

The Cerebral Cortex of Reptiles

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1. Introduction

Reptiles and mammals are the two groups of vertebrates with well-developed cerebral cortices. Ray-finned fishes have forebrains that develop by an eversion of the rostral neural tube that reduces the roof of the telencephalon to a thin membrane (Nieuwenhuys, 1982; Northcutt and Davis, 1983). They have olfactory cortices on the ventrolateral walls of their cerebral hemispheres (e.g., Braford and Northcutt, 1974), but the eversion process seemingly precludes the formation of a cortical roof to the telencephalon. Cartilaginous fishes (such as sharks), fleshy-finned fishes (lungfishes and coelacanths), amphibians, reptiles, birds, and mammals all have forebrains that develop via a fundamentally different process. This involves an evagination of the rostral neural tube resulting in paired lateral ventricles, interventricular foramina, and a neuronal roof to the telencephalon that can form an extensive cerebral cortex. However, the telencephalic roof of sharks forms a solid mass of neurons lacking the lamination usually associated with the cerebral cortex (Smeets *et al.*, 1983). Although amphibians (Northcutt and Kicliter, 1980) and lungfishes (Northcutt, 1986) have laminated cortices, they show little migration of neurons away from the ependyma. Birds have a small cerebral cortex, ostensibly resulting from a secondary reduction of the reptilian pattern (Benowitz, 1980). It is only in reptiles and mammals that the telencephalic roof develops into extensive and multilayered cortices.

A fundamental understanding of the nature and significance of such cortices clearly requires an understanding of the commonality and differences of

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design seen in the cerebral cortex of reptiles and mammals. However, the brains of reptiles are largely unmyelinated, which made it difficult to trace out even major fiber systems until the introduction of Nauta degeneration methods in the 1960s. The relatively small brain of reptiles made physiological studies using evoked potential techniques or large stimulation electrodes difficult, so there was little neurophysiological work on reptiles until the advent of microelectrode methods. Factual information about the central nervous systems of reptiles was consequently limited principally to cytoarchitectonic descriptions of the brain until roughly 1970 (reviews: Ariëns Kappers, 1921; Ariëns Kappers *et al.*, 1936; Goldby and Gamble, 1957; Northcutt, 1967).

Since 1970 there has been a dramatic increase in the information available about the brains of reptiles due to the application of modern neuroanatomical and behavioral methods. Some of this information is summarized in earlier reviews of forebrain or cortical organization of reptiles: Northcutt (1970, 1978, 1981), Butler (1978, 1980), Belekova (1979), Halpern (1980), Peterson (1980), Ulinski (1983), Parent (1986), and Schwerdtfeger and Smeets (1988). Most recently, *in vitro* preparations of reptilian eye cup (Baylor and Fettiplace, 1976), ear (Crawford and Fettiplace, 1980, 1981a,b), and whole brain (Mori and Shepherd, 1979; Mori *et al.*, 1981; Kriegstein, 1985) have been developed and used to greatly extend the body of information on the cellular physiology and pharmacology of the cerebral cortex of reptiles. It is, therefore, now possible for the first time to provide an adequate outline of how the cerebral cortex is organized in reptiles.

After providing some brief, background information on reptiles and their forebrains, this chapter reviews information on the structure and function of the cerebral cortex in reptiles with emphasis placed on work done since 1970. Wherever possible, an attempt has been made to place results within a common nomenclatorial framework. Thus, a uniform nomenclature for cortical areas and cell types is provided and information is presented using this nomenclature wherever such a synthesis seems warranted. The chapter concludes with a consideration of the differences and similarities in the cortices of reptiles and mammals.

2. Background Information

2.1. Phylogenetic Relationships

Reptiles living in Recent geological times are placed into four orders within the class Reptilia (e.g., Romer, 1956; Schmidt and Inger, 1957). The order Chelonia contains the turtles and tortoises which are characterized by their unique shells (Pritchard, 1967). It is a small order of about 200 species that live in both marine and freshwater environments as well as terrestrial habitats ranging from forests to deserts. Most neurobiological work has been done on turtles in the family Emydidae, which includes the closely related genera *Pseudemys* and *Chrysemys* in North America and the genus *Emys* in Europe.

The order Crocodylia includes crocodiles, alligators, and gavials, all characterized by the elongated rostrum or snout present in their skulls (e.g., Langston, 1973). There are about 20 species of crocodilians distributed in fresh and

brackish waters in the Americas, Africa, Asia, and Australia. Essentially all neurobiological information has been obtained on the American alligator, *Alligator mississippiensis*, and its close relatives, the caimans (e.g., *Caiman sklerops* and *C. crocodilus*) of South America.

The order Squamata includes about 5000 species of lizards, snakes, and amphisbaenians. Lizards occur throughout most of the world and typically have four legs, although several groups of lizards have elongate bodies and show limb reduction. Neurobiological work has been carried out principally on the green iguana (*Iguana iguana*), a herbivorous American lizard; on the tegu lizards (*Tupinambis teguixin* and *T. nigropunctatus*), moderate sized and omnivorous South American forms; on monitor lizards (*Varanus exanthematicus* and *V. niloticus*), large, carnivorous Asian lizards; and on the medium-sized European lizards of the genus *Lacerta*. Snakes are characterized by absence of all but vestigial hind limbs in some forms and a highly modified skull affording it the ability to swallow prey larger than its head. Work has been done on boa constrictors (*Constrictor constrictor*), garter snakes (*Thamnophis sirtalis*), water snakes [*Nerodia* (= *Natrix*) *sipedon*] and several species of rattlesnakes. The rattlesnakes and pythons have attracted particular interest (e.g., Berson and Hartline, 1988) because of their infrared detection systems used for prey capture. Amphisbaenians (Gans, 1978) are a small group of burrowing reptiles that some workers consider as closely related to lizards.

The fourth order, Rhynchocephalia, includes only a single living species. This is the sphenodon or tuatara (*Sphenodon punctatum*) that lives on a group of small islands off the coast of New Zealand. Sphenodons bear a superficial resemblance to medium-sized lizards. However, they demonstrate a number of technical characteristics that place them in a group that appeared in the fossil record in the Triassic period, but declined in numbers by the Cretaceous period.

Although a complete discussion of the evolutionary history of reptiles is beyond the scope of this chapter (see Carroll, 1969, 1987), a few points about the relationships of reptiles (Fig. 1) are immediately relevant to neurobiological issues. The first is that the species of Recent reptiles represent the surviving endpoints of a very large and successful radiation of vertebrates that flourished principally in the Mesozoic era, from 225 to 70 million years ago. It included species living in all conceivable habitats, from subterranean burrowers, to desert dwellers, to inhabitants of tropical rain forests to free-flying forms (the pterosaurs), as well as the highly diverse dinosaurs. It also included a lineage of reptiles that diverged early in reptilian evolution from the stem reptiles, and eventually gave rise to mammals midway through the Mesozoic (Hotton et al., 1986). Second, it is important to bear in mind that these synapsid reptiles were well on their evolutionary way prior to appearance in the fossil record of any of the four groups of reptiles represented in the Recent fauna. Mammals and lizards, for example, appear at roughly the same point in geological time, the results of long and independent lines of evolution. No evolutionary priority is accorded to being a mammal, and lizards and mammals must be viewed as being as equally advanced and equally specialized. There is no reason to view mammals as in any sense having evolved from or been derived from any of the Recent groups of reptiles.

A related point that has caused particular confusion in the neurobiological literature concerns the relationship between turtles and mammals. Several authors have taken the view that the brains of turtles are of particular value in

understanding the evolution of mammalian cortex because turtles appear early in the fossil record and have changed little during their evolution. It is true that with the rhynchocephalians, turtles appear in the fossil record earlier than representatives of the other Recent orders. However, reptilian evolution was well underway by the time turtles appeared, and the lines leading to mammals had separated off at least several million years before the first turtles appeared in the fossil record. Thus, turtles (unfortunately) provide no privileged view of the stem reptiles or the ancestors of mammals. The idea that turtles have not changed since their appearance is also misleading. There have been significant changes in the structure of the shell (Zangerl, 1969) and the first turtles could not retract their necks while modern turtles either fold their necks to the side (side-necked or pleurodiran turtles) or pull their necks into their shells (cryp-

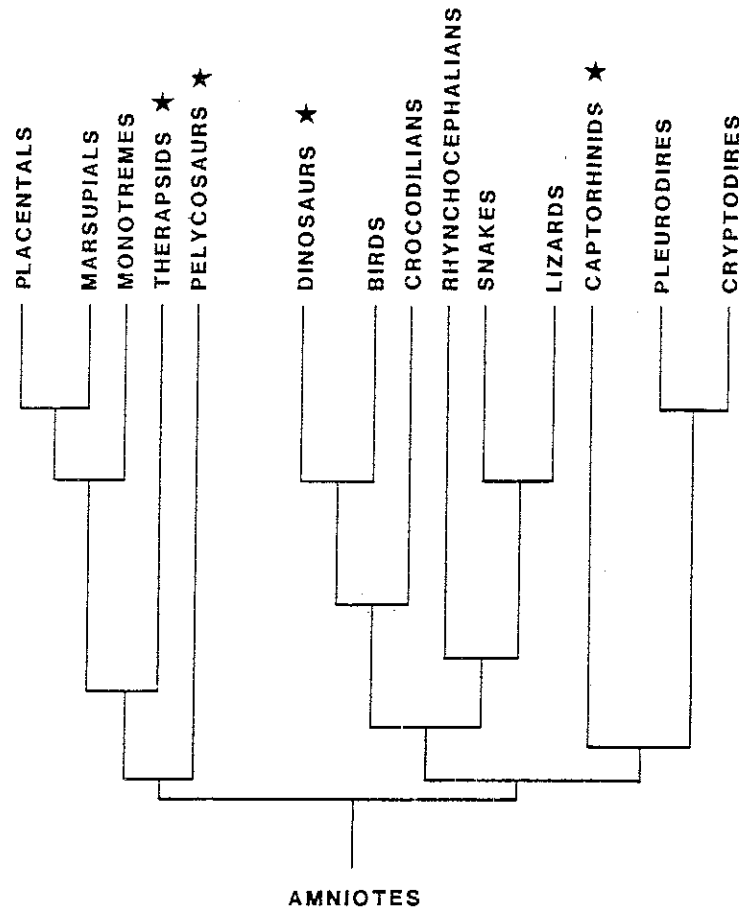


Figure 1. Phylogenetic relationships of major groups of reptiles. This is a cladogram summarizing the phylogenetic relationships of several major groups of reptiles. The relationship of birds and mammals to various groups of reptiles is also shown. The four orders of recent reptiles are the turtles (represented by two clades, the pleurodire or side-necked turtles and the cryptodires or turtles that withdraw their heads into their shells), lizards, snakes, rhynchocephalians (the sphenodon or tuatara) and crocodilians. Two extinct groups of reptiles (captorhinids and dinosaurs) are marked by stars. Notice that birds are the sister group of the dinosaurs. The cluster of clades on the left is composed of groups that diverged very early in evolutionary time from the stem reptiles and are represented in recent times by the placental, marsupial and monotreme mammals. Two extinct groups (the therapsids and pelycosaurs) are marked by stars.

todiran turtles). Relevant here, the cortex of cryptodiran turtles is a distinctly laminated structure throughout while that of pleurodiran turtles contains a nuclear structure (Riss *et al.*, 1969). Thus, observations on the cortex of cryptodiran turtles will not necessarily hold generally for turtles, let alone for all of the reptiles or mammals.

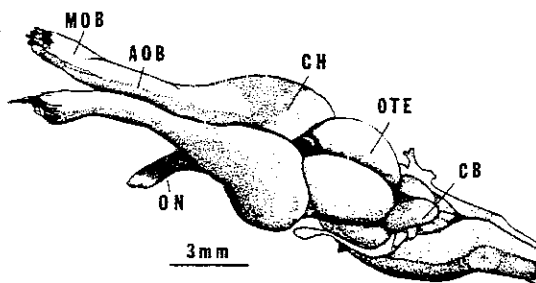
The idea of a close relationship between turtles and mammals has attracted attention over the years principally because of a general interest in reconstructing the evolutionary history of mammalian brains. Accepting a close relationship between turtles and mammals held out the promise of deducing the structure of the brain in an animal close to the phylogenetic origin of mammals, but it is now apparent that this approach is based upon a misunderstanding of evolutionary interrelationships of reptiles and mammals. A more profitable strategy is to avoid selecting any one species of reptile as particularly important in understanding the evolution of mammalian cortex, and to recognize that the members of the four orders of living reptiles are essentially random samples from the reptilian adaptive radiation. Thus, features of cortical organization that are common to the living reptiles are likely to be those that evolved early in the evolution of reptiles and have been retained throughout the evolution of each, independent lineage. An important goal of studies of cortical organization in reptiles is, then, to understand the basic pattern of cortical organization and determine how it resembles and differs from the pattern of cortical organization seen in mammals. This point is considered in more detail in Section 9.

2.2. General Structure of Forebrain

The forebrain in reptiles (Fig. 2) develops from the prosencephalon of the neural tube, which, as in all vertebrates, is divided into a rostral telencephalon and a caudal diencephalon (Senn, 1979). The walls of the diencephalon develop ventricular sulci that divide it into four basic components (Fig. 3). The epithalamus includes the roof organs such as the pineal and parapineal (see Quay, 1979) and the habenula (Fig. 3, HB). The structure and connections of the habenular nuclei in reptiles generally resemble those of mammals. In particular, the habenular nuclei in the monitor lizard, *Varanus benegalensis*, project to the interpeduncular nucleus and the superior raphe (Distel and Ebbesson, 1981).

Ventral to the epithalamus is the dorsal thalamus, which consists of several discrete nuclear groups (Papez, 1935; Cruce, 1974; Butler and Northcutt, 1973; Balaban and Ulinski, 1981a). There are considerable interspecific differences in the cytoarchitecture of the thalamus, and comparisons have been hampered because different nomenclature schemes have often been used for different

Figure 2. Brain of a reptile. This drawing of the brain of the eastern garter snake, *Thamnophis sirtalis* illustrates the general features of the brains of reptiles. It is shown in a dorsolateral view. AOB, accessory olfactory bulb; CB, cerebellum; CH, cerebral hemisphere; MOB, main olfactory bulb; ON, optic nerve; OTE, optic tectum. Drawing by Dr. D. M. Dacey.



species. One common feature is a large, ellipsoidal nucleus situated in the center of the thalamus (e.g. Rainey, 1979; Rainey and Ulinski, 1982a,b) called nucleus rotundus (Fig. 3, RO), which receives bilateral projections from the optic tectum (Hall and Ebner, 1970a) and is responsive to visual stimuli. A dorsal lateral geniculate complex (Fig. 3, DLGN) that receives direct projections from retinal ganglion cells has been identified in all of the groups of reptiles (see Ulinski, 1983, for references). There are considerable interspecific differences in the cytoarchitecture and neuronal organization of the dorsal lateral geniculate complex, some of which will be discussed in Section 7.1.1b. Nucleus rotundus is surrounded dorsally, medially, and ventrostrally by a group of nuclei that can be called collectively the perirotundal nuclei. They are interconnected with com-

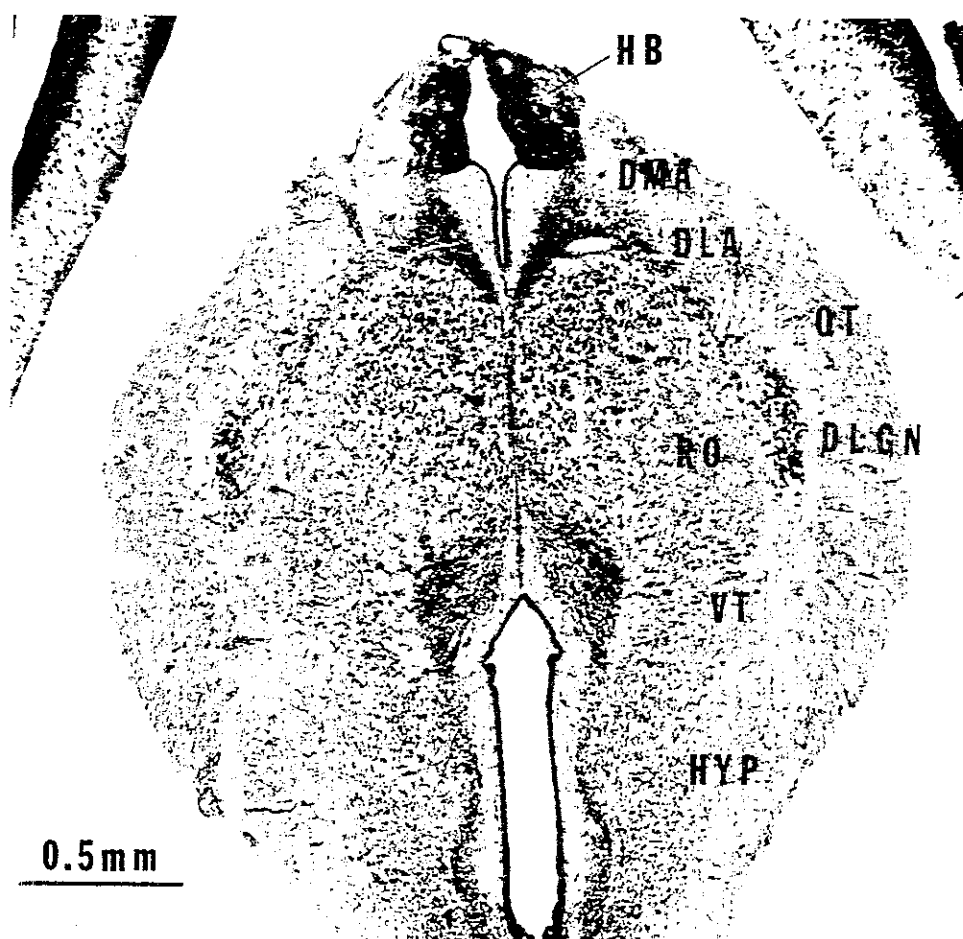


Figure 3. General feature of the diencephalon. This transverse Nissl section through the diencephalon of the red-eared turtle, *Pseudemys scripta elegans* shows the general organization of the diencephalon in reptiles. The epithalamus is represented by the habenula (HB). The dorsal thalamus includes the dorsal lateral geniculate nucleus (DLGN) situated internal to the optic tract (OT), nucleus rotundus (RO), and two "perirotundal nuclei": the dorsomedial anterior (DMA) and dorsolateral anterior (DLA) nuclei. The ventral thalamus (VT) is a narrow band of tissue ventral to the dorsal thalamus. The hypothalamus (HYP) comprises the ventral third of the diencephalon. It consists of both scattered cells laterally and a vertical plate of cells medially.

ponents of the limbic system. A nucleus that receives auditory input from the torus semicircularis (the midbrain homologue of the inferior colliculus) is present in all groups of reptiles, but has been called by different names in different species. The caudal thalamus also includes a nucleus that receives somatosensory information from the dorsal column nuclei and spinal cord.

The ventral thalamus (Fig. 3, VT) is a relatively small wedge of tissue situated ventral to the dorsal thalamus and dorsal to the forebrain bundle system, the major avenue by which the brain stem is interconnected with the telencephalon. The ventral lateral geniculate nucleus (not present in Fig. 3) is situated at the lateral edge of the ventral thalamus, medial to the optic tract. It receives direct retinal projections, has reciprocal connections with the optic tectum, and projects to the brain-stem reticular formation. The suprapeduncular nucleus is positioned dorsal to the forebrain bundles and receives descending projections from the striatum. The anterior entopeduncular nucleus is embedded in the forebrain bundle. It appears to be an analogue to the thalamic reticular or perigeniculate nucleus of mammals that contains GABAergic neurons and may be a source of inhibitory inputs to dorsal thalamic nuclei (Ulinski, 1987c).

The hypothalamus forms (Fig. 3, HYP) the floor of the diencephalon and contains several cytoarchitecturally distinct nuclei (Crosby and Showers, 1969; Cruce, 1974; Butler and Northcutt, 1973). Many neurons in the dorsal hypothalamus are arranged in plates of cells that parallel the third ventricle. A ventromedial nucleus is typically present as a discrete mass of neurons in the caudal, ventral hypothalamus. A cluster of nuclei in the caudal hypothalamus are called the mammillary nuclei. Hypothalamic neurons generally have multipolar, iso-dendritic dendritic fields (Franzoni and Fasolo, 1982; Subhedar and Rama Krishna, 1984; Prasada Rao *et al.*, 1981; Prasada Rao and Subhedar, 1977). Some have one or two processes that extend into the ependymal lining of the third ventricle and contact the cerebrospinal fluid. The hypothalamus is interconnected with limbic components of the forebrain.

The telencephalon (Fig. 4) contains lateral ventricles interconnected with the third ventricle through interventricular foramina (Fig. 4, asterisk). The anterior commissure is situated rostral and dorsal to these foramina, and the forebrain bundle system passes ventral to the anterior commissure. Its medial component, the medial forebrain bundle, courses between the ventral diencephalon and the ventromedial components of the telencephalon. Its lateral component, the lateral forebrain bundle (Fig. 4, LFB), is equivalent to the internal capsule of mammals and courses between the dorsal diencephalon and the dorsal components of the telencephalon, which it reaches by turning dorsally once it has passed rostral to the anterior commissure.

The paired cerebral hemispheres contain three major components. The pallium forms the roof of the hemispheres and lies dorsal to the lateral ventricles. In mammals, the entire pallium forms a cerebral cortex. In reptiles (and birds) the pallium has two quite distinct parts, although both contain antigens that cross-react with antisera prepared against mammalian pallium (Kriegstein *et al.*, 1986). The first is the cerebral cortex, which extends from the dorsal edge of the septum, over the lateral ventricles and down onto the ventrolateral surface of the hemispheres. The cortex (Fig. 4 M, DM, D, and L) is a laminated structure, and a consideration of its organization is the major focus of this chapter. As in mammals, the cerebral cortex of reptiles receives ascending projections from nuclei in the dorsal thalamus. Particular regions of the cortex give rise to efferent

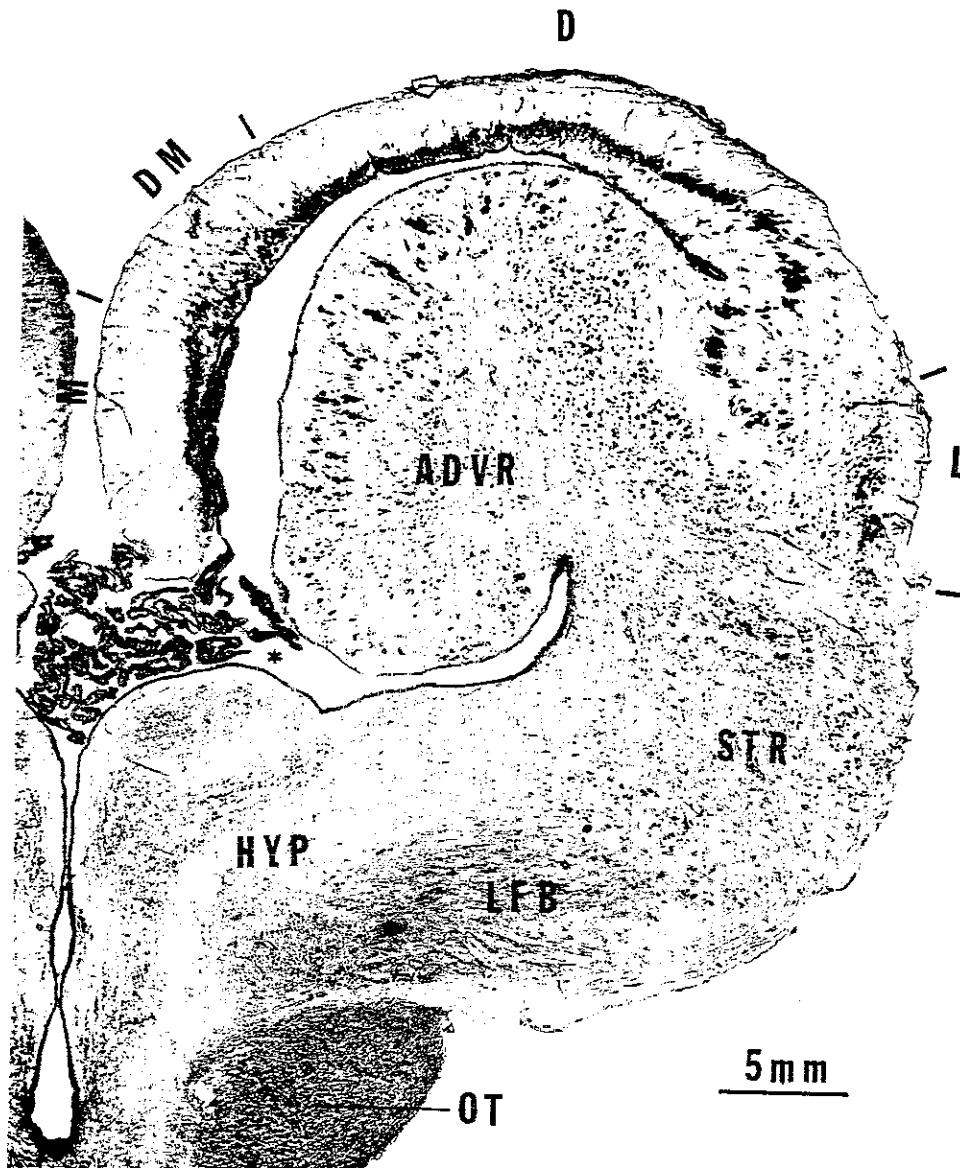


Figure 4. Cerebral hemisphere of a reptile. This transverse Nissl section through the cerebral hemisphere of the red-eared turtle, *Pseudemys scripta elegans* illustrates the general features of the telencephalon of reptiles. The section passes through the interventricular foramen (marked by the asterisk) which connects the third and lateral ventricles. The dorsal telencephalon or pallium has two components. The anterior dorsal ventricular ridge (ADVR) protrudes into the lateral ventricle. The cerebral cortex lies dorsal to the lateral ventricle. It contains four cytoarchitectonic areas: medial cortex (M), dorsomedial cortex (DM), dorsal cortex (D), and lateral cortex (L). The ventral lateral wall of the telencephalon is formed by the striatum (STR) which blends caudally with the hypothalamus (HYP). Fibers in the lateral forebrain bundle (LFB) system are seen coursing through the striatum. OT, optic tract.

projections to the septum and hypothalamus that generally resemble the fornix system of mammals. Also, the visual cortex has efferent projections to the dorsal lateral geniculate nucleus, nucleus rotundus, and the optic tectum (at least in some species). However, there is no indication that reptiles have efferent projections to the rhombencephalon or spinal cord that might resemble the corticospinal or corticobulbar tracts of mammals.

The second part of a pallium is unique to reptiles and birds. It is a ridge of tissue that protrudes into the lateral ventricles from the ventrolateral wall of the hemisphere and is therefore called the dorsal ventricular ridge (DVR). DVR is divided into two parts at about the level of the anterior commissure. The anterior dorsal ventricular ridge (Fig. 4, ADVR) receives ascending projections from several of the sensory relay nuclei of the dorsal thalamus. These projections are arranged in a pattern that is the same for the three orders of reptiles that have been studied (there are no data for *Sphenodon*). Nucleus rotundus projects to the lateral edge of ADVR, which is known to be responsive to visual stimuli in at least turtles and lizards. The somatosensory nuclei of the caudal thalamus project to a central region of ADVR in crocodilians and lizards. The auditory nucleus of the caudal thalamus projects to the medial region of ADVR in crocodilians and lizards. The organization of ADVR has been discussed extensively by Ulinski (1983). The basal dorsal ventricular ridge (BDVR; not present in Fig. 4) is situated caudal and ventral to ADVR. Its connections bear a general resemblance to the mammalian amygdala. BDVR in snakes, lizards, and *Sphenodon*, for example, contains a discrete structure called nucleus sphericus (Fig. 11B, NS). It receives inputs from the accessory olfactory bulb and projects to the ventromedial nucleus of the hypothalamus, and thus resembles the corticomедial nuclear group of the amygdala of mammals. There is less information on BDVR than there is on ADVR, but what little is known is reviewed by Ulinski (1983).

