavioral Neurobiology* (R. B. Masterson, ed.). Plenum Press, New York, pp. 119-614.
- Graham, J. (1977). An autoradiographic study of the efferent connections of the superior colliculus in the cat. *J. Comp. Neurol.* 173, 629-654.
- Graham, J., Berman, N., and Murphy, E. H. (1982). Effects of cortical lesions on receptive field properties of single units in the superior colliculus of rabbits. *J. Neurophysiol.* 47, 256-271.
- Graham, J., and Casagrande, V. A. (1980). A light microscopic study of the superficial layers of the superior colliculus of the tree shrew (*Tupaia glis*). *J. Comp. Neurol.* 191, 133-151.
- Granda, A. M., and O'Shea, P. J. (1972). Spectral sensitivity of the green turtle (*Chelonia mydas mydas*) determined by electrical responses to heterochromatic light. *Brain Behav. Evol.* 5, 143-154.
- Granda, A. M., and Stirling, C. E. (1965). Differential spectral sensitivity in the optic tectum and eye of the turtle. *J. Gen. Physiol.* 48, 901-917.
- Granda, A. M., and Yazulla, S. (1971). The spectral sensitivity of single units in the nucleus rotundus of pigeon (*Columba livia*). *J. Gen. Physiol.* 57, 363-384.
- Grantyn, A., and Grantyn, R. (1982). Axonal patterns and sites of termination of cat superior collicular neurons projecting in the tecto-bulbo-spinal tract. *Exp. Brain Res.* 46, 243-256.
- Grantyn, R., Ludwig, R., and Eberhardt, W. (1984). Neurons of the superior tectal gray: an intracellular HRP-study on the kitten superior colliculus *in vitro*. *Exp. Brain Res.* 55, 172-176.
- Graybiel, A. M. (1975). Anatomical organization of retinotectal afferents in the cat: an autoradiographic study. *Brain Res.* 96, 1-23.
- Graybiel, A. M. (1978). Organization of the nigrotectal connection: an experimental tracer study in the cat. *Brain Res.* 143, 339-348.
- Grobstein, P. (1988). Between the retinotectal projection and directed movements: topography of a sensorimotor interface. *Brain Behav. Evol.* 31, 34-48.
- Grobstein, P., Comer, C., Hollyday, M., and Archer, S. M. (1978). A crossed isthmotectal projection in *Rana pipiens* and its involvement in the ipsilateral visuotectal projection. *Brain Res.* 156, 117-123.
- Grobstein, P., Comer, C., and Kostyk, S. K. (1983). Frog prey capture behavior: between sensory maps and directed motor output. In *Advances in Vertebrate Neuroethology* (J.-P. Ewert, R. R. Capranica, and D. J. Ingle, eds.). Plenum Press, New York, pp. 331-348.
- Grover, B. G., and Sharma, S. C. (1981). Organization of extrinsic tectal connections in the goldfish (*Carassius auratus*). *J. Comp. Neurol.* 196, 471-488.
- Gruberg, E. R., Kicliter, E., Newman, E. A., Kass, L., and Hartline, P. H. (1979). Connections of the tectum of the rattlesnake *Crotalus viridis*: an HRP study. *J. Comp. Neurol.* 188, 31-42.
- Gruberg, E. R., and Lettvin, J. Y. (1980). Anatomy and physiology of a binocular system in the frog *Rana pipiens*. *Brain Res.* 192, 313-325.
- Gruberg, E. R., and Udin, S. (1978). Topographic projections between nucleus isthmi and the tectum of the frog *Rana pipiens*. *J. Comp. Neurol.* 179, 487-500.
- Gusel'nikov, V. I., Morenkov, E. D., and Pivovarov, A. S. (1970). On functional organization of the visual system of the tortoise (*Emys orbicularis*). *Fiziol. Zh. SSSR Sechenova* 56, 1377-1385.
- Hall, W. C., and Ebner, F. F. (1970a). Parallels in the visual afferent projections of the thalamus in the hedgehog (*Paraechinus hypomelas*) and the turtle (*Pseudemys scripta*). *Brain Behav. Evol.* 3, 135-154.
- Hall, W. C., and Ebner, F. F. (1970b). Thalamotelencephalic projections in the turtle *Pseudemys scripta*. *J. Comp. Neurol.* 140, 101-122.
- Hall, J. A., Foster, R. E., Ebner, F. F., and Hall, W. C. (1977). Visual cortex in a reptile, the turtle (*Pseudemys scripta* and *Chrysemys picta*). *Brain Res.* 130, 197-216.
- Halpern, M. (1973a). Retinal projections in blind snakes. *Science* (N.Y.) 182, 390-391.
- Halpern, M., and Frumin, N. (1973). Retinal projections in a snake (*Thamnophis sirtalis*). *J. Morphol.* 141, 359-382.
- Harkness, L. (1977). Chameleons use accommodation cues to judge distance. *Nature* (London) 267, 346-349.
- Harrell, J. V., Caldwell, R. B., and Mize, R. R. (1982). The superior colliculus neurons which project to the dorsal and ventral lateral geniculate nuclei in the cat. *Exp. Brain Res.* 46, 234-242.
- Harris, L. R. (1980). The superior colliculus and movements of the head and eyes in cats. *J. Physiol.* (London) 300, 367-391.
- Harting, J. K. (1977). Descending pathways from the superior colliculus: an autoradiographic analysis in the rhesus monkey (*Macaca mulatta*). *J. Comp. Neurol.* 173, 583-612.