The second major component of the cerebral hemispheres is the striatum (Fig. 4, STR), which makes up the ventral lateral walls of the hemispheres. The striatum of reptiles bears a general resemblance in its cytology, connections, and histochemistry to the caudate, putamen, and globus pallidus of mammals (Reiner *et al.*, 1984; Parent, 1986). Some attempts have been made to relate specific components of the striatum of reptiles to elements of the basal ganglia in mammals. However, these have not yielded clear results, and will not be pursued here.

The third major component of the cerebral hemispheres is the septum (Figs. 6 and 7, S). The precommissural part of the septum forms the ventromedial wall of the cerebral hemisphere, while its postcommissural part extends caudally over the anterior commissure. The septum contains dorsolateral, ventromedial, and ventrolateral nuclear groups. The majority of septal neurons are multipolar and isodendritic, but those lying adjacent to the midline are typically bipolar with the long axes of the dendritic fields oriented parallel to the surface of the brain (Ulinski, 1977a; Martin-Perez *et al.*, 1981). The septum contains neurons that stain positively for GABA and acetylcholinesterase (Schwerdtfeger *et al.*, 1986). The septum in tegu lizards projects caudally to the periventricular and mammillary nuclei of the hypothalamus and to the perirhinal thalamic nuclei (Hoogland *et al.*, 1978; Sligar and Voneida, 1981).

Using this overview of the forebrain of reptiles as a background, we can now turn to a more detailed consideration of the cortical component of the pallium.

3. Cytoarchitecture of Cortex

The cerebral cortex is a sheet of tissue between 0.5 and 1.0 mm thick that forms a fissureless roof for the cerebral hemisphere (Fig. 5). It contains three layers defined by variations in the density of neurons. The outer layer 1 is bounded dorsally by the end feet of ependymal tanycytes that extend radially through the cortex and by the pia (see Stark, 1979, for a review of the meninges of reptiles). It contains relatively few, scattered somata. The intermediate layer 2 contains a large number of more densely packed somata. It forms a continuous sheet of cells extending from the medial to the lateral edge of the cortex in many species. In others, breaks occur in layer 2 during the course of embryonic development and the edges of the intermediate region of layer 2 come to lie deep in the medial and lateral regions. The cortex thus has five layers in these regions, which are called the medial and lateral superpositions and marked by stars in Fig. 5. The configuration of the cortex within the superpositions resembles that present at the point where the dentate gyrus meets area CA3 within the hippocampal formation of mammals. The inner layer 3 contains a moderate number of loosely packed somata. A layer of fibers called the alveus (Fig. 5, AL) is situated deep in layer 3. A distinct, sheetlike aggregation of cells known as the cell plate (Fig. 5, CP) occurs in layer 3 in some reptiles (Unger, 1906; de Lange, 1911; Rose, 1923; Ulinski, 1974). The inner surface of layer 3 is bounded by ependymal cell somata (Fig. 5, E).

The cortex is divided into several cytoarchitectonic areas based on variations in cell density and the configuration of the three layers. The same areas can be recognized in representatives of all four orders (Figs. 6–9), but there are variations between taxa in the detailed cytoarchitecture of each area (see Table I for references). The areas are rostrocaudally elongate strips that extend from the caudal edge of the olfactory bulbs to the caudal pole of the cortex (Fig. 10). They constitute most of the cortex, but the cortex is reduced to thin membranes at some points. This typically occurs along the caudoventral surface of each cerebral hemisphere where the cortex becomes a noncellular membrane that forms the medial face of the lateral ventricle. The cortex is also reduced to a membrane in the olfactory cortex of anoline lizards that have a highly reduced olfactory system (Armstrong *et al.*, 1953). Several nomenclature systems have been used for the cortical areas over the years, but most workers now recognize four areas named (from medial to lateral): medial cortex, dorsomedial cortex, dorsal cortex, and lateral cortex.*

Medial cortex (also called small-celled medial cortex and ventral medial cortex) lies on the dorsal edge of the septum (Figs. 6–9, M). It is narrow in width rostrally where it blends with the anterior olfactory nucleus (Fig. 10, AON), and expands caudally so that it forms a relatively large percentage of the caudal pole of the hemisphere. Caudal to the septum it thus lies dorsal to the thin membrane mentioned in the previous paragraph. It is characterized in all forms by the

*Many authors recognize only three cortical areas in reptiles. These would correspond to the lateral area, dorsal area, and the combination of the dorsomedial and medial areas. However, most of the authors recognize two components in the medial of these three areas. Since the cytoarchitecture, cytology, and connections of these two components vary in all groups of reptiles, it seems preferable to distinguish them as distinct cytoarchitectonic areas.

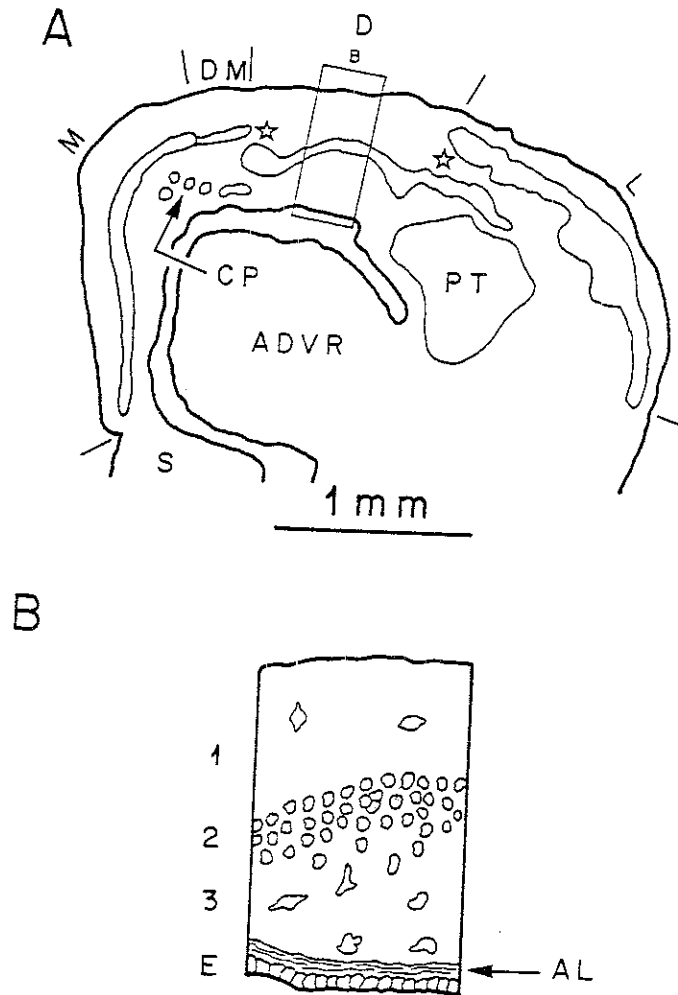


Figure 5. General features of cerebral cortex (A) Drawing of a transverse section through the pallium of a tegu lizard to illustrate the nomenclature of the major components of cerebral cortex in reptiles. The cortex is divided into four major cytoarchitectonic areas: medial cortex (M), dorsomedial cortex (DM), dorsal cortex (D) and lateral cortex (L). In some forms, a distinct cluster, or several clusters of cells, are seen in the lateral region of dorsal cortex. This component of dorsal cortex is sometimes called the pallial thickening (PT). The cortex in reptiles is fundamentally a three-layered cortex, but in some species the second layer is ruptured at the medial and lateral borders of dorsal cortex, resulting in the medial and lateral superpositions (marked by stars). In some species, clusters of cells occur in the deep layer of medial, dorsomedial and dorsal cortex. These are called the cell plate (CP). The rectangle marked 'B' in dorsal cortex is magnified in panel B. (B) Transverse section through dorsal cortex to illustrate the nomenclature of cortical layers. The cortex contains three layers. The outer layer 1 contains a few scattered cells (open profiles). The intermediate layer 2 contains many, densely packed somata. The deep layer 3 contains a moderate number of scattered somata. A distinct bundle of unmyelinated fibers, the alveus (AL), runs through the deep part of layer 3 of medial, dorsomedial, and dorsal cortex. The inner surface of the cortex is formed by the ependyma (E). ADVR, anterior dorsal ventricular ridge; S, septum.

presence of relatively few neurons in layers 1 and 3. Somata of neurons in layer 2 are small, densely packed, and stain intensely in Nissl stains.

Dorsomedial cortex (also called large-celled medial cortex and dorsal medial cortex) forms the dorsomedial convexity of the cerebral hemispheres. Like the medial cortex, it contains relatively few neurons in layers 1 and 3. The cells in dorsomedial cortex are always larger than those in medial cortex, but there are some marked interspecific differences in the cytoarchitecture of dorsomedial cortex. Dorsomedial cortex in squamates (Figs. 8 and 9, DM) has a densely packed layer 2, which is relatively narrow in lizards but wider in snakes. By contrast, neurons in layer 2 of dorsomedial cortex of turtles (Fig. 7, DM) and crocodilians (Fig. 6, DM) are loosely packed so that layer 2 is relatively thick in species in these taxa.

Dorsal cortex (also called general cortex) forms the dorsal surface of the cerebral hemispheres (Figs. 6–9, D). It has few neurons in layer 1, many densely packed neurons in layer 2, and a moderate number of loosely packed neurons in layer 3. It is usually possible to divide dorsal cortex into three subareas based on subtle differences in cytoarchitecture. These subareas have not been explicitly recognized by all authors, and—when recognized—have been subjected to a variety of nomenclatures. The simplest nomenclature recognizes medial, inter-

Table I. Studies of the Cytoarchitecture of Cortex in Reptiles^a

Turtles and tortoises	
<i>Chelydra serpentina</i>	Riss <i>et al.</i> (1969)
<i>Chrysemys picta</i>	Riss <i>et al.</i> (1969), Northcutt (1970)
<i>Podocnemis unifilis</i>	Riss <i>et al.</i> (1969)
<i>Pseudemys scripta</i>	Desan (1984)
<i>Testudo hermanni</i>	Platel <i>et al.</i> (1973)
Crocodilians	
<i>Alligator mississippiensis</i>	Crosby (1917)
<i>Alligator lucius</i>	Rose (1923)
<i>Caiman sklerops</i>	Riss <i>et al.</i> (1969)
<i>Crocodylus palustris</i>	Rose (1923)
Lizards	
<i>Anolis carolinensis</i>	Greenberg (1982)
<i>Chamaeleo lateralis</i> , <i>C. vulgaris</i>	Beckers <i>et al.</i> (1971/1972), Shanklin (1930)
<i>Gekko gekko</i>	Smeets <i>et al.</i> (1986)
<i>Iguana iguana</i>	Northcutt (1967)
<i>Lacerta viridis</i>	Beckers <i>et al.</i> (1971/1972), Goldby (1934)
<i>Scincus scincus</i>	Platel (1969)
<i>Tupinambis</i> sp.	Curwen (1937), Ebbesson and Voneida (1969)
Snakes	
<i>Coluber constrictor</i>	Carey (1967)
<i>Constrictor</i> (= <i>Boa</i>) <i>constrictor</i>	Ułinski (1974)
<i>Crotalus adamanteus</i> , <i>C. atrox</i>	Warner (1931, 1946)
<i>Eryx johni</i>	Ułinski (1974)
<i>Natrix</i> (= <i>Nerodia</i>) <i>sipedon</i>	Ułinski (1974)
Amphisbaenians	
<i>Monopeltis guentheri</i>	Beckers <i>et al.</i> (1971/1972)
Sphenodon	
<i>Sphenodon punctatum</i>	Cairney (1926), Durward (1930)

^aThis table is a selected list of references on the cytoarchitecture of cortex in reptiles, arranged by taxonomic group. Other, especially older, references are contained in the bibliographies of the papers listed.

mediate, and lateral subdivisions of dorsal cortex. Layer 2 of the medial and lateral subdivisions is sometimes slanted in adult forms and juts ventral to layer 2 of medial cortex and lateral cortex, respectively, resulting in the medial and lateral superpositions. Layer 2 retains its embryonic condition in other adult forms and is continuous with layer 2 of medial and lateral cortex. The lateral subdivision of dorsal cortex in cryptodiran turtles merits special comment (Fig. 7). It is greatly expanded and its lateral edge forms a scroll-like convolution that was named the pallial thickening by Johnston (1915). The pallial thickening is characterized by the presence of many large clusters of neurons with closely apposed somata.

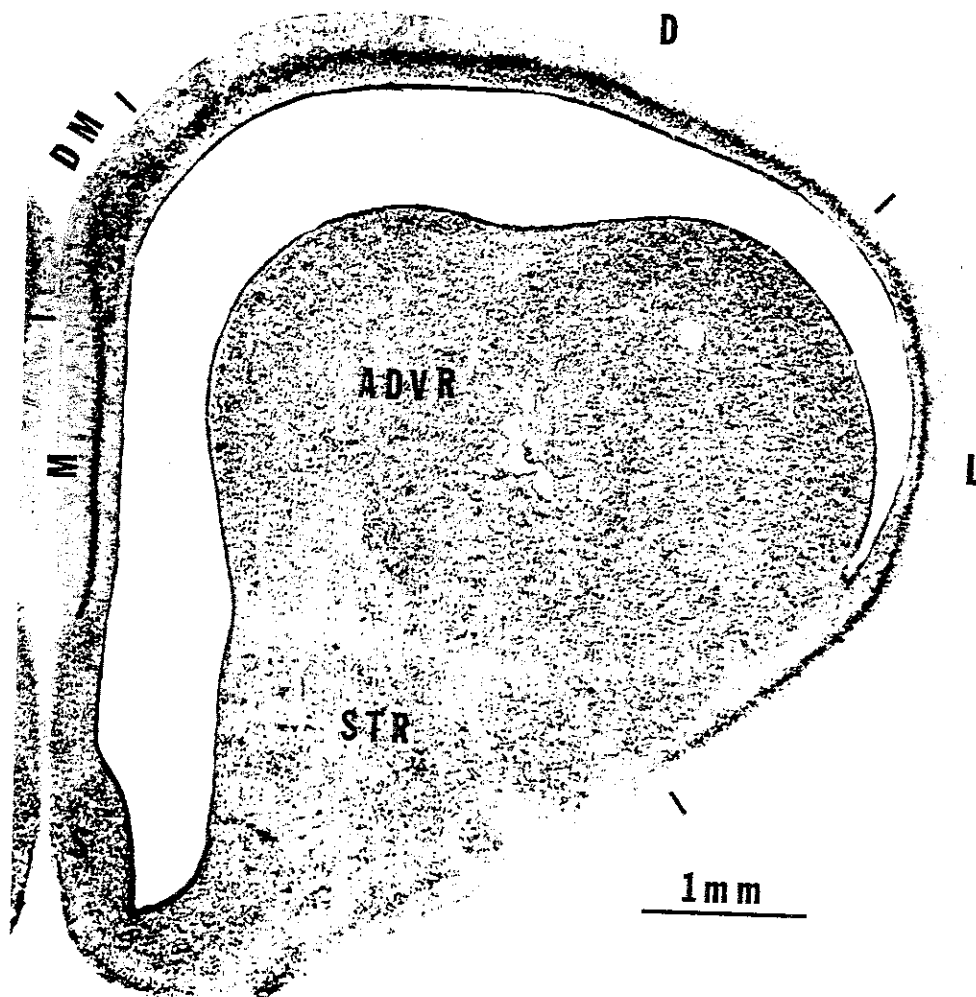


Figure 6. Telencephalon of a crocodilian. Figures 6 through 9 show examples of transverse sections through the telencephalons of representatives of each of the major groups of Recent reptiles. This is a Nissl section from the telencephalon of an alligator *Alligator mississippiensis*. The cortex is divided into medial cortex (M), dorsomedial cortex (DM), dorsal cortex (D) and lateral cortex (L). ADVR, anterior dorsal ventricular ridge; S, septum; STR, striatum.

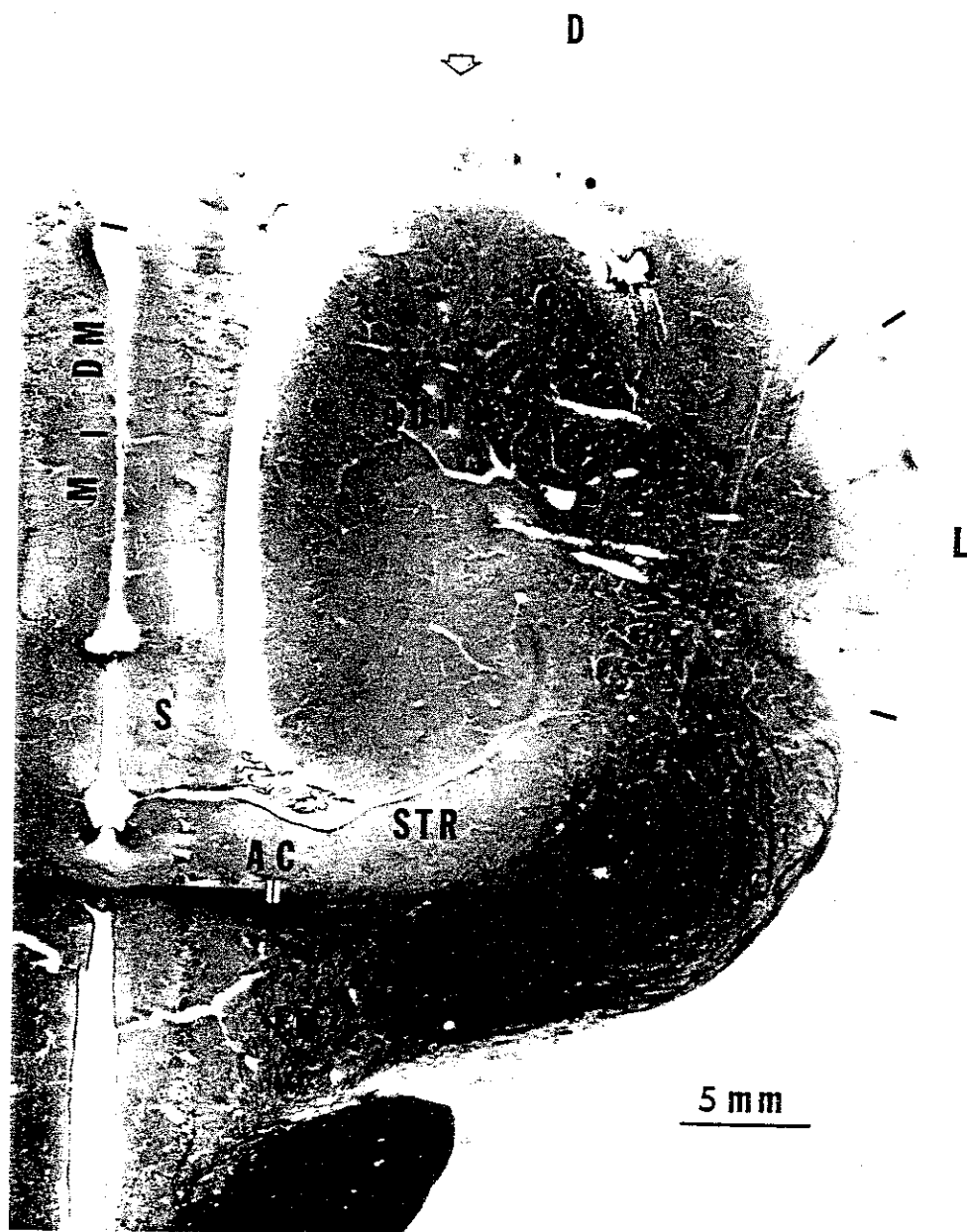


Figure 7. Telencephalon of a turtle. This is a section from the telencephalon of the red-eared turtle, *Pseudemys scripta elegans*, stained with a myelin stain. It is slightly rostral to the section shown in Fig. 3. The cortex is situated dorsal to the postcommissural septum (S). It contains medial cortex (M), dorsomedial cortex (DM), dorsal cortex (D), and lateral cortex (L). The open arrow marks the divisions of dorsal cortex that are designated D1 (laterally) and D2 (medially) by Desan (1984). The section passes through the anterior commissure (AC) and the forebrain bundles (FB) as they turn laterally into the striatum (STR). ADVL: anterior dorsal ventricular ridge.

Pallial thickening has often been regarded as a separate entity. However, Desan (1984) recently divided dorsal cortex of cryptodiran turtles into two divisions. His area D1 corresponds to the medial subarea of dorsal cortex; his area D2 includes the intermediate subarea and the pallial thickening. In *Sphenodon*, the lateral subarea of dorsal cortex curves ventrally and fuses during the course of ontogenesis with the cell-cluster zone of ADVR so that ADVR and cortex appear continuous in adult *Sphenodon* (Hines, 1923).

Lateral cortex forms the ventrolateral wall of the hemisphere. It is situated dorsal to the lateral olfactory tract, which carries the axons of mitral cells from the main olfactory bulb to lateral cortex. This cortical area is typically divided

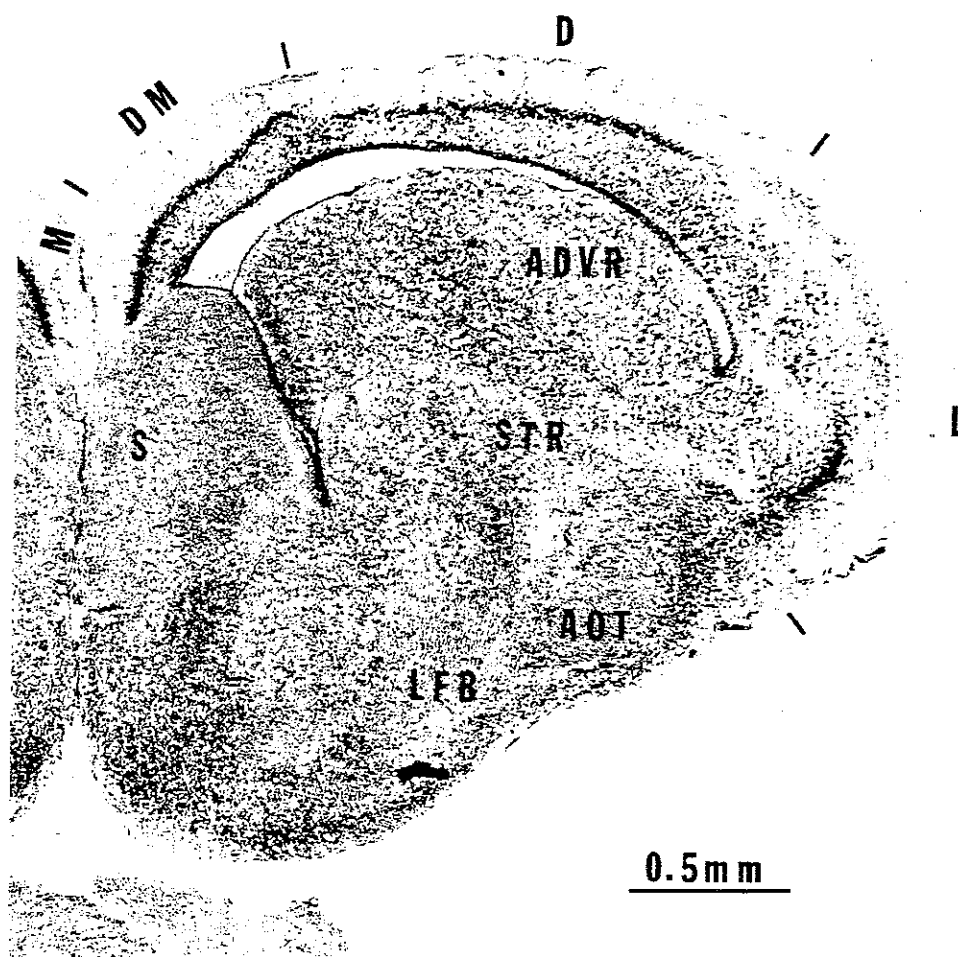


Figure 8. Telencephalon of a snake. This is a Nissl section from the telencephalon of a water snake, *Natrix sipedon*. At this level, more rostral than the section shown in Fig. 2, the cortex is situated dorsal to the precommissural septum (S). It contains medial cortex (M), dorsomedial cortex (DM), dorsal cortex (D), and lateral cortex (L). The accessory olfactory tract (AOT) carries fibers from the accessory olfactory bulb (see Fig. 2) to nucleus sphericus in the caudal telencephalon (see Fig. 11B). This tract, and the perifascicular nuclei that surround it, are best developed in snakes and some lizards. ADVR, anterior dorsal ventricular ridge; LFB, lateral forebrain bundle; STR, striatum.

into four subareas (Fig. 11). Two rostral areas (Fig. 11, drL, vrL) occupy the part of the lateral cortex that is situated rostral to the anterior commissure. Caudal areas (Fig. 11, dcL, vcL) are situated caudal to the anterior commissure. The rostral and caudal parts of lateral cortex are each divided into dorsal and ventral parts on cytoarchitectonic criteria. Thus, the dorsal rostral cortex has somata relatively densely packed in layer 2, while the ventral rostral cortex has somata

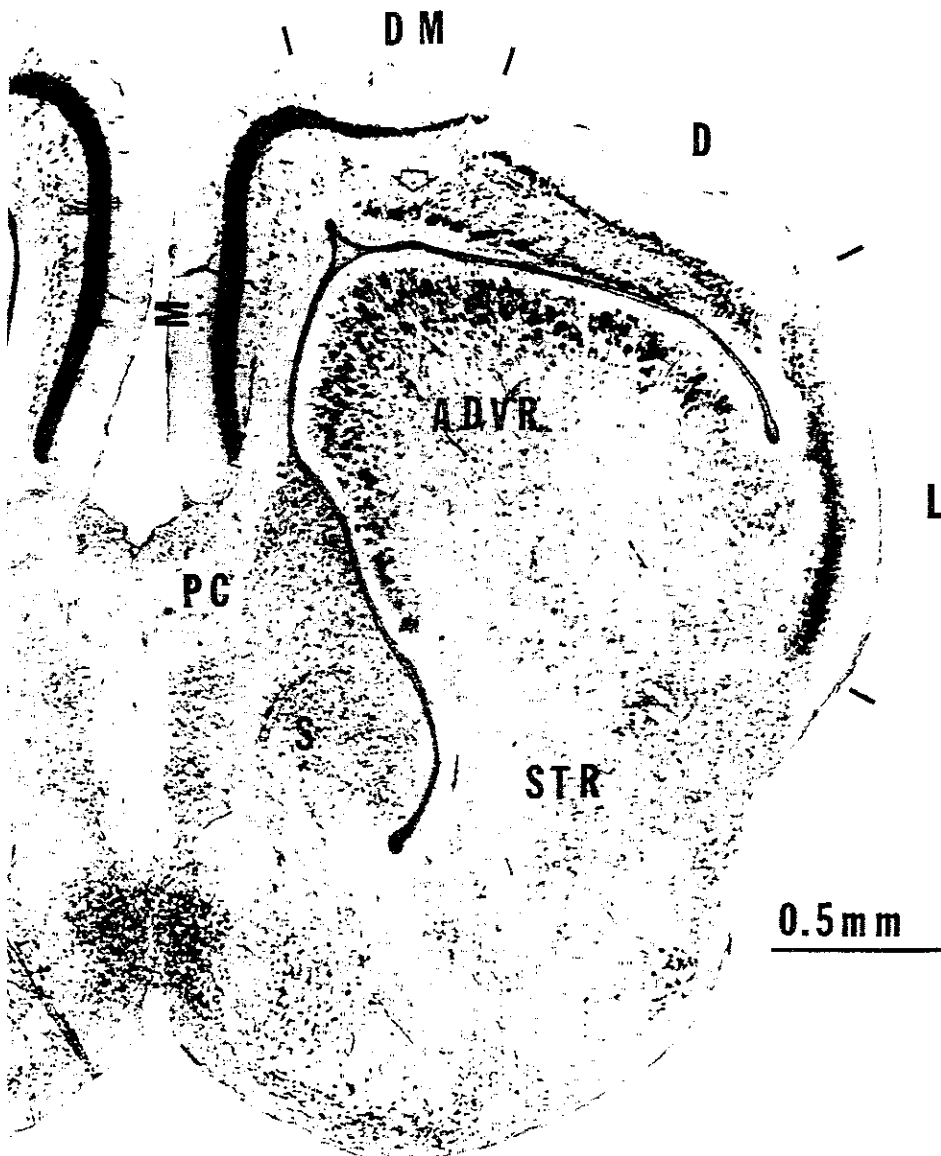


Figure 9. Telencephalon of a lizard. This is a Nissl section from the telencephalon of the tokay gecko *Gehko gecko*. At this level the pallial commissure (PC) connects the two cortices through the dorsal part of the precommissural septum (S). The cortex contains medial cortex (M), dorsomedial cortex (DM), dorsal cortex (D), and lateral cortex (L). Notice the distinct cell plate in dorsomedial and dorsal cortex. ADVR, anterior dorsal ventricular ridge; STR, striatum.

more loosely packed in layer 2. Layer 3 of rostral cortex usually has a distinct accumulation of loosely packed somata.

4. Development

The trilaminar pattern of cortex arises ontogenetically as a result of a radial migration of neuroblasts from a ventricular layer lining the inner surface of the cerebral hemispheres of embryos. General features of this process can be identified by studying sections through the forebrains of selected developmental stages of embryos (Herrick, 1892; Tandler and Kantor, 1907; Johnston, 1916; Kirsche, 1972; Hines, 1923; Reese, 1910; Hetzel, 1974; Warner, 1946; Kallen, 1951, 1956; Berquist and Kallen, 1954; Goffinet, 1983). The roof of the hemisphere consists of a neuroepithelium of actively dividing cells in early embryos. As neuroblasts begin to migrate from the neuroepithelium, an inner layer of scattered cells and a cell-free outer (or marginal) layer can be recognized. The trilaminar pattern of the adult cortex is evident in later embryonic stages in which layer 1 contains a few neurons, usually with horizontally aligned processes, layer 2 contains many neurons with bipolar, vertically aligned processes, and layer 3 contains a moderate number of scattered neurons. Layer 2 is initially

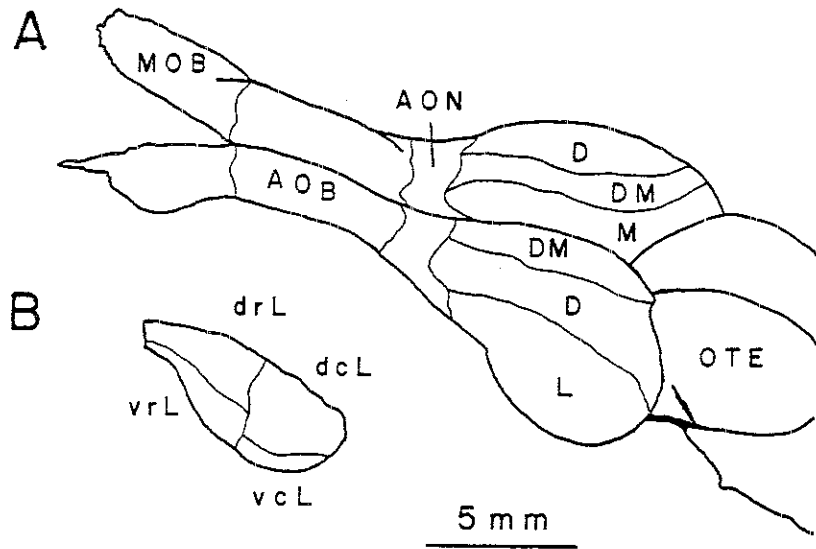


Figure 10. (A) Distribution of cortical areas. This is a drawing of the brain of a garter snake, *Thamnophis sirtalis*, similar to that shown in Fig. 2 to illustrate the position of the cortical areas upon the cerebral hemisphere. Because of the orientation of the brain, the drawing shows areas on the lateral surface of the left hemisphere and the medial surface of the right hemisphere. Medial (M), dorsomedial (DM), dorsal (D), and lateral (L) cortex have the form of rostrocaudally elongate strips. They abut rostrally with the anterior olfactory nucleus (AON), which encircles the peduncle of the olfactory bulb. Dorsal cortex is sometimes divided into three subareas (now shown). Lateral cortex is divided into four subareas. (B) Subareas of lateral cortex. This is a magnification of lateral cortex from panel A to show the position of the dorsal rostral lateral (drL), ventral rostral lateral (vrL), dorsal caudal lateral (dcL), and ventral caudal lateral (vcL) subareas. The cytoarchitecture of these areas is illustrated in Fig. 11.

a continuous stratum of cells in all species, but is ruptured medially and laterally to form the two superpositions in those species demonstrating this cytoarchitectonic feature.

Details of the migratory process have been investigated by tritiated thymidine labeling in the turtle *Emys orbicularis* and the lizard *Lacerta trilineata* (Goffinet *et al.*, 1986). Cortical neurons are born over a period of about 9 days late in the first half of embryogenesis. There are lateral-to-medial and rostral-to-caudal gradients in the timing of cortical migrations, so that, for example, neuroblasts migrate from the ventricular zone into lateral cortex earlier in development than they do in medial cortex. Migration occurs by means of an outside-in pattern within each cortical area with the first born neuroblasts migrating into layer 1 while those neuroblasts generated later in development migrate into layer 3. Glial cells continue to be born after the major wave of neuronal generation has subsided. Radial glial cells are present in embryos (Goffinet, 1983). Instances of neurons that are closely apposed to radial glial cells are sometimes seen in Golgi preparations of embryos, suggesting that radial glia play a role in guiding the migration of cortical neuroblasts in reptiles as they do in mammals.

Although the major fraction of cortical neurogenesis occurs during embryogenesis, two bits of evidence suggest some neurogenesis can occur in adult lizards of the genus *Lacerta*. The first is that there is a progressive increase in the

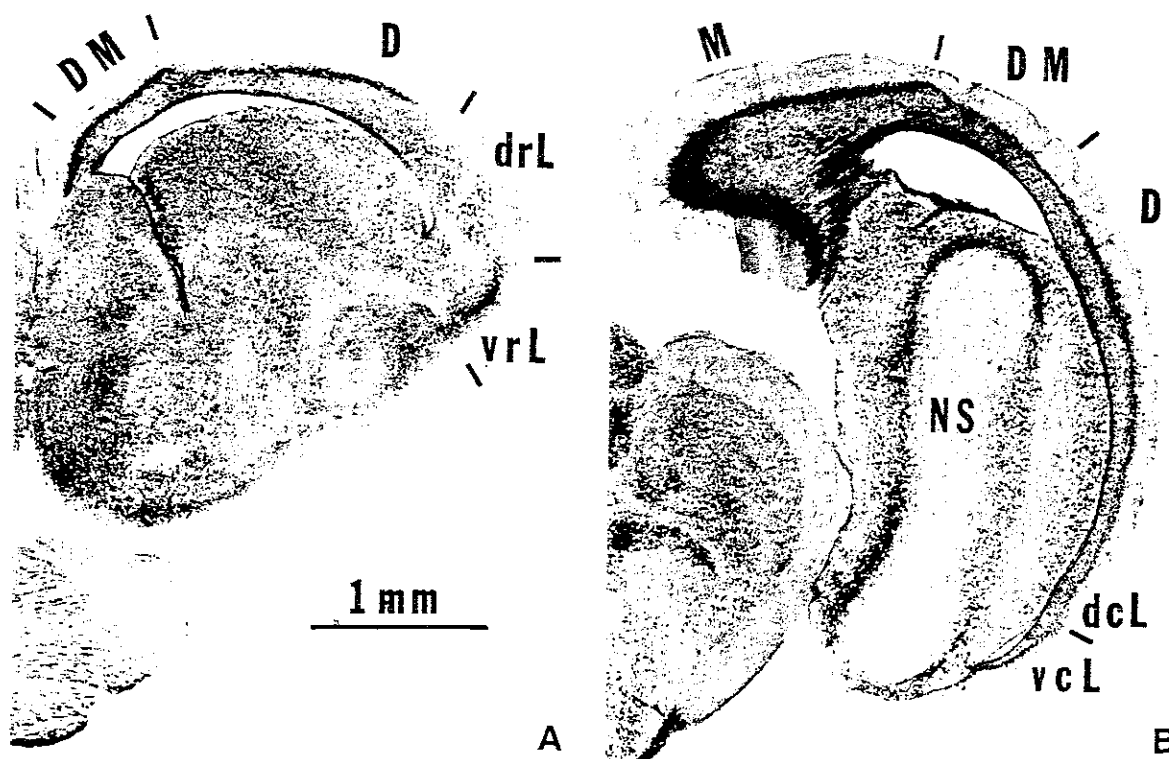


Figure 11. Cytoarchitecture of cortical areas. Shown are transverse sections through the brain of a water snake, *Nerodia sipedon*, to illustrate the cytoarchitecture of the cor-

tical areas identified in Fig. 10. (A) Section through the rostral hemisphere; (B) section through the caudal pole of the hemisphere. Abbreviations as in Fig. 10.

number of neurons in medial cortex of *Lacerta* with age (Lopez-Garcia *et al.*, 1984). The second is that spindle-shaped cells in layer 3 of medial cortex that appear to be immature, migrating neurons have been identified at both the light and electron microscope levels (Garcia-Verdugo *et al.*, 1986). These cells are in direct contact with the radial processes of ependymal tanycytes. They may originate from a subventricular or germinative zone that lines the lateral part of medial cortex (Kirsche, 1972; Garcia-Verdugo *et al.*, 1981).

5. Cortical Cells

5.1. Glial Cells

Cerebral cortex of reptiles contains two types of glial cells. First are ependymal cells or tanycytes (Fig. 12) that are the adult derivatives of the embryonic radial glial cells. The somata of these cells form a pseudostratified epithelium (the ependyma) that lines the ventricular surface of the cortex and the anterior

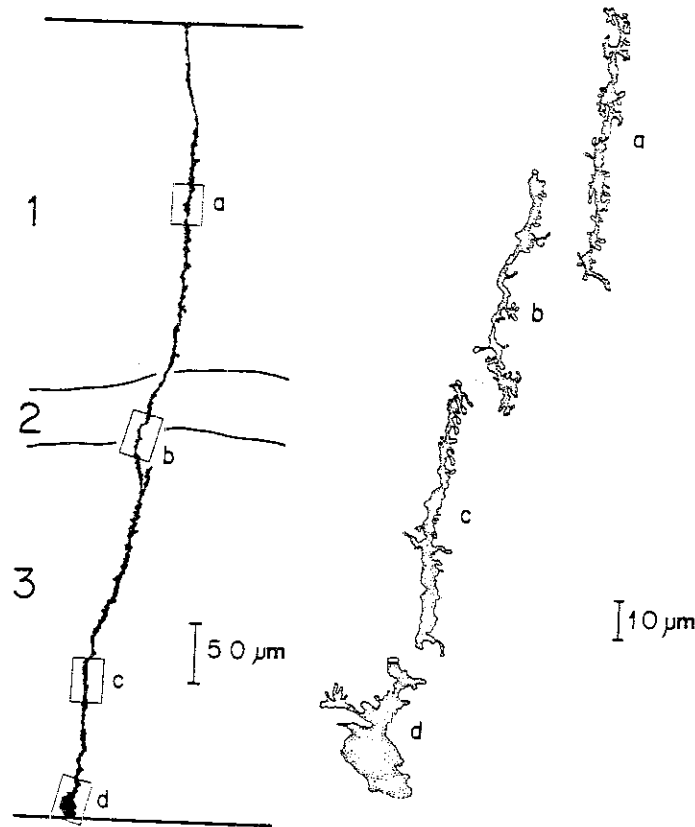


Figure 12. Ependymal cell. On the left is a camera lucida drawing of an ependymal cell from a Golgi preparation of the brain of a water snake, *Natrix sipedon*. The parts of the cell enclosed in rectangles are shown at higher magnification on the right. Most of the cell is covered by velate processes, which decrease in density as the cell passes through layer 2 of medial cortex. From Ulinski (1977a).

dorsal ventricular ridge. The ventricular surface of each tanycyte is heavily ciliated. The cell body itself is elongated, with its sides joined to those of its neighbors via junctional complexes (Ulinski, 1977a, 1979; Wouterlood *et al.*, 1981; Davila *et al.*, 1985; Weiss and Ulinski, 1985). The cell body contains a nucleus and a well-developed Golgi apparatus. A short neck region extends from the cell body and then continues into a long radial process that extends the full width of the cortex. These can span the cortex unbranched, or divide into daughter processes that continue toward the pia. The processes contain a core of microtubules and filaments surrounded by a rim of cytoplasm with many glycogen particles (Ulinski, 1977a, 1979; Garcia-Verdugo *et al.*, 1981; Wouterlood *et al.*, 1981; Weiss and Ulinski, 1985). The radial processes bear velate processes that extend into the neuropil. The velate processes can be unevenly distributed along the shaft of the radial process. In medial cortex, tufts of velate processes occur in layers 3 and 1, but there are fewer velate processes in layer 2, which is composed of many densely packed somata (Lacey, 1978). The velate processes contain glycogen and insinuate themselves between neuronal somata and dendrites (see Weiss and Ulinski, 1985). The radial processes end in footlike expansions just below the pial surface (Wouterlood *et al.*, 1981; Davila *et al.*, 1985). These contain many mitochondria and expand into horizontally elongate and thin processes. They overlap each other and are joined by gap junctions to form a glial limiting membrane, positioned internal to the basal lamina, that separates the brain from the pia.

Both the cell bodies and the radial processes of tanycytes are postsynaptic to axon terminals involved in chemical synapses (Ebner and Colonnier, 1975; Weiss and Ulinski, 1985). These involve asymmetric active zones and round synaptic vesicles. Intracellular recordings have been achieved from tanycytes with *in vitro* preparations of turtle dorsal cortex (Connors and Ransom, 1982). Recordings made from tanycytes while stimulating fiber systems within the cortex failed to produce any sign of postsynaptic potentials, so the function of neuron-tanycyte synapses is unclear. Weiss and Ulinski (1985) discuss several possibilities, including the modulation of transport of substances into or out of the ventricular system or a role in controlling the extracellular ionic environment by mediating movements of the velate processes.

The remaining glial cells are oligodendrocytes and astrocytes that are scattered throughout the cortex. They have not been extensively studied, but seem to resemble the glial cells of mammals both in Golgi preparations (Ramón, 1891, 1896; Conty, 1953; King, 1966; Kruger and Maxwell, 1967; Stensaas and Stensaas, 1968; Inoue *et al.*, 1974; Wouterlood *et al.*, 1981; Guirado *et al.*, 1984) and in electron microscopic material. Both fibrous and protoplasmic astrocytes have been described.

5.2. Cytology of Neurons

Cortical neurons are comparable in their cytology to small- and medium-sized neurons in other regions of vertebrate nervous systems (Davydova and Smirnov, 1969; Ulinski, 1977a, 1979; Ulinski and Rainey, 1980; Davila *et al.*, 1986). Small neurons have a modicum of cytoplasm that contains scattered ribosomes, but few organized stacks of rough endoplasmic reticulum. Larger neurons have more cytoplasm and some stacks of rough endoplasmic reticulum.

that appear as a diffuse basophilia at the light microscope level in Nissl stains. The organelles found in cortical neurons are generally unremarkable. However, neurons in the cortex of reptiles, and elsewhere in their central nervous system, have more glycogen than is commonly found in neurons in mammals. It appears as granules scattered generally throughout the cytoplasm and dendrites of most neurons. This abundance of glycogen may reflect differences between reptiles and mammals in their dependence upon aerobic versus anaerobic metabolism (e.g., Bennett and Dawson, 1976). Nuclei are frequently indented by fingers of cytoplasm.

Dendrites of cortical neurons can be divided into two types based on their cytology. Some have a cytoplasm filled with neurotubules and neurofilaments running within the core of the dendrite (Fig. 13). Others seemingly lack an extensive cytoskeleton (Fig. 14) and have been labeled as "pale" dendrites by some authors (Davydova and Smirnov, 1969; Ebner and Colonnier, 1975; Ulinski, 1977a). Some dendrites are smooth, or bear a series of swellings or dilations. Others are covered with excrescences or dendritic spines (Fig. 15). These vary in their morphology from simple, filiform appendages, to spines with a knoblike swelling distally to those with a relatively large head that end in a fingerlike extension invaginated into a presynaptic element (e.g., Ulinski, 1977a; Davydova and Goncharova, 1979; Martinez-Guijarro *et al.*, 1984). Spines are invariably postsynaptic to profiles that resemble axon terminals (Ebner and Colonnier, 1975; Ulinski, 1977a). The synaptic contacts involve asymmetric active zones and presynaptic elements with clear, round synaptic vesicles in the great majority of cases, but some instances of spinelike profiles postsynaptic to terminals with clear, pleomorphic vesicles have been reported (Ebner and Colon-

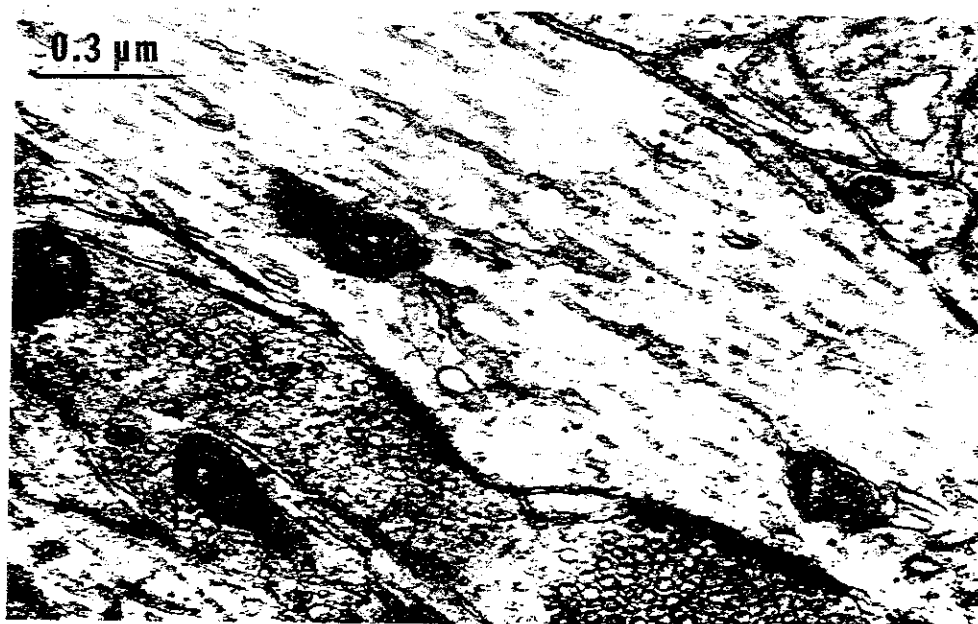


Figure 13. Dendrite. This is a longitudinal section through a dendrite from layer I of medial cortex of a water snake, *Natrix sipedon*. Like most dendrites, it contains many neurotubules. It is postsynaptic to two axon terminals.

nier, 1975) Spine apparatuses have not been described in reptiles. Dendrites frequently show structures called vacuolated invaginations (Ebner and Colonnier, 1975; Ulinski, 1979; Wouterlood *et al.*, 1981). These consist of regions of plasma membrane that invaginate into the dendrite forming a membrane-bound space confluent with the extracellular space (Fig. 16, VI). Several large membrane-bound vesicles are enclosed in this space. Vacuolated invaginations are often found adjacent to an axon terminal (Fig. 16, AT) that is presynaptic to the dendrite in which they occur, and in some sections it can be determined that the axon terminal gives rise to a flap of its plasma membrane that extends into the associated dendrite. Thus, the vesicles in the invagination are actually inside the axon terminal. The function of vacuolated invaginations is not known, but Wouterlood *et al.* (1982) found a fivefold increase in the number of vacuolated invaginations in the medial cortex of the lizard *Agama* following lesions of the adjacent dorsal and lateral cortical areas. These areas contain neurons that project to medial cortex (see Section 7.2), so the increase in vacuolated invaginations is correlated with the presence of degenerating axon terminals in medial cortex.

Cortical neurons show a marked tendency to form groups or clusters of cells with closely apposed somata. This is dramatically the case in layer 2 of medial cortex, which consists of many, very densely packed somata (Fig. 17). Electron microscopic observation shows that the plasma membranes of neighboring cells are closely apposed. The somata of neurons in other regions of the cortex are usually not as densely packed as in medial cortex, but the presence of clusters of neurons that are apposed to each other but isolated from neighboring cells is

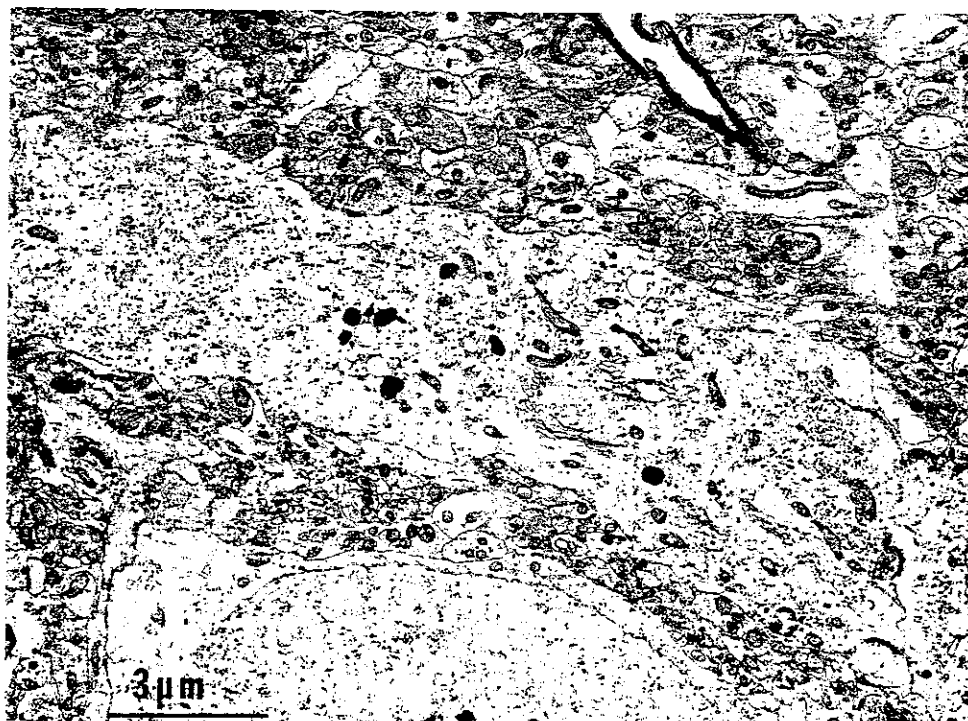


Figure 14. Pale dendrite. This is an example of a dendrite that lacks obvious neurotubules. It is from layer 3 of medial cortex of a water snake (*Natrix sipedon*).

common. Very large and distinct clusters are seen in the pallial thickening region of the dorsal cortex of cryptodiran turtles (Fig. 7). Smaller and less distinct clusters of neurons are seen throughout the cortex (e.g., Fig. 9) in many species. Three-dimensional reconstruction of layer 2 of turtle dorsal cortex indicates that clusters are present in medial dorsal cortex and that they become larger and more isolated in the pallial thickening. Such clusters are not unique to the cortex, but are actually a very dominant feature of the forebrains of reptiles and birds (see Ulinski, 1983). In some regions, such as the medial cortex of snakes (Fig. 17), apposed neurons are linked via membrane specializations that, according to Ulinski (1977a), resemble gap junctions. In other regions, membrane specializations have not been observed and the regions of contact resemble what Sotelo *et al.*, (1974) called "casual appositions." Ulinski (1977a) suggests that somatic appositions constitute a substrate for electrical interactions between cortical neurons, either via electrical synapses or via ephaptic interactions. However, Wouterlood *et al.* (1981) argue that the somatic appositions are more reminiscent of adhesive contacts between neurons in other regions of central nervous systems.

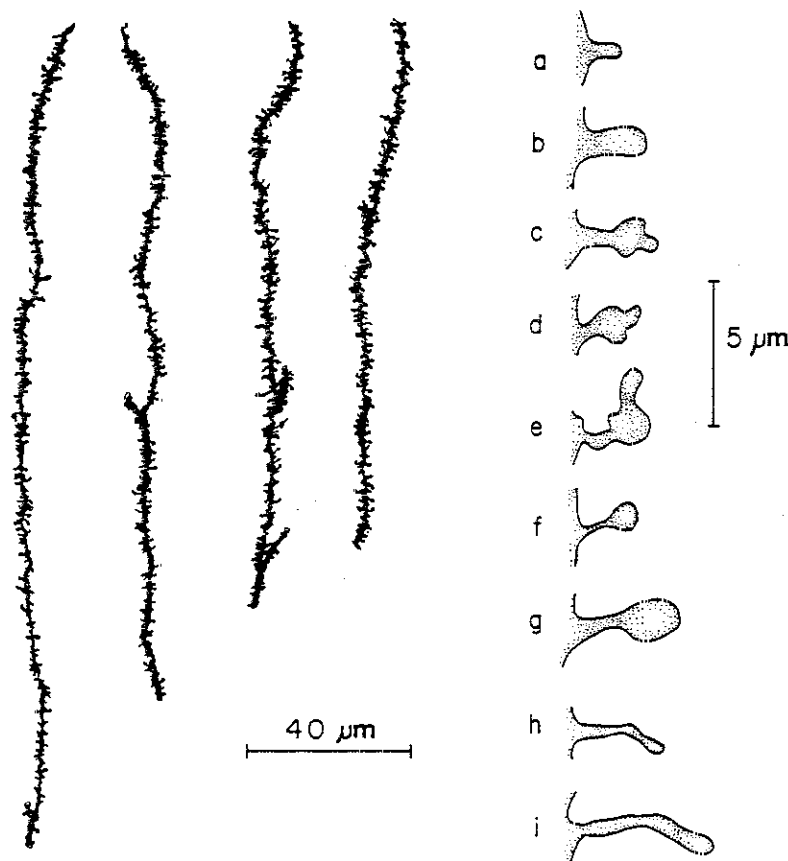


Figure 15. Dendritic spines. Shown are examples of spiny dendrites from a Golgi preparation of medial cortex of a water snake *Natrix sipedon*. Four examples of dendritic segments are shown on the left. On the right are the range of morphologies seen in dendritic spines. They range from small stubs (a, b), through pedunculated spines (c–g), through long, filiform appendages (h, i). From Ulinski (1977a)

The overall morphology of cortical neurons has been studied in Golgi preparations of several different species of reptiles. There have been a few recent studies that used intracellular injection of HRP to demonstrate the morphology of cortical neurons, but this method has not yet been employed systematically in reptiles. There is clearly a considerable variation in the morphology of cortical neurons. Most authors have used descriptive names to designate different groups of neurons, and there has been no systematic classification of cortical neurons in reptiles. The sketches in Fig. 18 summarize the major varieties of neurons that have been described.