- Harting, J. K., Hall, W. C., Diamond, I. T., and Martin, G. F. (1973). Anterograde degeneration study of the superior colliculus in *Tupaia glis*: evidence for a subdivision between superficial and deep layers. *J. Comp. Neurol.* 148, 361–386.
- Harting, J. K., Huerta, M. F., Frankfurter, A. J., Strominger, N. L., and Royce, G. J. (1980). Ascending pathways from the monkey superior colliculus: an autoradiographic analysis. *J. Comp. Neurol.* 192, 853–882.
- Hartline, P. H. (1971). Mid-brain responses of the auditory and somatic vibration systems in snakes. *J. Exp. Biol.* 54, 373–390.
- Hartline, P. H. (1984). The optic tectum of reptiles: neurophysiological studies. In *Comparative Neurology of the Optic Tectum* (H. Vanegas, ed.). Plenum Press, New York, pp. 601–618.
- Hartline, P. H., Kass, L., and Loop, M. S. (1978). Merging of modalities in the optic tectum: infrared and visual integration in rattlesnakes. *Science* (N.Y.) 199, 1225–1229.
- Hayes, B. P., and Webster, K. E. (1975). An electron microscopic study of the retinoreceptive layers of the pigeon optic tectum. *J. Comp. Neurol.* 162, 447–466.
- Heller, S. B., and Ulinski, P. S. (1987). Morphology of geniculocortical axons in the turtles, of the genera *Pseudemys* and *Chrysemys*. *Anat. Embryol.* 175, 505–515.
- Heric, T. M., and Kruger, L. (1965). Organization of the visual projection upon the optic tectum of a reptile (*Alligator mississippiensis*). *J. Comp. Neurol.* 124, 101–112.
- Heric, T. M., and Kruger, L. (1966). The electrical response evoked in the reptilian optic tectum by afferent stimulation. *Brain Res.* 2, 187–199.
- Hess, W. R., Burgi, S., and Bucher, V. (1946). Motorische Funktion des Tektal and Tegmentalgebietes. *Monatsschr. Psychiatr. Neurol.* 112, 1–52.
- Hikosaka, O., and Wurtz, R. H. (1983). Visual and oculomotor functions of monkey substantia nigra pars reticulata. IV. Relation of substantia nigra to superior colliculus. *J. Neurophysiol.* 49, 1285–1301.
- Holcombe, V., and Hall, W. C. (1981a). The laminar origin and distribution of the crossed tectoreticular pathways. *J. Neurosci.* 1, 1103–1112.
- Holcombe, V., and Hall, W. C. (1981b). Laminar origin of ipsilateral tectopontine pathways. *Neuroscience* 6, 255–260.
- Hoogland, P. V. (1977). Efferent connections of the striatum in *Tupinambis nigropunctatus*. *J. Morphol.* 152, 229–246.
- Hoogland, P. V. (1982). Brainstem afferents to the thalamus in a lizard, *Varanus exanthematicus*. *J. Comp. Neurol.* 210, 152–162.
- Hubel, D. H., Le Vay, S., and Wiesel, T. N. (1975). Mode of termination of retinotectal fibers in macaque monkey: an autoradiographic study. *Brain Res.* 96, 25–40.
- Huber, G. C., and Crosby, E. C. (1926). On thalamic and tectal nuclei and fiber paths in the brain of the American alligator. *J. Comp. Neurol.* 40, 97–227.
- Huber, G. C., and Crosby, E. C. (1933). The reptilian optic tectum. *J. Comp. Neurol.* 57, 57–164.
- Huber, G. C., and Crosby, E. C. (1943). A comparison of the mammalian and reptilian tecta. *J. Comp. Neurol.* 78, 133–168.
- Huerta, M. F., Frankfurter, A. J., and Harting, J. K. (1981). The trigemino-collicular projection in the cat: patch-like endings within the intermediate gray. *Brain Res.* 211, 1–14.
- Huerta, M. F., and Harting, J. K. (1982). Projections of the superior colliculus to the supraspinal nucleus and the cervical spinal cord gray of the cat. *Brain Res.* 242, 326–331.
- Huerta, M. F., and Harting, J. K. (1984). The mammalian superior colliculus: studies of its morphology and connections. In *Comparative Neurology of the Optic Tectum* (H. Vanegas, ed.). Plenum Press, New York, pp. 687–774.
- Hunt S. P., and Kunzle, H. (1976). Observations on the projections and intrinsic organization of the pigeon optic tectum: an autoradiographic study based on anterograde and retrograde axonal and dendritic flow. *J. Comp. Neurol.* 170, 153–172.
- Hunt, S. P., Streit, P., Kunzle, H., and Cuenod, M. (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. (1968). Visual releasers of prey-catching behavior in frogs and toads. *Brain Behav. Evol.* 1, 500–518.
- Ingle, D. (1973). Disinhibition of tectal neurons by pretectal lesions in the frog. *Science* (N.Y.) 180, 422–424.
- Ingle, D. (1976). Spatial vision in anurans. In *The Amphibian Visual System* (K. Fite, ed.). Academic Press, New York, pp. 119–140.
- Ingle, D. (1980). Some effects of pretectum lesions on the frog's detection of stationary objects. *Behav. Brain Res.* 39–163.
- Ingle, D. (1982). Organization of visuomotor behaviors in vertebrates. In *Analysis of Visual Behavior* (D. J. Ingle, M. A. Goodale, and R. J. M. Mansfield, eds.). MIT Press, Cambridge, Mass., pp. 67–110.
- Ingle, D., and Sprague, J. M. (1975). Sensorimotor functions of the midbrain tectum. *Neurosci. Res. Prog. Bull.* 13, 173–288.