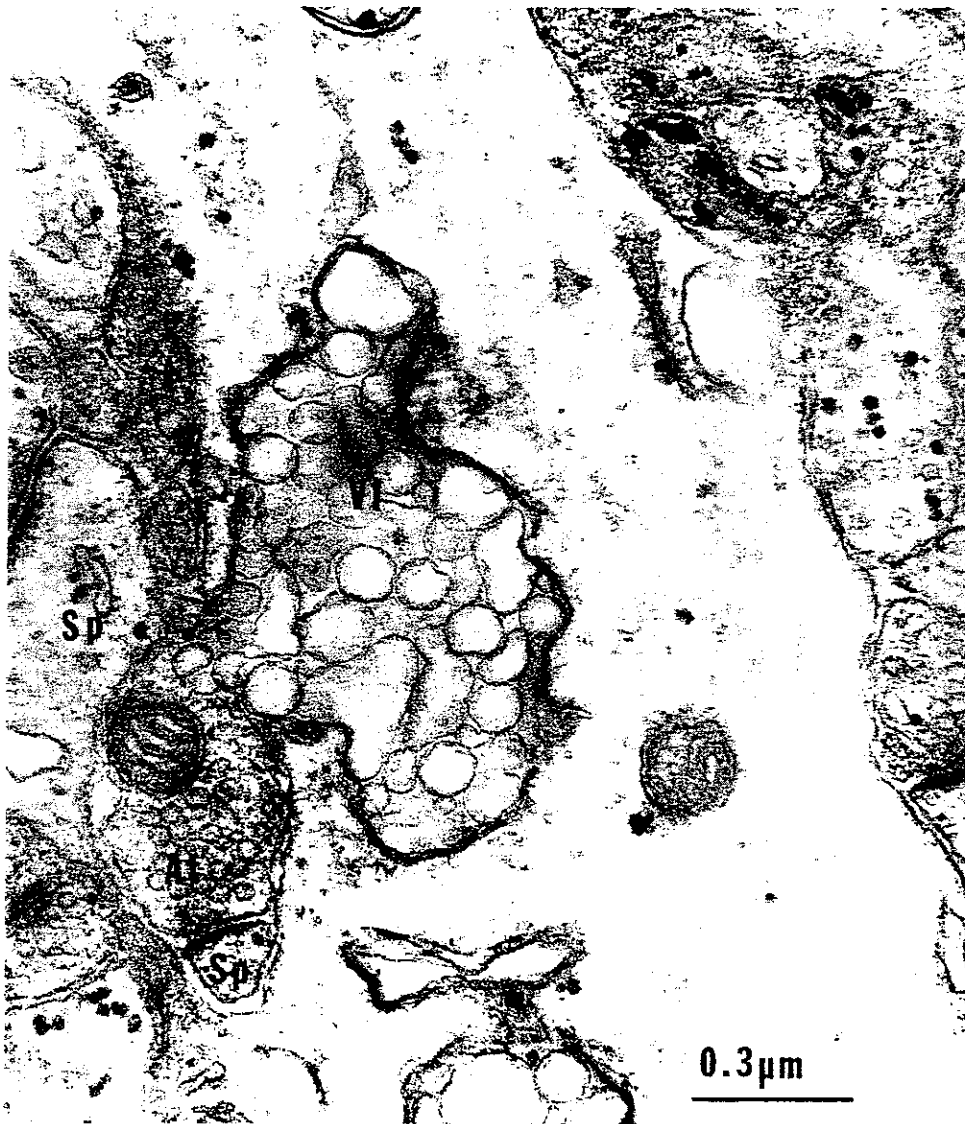


Figure 16. Vacuolated invagination. This is a vacuolated invagination in a dendrite from medial cortex of a water snake *Natrix sipedon*. The axon terminal to the left (At) contacts a small dendritic spine (Sp) and also invaginates into the large dendrite on the right. This vacuolated invagination (VI) contains many large membrane-bound vesicles.

Stellate neurons (Fig. 18A) have relatively small, oval or round somata and bear dendrites that radiate in a spherical dendritic field confined within a given cortical layer. They vary in the extent to which they bear dendritic spines. The axons of stellate cells have not been well characterized, but Desan (1984) did obtain good impregnations of stellate cells that had axon systems arborizing extensively within the vicinity of the cells' dendritic fields.

A second group of cortical neurons (Fig. 18B) have medium-sized somata that are fusiform or oval in shape and frequently have their long axes oriented vertically. These neurons have a single apical dendrite that extends vertically into adjacent cortical layers and several basal dendrites that extend toward the ependyma. The dendrites have a moderate cover of dendritic spines. Again, the axons have not been well characterized, but it has been established that some have collaterals that extend vertically into adjacent cortical layers. These neurons can be reasonably compared to the pyramidal neurons of mammalian cortex, and this term will be used here. However, two caveats are in order. The first is that the term *pyramidal* has been used promiscuously within the literature on reptile cortex and is often applied to cells that bear little real resemblance to

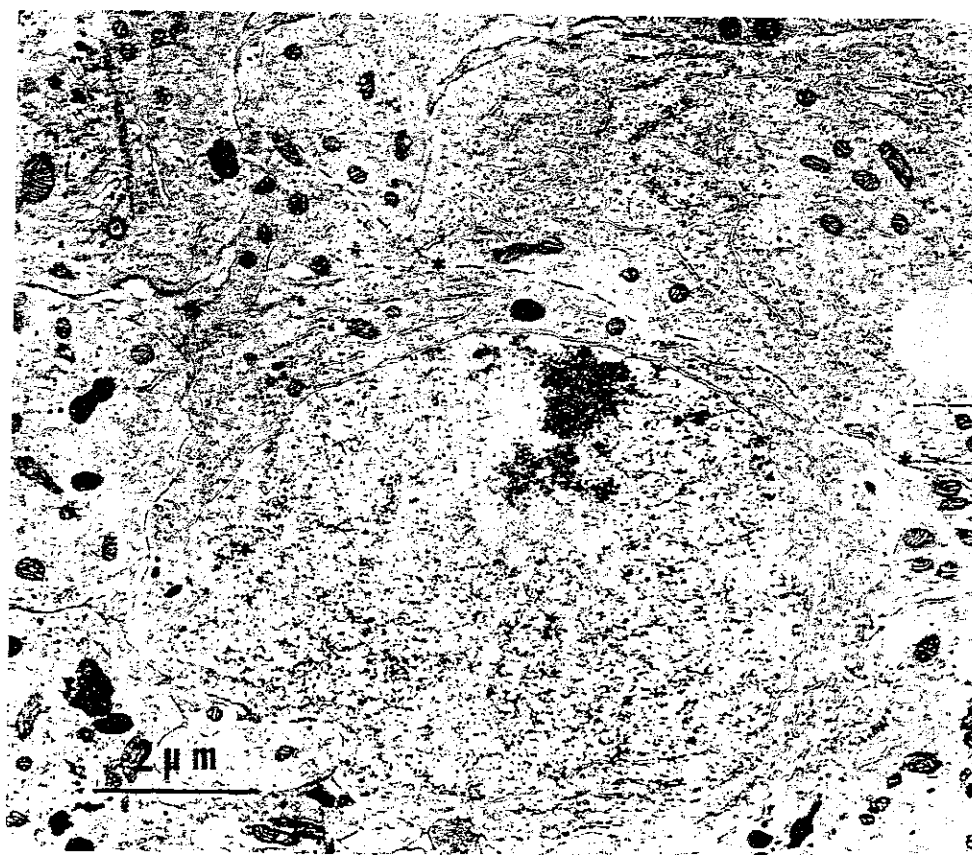


Figure 17. Neurons with apposed somata. This is an example of cortical neurons with apposed somata from medial cortex of a water snake *Natrix sipedon*. The soma that occupies the bottom of the figure is closely apposed to a second soma at the upper right. The line of apposition is marked by several specialized junctions (asterisks).

mammalian pyramidal cells. The second is that there remains some discussion as to what constitutes a pyramidal cell within the mammalian literature. In general, it seems appropriate to use the term *pyramidal* conservatively in describing reptilian neurons, and imprudent to attach too great a significance to the term

A third, and quite distinct, group of cells (Fig. 18C) can be designated as double pyramidal cells or bitufted cells. They have moderate-sized, oval or fusiform somata, but are distinguished by their possession of two tufts of vertically oriented dendrites, one from each pole of the soma. Each tuft of dendrites hence forms a pyramidal configuration, so the cell has two pyramids or tufts of

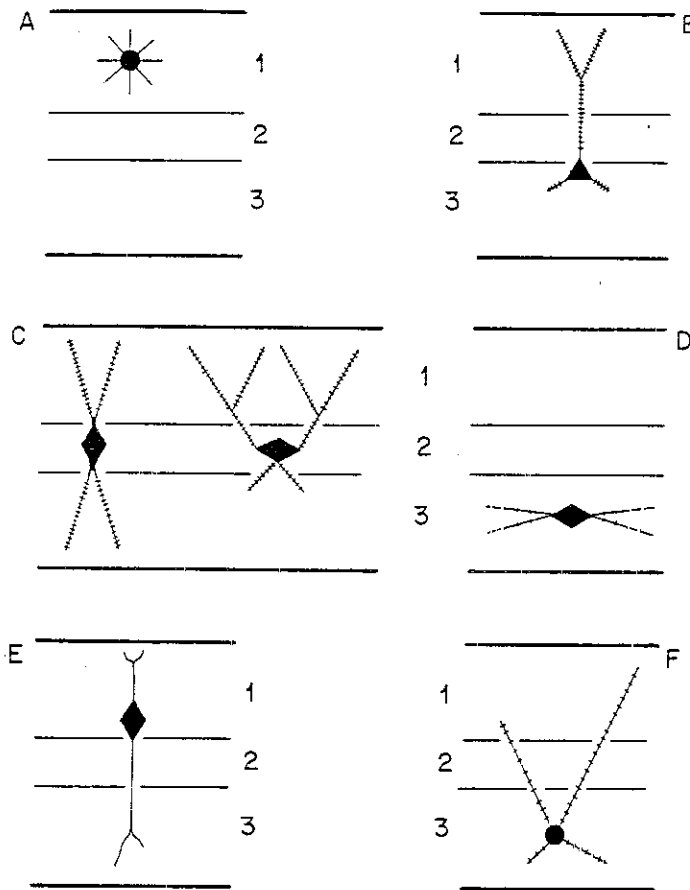


Figure 18. Cortical cell types. These drawings show, in cartoon form, the principal types of cells seen in cerebral cortex of reptiles. Each cell is positioned in a segment of cortex with layers 1, 2, and 3 indicated. (A) Stellate cells have oval or round somata that give rise to several dendrites, extending in all directions. They are most frequent in layer 1. (B) Pyramidal cells have triangular-shaped somata with a single ascending dendrite and several descending dendrites. They are found in layers 2 and 3. (C) Double pyramidal cells typically (like the cell shown on the left) have vertically fusiform somata that bear two conical tufts of dendrites. They occur in layers 2 and 3. However, double pyramidal cells frequently occur with reduced descending dendritic trees like the cell shown on the right. (D) Horizontal cells have horizontally elongated somata and bear dendrites that extend considerable distances from each pole. They occur in layer 3. (E) Bipolar cells have vertically fusiform somata and bear only a single, relatively unbranched dendrite from each pole. They occur in all three layers. (F) Multipolar cells have round or oval somata and give rise to several long dendrites that may cross laminar boundaries. They occur in all three layers.

dendrites. The dendrites are invested heavily with dendritic spines. Axons of double pyramidal cells can bear collaterals that either ascend or descend into adjacent cortical layers. There is clearly a range in the morphology of double pyramidal cells. All have a dendritic field extending vertically toward the pial surface. However, the extent to which the descending dendritic field is developed varies considerably.

Horizontal cells (Fig. 18D) are characteristic of the third layer of the cortex. They have fusiform somata whose long axes are oriented parallel to the pial surface. The somata bear dendrites from their poles. The dendrites usually extend for considerable distances within layer 3, but may eventually turn and ascend through layer 2 before terminating in layer 1.

Bipolar cells (Fig. 18E) have vertically elongate somata and a single dendrite that leaves each pole of the soma.

Multipolar cells (Fig. 18F) have oval or round somata that bear several dendrites in all directions. The dendrites extend throughout the depth of the cortex, branching several times and bearing relatively few spines.

5.3. Physiology of Neurons

Information on the cellular physiology of cortical neurons is limited to a few *in vivo* studies (e.g., Pivavarov and Trepakov, 1972) and, more recently, extensive, *in vitro* studies in turtles (Connors and Kriegstein, 1986; Kriegstein and Connors, 1986; Kriegstein, 1987; Larson-Prior and Slater, 1988). Membrane properties of cortical neurons are generally unremarkable, except that some pyramidal or double pyramidal cells have relatively long membrane time constants, i.e., 140 msec (Connors and Kriegstein, 1986). The cause or significance of this is not known.

A striking feature of cortical neurons is that they can be divided into two categories based on differences in their firing patterns (Fig. 19). Experiments in which cells were studied with intracellular recording techniques and then filled with markers such as Lucifer yellow or HRP suggest these physiological groupings correlate with morphological differences. Intracellular injection of current in neurons classified as pyramidal or double pyramidal cells on morphological grounds (Fig. 19A) produces a train of action potentials that have a relatively slow firing frequency and accommodate rapidly (Connors and Kriegstein, 1986; Shen and Kriegstein, 1987). Action potentials with two amplitudes are seen. Large-amplitude potentials have long (1–3 sec), hyperpolarizing afterpotentials and result principally from an inward sodium conductance, with some involvement of a calcium conductance. Action potentials with small amplitudes typically precede the large-amplitude potentials and may trigger them. They are distinct from action potentials triggered by antidromic activation of axons, and may represent dendritic spikes. A second group of neurons includes layer 1 stellate cells as well as layer 3 horizontal cells (Connors and Kriegstein, 1986; Shen and Kriegstein, 1987). Intracellular current injection in these cells produces a relatively high frequency of firing that accommodates slowly. Nothing is known of the ionic basis of the firing pattern of these cells.

Double pyramidal cells in dorsomedial cortex frequently discharge in periodic bursts of multiple action potentials (Shen and Kriegstein, 1987). In some instances, hyperpolarizing the cells reveals the presence of underlying EPSPs,

suggesting the cells burst as a result of synaptic activation. However, other cells show no sign of such EPSPs and appear to burst endogenously. Both types of bursting cells accelerate their firing as a result of orthodromic synaptic activation. Bursting also increases when the cortex is treated with bicuculline methiodide, either by focal application or by submerging the cortex in a bath containing the agent. This indicates bursting is normally suppressed by intrinsic GABAergic mechanisms. Similarly, intracellular studies of neurons in turtle medial cortex in *in vitro* preparations (Larson-Prior and Slater, 1988) show they are normally under the influence of large, spontaneous IPSPs. Application of bicuculline or picrotoxin blocks the IPSPs and leads to a large depolarizing shift and epileptiform discharge that can be blocked, in turn, by NMDA antagonists.

Cortical neurons generally show various mixtures of EPSPs and IPSPs when activated by either electrical (Kriegstein and Connors, 1986; Shen and Kriegstein, 1987; Kriegstein, 1987) or natural (Pivavarov and Trepakov, 1972; Kriegstein, 1987) stimulation. EPSPs can be elicited by focal application of L-glutamate. IPSPs can involve two components. The first is a short-latency hyperpolarizing event with a reversal potential of -70 mV. It is blocked by bicuculline methiodide and reversed by chloride injection. These responses are probably chloride conductances mediated via GABA A receptors. Long-latency hyperpolarizing events are insensitive to bicuculline and are not reversed by chloride injection. They have reversal potentials near the potassium reversal potential as calculated by the Nernst equation. They can be tentatively attributed to a potassium conductance mediated via a GABA B receptor.

Cortical neurons show both habituation and potentiation of their activity as the result of prolonged activation. Habituation is seen *in vivo* in turtle visual cortex (Gusel'nikov and Pivavarov, 1978). A neuron that responds to a moving stimulus shows decreased activity in response to repeated presentation of the stimulus. Consistent with this, paired application of cortical shocks with short interstimulus intervals results in a suppression of the activity of pyramidal cells in intracellular recordings (Kriegstein and Connors, 1986). On the other hand, pairs of pulses with long interstimulus intervals, up to several hundreds of

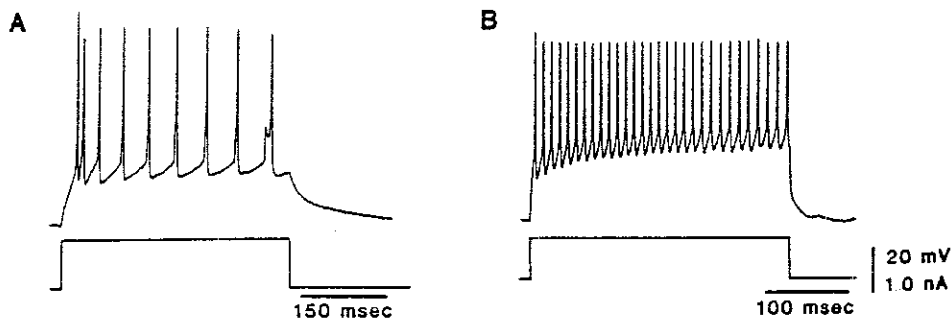


Figure 19. Physiological properties of cortical cells. Shown are the two firing patterns seen in cortical cells. Each panel represents an intracellular recording from a cortical cell during a depolarizing current pulse. (A) This firing pattern is typical of double pyramidal and pyramidal cells. It consists of a number of relatively broad action potentials and smaller "spikelets" which may be dendritic spikes. There is strong accommodation. (B) This firing pattern is typical of stellate and horizontal cells. Action potentials are relatively narrow. There are no spikelets and little accommodation. From Connors and Kriegstein (1986).

milliseconds, lead to an increased response in pyramidal cells that is apparently mediated by a greatly enhanced EPSP.

5.4. Neurotransmitters

There is considerable evidence for neurons in cerebral cortex that use GABA as a neurotransmitter. Immunohistochemical techniques have been used to localize GABA and related marker substances to cerebral cortex. Schwerdtfeger and Lorente (1988a,b) used monoclonal antibodies against GABA to study the distribution of GABA-like immunoreactivity in the lizard *Podarcis* (= *Lacerta*) *hispanica* at both the light and electron microscopic levels. GABA-positive somata are found in layers 1 and 3 of the medial and dorsomedial cortices and are typically associated with aspiny or sparsely spiny dendrites. GABA-positive axon terminals are plentiful, particularly in layer 1, and form symmetric active zones. They are typically presynaptic to unlabeled somata or dendrites. The distribution of GABA-positive neurons is similar in the medial and dorsomedial cortex of turtles (Shen and Kriegstein, 1987). Blanton *et al.* (1987) used antibodies against GABA and its synthetic enzyme glutamic acid decarboxylase (GAD) as well as histochemical procedures for the GABA degradative enzyme, GABA-transaminase, to study potential GABAergic neurons in the dorsal cortex of turtles. These markers label many neurons in layers 1 and 3 as well as a few neurons in layer 2. Labeled neurons include stellate, multipolar, and horizontal cells, but not pyramidal and double pyramidal cells. *In vitro* receptor binding studies using tritiated flunitrazepam indicate that benzodiazepine receptors (which are part of a complex containing GABA A receptors) are present in turtle cortex (Schlegel and Kriegstein, 1987). They are found in all layers and areas, but are relatively rare in dorsomedial cortex and plentiful in the outer third of layer 1 of the other areas. It is likely that stellate and horizontal cells throughout the cortex are GABAergic and responsible for generating IPSPs mediated by GABA A receptors and chloride channels in pyramidal and double pyramidal cells.

Both *in vivo* and *in vitro* studies on turtle embryos show that these GABAergic responses develop early in cortical differentiation (Blanton and Kriegstein, 1987; Shen *et al.*, 1987; Kriegstein and Shen, 1987; Kriegstein *et al.*, 1988). Experiments in which cells were labeled with HRP *in vitro* show that horizontal cells are the first relatively differentiated cells to develop in turtle cortex; stellate cells develop slightly later. Both are immunoreactive for GABA soon after they differentiate. Whole-cell patch-clamp studies of cells dissociated from embryonic cortex show that GABA-mediated chloride currents are also present early in development, indicating that GABA A receptors are present and functional before the formation of layer 2 or of synapses.

Neurons with somata in layer 2 of the cortex of turtle embryos stain positively with antibodies against the excitatory amino acid glutamate (Blanton and Kriegstein, 1987). Local application of L-glutamate in intracellular recording experiments results in EPSPs in several classes of cortical cells (Kriegstein and Connors, 1986). It appears likely then that some intracortical connections of pyramidal and double pyramidal cells may be mediated via glutaminergic mechanisms.

Immunohistochemical techniques have been used to localize the peptide substance P in the forebrains of both turtles and caiman (Brauth *et al.*, 1983;

Reiner *et al.*, 1984). Somata that stain positively for substance P are found in layers 1 and 2 of medial, dorsomedial, and dorsal cortical areas. Terminal labeling is found in lateral cortex, principally in layers 2 and 1. These observations raise the possibility that projections from medial cortex to lateral cortex use substance P as a neurotransmitter.

Members of the enkephalin family of peptides are found in neurons throughout the cortex of *Caiman* (Brauth, 1984), turtles (Reiner, 1983), and lizards (Naik *et al.*, 1981), principally in layer 2. A small number of neurons that stain positively for somatostatin have been reported in dorsal cortex of turtles (Bear and Ebner, 1983) and the lizard *Ctenosauria pectinata* (Goossens *et al.*, 1980).

Although neurons that stain positively with antibodies against the acetylcholine synthetic enzyme, choline acetyltransferase, are found in the basal forebrain of turtles (Desan, 1984; Hohmann *et al.*, 1983), there is no indication of cholinergic neurons within the cortex.

6. Neuronal Organization of Cortical Areas

Representatives of the morphological groups of neurons described in Section 5.2 are found in all four cytoarchitectonic areas of cortex, but each area contains a particular mixture of cell types and morphological varieties, giving it a distinct neuronal organization.

6.1. Medial Cortex

Layer 1 of medial cortex contains a small number of cells (Minelli, 1966; Lacey, 1978; Davydova and Goncharova, 1979; Ulinski, 1977a; Davila *et al.*, 1985; Berbel *et al.*, 1987). Some are stellate in configuration; others resemble small horizontal cells. In snakes (Ulinski, 1977a), they have oval or round somata, 5 to 10 μm in diameter, that bear two to five dendrites (Fig. 20). The dendrites contain a flocculent cytoplasm with few neurotubules and are relatively smooth, bearing few dendritic spines. They form arbors 200 to 400 μm in diameter. Axons of these stellate cells have not been well characterized, but seem to extend some distance horizontally in layer 1 before branching. Both the somata and dendrites of stellate cells receive many synaptic contacts, predominantly from axon terminals with clear, round synaptic vesicles and forming asymmetric contacts.

Layer 2 is characterized by a large number of small double pyramidal cells with densely packed somata that frequently form casual appositions (Garcia-Verdugo *et al.*, 1981; Davila *et al.*, 1985) or are linked by specialized junctions (Ulinski, 1977a; Wouterlood *et al.*, 1981). They are morphologically quite heterogeneous (Minelli, 1966; Ramón, 1896; Davydova and Goncharova, 1979; Ulinski, 1977a; Lacey, 1978; Davila *et al.*, 1985; Berbel *et al.*, 1987; Guirado *et al.*, 1984; Ebbesson and Voneida, 1969), and we do not know how many cell types are actually present. One clear type is the candelabra cell described by Ulinski (1977a) in the snake *Natrix* (Fig. 21). These neurons have vertically oriented, fusiform somata that bear an extensive array of dendrites in layer 1. The dendrites branch once or twice and ultimately reach the pial surface. They are

heavily covered by dendritic spines that range from slender, filiform appendages to mushroom-like in appearance. The spines and shafts of these dendrites are postsynaptic to axon terminals, the great majority of which contain clear, round synaptic vesicles and form asymmetric contacts. The lower pole of each candelabra cell soma gives rise to a single dendrite that is initially smooth, but soon divides into several spinous branches that descend throughout the upper part of layer 3. Proximal shafts of the descending dendrites give rise to one or sometimes two axons that invariably descend into layer 3. Each axon has collateral branches containing many varicosities *en passant*, superficially in layer 3, and then enters the alveus deep in layer 3 where it bifurcates into a medial branch that enters the septum and a lateral branch that courses toward dorsomedial cortex. Both branches bear varicosities *en passant*. Electron microscopic studies of the alveus (Ulinski, 1977a) show it consists of fascicles of tightly packed, unmyelinated axons that dilate into varicosities at intervals. These contain clear, round synaptic vesicles that form asymmetric contacts on dendrites and somata in layer 3. The candelabra cells are the source of major efferent projections from the cortex, which will be described in Section 7.3.

Other layer 2 neurons can be viewed as variants of candelabra cells. One type that has been described frequently in lizards are the superficial fusiform cells first described by Pedro Ramón (1896) in *Lacerta* (Fig. 22), but since reported in several lizards (Lacey, 1978; Davila *et al.*, 1985; Berbel *et al.*, 1987). They generally resemble candelabra cells, but have ascending dendrites that run for a considerable distance along the inner border of layer 2 before turning into layer 1.

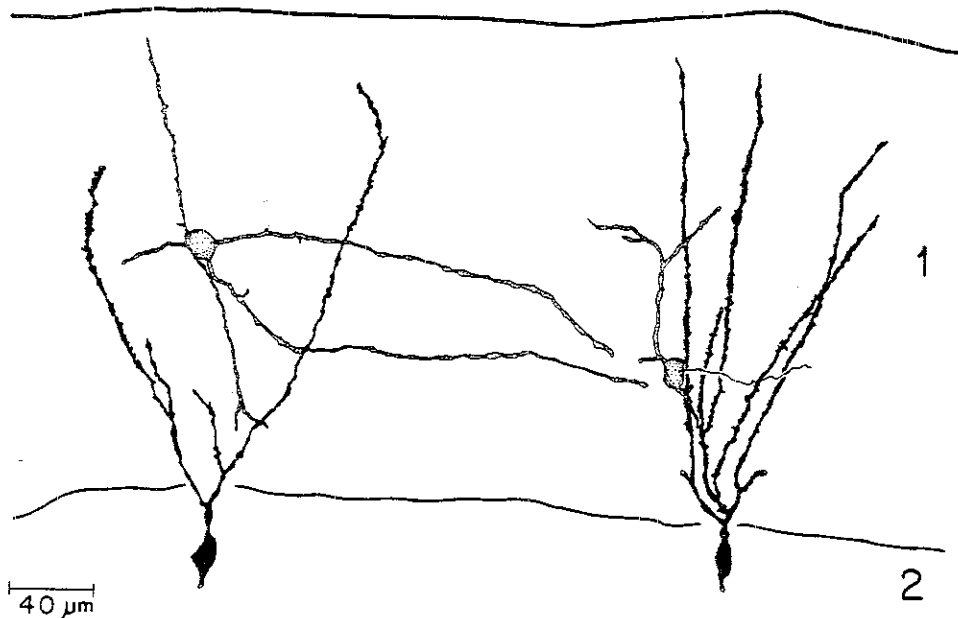


Figure 20. Stellate cells from medial cortex. This is a camera lucida drawing of two stellate cells from Golgi preparations of medial cortex of a water snake, *Natrix sipedon*. The stellate cells are situated in layer 1 and bear several dendrites that extend in all directions. The cell on the right bears an axon that runs horizontally intersecting the dendrites of candelabra cells. From Ulinski (1977a).