- Ito, H. (1970). Fine structure of the carp tectum opticum. *J. Hirnforsch.* 12, 325–354.
- Kaas, J. H. (1982). The segregation of function in the nervous system: why do sensory systems have so many subdivisions? *Contributions Sensory Physiol.* 7, 201–240.
- Karten, H. J. (1965). Projections of the optic tectum of the pigeon (*Columba livia*). *Anat. Rec.* 151, 369.
- Karten, H. J., Hodos, W., Nauta, W. J. H., and Revzin, A. M. (1973). Neural connections of the "visual Wulst" of the avian telencephalon: experimental studies in the pigeon and owl. *J. Comp. Neurol.* 150, 253–278.
- Kass, L., Loop, M. S., and Hartline, P. M. (1978). Anatomical and physiological localization of visual and infrared cell layers in the tectum of pit vipers. *J. Comp. Neurol.* 182, 811–820.
- Kawamura, K., Brodal, A., and Hodevik, G. (1974). The projection of the superior colliculus onto the reticular formation of the brainstem: an experimental anatomical study in the cat. *Exp. Brain Res.* 19, 1–19.
- Kawamura, S., Fukushima, N., Hattori, S., and Kudo, M. (1980). Laminar segregation of cells of origin of ascending projections from the superficial layers of the superior colliculus in the cat. *Brain Res.* 184, 486–490.

- Kawamura, K., and Hashikawa, T. (1978). Cell bodies of origin of the reticular projection from the superior colliculus in the cat: an experimental study with the use of horseradish peroxidase as a tracer. *J. Comp. Neurol.* 182, 1-16.
- Kawamura, S., and Kobayashi, E. (1975). Identification of laminar origin of some tectothalamic fibers in the cat. *Brain Res.* 9, 281-285.
- Kawamura, S., Sprague, J. M., and Niimi, K. (1974). Corticofugal projections from the visual cortices to the thalamus, pretectum and superior colliculus in the cat. *J. Comp. Neurol.* 158, 339-362.
- Keller, E. L. (1974). Participation of medial pontine reticular formation in eye movement generation in monkey. *J. Neurophysiol.* 37, 316-332.
- Killackey, H. P., and Erzurumlu, R. H. (1981). Trigeminal projections to the colliculus of the rat. *J. Comp. Neurol.* 201, 221-242.
- Kishida, R., Amemiya, F., Kusunoki, T., and Terashima, S. (1980). A new tectal afferent nucleus of the infrared sensory systems in the medulla oblongata of crotaline snakes. *Brain Res.* 195, 271-279.
- Knapp, H., and Kang, D. (1968a). The visual pathways of the snapping turtle (*Chelydra serpentina*). *Brain Behav. Evol.* 1, 19-42.
- Knapp, H., and Kang, D. (1968b). The retinal projections of the side-necked turtle (*Podocnemis unifilis*) with some notes on the possible origin of the pars dorsalis of the lateral geniculate body. *Brain Behav. Evol.* 1, 369-404.
- Kolb, H. (1982). The morphology of the bipolar cells, amacrine cells and ganglion cells in the retina of the turtle *Pseudemys scripta elegans*. *Phil. Trans. R. Soc. Lond.* B298, 355-393.
- Kosareva, A. A. (1967). Projection of optic fibers to visual centers in a turtle (*Emys orbicularis*). *J. Comp. Neurol.* 130, 263-276.
- Kosareva, A. A. (1974). Afferent and efferent connections of the nucleus rotundus in the tortoise *Emys orbicularis*. *Zh. Evol. Biokhim. Fiziol.* 10, 395-399.
- Kruger, L. (1969). The topography of the visual projection to the mesencephalon: a comparative survey. *Brain Behav. Evol.* 3, 169-177.
- Kusunoki, T. (1971). The chemoarchitectonics of the turtle brain. *Yohokama Med. Bull.* 22, 1-29.
- Langer, T. P., and Lund, R. D. (1974). The upper layers of the superior colliculus of the rat: a Golgi study. *J. Comp. Neurol.* 158, 405-434.
- Lara, R., Arbib, M. A., and Cromarty, A. S. (1982). The role of the tectal column in facilitation of amphibian prey-catching behavior: a neural model. *J. Neurosci.* 2, 521-530.
- Lazar, G., and Szekely, G. (1967). Golgi studies on the optic center of the frog. *J. Hirnforsch.* 9, 329-344.
- Lee, C., Rohrer, W. H., and Sparks, D. L. (1988). Population coding of saccadic eye movements by neurons in the superior colliculus. *Nature* 332, 357-360.
- Leghissa, S. (1962). L'evoluzione del tetto ottico nei bassi vertebrati. *Arch. Ital. Anat. Embryol.* 67, 334-413.
- Lennie, P. (1980). Parallel visual pathways: a review. *Vision Res.* 20: 561-594.
- Leresche, N., Hardy, O., and Jassik-Gerschenfeld, D. (1983). Receptive field properties of single cells in the pigeon's optic tectum during cooling of the "visual Wulst." *Brain Res.* 267, 225-236.
- Lohman, A. H. M., and van Woerden-Verkley, I. (1978). Ascending connections to the forebrain in the tegu lizard. *J. Comp. Neurol.* 182, 555-594.
- Luiten, P. G. M. (1981). Afferent and efferent connections of the optic tectum in the carp (*Cyprinus carpis*). *Brain Res.* 220, 51-65.
- Lund, J. S. (1981). Intrinsic organization of the primate visual cortex, Area 17, as seen in Golgi preparations. In *The Organization of the Cerebral Cortex* (F. O. Schmitt, F. G. Worden, G. Adelman, and S. G. Dennis, eds.). MIT Press, Cambridge, Mass., pp. 105-124.
- Lund, R. D. (1969). Synaptic patterns of the superficial layers of the superior colliculus of the rat. *J. Comp. Neurol.* 135, 179-208.
- Lund, R. D. (1972). Synaptic patterns in the superficial layers of the superior colliculus of the monkey (*Macaca mulatta*). *Exp. Brain Res.* 15, 194-211.
- Magalhaes-Castro, H. H., Dolabela de Lima, A., Saraiva, P. E. S., and Magalhaes-Castro, B. (1978). Horseradish peroxidase labeling of cat tectotectal cells. *Brain Res.* 148, 1-13.
- Marchiafava, P. L., and Wagner, H. G. (1981). Interactions leading to colour opponency in ganglion cells of the turtle retina. *Proc. R. Soc. London, Ser. B* 211, 261-267.
- Marchiafava, P. L., and Weiler, R. (1980). Intracellular analysis and structural correlates of the organization of inputs to ganglion cells in the retina of the turtle. *Proc. R. Soc. Lond., Ser. B* 208, 103-113.
- Martin, G. F. (1969). Efferent tectal pathways of the opossum, *Didelphis virginiana*. *J. Comp. Neurol.* 125, 209-224.
- Masai, H. (1973). Structural patterns of the optic tectum in Japanese snakes of the family Colubridae, in relation to habit. *J. Hirnforsch.* 14, 367-374.
- Maxwell, J. H., and Granda, A. M. (1979). Receptive fields of movement-sensitive cells in the pigeon thalamus. In *Neural Mechanisms of Behavior in the Pigeon* (C. A. M. Granda and J. H. Maxwell, eds.). Plenum Press, New York, pp. 177-198.
- May, P. J., and Hall, W. C. (1981). A relationship between nigrotectal and crossed tectoreticular pathways in the grey squirrel. *Neurosci. Abst.* 7, 776.
- May, P. J., Lin, C.-S., McIlwain, J. T., and Hall, W. C. (1982). Morphology of tecto-pulvinar neurons in the grey squirrel. *Neurosci. Abst.* 8, 406.
- 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 cats' superior colliculus. *J. Neurophysiol.* 47, 167-178.
- Meek, J. A. (1981a). A Golgi-electron microscopic study of the goldfish optic tectum. I. Description of afferents, cell types, and synapses. *J. Comp. Neurol.* 199, 149-174.
- Meek, J. A. (1981b). A Golgi-electron microscopic study of the goldfish optic tectum. II. Quantitative aspects of synaptic organization. *J. Comp. Neurol.* 199, 175-190.
- Mendez-Otero, R., Rocha-Miranda, C. E., and Perry, V. H. (1980). The organization of the parabigemino-tectal projections in the opossum. *Brain Res.* 198, 183-189.
- Mesulam, M.-M. (1982). *Tracing Neural Connections with Horseradish Peroxidase*. John Wiley, New York.
- Miceli, D., Peyrichoux, J., and Repérant, J. (1975). The retino-thalamo-hyperstriatal pathway in the pigeon (*Columba livia*). *Brain Res.* 100, 125-131.

- Mize, R. R., Spencer, R. F. S., and Sterling, P. (1981). Neurons and glia in cat superior colliculus accumulate ^3H -gamma-aminobutyric acid (GABA). *J. Comp. Neurol.* 202, 300–312.
- Mize, R. R., and Sterling, P. (1976). Synaptic organization of the superficial gray layer of cat superior colliculus analyzed by serial section cinematography. *Invest. Ophthalmol. Vis. Sci.* 15, 47.
- Molenaar, G. J. (1974). An additional trigeminal system in certain snakes possessing infrared receptors. *Brain Res.* 78, 340–344.
- Molenaar, G. J., and Fizaan-Oostveen, J. L. F. P. (1980). Ascending projections from the lateral descending and common sensory trigeminal nuclei in python. *J. Comp. Neurol.* 189, 555–572.
- Morenkov, E. D., and Pivavarov, A. S. (1973). Peculiarities of the organization of the visual system in reptiles. In *Functional Organization and Evolution of the Vertebrate Visual System*. Nauka, Leningrad, pp. 95–107.
- Morenkov, E. D., and Pivavarov, A. S. (1975). Peculiarities of cell reactions in turtle dorsal and ventral thalamus to visual stimuli. *Zh. Evol. Biokhim. Fiziol.* 11, 70–75.
- Moschovakis, A. K., Karabelas, A. B., and Highstein, S. M. (1988a). Structure-function relationships in the primate superior colliculus. I. Morphological classification of efferent neurons. *J. Neurophysiol.* 60, 232–262.
- Moschovakis, A. K., Karabelas, A. B., and Highstein, S. M. (1988b). Structure-function relationships in the primate superior colliculus. II. Morphological identity of presaccadic neurons. *J. Neurophysiol.* 60, 263–302.
- Murray, E. A., and Coulter, J. D. (1982). Organization of tectospinal neurons in the cat and rat superior colliculus. *Brain Res.* 243, 201–214.
- Nagata, T., Magalhaes-Castro, H. H., Saraiva, P. E. S., and Magalhaes-Castro, B. (1980). Absence of tectotectal pathway in the rabbit: an anatomical and electrophysiological study. *Neurosci. Lett.* 17, 125–130.
- Newman, D. B., and Cruce, W. L. R. (1982). The organization of the reptilian brainstem reticular formation: a comparative study using Nissl and Golgi techniques. *J. Morphol.* 173, 325–349.