There is considerable reason to believe that the axons of cells in layer 2 of medial cortex contain zinc. Zinc can be detected histochemically using the method of Timm in several areas of cerebral cortex of lizards (Lopez-Garcia *et al.*, 1983; Perez-Clausell, 1988), including layer 3 of medial cortex and layers 1 and 3 of dorsomedial cortex, as well as the dorsal septum. These contain abundant Timm-reactive presynaptic boutons which make asymmetric contacts with dendrites and dendritic spines. The only known fiber system with a distribution that correlates precisely with the Timm-positive regions of the telencephalon are the efferent fibers from medial cortex to the septum and dorsomedial cortex (Olucha *et al.*, 1988). Recent work in mammals suggests zinc may be released by synaptic terminals and can differentially modulate the activity of different classes of excitatory amino acid receptors (Westbrook and Mayer, 1987; Peters *et al.*, 1987). Since both afferents to the cortex and intracortical axons may be glutaminergic, cells in layer 2 of medial cortex could play a complicated role in

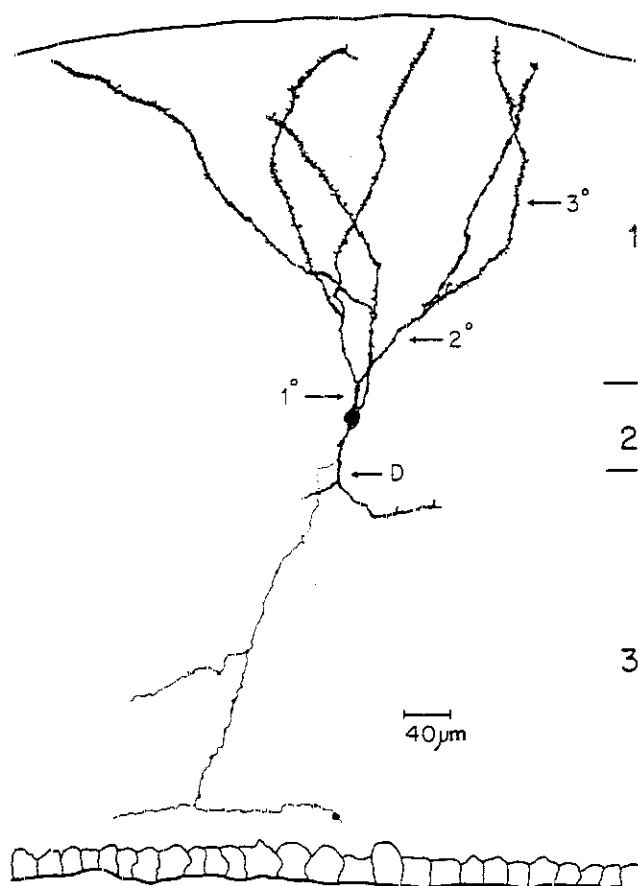


Figure 21. Candelabra cell. This is a camera lucida drawing showing the morphology of a candelabra cell, a type of modified double pyramidal cell characteristic of medial cortex. It is from Golgi preparations of a water snake, *Natrix sipedon*. Ascending dendrites extend in layer 1 and consist of proximal portions (1°) and distal portions (2° and 3°). Descending dendrites (D) branch in the upper half of layer 3. The axon descends through layer 3 and bifurcates into medial and lateral branches in the alveus. From Ułinski (1977a).

controlling the overall activity of neurons in dorsomedial cortex and the septum through the release of both a traditional neurotransmitter as well as an ion with a neuromodulatory function.

Layer 3 typically contains a moderate number of scattered neurons, but there is a tendency in some species for cells deep in layer 3 to form clusters or a more extensive cell plate. In snakes (Ulinski, 1977a), these periventricular cells are pyramidal cells with fusiform somata (Fig. 23), oriented horizontally in layer 3, and joined to their neighbors by rows of appositions resembling those seen on candelabra cells. Descending, spiny dendrites spread tangentially from the somata within the alveus. A single ascending dendrite extends radially from each soma through layer 3 and into layer 2. It is initially 2 μ m thick and lacks dendritic spines, but eventually bifurcates into spinous branches as it leaves layer 2. In lizards, layer 3 contains neurons that range from spiny multipolar cells to pyramidal cells to horizontal cells (Davila *et al.*, 1985; Berbel *et al.*, 1987; Guirado *et al.*, 1984). The horizontal cells have thick dendrites that are presynaptic to Timm-positive boutons, which suggests they are postsynaptic to layer 2 cells. A population of multipolar cells with distinctive, long dendritic spines are also postsynaptic to Timm-positive boutons (Lopez-Garcia *et al.*, 1988). They are GABA-positive and bear axons that ascend to layer 1. Thus, they are probably inhibitory interneurons.

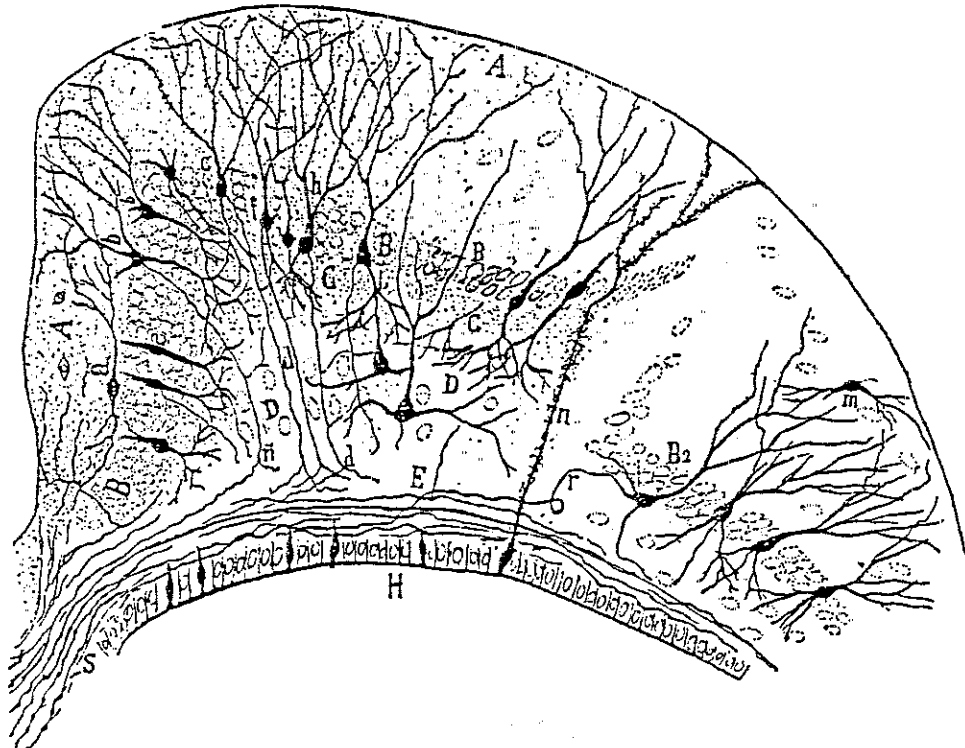


Figure 22. Lizard cortex. This is a drawing of a Golgi preparation through medial, dorsomedial, and dorsal cortex in a lizard *Lacerta*. It shows several cell types. Note in particular the candelabra cells and the "superficial fusiform cell" (a) in medial cortex. From Ramón (1896).

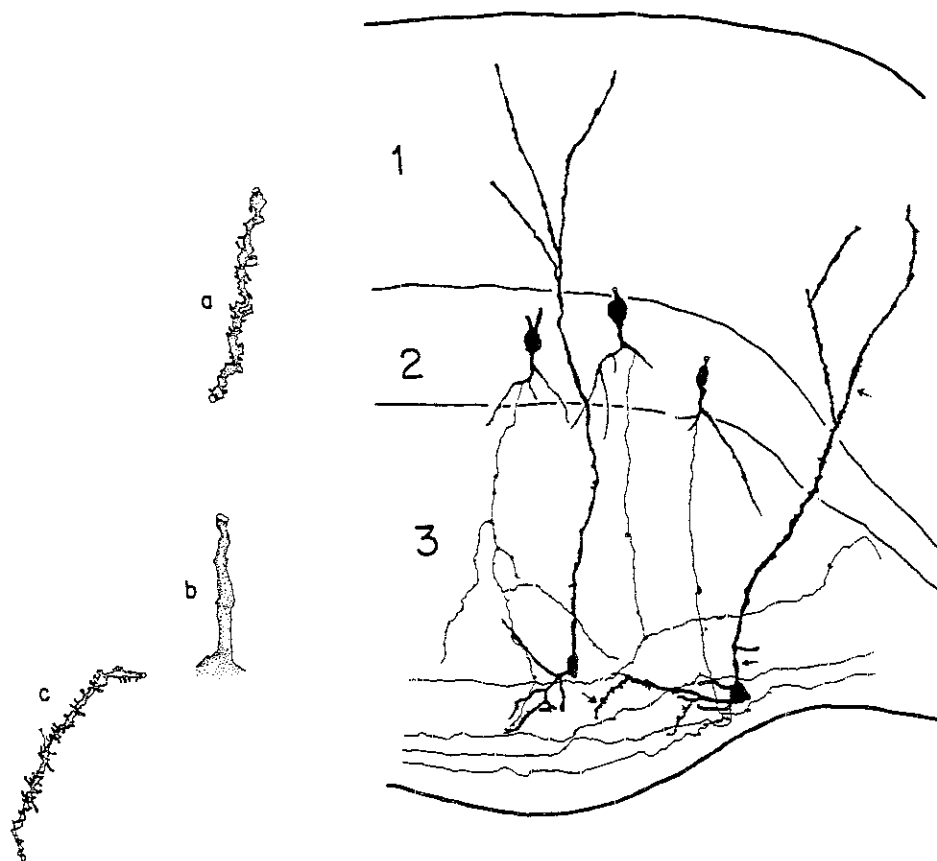


Figure 23. Pyramidal cells. This is a camera lucida drawing of pyramidal cells from the cell plate of medial cortex. It is from Golgi preparations of a water snake, *Natrix sipedon*. the somata and descending dendrites of the cells lie in the alveus; their ascending dendrites extend through layer 1. An axon originates from the soma on the right and runs into the alveus. The insets show details of the descending dendrite (c), proximal (b) and distal ascending (a) dendrites from the cell on the right at the levels indicated by the arrows. Note that descending axons of candelabra cells intersect the pyramidal cells. From Ulinski (1977a)

6.2. Dorsomedial Cortex

Bipolar cells in layer 1 of dorsomedial cortex have fusiform, vertically oriented somata with three to five dendrites that extend up to 150 μm from the soma (Minelli, 1966; Ulinski, 1979; Lacey, 1978). Some are devoid of spines or excrescences, while others bear a moderate number of spines. The morphology of their axons is poorly known.

Layer 2 is characterized by double pyramidal cells (Fig. 24) distinctly larger than those present in layer 2 of medial cortex (Ramón, 1891; Minelli, 1966; Ebbesson and Voneida, 1969; Davydova and Goncharova, 1979; Lacey, 1978; Ulinski, 1979). They have fusiform, vertically oriented somata that are distinguished ultrastructurally by a relatively large number of lysosomes and lipofuchsin granules (Ulinski, 1979). They are relatively loosely packed, so con-

tacts with neighboring somata are rarer than in medial cortex and the appositions characteristic of candelabra cells are not found in dorsomedial cortex. Each pole of the soma gives rise to a tuft of dendrites, consisting of a smooth proximal shaft that branches into several spinous daughter branches. The shafts are contacted by axon terminals containing clear, round vesicles and forming symmetric contacts (Ulinski, 1979). The spines are contacted by axons with clear, round vesicles and forming asymmetric contacts (Ulinski, 1979; Guirado *et al.*, 1984). The ascending dendrites extend through layer 1 almost to the pial surface. The descending dendrites extend through the upper half of layer 3. There are some variations in the size and shape of the dendritic fields (see Ulinski, 1979). Axons originate either from the somata of double pyramidal cells or from proximal dendrites near the soma. They descend into layer 3 and arborize into a series of branches forming a conical field. Some branches extend medially and participate in the commissural connections described in Sections 7.2.

Layer 3 contains several distinct types of neurons (Ramón, 1891; Minelli, 1966; Ulinski, 1979). First is a population of "displaced" double pyramidal cells that resemble the layer 2 cells. Second is a population of multipolar cells with round or oval somata (Fig. 26). Dendrites originate from all parts of their somata. They are initially smooth, but eventually are covered by dendritic spines. The ascending dendrites are long and can extend into layer 2; the descending

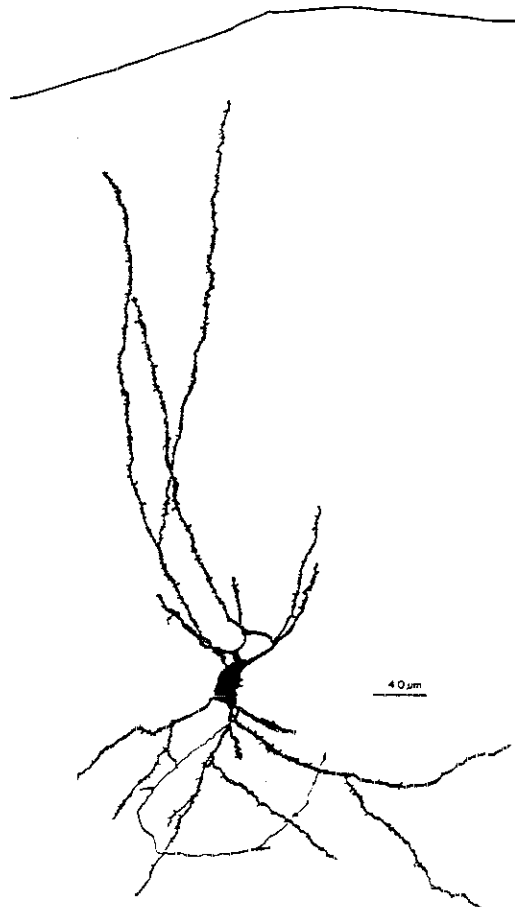


Figure 24. Double pyramidal cell. A camera lucida drawing of a double pyramidal cell from a Golgi preparation of dorsomedial cortex of a water snake, *Natrix sipedon*. The soma of the cell is located in layer 2. From Ulinski (1979).

dendrites are shorter and extend through layer 3 to the ependyma. Finally, horizontal cells have somata in the inner half of layer 3 (Fig 25). These are fusiform and oriented horizontally. Each pole of the soma gives rise to one or two dendrites that eventually branch and extend for considerable distances in layer 3 parallel to the ventricular surface. The dendrites bear relatively few spines, but sometimes have dilatations.

6.3. Dorsal Cortex

The cytoarchitecture of dorsal cortex varies considerably between species, but the only detailed investigations of its cellular structure have been carried out in cryptodiran turtles (Davydova and Smirnov, 1969; Northcutt, 1970; Davydova and Goncharova, 1979; Desan, 1984) and, to a lesser extent, in lizards (Ramón, 1891; Ebbesson and Voneida, 1969; Guirado *et al.*, 1987).

Layer 1 contains scattered stellate cells. Stellate cells have their somata situated deeper in layer 1 and dendrites that extend in all direction from their somata. The dendrites are generally confined to layer 1 and can vary in morphology from smooth to beaded to sparsely spinous to those covered with a moderate number of spines. The axons of these cells arborize extensively within layer 1 bearing many varicose collaterals. Horizontal cells are situated in the upper part of layer 1, nearer the pia, and have dendritic fields that are more dorsoventrally flattened with individual dendrites extending roughly parallel to the pial surface. The axons of these cells also extend horizontally. The stellate cells are GABAergic and demonstrate a tonic firing pattern (Section 5).

Layer 2 of turtles contains two distinct cell types (Northcutt, 1970; Davydova and Goncharova, 1979; Minelli, 1966; Desan, 1984). The majority are double

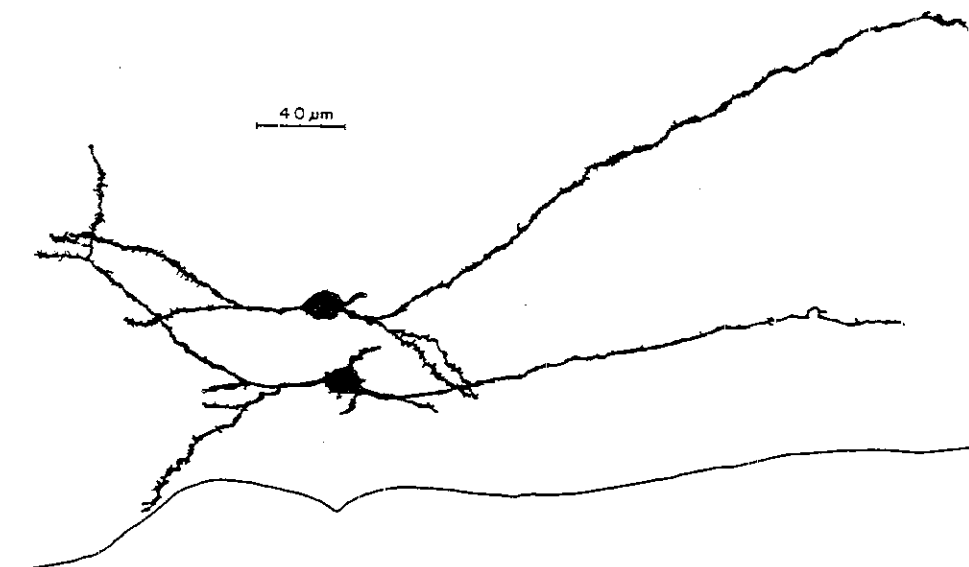


Figure 25. Horizontal cells. Camera lucida drawing of two horizontal cells from Golgi preparations of dorsomedial cortex of a water snake *Natrix sipedon*. The ventricular surface of dorsomedial cortex is shown at the bottom of the drawing. From Ulinski (1979).

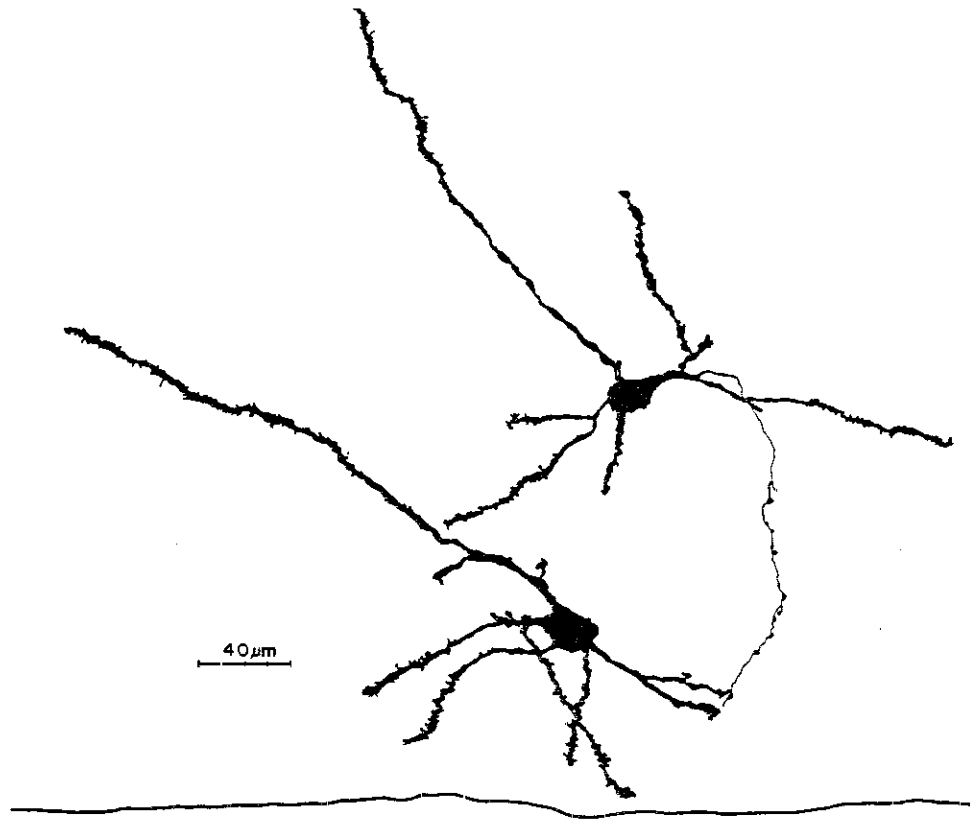


Figure 26. Multipolar cells. Camera lucida drawing of two multipolar cells from a Golgi preparation of dorsomedial cortex of a water snake, *Natrix sipedon*. The somata of the cells are situated in layer 3. The ventricular surface is shown at the bottom of the drawing. From Ulinski (1979)

pyramidal cells, each having two conical dendritic fields, one ascending into layer 1 and the other descending into layer 3 (Fig. 27). The proximal dendrites are free of dendritic spines, but spines gradually appear as the dendrites are followed out from the somata and then decrease in number toward the distal tips of the dendrites. Some of the spines are long or filiform, others are pedunculated, and many end in complex heads that invaginate into presynaptic axon terminals. The spines are postsynaptic to axon terminals that almost always contain clear, round synaptic vesicles and form asymmetric junctional contacts. The morphology of the axons of double pyramidal cells has not been systematically studied, but many descend into layer 3 where they collateralize. Some collaterals ascend obliquely into layer 1; others run in layer 3 into adjacent cortical layers. Although most double pyramidal cells have two dendritic fields, they vary systematically in their development according to the position of the cell in dorsal area. Layer 2 is situated close to the ependyma at the medial edge of dorsal area, and the double pyramidal cells in this region have very reduced basal dendritic fields. The size of the basal dendritic fields increases in cells situated at progressively more lateral regions in dorsal cortex, so those in the pallial thickening (the convoluted region adjacent to lateral cortex) have ascending and descending fields that are of equal size. The double pyramidal cells

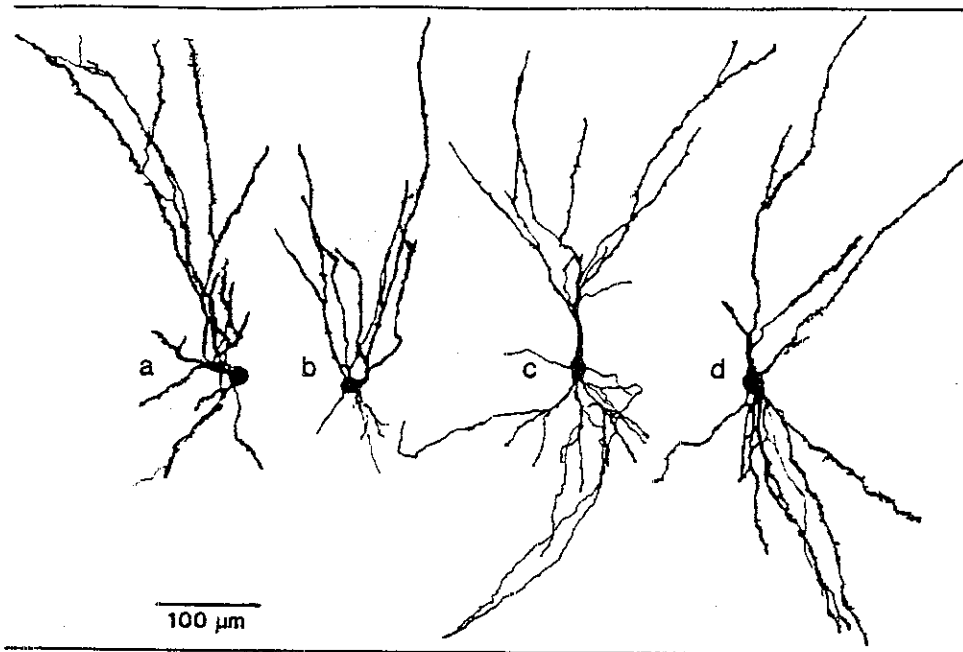


Figure 27. Double pyramidal cells. Drawings of double pyramidal cells from dorsal cortex of the red-eared turtle, *Pseudemys scripta elegans*. These cells are all from area D2 of Desan (1984) and illustrate the way in which the morphology of double pyramidal cells in this area varies as a function of mediolateral position. Cell a is situated toward the medial border of area D2; other cells are situated at progressively more lateral positions. Note the way in which the length of the descending tuft of dendrites increases as cells are situated more laterally. From Connors and Kriegstein (1986)

exhibit a slow firing pattern, a tendency to accommodate, and, possibly, dendritic spikes. The second type of cell present in layer 2 of dorsal cortex is a multipolar cell that has a round soma and several smooth dendrites that extend into layers 1 and 3. Layer 2 of lizards contains double pyramidal and multipolar cells, but also contains distinct populations of pyramidal cells (Ramón, 1891; Ebbesson and Voneida, 1969; Guirado *et al.*, 1987).

Layer 3 contains principally horizontal cells with fusiform somata and dendrites that extend from their poles, running concentric with the ependymal surface. Little is known about the axons of the horizontal cells, except that at least some project out of the cortex to the brain stem (Ulinski, 1986b). Many of the horizontal cells stain positively for markers associated with GABA (Shen and Kriegstein, 1987). In addition, layer 3 may contain bipolar cells.

6.4. Lateral Cortex

The cellular composition of lateral cortex has been most extensively studied in the snakes *Constrictor*, *Thamnophis* and *Natrix* (Ulinski and Rainey, 1980) with a few observations available in lizards (Ebbesson and Voneida, 1969) and turtles (Minelli, 1966; Davydova and Goncharova, 1979). Layer 1 of all four cytoarchitectonic subareas of lateral cortex is characterized by stellate cells with oval or round somata and dendrites confined to layer 1. The dendrites vary from

smooth to heavily decorated with spines. The axons of stellate cells appear to collateralize in layer 1, within the dendritic field of the parent cell. However, each of the four cytoarchitectonic areas has a distinct mixture of cell types in layers 2 and 3.

The rostral and caudal parts of lateral cortex are distinguished principally by differences in layer 2. Rostral lateral cortex is characterized by a population of distinct layer 2 cells, called bowl cells by Ulinski and Rainey (1980) (Fig. 28). These neurons have fusiform somata that give rise to a dendritic arbor, about 600 μm in diameter, extending into layer 1 with an overall bowl-shaped configuration. The somata are densely packed, with their plasma membranes touching in casual appositions (Ulinski and Rainey, 1980; Garcia-Verdugo *et al.*, 1986), and receive relatively few axonal contacts. The proximal shafts of bowl cell dendrites are smooth. The more distal primary and secondary branches are heavily covered by dendritic spines that are postsynaptic to axon terminals with clear, round synaptic vesicles and forming asymmetric junctions. The axons of bowl cells descend into layer 3 and collateralize extensively. One branch of each cell is efferent from lateral cortex. Bowl cells in ventral rostral lateral cortex have axons that course ventrally. Bowl cells in dorsal rostral lateral cortex have axons that course dorsally and form a fascicle of axons, each bearing varicosities *en passant*, that courses over the dorsal surface of the brain to end in medial cortex (Fig. 29). Rostral lateral cortex also is characterized by a cell plate or "secondary lamina" of somata in layer 2 which seems to be composed principally of stellate cells. These have relatively large somata and dendrites that extend both within layer 3, and reach some distance through layer 2 and into layer 1.

Caudal lateral cortex is characterized by pyramidal cells in layers 2 and 3 (Fig. 30). Some have a distinctly pyramidal-shaped somata and an apical dendrite

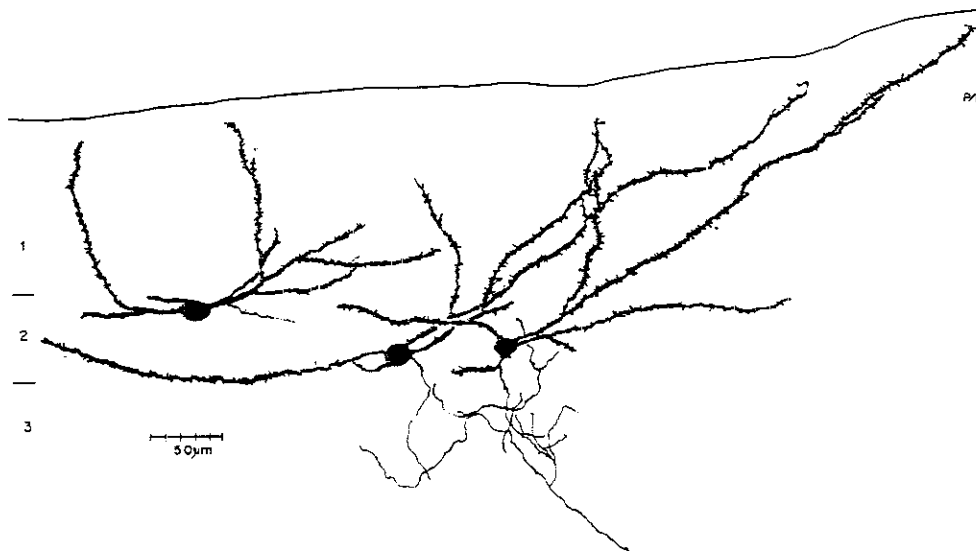


Figure 28. Bowl cells. Camera lucida drawing of bowl cells, a form of modified double pyramidal cell characteristic of lateral cortex. These are from Golgi preparations of lateral cortex of a water snake, *Natrix sipedon*. All of the cells are from dorsal lateral cortex. The pial surface is represented by the line at the top of the drawing and the borders of layer 2 are indicated by horizontal lines on the left. From Rainey and Ulinski (1980).

that ascends vertically and unbranched through layers 3 and 2. Others, more often found in layer 3, have horizontally oriented fusiform somata that bear an apical dendrite from one pole. This dendrite then curves sharply and ascends through layer 2. The proximal shafts of the apical dendrites are relatively smooth, but branch within layer 1 into a conical arbor of spiny dendrites. The basal dendrites of pyramidal cells are moderately spiny and form a conical arbor in layer 3.

Horizontal and double pyramidal cells are found in lateral cortex, but constitute a relatively small percentage of the total neuronal population as compared to other cortical areas.

7. Cortical Connections

7.1. Afferents to Cortex

The overall pattern of afferents to the cortex from subcortical structures has been studied in turtles (Desan, 1984) and lizards (Bruce and Butler, 1984a) using the retrograde transport of HRP. These studies indicate cortex receives inputs

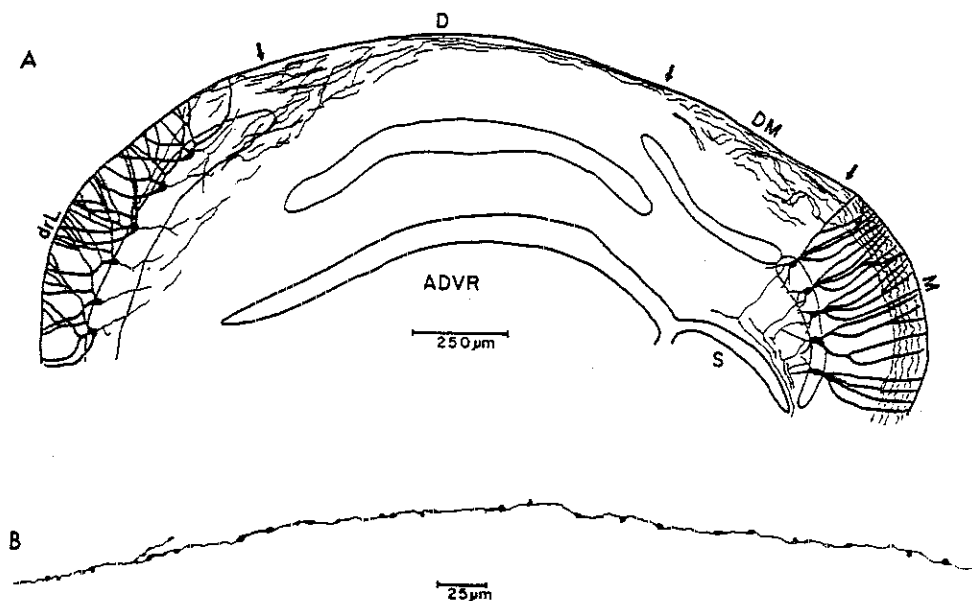


Figure 29. Bowl cell projections to medial cortex. (A) This is a drawing of the dorsal half of a coronal section through dorsal lateral cortex in a water snake, *Natrix sipedon*. Dorsal rostral lateral cortex (drL) is at the left. Examples of several bowl cells are depicted to illustrate the course of bowl cell axons. Notice that the axons of cells whose somata are situated ventrally in drL proceed medially through layer 3 and then curve dorsally. The axons of cells whose somata are situated ventrally course through layer 2 and dorsally into layer 1. Both sets of axons course together at the border of drL and dorsal cortex (D), which is marked by the arrow on the left. The bowl cell axons course across dorsal cortex just below the pial surface and enter dorsomedial cortex (DM). At this point the fascicle expands so that the fibers occupy the outer third of layer 1 in medial cortex (M). They intersect the distal ascending dendrites of the candelabra cells. (B) Camera lucida drawing of a segment of a bowl cell axon. It could be traced out of drL across the full width of dorsal area and into dorsomedial area. Note the varicosities, which can be seen along its trajectory. From Rainey and Ułinski (1980).

from a considerable variety of subcortical structures, which can be grouped into three categories for the purposes of discussion: (1) sources of sensory information, (2) structures related to the limbic system, and (3) brain-stem and basal forebrain systems.

7.1.1. Sources of Sensory Input

7.1.1a. Olfactory System. All reptiles have a main olfactory bulb that receives input from the olfactory mucosa of the nasal cavity. In addition, snakes, *Sphenodon*, and many lizards have accessory olfactory bulbs that receive input from the vomeronasal or Jacobson's organs. These are particularly well developed in forms with bifid tongues used to transport substrate-bound odorants to the vomeronasal cavities. Crocodilians lack vomeronasal organs; it is still uncertain whether or not turtles have vomeronasal organs (see Parsons, 1970). The accessory olfactory bulbs, when present, project to a distinctive nucleus in the amygdalar complex known as nucleus sphericus (Halpern, 1976; Ulinski and

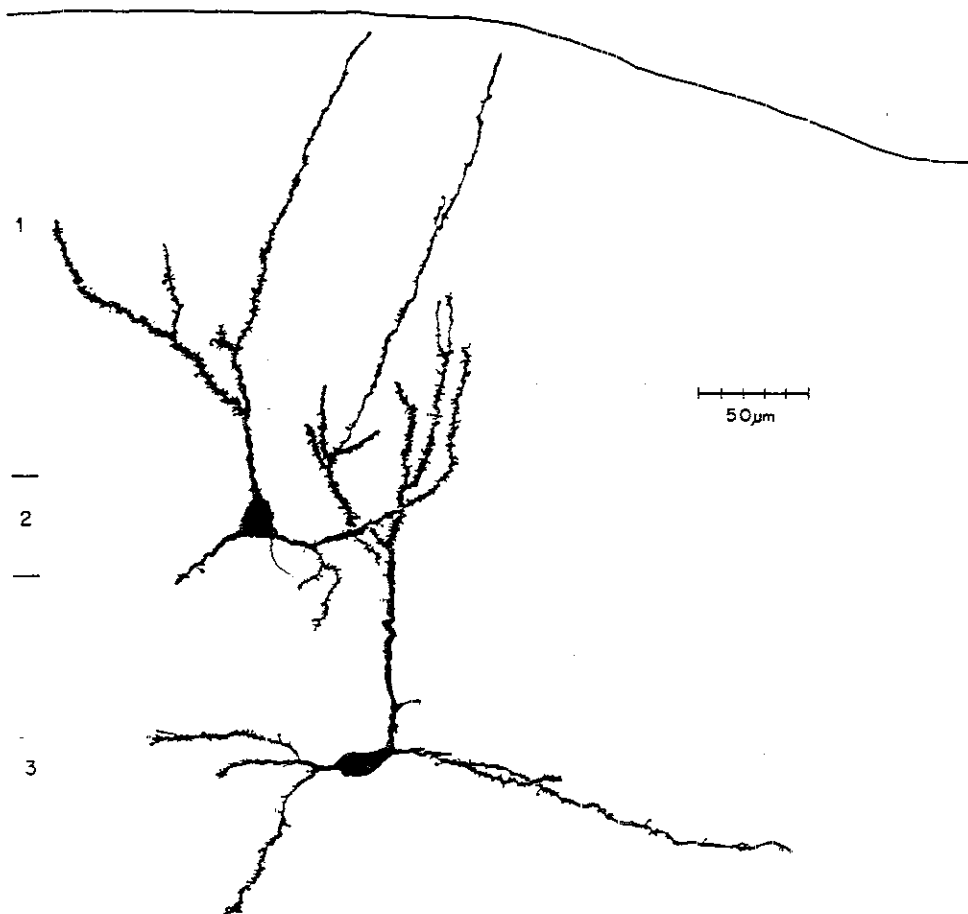


Figure 30. Pyramidal cells. Camera lucida drawing of pyramidal cells from Golgi preparation of lateral cortex of a water snake, *Natrix sipedon*. The pial surface is shown at the top of the drawing and the boundaries of layer 2 are demarcated by horizontal lines on the left. Note that the cell whose soma is positioned in layer 2 has a basal dendrite that recurves into layer 1, while the layer 3 pyramidal cell has its basal dendrites confined to layer 3. From Rainey and Ulinski (1980).

Kanarek, 1973; Heimer, 1969; Ulinski and Peterson, 1981). The main olfactory bulbs project to several structures situated around the rostral telencephalon (e.g., Halpern, 1976; Ulinski and Peterson, 1981; Scalia *et al.*, 1969; Reiner and Karten, 1985). These include the olfactory tubercle, diagonal band nuclei, and lateral cortex (Fig. 31).

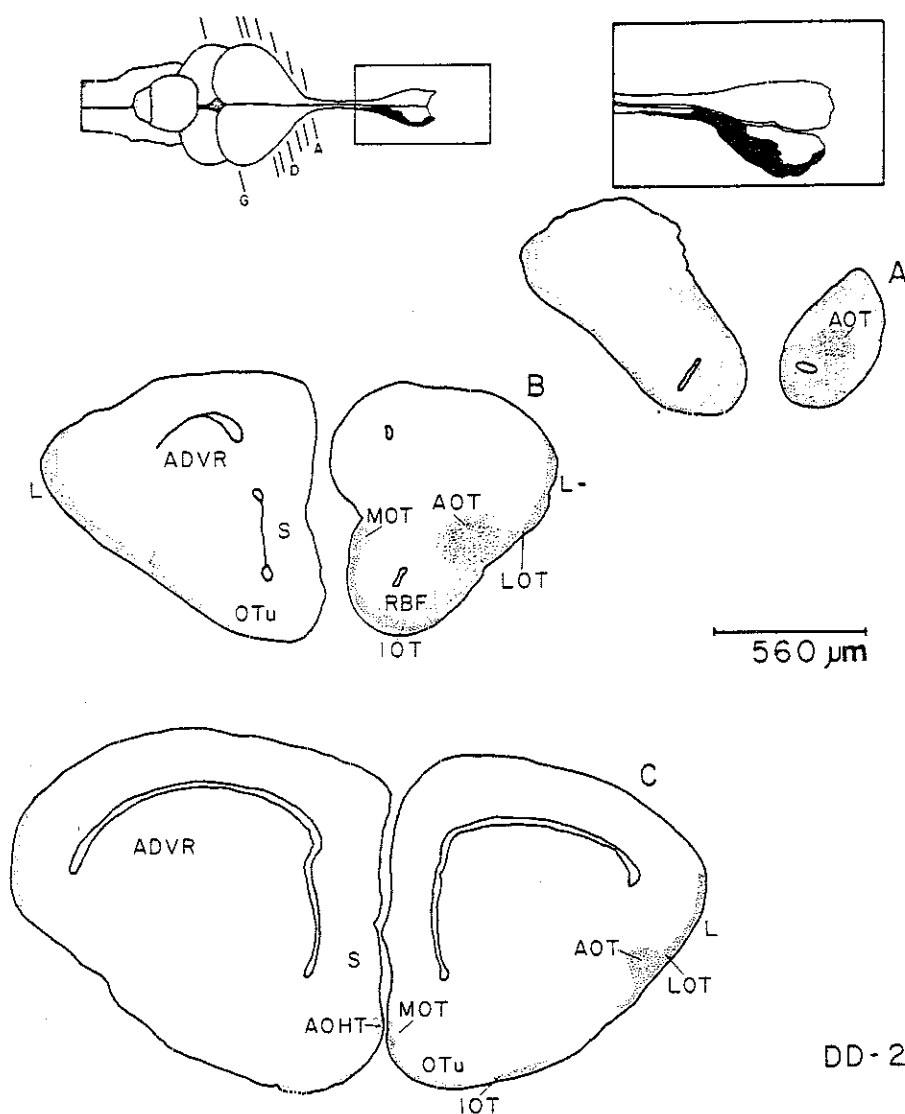


Figure 31. Olfactory projections. This is an experiment that shows the total efferent projections of the main and accessory olfactory bulbs in a desert iguana, *Dipsosaurus dorsalis*. The lizard underwent a transection of the olfactory peduncle caudal to the bulbs and survived for 14 days. The location and extent of the lesion are shown in the inset on the right. The planes of the transverse sections A through G are shown on the dorsal view of the brain on the left. Note that the sections are oriented obliquely relative to the brain's long axis so that the right half of the brain in each section is rostral to the left half. The appearance of degenerated elements in Fink-Hemier preparations is charted on sections A through G. Axons from mitral cells in the main olfactory bulb run through the lateral olfactory tract (LOT) to the rostral subareas of the ipsilateral lateral cortex (L). They also cross the

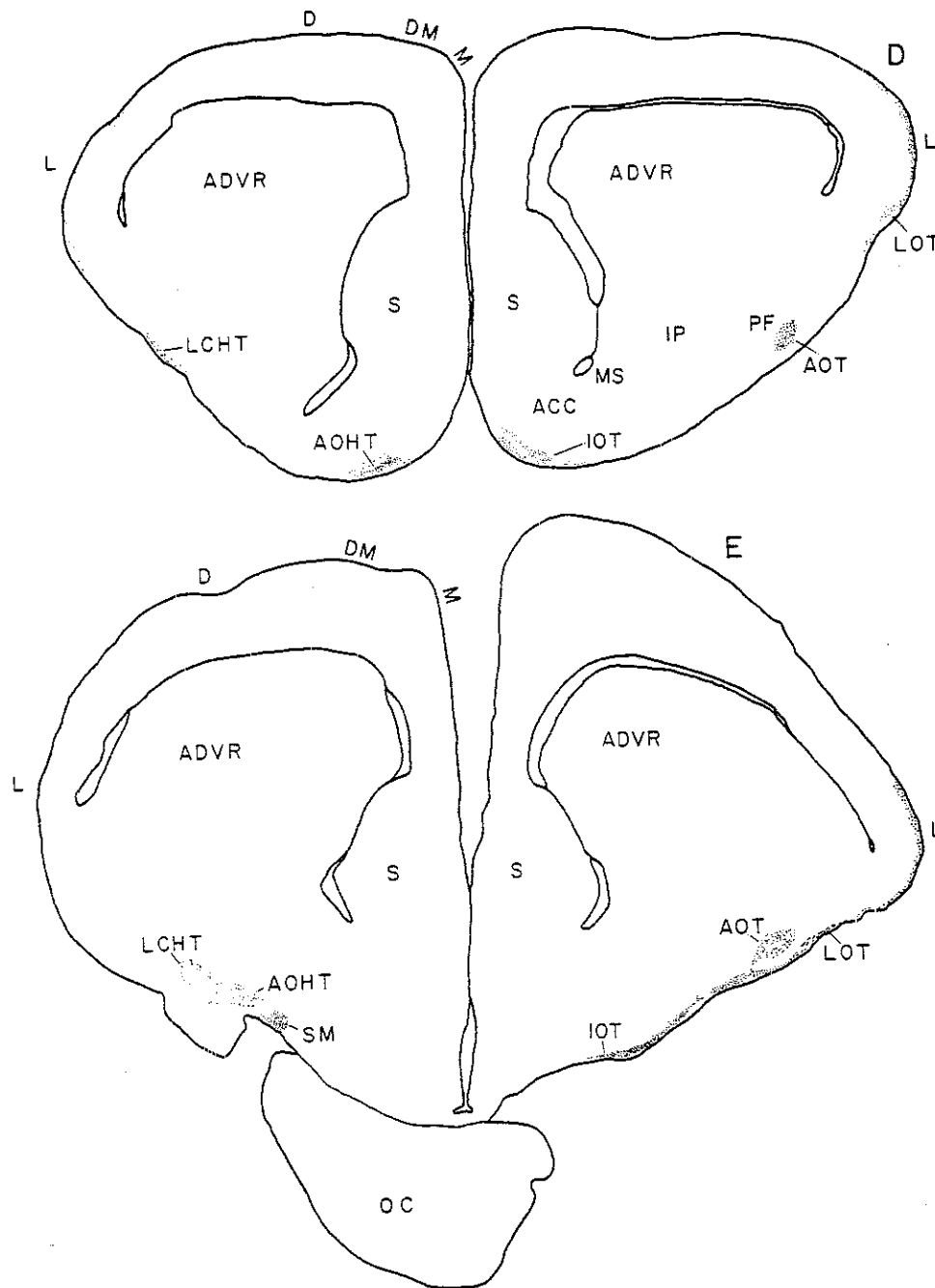


Figure 31. (Continued)

midline through the stria medullaris system (SM) and habenular commissure (HC) to reach the contralateral lateral cortex. Axons from the accessory olfactory bulb run through the accessory olfactory tract (AOT) to the nucleus sphericus. AC, anterior commissure; ACC nucleus accumbens; ADVR anterior dorsal ventricular ridge; AOHT, anterior olfactohabenular tract; D dorsal cortex; DM, dorsomedial cortex; IOT, intermediate olfactory tract; IP intrapeduncular nucleus of the striatum; LCHT, lateral corticohabenular tract; M, medial cortex; MOT, medial olfactory tract; MS, medial striatal nucleus; OC, optic chiasm; OT, optic tract; OTu, olfactory tubercle; PF perirhinal cortex; RBF retrobulbar formation; S septum; T, optic tectum. From Ulinski and Peterson (1981)

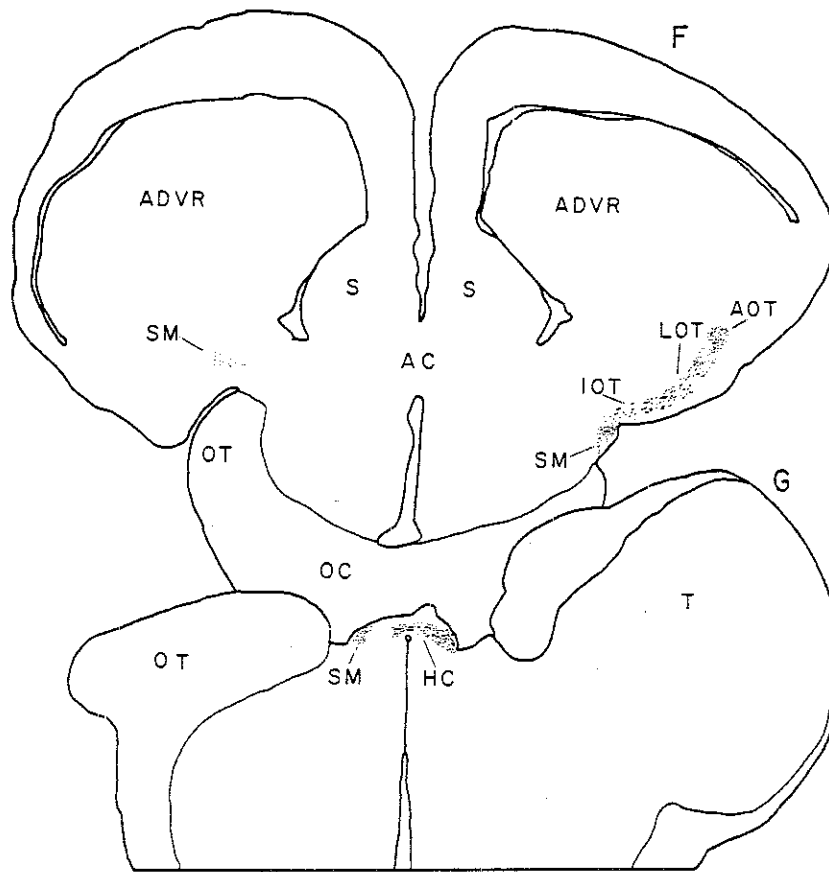


Figure 31. (Continued)

Efferent fibers from the main olfactory bulb exit its lateral surface and run into the ipsilateral lateral cortex via the lateral olfactory tract. The pattern of main olfactory bulb input to lateral cortex varies between species. In snakes, it terminates throughout the dorsoventral extent of the rostral lateral cortex, but ends precisely at its border with the caudal lateral cortex (Halpern, 1976; Ulinski and Rainey, 1980). The same situation is present in the fence lizard *Lacerta viridis* and the desert iguana *Dipsosaurus dorsalis* (Ulinski and Peterson, 1981). Anoles of the genus *Anolis* have relatively reduced olfactory systems (Armstrong *et al.*, 1953). The olfactory bulb complex is small and the rostral lateral cortex is reduced to a pallial membrane and receives only a sparse olfactory bulb input. Heimer (1969) reported a rather different situation in the tegu lizard *Tupinambis*. He found main olfactory bulb inputs to the full rostrocaudal extent of lateral cortex. This resembles the pattern of olfactory bulb projections in turtles (Gamble, 1956; Balaban, 1977; Skeen *et al.*, 1984; Reiner and Karten, 1985) and *Caiman* (Scalia *et al.*, 1969) in which the olfactory bulbs project all along the ventrolateral surface of the cortex.

In contrast to mammals, there are direct projections to the contralateral lateral cortex in reptiles. These are effected via the habenular commissure by fibers that run caudally in the lateral olfactory tract and then cross the base of

the hemisphere, join the stria medullaris and thereby gain access to the habenular commissure. They turn rostrally and run through the contralateral stria medullaris and lateral corticohabenular tracts to reach the caudal edge of the contralateral cortex. Orrego (1961, 1962) found that electrical stimulation of the olfactory bulb produced a surface negative evoked potential in the contralateral olfactory cortex with a latency of 50–100 msec.

Main olfactory bulb projections are limited to the outer one-quarter of layer 1 of lateral cortex (Ulinski and Rainey, 1980; Ulinski and Peterson, 1981; Skeen *et al.* 1984). Individual fibers run caudally in the lateral olfactory tract (Peterson and Ulinski, 1981). They initially have dorsoventral trajectories, but gradually turn to run rostrocaudally in layer 1. They consist of thin axons bearing many varicosities *en passant* and terminate principally upon dendritic spines via axon terminals that form asymmetric active zones and contain clear, round synaptic vesicles (Rainey and Ulinski, 1980). There have been no intracellular studies of their synaptic activity, but Orrego's (1961, 1962) finding that electrical stimulation of the olfactory bulbs of turtles elicits surface negative evoked potentials in lateral cortex suggests they give rise to EPSPs in cortical neurons. The orientation of the dendrites of bowl cells and their numerical predominance in the rostral lateral cortex suggest they are the principal postsynaptic targets of olfactory bulb afferents.

HRP experiments in lizards (Bruce and Butler, 1984a; Martinez-Garcia *et al.*, 1986) show the rostral lateral cortex receives olfactory information indirectly via structures in the basal telencephalon as well as directly from the main olfactory bulbs. HRP injections retrogradely label somata in the diagonal band nuclei and the nucleus of the lateral olfactory tract. These structures receive inputs from the main olfactory bulbs and could serve as an indirect relay of olfactory information to lateral cortex. The relationship of the direct and indirect olfactory inputs within lateral cortex is not known.

7.1.1b Dorsal Lateral Geniculate Nucleus. Early theories of telencephalic evolution held that the cerebral hemispheres of nonmammals were dominated by olfactory inputs and received little or no nonolfactory sensory input. This was consistent with the view that there are no direct thalamic projections to the dorsal telencephalon in reptiles (e.g., Powell and Kruger, 1960; Kruger and Berkowitz, 1960). However, in 1970 Hall and Ebner (Hall and Ebner, 1970b) used Nauta degeneration techniques to convincingly demonstrate a projection from the dorsal lateral geniculate nucleus to the cortex in turtles. Genulocortical projections have since been studied extensively in turtles and demonstrated in several lizards. Their presence is problematic in snakes and crocodilians, and unexplored in *Sphenodon*.

The dorsal lateral geniculate complex in turtles is a rostrocaudally elongate structure situated internal to the optic tract. It consists of a cell plate of densely packed neurons that makes up its medial face and a neuropil of scattered cells situated between the cell plate and the optic tract (Rainey and Ulinski, 1986). The cell plate cells have dendrites that extend radially into the neuropil. The neuropil cells have dendrites arranged parallel to the optic tract (Rainey and Ulinski, 1986). The retina projects bilaterally and topographically to the geniculate complex (Hall and Ebner, 1970a; Knapp and Kang, 1968a,b; Bass and Northcutt, 1981a,b; Ulinski and Nautiyal, 1988). The retinogeniculate axons form restricted terminal arbors (Sjostrom and Ulinski, 1985) that synapse on

geniculate neurons via synapses with clear, round synaptic vesicles and asymmetric junctional complexes (Ulinski and Nautiyal 1988). These terminals form triadic relationships with pairs of cell plate dendrites as well as making relatively isolated contacts along the more proximal shafts of the cell plate cells. The geniculate neurons have axons that exit the medial face of the geniculate complex (Heller and Ulinski, 1987), course ventrally and join the dorsal peduncle of the lateral forebrain bundle (Fig. 32). They proceed rostrally into the striatum where they initially lie at the very superficial edge of the dorsal peduncle as it passes beneath the floor of the lateral ventricle (Hall and Ebner, 1970b; Heller and Ulinski, 1987). However, they eventually turn laterally and extend dorsally between the inner edge of the lateral cortex and the anterior dorsal ventricular ridge. Both the Hall and Ebner and Heller and Ulinski studies are subject to some ambiguity because of the difficulty of restricting lesions or injections of tracer substances solely to the geniculate complex. However, the trajectory suggested for the geniculocortical fibers by these studies is consistent with the pattern of labelling seen in the cortex following the transsynaptic transport of tritiated amino acids (Desan, 1984).

Geniculate neurons can be retrogradely labeled following cortical HRP injections (Hall *et al.*, 1977; Belekova *et al.*, 1979), and Ulinski (1987b) was able to label neurons in the neuropil layer as well as both sublayers of the cell plate by cortical injections. It therefore appears that all of the cell populations in the geniculate project to the cortex. It is less certain whether all of the individual cells in each population project to the cortex, but it seems likely from the density of retrograde labeling that at least a sizable majority do. This implies that the geniculate may lack true interneurons, although interactions between geniculate neurons can occur via dendrodendritic synapses (Ulinski, 1987a) and there may be a population of neurons in the lateral forebrain bundle that effectively serve as thalamic interneurons (Ulinski, 1987c).

Both the earlier orthograde degeneration study of Hall and Ebner (1970b) and the most recent orthograde HRP study of Heller and Ulinski (1987) indicate that once the geniculocortical axons reach the dorsal telencephalon, they run through the pallial thickening and then course dorsally into dorsal cortex. They are situated around the somata of layer 2 neurons in the pallial thickening, but occupy the outer one-third of layer 1 within dorsal cortex where they terminate precisely at the boundary between areas D1 and D2 of Desan (1984). Hall and Ebner interpreted degeneration in the pallial thickening as fibers passing through the pallial thickening without synapse. However, the Golgi-like HRP fills of geniculocortical axons obtained by Heller and Ulinski show that the axons have varicosities *en passant* as they pass through the pallial thickening. Individual axons could synapse upon the proximal dendrites or somata of neurons in the pallial thickening and then pass medially, approximately in the transverse plane, to synapse upon the distal dendrites of neurons in the medial part of D2. Because it is not possible to determine the precise arrangement of geniculocortical afferents in traditional sections, Mulligan and Ulinski (1990) used orthograde transport of HRP in an *in vitro* whole brain preparation to determine their trajectories. They folded back the cerebral cortex and made pressure or iontophoretic HRP injections in the superficial part of the lateral forebrain bundle as it passes beneath the lateral ventricle. Following sacrifice, the cortex was removed and processed as a whole-mount preparation. Orthogradely labeled axons could be traced out of the lateral forebrain bundle and into the cortex.