- Newman, D. B., Cruce, W. L. R., and Bruce, L. L. (1982). The sources of supraspinal afferents to the spinal cord in a variety of limbed reptiles. I. Reticulospinal systems. *J. Comp. Neurol.* 215, 17–32.
- Newman, E. A., Gruberg, E. R., and Hartline, P. H. (1980). Infrared trigemino-tectal pathway in the rattlesnake and in the python. *J. Comp. Neurol.* 191, 465–478.
- Newman, E. A., and Hartline, P. H. (1981). Integration of visual and infrared information in bimodal neurons of the rattlesnake optic tectum. *Science* (N.Y.) 213, 789–791.
- Niida, A., Oka, H., and Iwata, K. S. (1980). Visual responses of morphologically identified tectal neurons in the carp. *Brain Res.* 201, 361–371.
- Northcutt, R. G. (1978). Forebrain and midbrain organization in lizards and its evolutionary significance. In *The Behavior and Neurology of Lizards* (N. Greenberg and P. D. MacLean, eds.). National Institute of Mental Health, Rockville, Md., pp. 11–64.
- Northcutt, R. G. (1981). Evolution of the telencephalon in nonmammals. *Ann. Rev. Neurosci.* 4, 301–350.
- 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 *Comparative Neurology of the Optic Tectum* (H. Vanegas, ed.). Plenum Press, New York, pp. 547–600.
- Northcutt, R. G., Braford, M. R., Jr., and Landreth, G. E. (1974). Retinal projections in the tuatara, *Sphenodon punctatus*: an Autoradiographic study. *Anat. Rec.* 178, 428.
- Northcutt, R. G., and Butler, A. B. (1974a). Retinal projections in the northern water snake, *Natrix sipedon sipedon*. *J. Morphol.* 142, 117–136.
- Northcutt, R. G., and Butler, A. B. (1974b). Evolution of reptilian visual systems: retinal projections in a nocturnal lizard, *Gekko gecko* (Linnaeus). *J. Comp. Neurol.* 157, 453–465.
- Palmer, L. A., and Rosenquist, A. C. (1974). Visual receptive fields of single striate cortical units projecting to the superior colliculus in the cat. *Brain Res.* 67, 27–42.
- Parent, A. (1979). Monoaminergic systems in reptile brains. In *Biology of the Reptilia* (C. Gans, R. G. Northcutt, and P. S. Ulinski, eds.). Academic Press, London, Vol. 10, pp. 247–285.
- Pedersen, R. (1973). Ascending spinal projections in three species of side-necked turtle: *Podocnemis unifilis*, *Pelusios subreger*, and *Pelomedusa subrufa*. *Anat. Rec.* 175, 409.
- Peterson, E. H. (1978a). Size classes of ganglion cells which project to the optic tectum in the turtle, *Pseudemys scripta*. *Anat. Rec.* 190, 509–510.
- Peterson, E. H. (1978b). Horizontal cells in the optic tectum of the turtle, *Pseudemys scripta elegans*. *Am. Zool.* 18, 587.
- Peterson, E. H. (1981). Regional specialization in the retinal ganglion cell projection to the optic tectum of *Dipsosaurus dorsalis* (Iguanidae). *J. Comp. Neurol.* 196, 225–252.
- Peterson, E. H. (1982). Morphology of retinal ganglion cells in a turtle, *Pseudemys scripta*. *Neurosci. Abstr.* 8, 48.
- Peterson, E. H., and Ulinski, P. S. (1979). Quantitative studies of retinal ganglion cells in a turtle, *Pseudemys scripta elegans*. I. Number and distribution of ganglion cells. *J. Comp. Neurol.* 186, 17–42.
- Peterson, E. H., and Ulinski, P. S. (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.
- Pitts, W. H., and McCulloch, W. S. (1947). How we know universals, the perception of auditory and visual forms. *Bull. Math. Biophys.* 9, 127–147.
- Pritz, M. B. (1975). Anatomical identification of a telencephalic visual area in crocodiles: ascending connections of nucleus rotundus in *Caiman crocodilus*. *J. Comp. Neurol.* 164, 323–338.
- Quiroga, J. C. (1978). The tectum opticum of *Pantodactylus schreiberii* (Teiidae, Lacertilia, Reptilia). *J. Hirnforsch.* 19, 109–131.

- Rainey, W. T. (1979). Organization of nucleus rotundus, a tectofugal thalamic nucleus in turtles. I. Nissl and Golgi analyses. *J. Morphol.* 160, 121–142.
- Rainey, W. T., and Ulinski, P. S. (1982a). Organization of nucleus rotundus, a tectofugal thalamic nucleus in turtles. II. Ultrastructural analyses. *J. Comp. Neurol.* 209, 187–207.
- Rainey, W. T., and Ulinski, P. S. (1982b). Organization of nucleus rotundus, a tectofugal thalamic nucleus in turtles. III. The tectorotundal projection. *J. Comp. Neurol.* 209, 208–223.
- Ramón, P. (1896). Estructura de encefalo del camaleon. *Rev. Trim. Micrograf.* 1, 146–182.
- Ramón y Cajal, S. (1911). *Histologie du Système Nerveux de l'Homme et des Vertèbres*. Maloine, Paris.
- Reiner, A., Brauth, S. E., Kitt, C. A., and Karten, H. J. (1980). Basal ganglionic pathways to the tectum: studies in reptiles. *J. Comp. Neurol.* 193, 565–589.
- Repérant, J. (1973). Les voies et les centres optiques primaires chez la vipere (*Vipera aspis*). *Arch. Anat. Micr. Morph. Exp.* 62, 323–352.
- Repérant, J. (1975). Nouvelles données sur les projections rétiniennes chez *Caiman sclerops*. Etude radio-autographique. *C. R. Acad. Sc. Paris, Serie D.* 280, 2881–2884.
- Repérant, J., Peyrichoux, J., and Rio, J.-P. (1981). Fine structure of the superficial layers of the viper optic tectum: a Golgi and electron-microscopic study. *J. Comp. Neurol.* 199, 393–417.
- Repérant, J., Raffin, J.-P., and Miceli, D. (1974). La voie retino-thalamo-hyperstriatale chez le pouissin (*Callus domesticus*). *C. R. Acad. Sci. Paris* 279, 279–281.
- Repérant, J., and Rio, J.-P. (1976). Retinal projections in *Vipera aspis*: a reinvestigation using light radio-autographic and electron microscopic degeneration techniques. *Brain Res.* 107, 603–609.
- Repérant, J., Rio, J.-P., Miceli, D., and Lemire, M. (1978). A radioautographic study of retinal projections in Type I and Type II lizards. *Brain Res.* 142, 401–411.
- Revzin, A. M. (1970). Some characteristics of wide-field units in the brain of the pigeon. *Brain Behav. Evol.* 3, 195–204.
- Revzin, A. M. (1979). Functional localization in the nucleus rotundus. In *Neural Mechanisms of Behavior* (A. M. Granda and J. H. Maxwell, eds.). Plenum Press, New York, pp. 165–176.
- Revzin, A. M., and Karten, H. J. (1966). Rostral projections of the optic tectum and nucleus rotundus in the pigeon. *Brain Res.* 3, 264–276.
- Rhoades, R. W., Kuo, D. C., Polcer, J. D., Fish, S. E., and Voneida, T. J. (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.
- Rhoades, R. W., Mooney, R. D., Rhorer, W. H., Nikolettseas, M. M., and Fish, S. (1989). Organization of the projection from the superficial to the deep layers of the hamster's superior colliculus as demonstrated by the anterograde transport of *Phaseolus vulgaris* leucoagglutinin. *J. Comp. Neurol.* 283, 54–70.
- Robbins, D. O. (1972). Coding of intensity and wavelength in optic tectal cells of the turtle. *Brain Behav. Evol.* 5, 124–142.
- Robinson, D. A. (1981). The use of control systems analysis in the neurophysiology of eye movements. *Ann. Rev. Neurosci.* 4, 463–503.
- Robinson, L. R. (1969). Bulbosplinal fibres and their nuclei of origin in *Lacerta viridis* demonstrated by axonal degeneration and chromatolysis respectively. *J. Anat.* (London) 105, 59–88.
- Robson, J. A., and Hall, W. C. (1976). Projections from the superior colliculus to the dorsal lateral geniculate nucleus of the grey squirrel (*Sciurus carolinensis*). *Brain Res.* 113, 379–385.
- Rodieck, R. W. (1979). Visual pathways. *Ann. Rev. Neurosci.* 2, 193–226.
- Rosenquist, A. C., and Palmer, L. (1979). Visual receptive fields of cells of the superior colliculus after cortical lesions in the cat. *Exp. Neurol.* 33, 629–652.
- Roucoux, A., and Crommelinck, M. (1976). Eye movements evoked by superior colliculus stimulation in the alert cat. *Brain Res.* 106, 349–363.
- Rowe, M. H., and Stone, J. (1977). The naming of neurones: the classification and naming of cat retinal ganglion cells. *Brain Behav. Evol.* 14, 185–216.
- Rubinson, K. (1968). Projections of the tectum opticum of the frog. *Brain Behav. Evol.* 1, 529–561.
- Schapiro, H., and Goodman, D. G. (1969). Motor functions and their anatomical basis in the forebrain and tectum of the alligator. *Exp. Neurol.* 24, 187–195.
- Schechter, P. B., and Ulinski, P. S. (1979). Interactions between tectal radial cells in the red-eared turtle, *Pseudemys scripta elegans*: an analysis of tectal modules. *J. Morphol.* 162, 17–36.
- Schiller, P. H., and Stryker, M. (1972). Single unit recording and stimulation in superior colliculus of the alert rhesus monkey. *J. Neurophysiol.* 35, 915–924.
- Schroeder, D. M. (1981a). Retinal afferents and efferents of an infrared sensitive snake, *Crotalus viridis*. *J. Morphol.* 170, 29–42.
- Schroeder, D. M. (1981b). Tectal projections of an infrared sensitive snake, *Crotalus viridis*. *J. Comp. Neurol.* 195, 477–500.
- Schroeder, D. M., and Ebbesson, S. O. E. (1975). Cytoarchitecture of the optic tectum in the nurse shark. *J. Comp. Neurol.* 160, 443–462.
- Schroeder, D. M., and Loop, M. S. (1976). Trigeminal projections in snakes possessing infrared sensitivity. *J. Comp. Neurol.* 169, 1–14.
- Senn, D. G. (1966). Über das optische System im Gehirn squamater Reptilien. *Acta Anat., Suppl.* 52, 65, 1–87.
- Senn, D. G. (1968a). Über den Bau von Zwischen- und Mittelhirn von *Anniella pulchra* Gray. *Acta Anat.* 69, 239–261.
- Senn, D. G. (1968b). Bau und Ontogenese von Zwischen- und Mittelhirn bei *Lacerta sicula* (Rafinesque). *Acta Anat., Suppl.* 55, 71, 1–150.
- Senn, D. G. (1969). Über das Zwischen- und Mittelhirn von zwei typhlopiden Schlangen, *Anomalepis aspinosus* und *Liotyphlops albirostris*. *Verhandl. Naturf. Ges. Basel.* 80, 32–48.