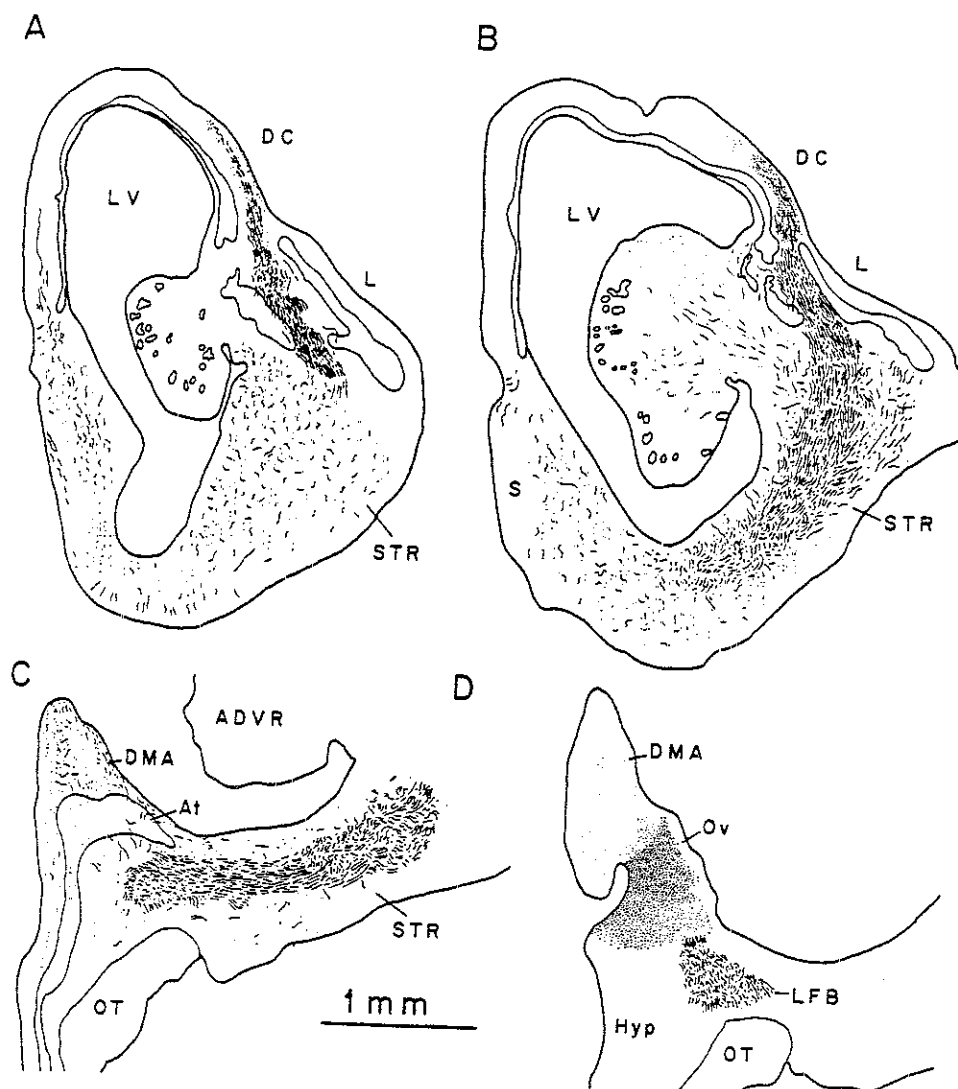


Figure 32. Thalamotelencephalic projections in turtle. This figure illustrates the general course of thalamotelencephalic projections as demonstrated by the anterograde transport of HRP. These are spaced serial sections from a turtle that received a relatively large injection of HRP *in vivo*. The injection site encroached on several thalamic nuclei, including the geniculate complex. Section A is the most rostral; section D is the most caudal. Section D shows the rostral edge of the injection site, which includes subnucleus ovalis (Ov) of the geniculate complex. Labeled axons course ventrolaterally from the injection site to the lateral forebrain bundle (LFB). Section C passes through the junction of the diencephalon and telencephalon. Labeled axons are seen coursing in the transverse plane into the striatum (STR). Section B is through midtelencephalic levels. Labeled axons run into the septum (S) and through the striatum (STR) into the anterior dorsal ventricular ridge (ADVR) and medial to the lateral cortex (L). This latter set of fibers pass through the pallial thickening and into the dorsal cortex (DC). At, area triangularis of the ventral thalamus; DMA, dorsomedial anterior nucleus; Hyp, hypothalamus; LV, lateral ventricle; OT, optic tract. From Heller and Ulinski (1987).

Individual axons fan out as they enter the cortex and run radially from lateral to medial across dorsal cortex, bearing varicosities *en passant* at irregular intervals. Thus, an individual geniculocortical axon can synapse upon a band of cortical neurons that extends from lateral to medial across dorsal cortex. The functional implications of this arrangement will be considered in Section 8.2.

The ultrastructure of geniculocortical afferents has been studied by Ebner and Colonnier (1975, 1978) and Smith *et al.* (1980). They made large thalamic lesions and sampled degenerating synapses along a strip of tissue situated at the boundary of D2 and D1. Thalamic synapses—presumably including the geniculocortical synapses—involve presynaptic elements that contain clear, round synaptic vesicles and form asymmetric junctional complexes. They occur upon the dendritic spines of cortical neurons and the smooth dendritic shafts of layer 1 stellate cells. Smith *et al.* estimate that each double pyramidal cell receives 300 thalamic synapses and each stellate cell receives 1800 thalamic synapses.

Pivovarov and Trepakov (1972) and Kriegstein (1987) recorded intracellularly from layer 1 and layer 2 neurons following electrical stimulation of the optic nerve or photic stimulation of the retina. Such recordings show EPSPs that are often followed by IPSPs. The EPSPs can be attributed to geniculocortical afferents. The EPSPs recorded in cortical cells following activation of the geniculocortical path resemble those obtained following intracortical application of L-glutamate (Kriegstein and Connors, 1986), and they are blocked by antagonists of the quisqualate and kainate types of excitatory amino acid receptors (Larson-Prior *et al.*, 1989).

The organization of the dorsal lateral geniculate complex in reptiles other than turtles is less completely understood. The diencephalon of lizards and snakes contains several cytoarchitecturally distinct structures that receive retinal inputs (see Ulinski, 1983, for references), and it is not certain how to relate these to the dorsal lateral geniculate nuclei of mammals. Most workers would agree that a structure named the dorsal lateral geniculate nucleus should receive direct retinal input and project to the telencephalon, while the ventral lateral geniculate nucleus should receive direct retinal input and have reciprocal projections with the optic tectum. Using these criteria, it appears that only the very rostralmost of the several retinorecipient structures in the diencephalon of squamates qualifies as the dorsal lateral geniculate nucleus; the several more caudal structures should be considered the ventral lateral geniculate nucleus.

A candidate for the dorsal lateral geniculate nucleus has been identified in three genera of lizards. Lohman and van Woerden-Verkely (1978) used orthograde degeneration and retrograde HRP transport to show that a plate of cells in the rostral diencephalon of the tegu lizard, *Tupinambis*, known to receive retinal input, projects to the lateral telencephalic wall. Bruce and Butler (1984b) used the retrograde transport of HRP following telencephalic injections in the tokay gecko, *Gekko gekko*, and the green iguana, *Iguana iguana*, to show that a similarly placed structure (named nucleus intercalatus) projects to the lateral telencephalic wall. The region of the telencephalon that receives geniculate inputs is situated between the anterior dorsal ventricular ridge and lateral cortex, ventral to the edge of dorsal cortex in each species and corresponds to the area that has often been designated as the pallial thickening. It consists of rather distinct clusters of cells in *Gekko*, but is less clearly defined in *Iguana* (Bruce and Butler, 1984a,b) and *Tupinambis* (Ebbesson and Voneida, 1969). Nothing is known of the organization of the geniculotelencephalic projections in lizards.

Until quite recently it appeared that the organization of the thalamic visual nuclei of snakes was quite different from that of other reptiles. Snakes seemed to lack a nucleus rotundus while having a relatively large dorsal lateral geniculate complex (e.g., Ulinski, 1977b). This situation was related to theories about the phylogenetic history of snakes (Northcutt and Butler, 1974; Senn and Northcutt, 1973) and to general patterns of brain evolution (Ebbesson, 1980). However, Dacey and Ulinski (1983) reexamined the problem and were able to use HRP techniques to show that snakes have a nucleus rotundus which is prominent, but situated more caudally in the thalamus than in other reptiles. Also, du Lac and Dacey (1981) analyzed the geniculate complex in snakes in some detail and argued that only the most rostral part of the complex, the nucleus ovalis of Warner (1931) and other authors (Halpern and Frumin, 1973), represents the dorsal lateral geniculate complex. The nucleus ovalis receives bilateral retinal projections and possibly gives rise to a small projection to the telencephalic wall between the anterior dorsal ventricular ridge and lateral cortex (Ulinski, unpublished observations). The remainder of the geniculate complex contains several cytoarchitecturally distinct regions that jointly correspond to the ventral lateral geniculate complex. These have reciprocal, topographically organized projections with the optic tectum (du Lac and Dacey, 1981; Dacey and Ulinski, 1983, 1986a,b) and project to the brain-stem reticular formation (Ulinski *et al.*, 1983).

7.1.1c. Dorsal Ventricular Ridge. In addition to demonstrating a source of visual input to cerebral cortex in turtles, Hall and Ebner (1970b) showed that nucleus rotundus—which receives inputs from the optic tectum—projects to the anterior dorsal ventricular ridge. Sensory inputs to ADVR have since been extensively studied in both reptiles and birds (see Ulinski, 1983), and it appears there is a general pattern in which auditory information projects to the medial, caudal region of ADVR, somatosensory information projects via the spinal cord and dorsal column nuclei to the central region of ADVR, and visual information projects via the optic tectum to a lateral region of ADVR. It is possible that the trigeminal sensory nuclei project directly to a ventrolateral region of ADVR (see Clark and Ulinski, 1984; Bruce and Butler, 1984b) and that the vestibular nuclei project to a region of ADVR immediately internal to lateral cortex (Kunzle, 1985).

There is some indication that ADVR provides a second route by which visual information reaches visual cortex. HRP injections in visual cortex retrogradely label neurons in the dorsal area of ADVR of turtles (Balaban, 1978, 1979; Desan, 1984). This is part of ADVR that receives projections from nucleus rotundus in turtles (e.g., Balaban and Ulinski, 1981a,b) and is responsive to visual stimuli (Dunser *et al.*, 1981). Belekova *et al.* (1979) provided physiological evidence for this projection by demonstrating a cortical response to visual stimuli in turtles that had sustained lesions of the dorsal lateral geniculate complex. These responses could reach the cortex via a relay in ADVR, and have a latency that is 20 msec longer than the early cortical response due to the geniculocortical pathway. Similarly, HRP injections in the lateral part of dorsal cortex retrogradely label neurons in that lateral region of ADVR in *Gekko* (Bruce and Butler, 1984b).

Whether or not there are projections to the cortex from the auditory and somatosensory areas of ADVR is unknown. However, Orrego and Lissenby

(1962) recorded evoked potentials in the cortex of turtles following somatosensory stimulation and Moore and Tschirigi (1962) found auditory, somatosensory, and visual multimodal responses in dorsal cortex of alligator. There is no indication of direct projections from the auditory thalamic nuclei to the cortex in any reptile. The organization of the somatosensory nuclei of the thalamus is not clearly established, but there is some evidence for spinal cord projections to the rostral thalamus in turtles (Kunzle and Schnyder, 1984). Since some of the perirhinal nuclei in this region project to the cortex, they may participate in a route by which somatosensory information can reach the cortex.

7.1.2. Limbic System Structures

7.1.2a. Hypothalamus. Each of the four cortical areas receives projections from one or more hypothalamic nuclei (Desan, 1984; Bruce and Butler, 1984a). The medial area receives projections principally from the mammillary nuclei, bilaterally, and a sparser projection from the periventricular region of the ipsilateral hypothalamus. Dorsomedial cortex receives a sparse projection from the ipsilateral mammillary nuclei. Dorsal cortex receives a bilateral projection from the mammillary nuclei, as well as projections from the lateral, preoptic, and paraventricular areas of the hypothalamus. Lateral cortex receives projections from the ipsilateral paraventricular nucleus.

The laminar organization of hypothalamic-cortical projections within the various areas is not known, but clues as to which neurotransmitters may be used are provided by Reiner *et al.* (1985) who employed immunohistochemical techniques to show that axons within layer 2 of turtle cortex that show substance P- or cholecystokinin-like immunoreactivity are absent from animals that have undergone hypothalamic lesions. Also, the periventricular hypothalamus contains somata that stain positively with antibodies against dopamine (Smeets *et al.*, 1986, 1987; Smeets, 1988). Fibers that stain with dopamine-like immunoreactivity are present in all of the cortical areas, although the details of their distribution vary between species. In *Pseudemys*, scattered fibers are found in layers 1 and 2 of both medial and dorsomedial areas, in layer 1 of D1, layer 2 of the pallial thickening, and layers 2 and 3 of both the dorsal and ventral parts of lateral cortex (Smeets *et al.*, 1987). In *Gekko*, labeled fibers are found in layers 1 and 3 of medial cortex, the outer part of layer 1 of dorsomedial cortex, layers 1 and 2 of dorsal cortex, and densely in layer 2 of the ventral rostral lateral cortex (Smeets *et al.*, 1986). In *Python*, fibers are found in layers 1 and 3 of medial and dorsomedial cortex, throughout dorsal cortex (but particularly in layer 3), and throughout lateral cortex (but particularly in layer 2 of ventral rostral lateral cortex) (Smeets, 1988). The significance of these differences is not known.

7.1.2b. Septum. The septum projects to one degree or another to medial, dorsomedial, and lateral cortical areas. These projections have been studied using the retrograde transport of HRP in snakes (Reperant, 1976), lizards (Lohman and van Woerden-Verkely, 1978; Bruce and Butler, 1984a), and turtles (Desan, 1984). Orthograde tracing studies in tegu lizards (Lohman and van Woerden-Verkely, 1976; Hoogland *et al.*, 1978; Sligar and Voneida, 1981) indicate that the precommissural septum projects to layer 1 of the medial and intermediate parts of dorsal cortex.

7.1.2c. Periotundal Nuclei. These are a set of nuclei that partially cover the rostral face of nucleus rotundus. They vary in character and extent between species, but dorsomedial and dorsolateral anterior nuclei (Fig. 3) are generally distinguished. The dorsomedial anterior nucleus lies between nucleus rotundus and the third ventricle and continues dorsally to lie between nucleus rotundus and the habenula. The dorsolateral anterior nucleus is situated between the dorsomedial anterior nucleus and the lateral geniculate complex. An anterior nucleus is recognized lying ventral to the rostral pole of nucleus rotundus in turtles. Nothing is known of the neuronal organization or transmitter profile of the periotundal nuclei, except that cortical injections in *Caiman* can label more than 99% of the neurons in the dorsolateral anterior nucleus, which suggests this nucleus has few intrinsic neurons (Pritz and Stritzel, 1987).

There have been no systematic studies of the afferents of the periotundal nuclei. However, orthograde tracing studies (Hoogland *et al.*, 1978; Sligar and Voneida, 1981) show the septal nuclei project to the ipsilateral periotundal nuclei. Since the septum receives projections from the medial and dorsal areas of the cortex, it then forms a link between the cortex and periotundal nuclei. Also, Halpern (1974) reports a direct projection from the medial area of the cortex to the anterior thalamus in garter snakes, *Thamnophis sirtalis*.

Retrograde HRP experiments establish that the periotundal nuclei project widely to the telencephalon. They have been retrogradely labeled following injections of HRP into the anterior dorsal ventricular ridge of turtles (Belekhova *et al.*, 1979; Balaban and Ulinski, 1981a) and lizards (Lohman and van Woerden-Verkely, 1978; Bruce and Butler, 1984a). They are also labeled following HRP injections restricted to specific cortical areas in turtles (Hall *et al.*, 1977; Ouimet *et al.*, 1985; Desan, 1984), lizards (Lohman and van Woerden-Verkely, 1978; Bruce and Butler, 1984a), and *Caiman* (Pritz and Stritzel, 1987). The projection appears to be a diffuse one, so the results of injections are sometimes difficult to interpret. However, there seems to be a pattern to the projection of the periotundal nuclei upon the cortex. For example, Bruce and Butler recognized three periotundal nuclei: the dorsomedial nucleus, the dorsolateral anterior nucleus, pars magnocellularis (DLAm), and the dorsolateral anterior nucleus, pars parvocellularis (DLAp). DLAm projects bilaterally to the medial area of cortex. DLAm and DLAp project bilaterally to the dorsomedial area, with cortical injections retrogradely labeling more cells in DLAp than in DLAm. DLAp also projects bilaterally to the dorsal area and sparsely to the ipsilateral lateral cortex.

Experiments designed to study the laminar organization of periotundal projections to cortex have yielded contradictory results. On the one hand, Balaban and Ulinski (1981a) used autoradiographic tracing methods to suggest that the periotundal nuclei project diffusely throughout the depth of medial cortex in turtles. On the other hand, Lohman and van Woerden-Verkely (1978) used orthograde degeneration methods to suggest that the periotundal nuclei terminate in a fairly discrete band within the medial third of layer I in tegu lizards. Desan (1984) used autoradiographic methods on turtles and suggested that periotundal projections to cortex involve both diffuse and specific systems. Thus, a discrete band of label is present in the middle third of layer I of medial and dorsomedial cortex, but some diffuse label above background is also present.

7.1.3. Brain Stem and Basal Forebrain

7.1.3a. Locus Coeruleus. Noradrenergic neurons in reptiles have been studied using the Falck–Hillarp histofluorescence methods (Baumgarten and Braak, 1968; Parent and Poirer, 1971; Yamamoto and Shimizu, 1977; see Parent, 1979, 1986, for reviews) and immunohistochemical methods employing antibodies against the synthetic enzyme tyrosine hydroxylase (Wolters *et al.*, 1984; Brauth, 1988). These studies demonstrate a cluster of catecholaminergic neurons in the dorsolateral isthmus region of the brain that have been designated the locus coeruleus (Cruce and Nieuwenhuys, 1974; ten Donkelaar and Nieuwenhuys, 1979). Transections of the brain stem rostral to the locus coeruleus result in a reduction of fluorescence in the forebrain (Parent and Poitras, 1974), and HRP injections in both the dorsal ventricular ridge (Balaban and Ulinski, 1981a) and dorsal cortex (Bruce and Butler, 1984a; Ouimet *et al.*, 1985) retrogradely label neurons in the locus coeruleus. The existence of a coeruleocortical pathway to the pallium is therefore well established in at least turtles and lizards.

Both Falck–Hillarp and glyoxylic acid fluorescence methods demonstrate a plexus of noradrenergic fibers in dorsal cortex (Parent, 1973; Parent and Poitras, 1974; Ouimet *et al.*, 1981, 1985). Fibers are varicose and present predominantly in the outer 100 μ m of layer 1. Fluorescence is depleted by pretreatment with reserpine (Ouimet *et al.*, 1985), and biochemical analysis shows this region of cortex to have a high norepinephrine concentration (Ouimet *et al.*, 1981). Ultrastructural analysis using tissue fixed with potassium permanganate (Ouimet *et al.*, 1981) shows that noradrenergic terminals contain small granular vesicles and are presynaptic to dendritic spines. The cytology of their active zones varies, with some being symmetric and others asymmetric.

7.1.3b. Raphe Nuclei. The distribution of indoleaminergic neurons in reptiles has been studied with histofluorescence techniques in lizards (Braak *et al.*, 1968) and turtles (Parent, 1973, 1979; Parent and Poitras, 1974), and with immunohistochemical techniques in lizards (Wolters *et al.*, 1985; Smeets and Steinbusch, 1988) and turtles (Umeda *et al.*, 1983). Serotonergic neurons are distributed in the several raphe nuclei spread throughout the rostrocaudal extent of the brain stem (for cytoarchitectonic descriptions of the raphe nuclei see Cruce and Nieuwenhuys, 1974; Newman and Cruce, 1982; ten Donkelaar and Nieuwenhuys, 1979; Wolters *et al.*, 1985; ten Donkelaar *et al.*, 1987). Neurons in the medial superior raphe nucleus are retrogradely labeled following injections of HRP in the dorsomedial and dorsal cortical areas (Lohman and van Woerden-Verkely, 1978; Bruce and Butler, 1984a; Ouimet *et al.*, 1985). Serotonergic fibers are present in the inner half of layer 1 of dorsal cortex of the turtle *Pseudemys* (Ouimet *et al.*, 1985). In *Gekko* (Smeets and Steinbusch, 1988) serotonergic fibers are found in layers 1 and 3 of medial and dorsomedial cortex, layer 2 of dorsal cortex, and throughout lateral cortex.

7.1.3c. Reticular Formation. The midbrain reticular formation gives rise to a bilateral projection to the cortex in the snakes *Thamnophis sirtalis* and *Natrix sipedon* (Ulinski, 1981). The projection arises from isodendritic, multipolar neurons situated in the dorsolateral midbrain tegmentum. Their axons ascend in the medial forebrain bundle and some cross the midline in the anterior pallial commissure. Fibers turn dorsally on both sides of the brain and pass through the

septum to enter the cortex. They run laterally in the alveus and turn to terminate in layer 1 of medial cortex and layers 1, 2, and 3 of dorsomedial cortex. They synapse upon dendritic spines as boutons with round synaptic vesicles and forming asymmetric active zones. Khatchaturian *et al.* (1984) report the presence of a group of neurons in the dorsolateral midbrain tegmentum of the lizard *Anolis* that stain with antibodies against β -endorphin, ACTH, and α -melanocyte stimulating hormone (all peptides in the proopiomelanocorticotropin family). Fibers that show immunoreactivity against these antisera are also found in the cortex of *Anolis*, so these peptides may be associated with the reticulocortical system.

7.1.3d. Basal Forebrain. It is now generally agreed that the basal forebrain of mammals contains several nuclear groups that give rise to cholinergic projections to the cortex; a similar system seems to be present in reptiles. Injections of HRP in both the dorsal and lateral cortical areas of geckos (Bruce and Butler, 1984a) and turtles (Desan, 1984) retrogradely label neurons in the nuclei of the diagonal band and in a cell group situated dorsal to the diagonal band, but ventral to the septal complex. These groups also contain neurons that stain positively with antibodies against choline acetyltransferase in turtles (Desan, 1984; Mufson *et al.*, 1984). Studies combining choline acetyltransferase immunocytochemistry with retrograde HRP labeling have not been done on reptiles, but it seems likely these two groups are equivalent to the cholinergic groups in the basal telencephalon. Thus, as in mammals, the diagonal band complex contains cholinergic neurons that project to the cortex. The more dorsal group in reptiles generally resembles the basal nucleus of Meynert of mammals.

The outer part of layer 1 of dorsal cortex of turtles stains positively for acetylcholinesterase and contains high levels of choline acetyltransferase and ACh (Hohmann *et al.*, 1983). Also, receptor binding techniques show that the entire dorsal cortex, including the pallial thickening, contains a moderate concentration of muscarinic cholinergic receptors (Schlegel and Kriegstein, 1987). Both extracellular and intracellular recordings in turtle dorsal cortex following focal application of ACh demonstrate a biphasic response of cortical neurons to ACh (Blanton *et al.*, 1986). A hyperpolarization, lasting from 250 msec to 15 sec, that may be associated with a potassium current, is followed by a voltage-sensitive depolarization that lasts up to 60 sec and is associated with a decrease in membrane conductance. These responses can be mimicked by electrical stimulation of the nucleus basalis, so there is evidence that the basal forebrain can modulate cortical activity via a cholinergic projection to at least the dorsal and lateral cortical areas.

7.2. Intracortical Connections

The four cytoarchitectonic areas of the cortex are interconnected via an extensive set of association and commissural connections, which have been studied in lizards (Voneida and Ebbesson, 1969; Lohman and Mentink, 1972; Lohman and van Woerden-Verkely, 1976), snakes (Ulinski, 1976), and turtles (Desan, 1984). It should be noted that experiments on the intracortical connections are technically difficult because of the problems involved in localizing lesions or injections of tracer substances to individual areas, which are very small,

and ambiguities caused by fiber-of-passage problems. Nonetheless, some general patterns have been established and the introduction of new tracing techniques such as the use of *Phaseolus vulgaris* leucoagglutinin as a tracer substance, promises that future studies will have greater resolution than has been possible so far. The intracortical connections can be divided into several sets for the purposes of discussion.

First are projections from the lateral, dorsal, and dorsomedial areas to the ipsilateral medial area (Fig. 33). These have a laminar organization such that axons from each of the three areas terminate in a discrete band within medial cortex (Fig. 34). Since the candelabra cells of medial cortex have their somata densely packed in layer 2, both the ascending and descending components of their dendritic trees are in register. Consequently, each segment of the dendritic tree of a candelabra cell receives inputs from a different cortical area. Axons from the bowl cells of layer 2 of the dorsal part (Desan, 1984) of lateral cortex run as a distinct fascicle in the superficial part of layer 1 of dorsal and dorsomedial cortex (Rainey and Ulinski, 1980). When the fascicle reaches medial cortex, it expands to occupy the outer third of layer 1 (Ulinski, 1976; Martinez-Garcia *et al.*, 1986). Each individual axon bears varicosities *en passant* and extends across the full medial-to-lateral extent of medial cortex, intersecting, and presumably synapsing upon, the dendrites of many candelabra cells. Since the outer third of layer 1 contains predominantly axon terminals with clear, round synaptic vesicles synapsing upon dendritic spines via asymmetric junctions, it is likely that the bowl cell terminals have these characteristics.

Fink-Heimer degeneration (Lohman and Mentink, 1972; Ulinski, 1976) and orthograde HRP studies (Desan, 1984) show dorsal cortex projects to the middle third of layer 1 of medial cortex. It is not entirely certain which of the three subareas of dorsal area give rise to this projection. However, there is some indication (Desan, 1984) that the more lateral subareas of dorsal cortex (e.g., area D2 of Desan in turtles) project to the medial subarea of dorsal cortex (i.e.,

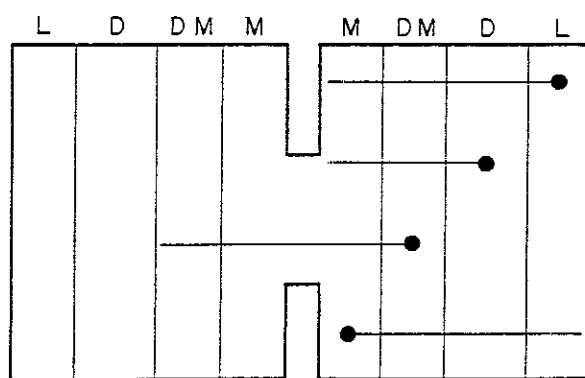


Figure 33. Commissural and association projections. This figure illustrates the organization of the major commissural and association projections that interconnect the four cortical areas. The cortical areas of the two cerebral hemispheres are diagrammed as if they have been flattened into rostrocaudally elongate strips. The two cortices are connected across the midline by the pallial commissure. Commissural and association projections tend to run in trans-

verse planes. Three association projections are shown. First, lateral cortex (L) projects medially through dorsal (D) and dorsomedial (DM) cortex to medial cortex (M). Second, dorsal cortex projects medially to medial cortex. Third, medial cortex projects lateral to dorsomedial, dorsal, and lateral cortices. The principle association projection involves projections from dorsomedial cortex, through the ipsilateral and contralateral medial cortices, to the contralateral dorsomedial cortex. Lizards have commissural projections linking the two lateral cortices through the habenular commissure; these are now shown.

area D1 of Desan), which projects in turn to medial area. Electron microscopic degeneration studies in the lizard *Agama* (Wouterlood *et al.*, 1982) indicate that axons originating in dorsal cortex terminate as boutons with clear, round synaptic vesicles, predominantly upon dendritic spines in medial cortex.

The dorsomedial area (Lohman and Mentink, 1972; Ulinski, 1976) gives rise to a projection to the inner third of layer 1 and the outer half of layer 3 of medial cortex. Thus, lateral and dorsal cortex project to the ascending dendrites of the candelabra cells, but dorsomedial cortex projects to both the ascending and descending dendrites.