- Senn, D. G. (1970). Zur Ontogenese des Tectum opticum von *Natrix natrix* (L.). *Acta Anat.* 76, 545–563.

- Senn, D. G. (1979). Embryonic development of the central nervous system. In *Biology of the Reptilia* (C. Gans, R. G. Northcutt, and P. S. Ulinski, eds.), 9A, 173–244.
- Senn, D. G., and Northcutt, R. G. (1973). The forebrain and midbrain of some squamates and their bearing on the origin of snakes. *J. Morphol.* 140, 135–152.
- Sereno, M. I. (1985). Tectoreticular pathways in turtles: I. Organization and morphology of tectoreticular axons. *J. Comp. Neurol.* 233, 48–90.
- Sereno, M. I., and Ulinski, P. S. (1985). Tectoreticular pathways in turtles: II. Morphology of tectoreticular cells. *J. Comp. Neurol.* 233, 91–114.
- Sereno, M. I., and Ulinski, P. S. (1987). Caudal topographic nucleus isthmi and the rostral nontopographic nucleus isthmi in the turtle, *Pseudemys scripta*. *J. Comp. Neurol.* 261, 319–346.
- Sherk, H. (1979). Connections and visual field mapping in cat's parabigeminal circuit. *J. Neurophysiol.* 42, 1656–1688.
- Sligar, C. M., and Voneida, T. J. (1976). Tectal efferents in the blind cavefish, *Astynax hubbsi*. *J. Comp. Neurol.* 165, 107–124.
- Smeets, W. J. A. J. (1981). Efferent tectal pathways in two chondrichthyans, the shark, *Scyliorhinus canicula* and the ray, *Raja clavata*. *J. Comp. Neurol.* 195, 13–24.
- 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. (1986). Translation of sensory signals into commands for control of saccadic eye movements: role of primate superior colliculus. *Physiol. Rev.* 66: 118–171.
- Sparks, D. L., Holland, R., and Guthrie, B. L. (1976). Size and distribution of movement fields in the monkey superior colliculus. *Brain Res.* 113, 21–34.
- Sparks, D. L., and Mays, L. E. (1980). Movement fields of saccade-related burst neurons in the monkey superior colliculus. *Brain Res.* 190, 39–50.
- Sparks, D. L., and Nelson, J. S. (1987). Sensory and motor maps in the mammalian superior colliculus. *Trends Neurosci.* 10: 312–317.
- Stanford, L. R., Schroeder, D. M., and Hartline, P. H. (1981). The ascending projection of the nucleus of the lateral descending trigeminal tract: a nucleus in the infrared system of the rattlesnake, *Crotalus viridis*. *J. Comp. Neurol.* 201, 161–173.
- Stein, B. E., and Clamann, H. P. (1981). Control of pinna movements and sensorimotor register in cat superior colliculus. *Brain Behav. Evol.* 19, 180–192.
- Stein, B. E., and Gaither, N. S. (1981). Sensory representation in reptilian optic tectum: some comparisons with mammals. *J. Comp. Neurol.* 202, 69–87.
- Stein, B. E., and Gaither, N. S. (1983). Receptive-field properties in reptilian optic tectum: some comparisons with mammals. *J. Neurophysiol.* 50, 102–124.
- Sterling, P. (1971). Receptive field and synaptic organization of the superficial gray layers of the cat superior colliculus. *Vision Res.* 11, Suppl. 3, 309–328.
- Sterling, P. (1983). Microcircuitry of the cat retina. *Ann. Rev. Neurosci.* 6, 149–186.
- Stone, J. (1981). *The Whole Mount Handbook*. Maitland, Sydney, Australia.
- Stone, J., and Freeman, J. A. (1971). Synaptic organization of the pigeon optic tectum: a Golgi and current source-density analysis. *Brain Res.* 27, 203–221.
- Streit, P., Knecht, E., Reubi, J.-C., Hunt, S. P., and Cuenod, M. (1978). GABA-specific presynaptic dendrites in pigeon optic tectum: a high resolution autoradiographic study. *Brain Res.* 149, 204–210.
- Szekely, G., and Lazar, G. (1976). Cellular and synaptic architecture of the optic tectum. In *Frog Neurobiology* (R. Llinas and W. Precht, eds.). Springer-Verlag, Berlin-Heidelberg, pp. 407–434.
- Szekely, G., Setalo, G., and Lazar, G. (1973). Fine structure of the frog's optic tectum: optic fiber termination layers. *J. Hirnforsch.* 14, 189–225.
- ten Donkelaar, H. J. (1976a). Descending pathways from the brainstem to the spinal cord in some reptiles. I. Origin. *J. Comp. Neurol.* 167, 421–442.
- ten Donkelaar, H. J. (1976b). Descending pathways from the brain stem to the spinal cord in some reptiles. II. Course and site of termination. *J. Comp. Neurol.* 167, 443–464.
- ten Donkelaar, H. J., and De Boer-van Huizen, R. (1978). Cells of origin of pathways descending to the spinal cord in a lizard (*Lacerta galloti*). *Neurosci. Lett.* 9, 123–128.
- ten Donkelaar, H. J., and De Boer-van Huizen, R. (1981). Basal ganglia projections to the brain stem in the lizard *Varanus exanthematicus* as demonstrated by retrograde transport of horseradish peroxidase. *Neuroscience* 6, 1567–1590.
- ten Donkelaar, H. J., Kusuma, A., and De Boer-van Huizen, R. (1980). Cells of origin of pathways descending to the spinal cord in some quadrupedal reptiles. *J. Comp. Neurol.* 192, 827–851.
- Terashima, S., and Goris, R. C. (1975). Tectal organization of pit viper infrared reception. *Brain Res.* 83, 490–494.
- Tigges, M., Tigges, J., Luttrell, G. L., and Frazier, C. M. (1973). Ultrastructural changes in the superficial layers of the superior colliculus in *Galago crassicaudatus*. *Z. Zellforsch. Mikrosk. Anat.* 140, 291–307.
- Tokunaga, A., and Otani, K. (1976). Dendritic patterns of neurons in the rat superior colliculus. *Exp. Neurol.* 52, 189–205.
- Torrealba, F., Partlow, G. D., and Guillery, R. W. (1981). Organization of the projection from the superior colliculus to the dorsal lateral geniculate nucleus of the cat. *Neuroscience* 6, 1341–1360.
- Ulinski, P. S. (1977). Tectal efferents in the banded water snake (*Natrix sipedon*). *J. Comp. Neurol.* 173, 251–274.
- Ulinski, P. S. (1978). Distribution of neurons in the optic tectum of the turtle *Pseudemys scripta*. *Anat. Rec.* 199, 568.
- Ulinski, P. S. (1983). *Dorsal Ventricular Ridge: a Treatise on Forebrain Organization in Reptiles and Birds*. John-Wiley Interscience, New York.
- Ulinski, P. S., du Lac, S., and Dacey, D. M. (1983). Descending projections of the geniculate complex. *Invest. Ophthalmol. Vis. Sci.* 24, 64.
- Valverde, F. (1973). The neuropil in superficial layers of the superior colliculus of the mouse. *Z. Anat. Entwickl.* 142, 117–147.
- Vanegas, H. (1975). Cytoarchitecture and connexions of the teleostean optic tectum. In *Vision in Fishes* (M. A. Ali, ed.). Plenum Press, New York, pp. 151–158.
- von Düring, M., and Miller, M. R., (1979). Sensory nerve endings of the skin

- and deeper structures of reptiles. In *Biology of the Reptilia* (C. Gans, R. G. Northcutt, and P. S. Ulinski, eds.). New York: Academic Press, 9, 407-441.
- Voneida, T. J., and Sligar, C. M. (1979). Efferent projections of the dorsal ventricular ridge and the striatum in the tegu lizard, *Tupinambis nigropunctatus*. *J. Comp. Neurol.* 186, 43-64.
- Walls, G. L. (1940). Ophthalmological implications for the early history of snakes. *Copeia*, 1940, 1-8.
- Walls, G. L. (1942). *The Vertebrate Eye*. Cranbrook Institute of Science, Bloomfield Hills, Mich.
- Wang, S.-J., Yan, K., and Wang, Y.-T. (1981). Visual field topography in the frog's nucleus isthmi. *Neurosci. Lett.* 23, 37-41.
- Wickelgren, B. G., and Sterling, P. (1969). Influence of visual cortex on receptive fields in the superior colliculus of the cat. *J. Neurophysiol.* 32, 16-23.
- Wilczinski, W., and Northcutt, R. G. (1977). Afferents to the optic tectum of the leopard frog: an HRP study. *J. Comp. Neurol.* 173, 219-230.
- Woodburne, R. T. (1936). A phylogenetic consideration of the primary and secondary centers and connections of the trigeminal complex in a series of vertebrates. *J. Comp. Neurol.* 65, 403-501.
- Wurtz, R. H., and Albano, J. E. (1980). Visual-motor functions of the primate superior colliculus. *Ann Rev. Neurosci.* 3, 189-226.
- Zagorul'ko, T. M. (1968). Effect of intensity and wavelength of photic stimulus on evoked responses of general cortex and optic tectum in turtles. *Fiziol. Zh. SSSR Sechenova* 54, 436-446.

Anatomy and Physiology of Infrared Sensitivity of Snakes

GERARD J. MOLENAAR

Contents

| | |
|---|-----|
| I. Introduction | 368 |
| II. Peripheral Structures | 370 |
| A. The Receptor | 370 |
| B. Innervation | 372 |
| C. The Ganglion | 374 |
| D. Properties of the Receptor and of the Peripheral Units | 375 |
| E. Geometry | 382 |
| F. Concluding Remarks | 383 |
| III. The Sensory Trigeminal System | 385 |
| A. General | 385 |
| B. The Common Sensory Trigeminal System | 389 |
| C. The Lateral Descending Trigeminal System | 391 |
| D. Concluding Remarks | 403 |
| IV. Efferent Projections from the Sensory Trigeminal Nuclei | 404 |
| A. Introduction | 404 |
| B. Normal Morphology of the Tertiary Trigeminal Structures | 405 |
| C. Ascending Projections of the Common Sensory Trigeminal Nuclei in <i>Python</i> | 409 |
| D. Projections of the Lateral Descending Nucleus in <i>Python</i> | 416 |
| E. Projections from the LTTD in Pit Vipers | 418 |
| F. Comparison of Secondary Infrared Pathways | 420 |
| G. Concluding Remarks | 421 |
| V. Higher-order Infrared Perceiving Structures | 422 |
| A. The Tectum | 422 |
| B. Forebrain Structures | 431 |
| C. Concluding Remarks | 433 |
| VI. Biological Role of the Infrared-sensitive System | 434 |
| A. Spatial Orientation | 434 |
| B. Role in Behavior | 435 |
| VII. Conclusions | 436 |
| A. Comparison of Thermosensitive Pathways | 436 |
| Acknowledgments | 441 |
| Appendix: Reptilian Species Discussed | 441 |
| References | 443 |