Medial cortex of snakes and lizards gives rise to a laterally directed projection that reciprocates the projections just described (Ulinski, 1976; Desan, 1984). It arises from the candelabra cells, whose axons descend to layer 3 and bifurcate within the alveus. The medially directed branches give rise to an efferent projection to the septum that is described below. The laterally directed branches project back to dorsomedial, dorsal, and lateral areas. The laminar organization of these projections is not as well documented as are the projections to medial area. However, the projection to dorsomedial area appears to involve collaterals of candelabra cell axons that ascend from the alveus and extend through most of the depth of dorsomedial cortex, sparing only the outer part of layer 1 which remains unstained in Timm-stained material (Perez-Clausell, 1988). The projection to dorsal cortex involves all but the most superficial part of layer 1. The

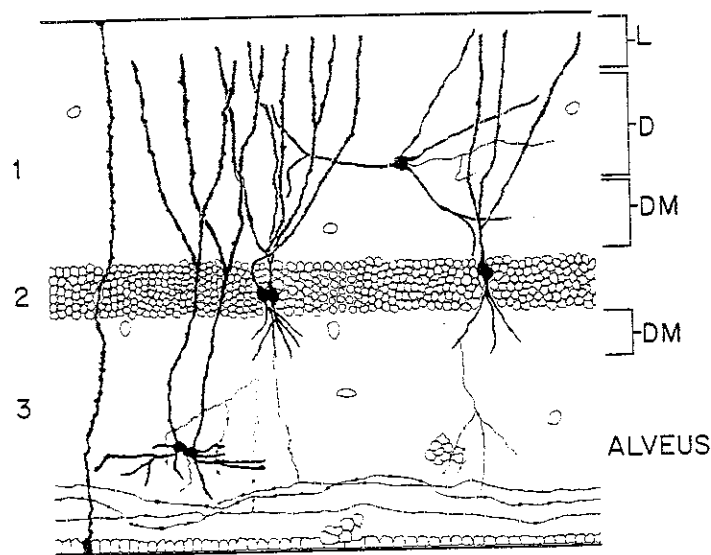


Figure 34. Laminar organization of medial cortex. This is a semidiagrammatic depiction of snake medial cortex. The somata of candelabra cells are densely packed in layer 2, so that their ascending and descending dendrites are in register in layers 1 and 3 respectively. Afferent systems tend to run through medial cortex in the transverse plane and therefore intersect the dendrites of the candelabra cells. Afferents from lateral cortex (L) run in the outer part of layer 1. Afferents from dorsal cortex (D) run in the intermediate part of layer 1. Afferents from the dorsomedial cortex (DM) run in the inner part of layer 1 and the upper part of layer 3. The axons of the candelabra cells descend in layer 3 and bifurcate to run in the alveus. The laterally directed branch gives rise to association projections to dorsal, dorsomedial and lateral cortices; the medially directed branch gives rise to efferent projects to the septum and hypothalamus. From Ulinski (1977a).

projection to lateral cortex involves the inner part of layer 1, thus complementing the projection of the ipsilateral and contralateral olfactory bulbs which terminate superficially in lateral cortex (Section 7.1.1a). Desan (1984) provides evidence that the analogous feedback projections in turtles arise from cells in both medial and dorsomedial cortex. Injections of lateral cortex with HRP retrogradely label neurons at the border of dorsal and dorsomedial cortex, while injections in D1 retrogradely label neurons at the border of medial and dorsomedial cortex.

Both the medially and laterally directed association connections conform to a lamellar organization such that both sets of axons run in approximately transverse planes (Ulinski, 1976; Ulinski and Rainey, 1980). Thus, bowl cells in a rostrocaudally compact band of lateral cortex project to a row of candelabra cells situated at roughly the same rostrocaudal level, and those candelabra cells project back to the same set of bowl cells. Because the axons that effect these projections bear varicosities *en passant*, it is likely that each candelabra cell in such a band is contacted by the axons of many bowl cells in the corresponding band.

In addition to these reciprocal projections in the transverse plane, there is evidence for association projections running rostrocaudally within the cortex. A rostrocaudally directed fascicle of fibers was described in normal sections of lizard cortex (Lohman and Mentink, 1972). Desan (1984) reported, on the basis of both anterograde HRP and tritiated proline injections, that axons run considerable rostrocaudal distances within specific cortical areas in turtles. Also, the projection from D2 to D1 involves a fascicle of fibers that course from D2 and run rostrocaudally along the medial border of D1.

There have been some claims that dorsal cortex (Ware, 1974; Gaidenko, 1978) participates in commissural connections with homotypic areas in the contralateral hemisphere, but these have not been generally substantiated and their existence should be regarded as provisional. There is evidence for commissural connections between lateral cortex on the two sides of the brain in lizards (Martinez-Garcia *et al.*, 1986; Butler, 1976) in which neurons in lateral cortex on one side of the brain project to the contralateral lateral cortex via the habenular commissure. However, commissural connections between the two lateral cortices seem to be absent in turtles.

There is clear evidence for commissural projections between the dorsomedial areas of the two hemispheres (Lohman and Mentink, 1972; Ulinski, 1976)(Fig. 35). These undoubtedly involve axons of layer 2 double pyramidal cells whose axons run medially through medial cortex. It is not known if single double pyramidal cells both project to medial cortex and participate in the commissural projections. Axons from dorsomedial cortex cross the midline through the pallial commissure (a U-shaped band of axons situated dorsal to the anterior commissure), run through the contralateral septum, and terminate in the contralateral medial and dorsomedial areas. The terminal zone in the medial area overlaps that originating from the ipsilateral dorsomedial area. The terminal zone in dorsomedial cortex is principally in layer 1. It is positioned deep in layer 1 at the medial edge of dorsomedial cortex, but then slants dorsally so that it extends superficially in layer 1 at the lateral edge of dorsomedial cortex. This terminal zone complements the projection from medial cortex to dorsomedial cortex and corresponds to the clear zone in Timm-stained material.

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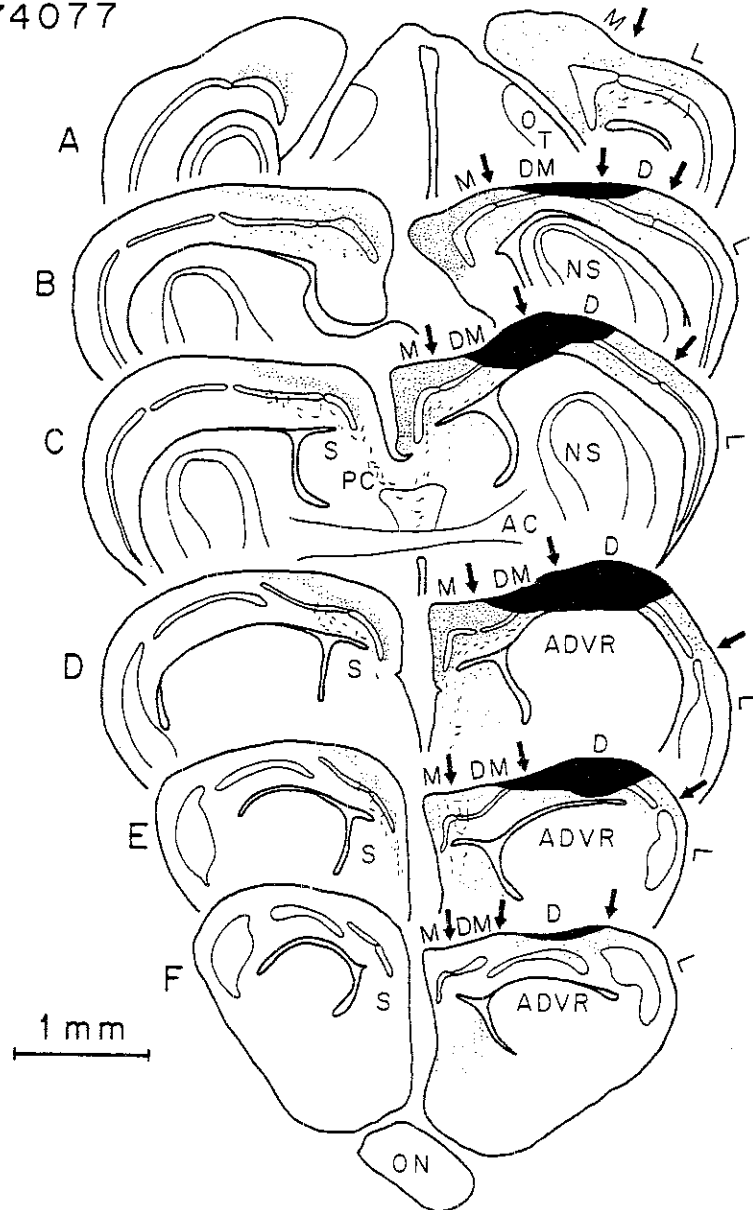


Figure 35. Commissural projections from dorsomedial cortex. The projections of dorsomedial cortex are shown in an anterograde degeneration experiment in which a lesion was made involving dorsomedial cortex (DM). Since dorsal cortex (D) and lateral cortex (L) do not project to the contralateral hemisphere in snakes, all of the commissural projections can be attributed to damage to dorsomedial cortex. Commissural axons cross the midline in the pallial commissure (PC) and run in layer 1 and 3 of the contralateral medial cortex (M). They terminate in layer 1 of the contralateral dorsomedial cortex. AC, anterior commissure; ADVR, anterior dorsal ventricular ridge; NS, nucleus sphericus; ON, optic nerve; OT, optic tract; S, septum. From Ulinski (1976)

7.3. Cortical Efferents

No projections from dorsomedial cortex to noncortical structures are known. However, each of the other cortical areas has projections efferent from the cortex. These have been studied in lizards (Butler, 1976; Lohman and Mentink, 1972; Lohman and van Woerden-Verkely, 1976), snakes (Halpern, 1974; Ulinski, 1975), and turtles (Gaidenko, 1978; Desan, 1984).

Lateral cortex receives bilateral projections from the main olfactory bulb as well as several olfactorecipient structures (Section 7.1.1a). Its dorsal rostral and dorsal caudal parts give rise to the projection that courses over the dorsal surface of the cortex to medial cortex, as described in Section 7.2.

Dorsal cortex gives rise to three sets of efferent projections. First are projections to the ipsilateral septum (Lohman and Mentink, 1972; Lohman and van Woerden-Verkely, 1976) involving axons that run medially through layer 3 and turn ventrally to enter the septum (Fig. 36). They terminate in the ventrolateral part of the septum along the full rostrocaudal length of both the parts of the septum situated rostral to the anterior commissure (precommissural septum) and those caudal to the anterior commissure (postcommissural septum). In tegu lizards, this projection originates from dorsal cortex (Lohman and van Woerden-Verkely, 1976). Second, dorsal cortex projects to the anterior dorsal ventricular ridge (Butler, 1976). Neurons in D2 project throughout the dorsal area of the anterior dorsal ventricular ridge in turtles (Balaban, 1978; Desan, 1984). Since D2 receives projections from the dorsal lateral geniculate complex and dorsal

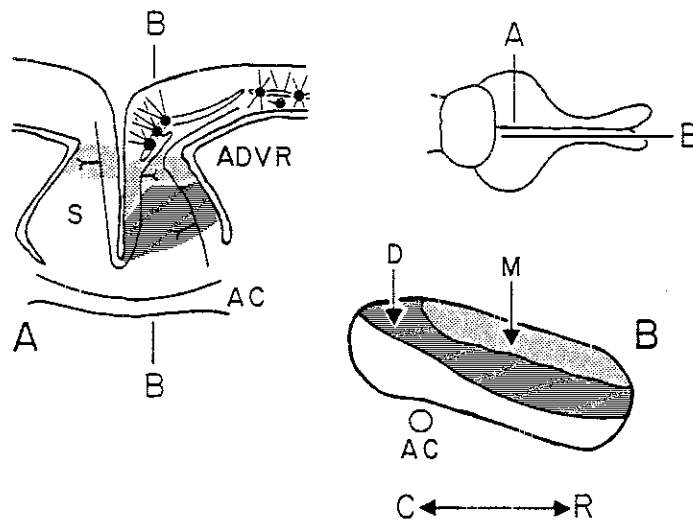


Figure 36. Corticoseptal projections. This figure illustrates the general organization of corticoseptal projections in snakes. The sketch of the snake brain shows the levels of the diagrammatic sections depicted in A and B. (A) Transverse section showing the course and termination (stipple) of axons of candelabra cells in medial cortex to the dorsal septum bilaterally and the course of the axons of unknown cells in dorsal cortex to their termination (stripes) in ventral septum ipsilaterally. (B) Parasagittal section of the septum showing the positions of the terminal fields of projections from medial cortex (stipple) and dorsal cortex (stripes) relative to the anterior commissure (AC). ADVR, anterior dorsal ventricular ridge; D, dorsal cortex; M, medial cortex; S, septum. From Ulinski (1975).

area of ADVR receives projections from nucleus rotundus. the projection from D2 to dorsal area serves to interconnect the telencephalic visual areas. Finally, dorsal cortex gives rise to efferent projections to visual structures in the brain stem. These have been best documented in turtles in which area D2 of Desan projects to the dorsal lateral geniculate complex, nucleus rotundus, and, perhaps, the optic tectum. Lesions of dorsal cortex (Gaidenko, 1978; Hall *et al.*, 1977) and HRP injections in D2 (Ulinski, 1986b; Desan, 1984) demonstrate that fibers course ventrally from dorsal cortex, proceed medial to lateral cortex and through the striatum to reach into the brain stem through the ventral peduncle of the lateral forebrain bundle. Axons turn dorsally and run into either nucleus rotundus or the dorsal lateral geniculate complex. These axons are rectilinear, of fine caliber, and bear varicosities *en passant*. Those entering nucleus rotundus extend from ventral to dorsal through the nucleus and can, therefore, intersect the dendritic fields of neurons scattered throughout rotundus. Those entering the dorsal lateral geniculate complex run from ventral to dorsal in the inner part of the structure's neuropil layer. These axons are also of fine caliber and bear varicosities *en passant*. They are positioned so as to intersect the smooth, proximal shafts of cell plate cells. Some axons can be traced caudally in the forebrain bundle into the midbrain tegmentum, where they turn dorsally and apparently terminate in the deep layers of the optic tectum. The existence of corticotectal cells has not been demonstrated with full certainty in turtles, but has been shown in the lizard *Agama* (Elprana *et al.*, 1980).

? Desan
layer 1 function

One issue surrounding the projections from dorsal cortex to the brain stem concerns their precise origin from within dorsal cortex. Desan (1984) used HRP injections to show that area D1 gives rise to intracortical projections to medial cortex, while area D2 gives rise to projections to the brain stem. This latter point has been confirmed using the retrograde transport following injections of HRP in the thalamus (Ulinski, 1986b). Such injections produce retrogradely labeled cells scattered throughout layers 2 and 3 of area D2, which include pyramidal, multipolar, or stellate cells and horizontal cells. A second question is whether a single cell projects to several structures (such as the geniculate complex, rotundus, and tectum) via collateral branches, or whether a single cell projects to only one structure. Definitive resolution of this issue requires double labeling experiments, but the available evidence favors a single cell projecting to multiple targets (Ulinski, 1986b).

Like dorsal cortex, medial cortex gives rise to efferent projections to the septum (Ulinski, 1975; Halpern, 1980). Axons run from medial cortex medially in the alveus to terminate in the dorsal part of the ipsilateral precommissural septum, complementing the projections of dorsal cortex more ventrally in the septum (Fig. 32). In addition, the axons continue ventrally, cross the midline in the pallial commissure, and proceed dorsally to give rise to a less dense terminal zone in the contralateral precommissural septum. Halpern (1974, 1980) reported that lesions of medial cortex in snakes also produce a bundle of degenerated axons that continues through the septum, passes caudal to the anterior commissure, and continues medially through the thalamus to terminate in the caudal hypothalamus. Degeneration was also found in the anterior thalamus, but could not be unequivocally attributed to an origin in the medial cortex because lesions in dorsal cortex also produce degeneration in the anterior thalamus.

8. Functional Organization of Cortical Areas

Previous sections have reviewed the cellular, neurochemical, and connective properties of the four cortical areas. This section considers what little information is available on the function of each of the areas

8.1. Lateral Cortex

Lateral cortex receives information from the main olfactory bulb both directly via the lateral olfactory tract and indirectly via olfactorecipient structures in the base of the forebrain. It receives a feedback projection from medial cortex and ascending projections from the peritubal nuclei of the thalamus, the median raphe, dopaminergic cell groups in the hypothalamus, and the cholinergic cells of the diagonal band-basal forebrain system. It gives rise to a major efferent projection to medial cortex, providing it with potential influence over the septum and hypothalamus. Finally—at least in lizards—there are commissural connections between the dorsal rostral lateral cortices.

Orrego (1961, 1962) studied the physiology of lateral cortex in turtles using electrical stimulation of the olfactory bulbs and showed that neurons in lateral cortex are activated by stimulation of the olfactory bulb. These findings have been confirmed by other workers (see Belekova, 1979), although the precise role of lateral cortex in olfactory behaviors is not known (see Ulinski and Peterson, 1981, for a review).

8.2. Dorsal Cortex

It is clear that dorsal cortex of turtles is involved in visual information processing. It receives an organized, although not topographic, projection from the dorsal lateral geniculate complex and projects back to visual structures in the brain stem such as the dorsal lateral geniculate complex, nucleus rotundus, and the optic tectum. Also, presentation of visual stimuli alters the electrical activity of dorsal cortex in both extracellular and intracellular recording experiments (Orrego, 1962; Bass *et al.*, 1983; Pivovarov and Trepakov, 1972; Kriegstein, 1987). Nonetheless, the precise role of dorsal cortex in the visual behavior of turtles has been problematic. Neurophysiological experiments have failed to find neurons with easily interpretable receptive field properties, and lesions of dorsal cortex do not produce obvious deficits in visual tasks such as pattern recognition (Bass *et al.*, 1973; Cranny and Powers, 1983).

However, the receptive field properties of cortical neurons suggest involvement in behavioral responses to moving objects in the turtle's environment. Neurons respond well to small, moving stimuli anywhere in the turtle's visual space (Mazurskaya, 1973; Mazurskaya *et al.*, 1976). They habituate rapidly (Gusel'nikov and Pivovarov, 1978), and the habituation shows some directional tuning so that repeated presentation of the stimulus moving in one direction causes habituation in a cortical neuron, whereas presentation of a stimulus moving in another direction elicits a brisk response. In addition to responding to a continuous moving stimulus, cortical cells also respond well to two small stimuli

presented at two disjunct points in visual space (Mazurskaya, 1973). Units located superficially in the cortex (presumably stellate cells) have response properties that differ from those located deep in the cortex (presumably double pyramidal cells). Superficial units respond preferentially to stimuli presented simultaneously, while deep units respond preferentially to stimuli presented successively, with some temporal delay, at two disjunct points. The optimum interstimulus interval varies as a function of the positional disparity of the two points, being—for example—200 msec for a disparity of 20° of visual arc. From a behavioral viewpoint, these properties are consistent with the idea that dorsal cortex is involved in analyzing moving stimuli as they move through the turtle's visual world. Thus, individual cells can respond to a give stimulus at different points in visual space and over time spans that would occur as turtles encounter moving objects.

Some of these properties can be explained in terms of the known anatomy and cellular physiology of neurons in dorsal cortex. Cortical cells have wide-field receptive fields that require a convergence of information from all points of visual space onto neurons situated throughout dorsal cortex. The dorsal lateral geniculate complex receives a topographically organized representation of the retinal surface (Ulinski and Nautiyal, 1988), and although a few geniculate neurons have wide-field receptive fields, most have receptive fields that subtend about 30° of visual arc (Boiko, 1980). Some convergence occurs in the projections from the retina to the geniculate, but a further convergence must occur deeper into the geniculocortical pathway. This convergence occurs in two steps (Mulligan and Ulinski, 1990; Cosans and Ulinski, 1990; Ulinski, 1988). Information about points along the vertical meridians of visual space apparently converges upon cortical neurons as a result of the point-to-line character of geniculocortical projections, while information about points along the horizontal meridians converges upon cortical neurons as a result of intracortical connections.

The tendency for cortical neurons to habituate strongly is expected of a motion analysis system and is consistent with the presence of inhibitory neurons in the cortex. Both the layer 1 stellate cells and the double pyramidal cells of layer 2 receive thalamic inputs (Smith *et al.*, 1980) which are apparently excitatory (Pivovarov and Trepakov, 1972; Kriegstein, 1987). The stellate cells make GABAergic synapses upon double pyramidal cells. Thus, activation of the geniculocortical system evokes an EPSP-IPSP sequence in double pyramidal cells. Since the stellate cells make extensive synaptic contacts in layer 1 (Desan, 1984) and have a tonic firing pattern (Connors and Kriegstein, 1986), activation of geniculate neurons would lead to initial activation of double pyramidal cells followed by a strong inhibition. Since stellate cells respond preferentially to stimuli that occur simultaneously in different regions of visual space, they will tend to bias double pyramidal cells toward transitory responses to local moving stimuli. At this point, we have only the most rudimentary idea of how dorsal cortex contributes to the turtle's ability to respond to moving stimuli. However, what is known suggests that it is involved in a smooth pursuit system functionally similar to the motor systems in primates that allow them to follow a moving target with their eyes (Lissberger *et al.*, 1987).

Although these results on turtles seem promising, they shed little light on the variations in the cytoarchitecture and connections of dorsal cortex that are seen between members of different groups of reptiles. Indeed, dorsal cortex is

the cortical area that shows the greatest interspecific variation. It is particularly interesting that cryptodiran turtles have a large input to dorsal cortex from the dorsal lateral geniculate complex while this system is relatively modest in lizards and perhaps absent in crocodilians. Members of each of the major orders of reptiles vary in the relative development of their eyes and the extent to which they use visual behavior in their day-to-day lives. However, many lizards—including those species that have been studied using anatomical techniques—use visual cues extensively both in feeding behaviors and in social communication. Why the geniculocortical system should be significantly smaller in size in these animals than in turtles is not at all obvious. The lateral regions of dorsal cortex, which receive geniculate input, also vary in their cytoarchitecture between species. Some forms have a large pallial thickening area adjacent to lateral cortex, while in others the geniculate input terminates in only a small cluster of neurons. Thus, the fraction of dorsal cortex that corresponds to a visual area is quite large in turtles but quite small in lizards.

It seems clear that dorsal cortex as classically defined is not a unitary structure, but it is not certain how to relate the subdivisions of dorsal cortex in one species to its subdivisions in another species. One suggestion (e.g., Butler, 1976) is that dorsal cortex contains two major components. A lateral part receives geniculate input and is a primary visual cortex. The medial part receives inputs from the lateral part, but not directly from the geniculate. It thus serves to relay visual information to the dorsomedial and medial cortical areas. Desan's (1984) subdivision of dorsal cortex into a lateral area (D2) which includes pallial thickening and a medial area (D1) reflects this idea in that there is a sequential projection from the geniculate to D2 to D1 and then to medial cortex. The medial part may also receive inputs from other sensory modalities (e.g., Moore and Tschirigi, 1962; Orrego and Lissensby, 1962; Belekova, 1979).

8.3. Dorsomedial Cortex

Dorsomedial cortex lacks efferent projections that leave the cortices of the two hemispheres, so it seems to play a role in interconnecting the cortical areas. Its most obvious connections form the largest commissural system in the cortex, linking the dorsomedial area of one side of the brain with its opposite member and a reciprocal connection with medial cortex. In at least turtles, the double pyramidal cells that are the major cell type found in layer 2 of dorsomedial cortex tend to fire in bursts of action potentials, either as a result of endogenous bursting properties or as a result of a rhythmic synaptic drive (Shen and Kriegstein, 1987).

Electroencephalographic studies on crocodilians (Pyrethon and Dusan-Pyrethon, 1969; Flannigan *et al.*, 1973), turtles (Herman *et al.*, 1964; Pyrethon and Dusan-Pyrethon, 1969; Karmanova and Churnosov, 1972; Vasilescu, 1970; Flannigan, 1974b; Flannigan *et al.*, 1974; Walker and Berger, 1973), lizards (Flannigan, 1974a) and snakes (Pyrethon and Dusan-Pyrethon, 1969) show that rhythmic discharges can be recorded from the cortex, olfactory bulbs, and optic tectum of reptiles. Reptiles generally demonstrate a variety of behavioral arousal states, including periods of quiescence that resemble mammalian sleep periods in that the animal assumes a species-specific, stereotypic rest posture, shows an elevated behavioral response threshold and decreased respiration. Changes in

behavioral state are correlated with EEG changes in that alert and active states are correlated with low-amplitude EEG patterns and quiescent periods are correlated with the presence of high-amplitude spikes in the EEG record. Whether these spikes correspond to the slow waves seen in mammalian sleep or to "limbic system spikes" recorded from the hippocampus of mammals during sleep (Hartse and Rechtschaffen, 1974) is not clear (see Walker and Berger, 1973). However, Hartse and Rechtschaffen (1974) showed that systemic administration in the tortoise *Geochelone carbonaria* of atropine sulfate, a drug that acts on central muscarinic cholinergic receptors, increases the frequency of high-voltage spikes in the EEG record. Since ACh hyperpolarizes neurons in dorsal cortex via muscarinic receptors, it is possible that atropine sulfate disinhibits neurons in dorsal cortex, thereby increasing the synaptic drive to endogenously bursting neurons in dorsomedial cortex. Thus, dorsomedial cortex may play a role in organizing the cortical rhythmic activities that mediate the animal's arousal state.

8.4. Medial Cortex

Medial cortex receives projections from a number of subcortical structures as well as each of the other three cortical areas. Its afferents show a complex organizational pattern, including a lamination of afferents such that many sets of afferents synapse upon a particular segment of the dendrites of layer 2 neurons. It is not possible to say much about the functional significance of these afferent systems except that medial cortex is in potential receipt of information from the main olfactory bulb via lateral cortex and of nonolfactory sensory information via dorsal cortex. Neurophysiological studies have confirmed such predictions made on the basis of the anatomical connections of medial cortex in that responses to electrical stimulation of the olfactory bulbs and activation of other sensory systems via either natural or electrical stimulation have been found to elicit neuronal activity in medial cortex of turtles (e.g., Pivavarov and Trepakov, 1972; Bass *et al.*, 1983) and lizards (see Belekova, 1979). The latency of responses in medial cortex are always longer than those in dorsal cortex or lateral cortex.

Some of the efferent projections from medial cortex involve feedbacks to other cortical areas, but others leave the cortex and terminate in the hypothalamus, septum, or anterior thalamus. These presumably play some role in mediating behavior, but there is no real information on what this role might be.

8.5. Cortex as a Whole

There have been several studies examining the effect of cortical lesions on various aspects of behavior. The intention has usually been to investigate the role of a specific cortical area, but given the degree to which the cortical areas are interconnected and the fact that most systems afferent to one cortical area pass through one or more other areas en route to their eventual targets, it is unlikely that any of the experiments conducted to date can yield unambiguous conclusions about a given cortical area. The application of newer methods of inducing chemical lesions, which potentially circumvent the problems that attend fibers of

passage, may help. In the meantime, work carried out so far may shed some light on the overall function of the cortex in reptiles on the assumption that any lesion in the cortex is likely to result in a global alteration of cortical activity.

One conclusion that comes from most of the lesion studies is that the cortex in reptiles does not play a simple role in discriminative function. Thus, lesions of dorsal cortex in lizards (Peterson, 1980) and turtles (Hayes and Hertzler, 1967; Hertzler and Hayes, 1967; Bass *et al.*, 1973; Morlock, 1972; Reiner and Powers, 1983) have generally failed to produce any noticeable deficit in the animal's ability to discriminate luminance levels or visual patterns, or perform a variety of visual locomotor tasks. On the other hand, cortical lesions do produce deficits in behaviors that require the animal to alter its pattern of behavior. Killackey *et al.*, (1972) found that lesions of dorsal cortex produce a deficit in the animal's ability to habituate to visual stimuli. Turtles were held so that they faced an instrument that released a Ping-Pong ball, causing it to fall toward the turtle's nose. Normal animals initially retract their neck and head when the ball is released, but then habituate to the stimulus. However, lesions of dorsal cortex eliminated the habituation response. Peterson (1980) studied the effects of lesions of dorsal cortex on spatial learning of desert iguanas (*Dipsosaurus dorsalis*) using mazes introduced by Lashley (1929). Normal animals were able to learn to locate a warm plate in a maze, but lesioned animals tended to wander into one cul-de-sac of the maze and stay there. Lesions of dorsal cortex also produced a deficit in reversal learning in these animals. Normal animals could be trained to go to one arm of a maze to find a warm plate. When they reached criterion on one arm, they could subsequently be trained to reverse themselves and go to the other arm of the maze. Lesioned animals could not learn this reversal task, and their errors tended to increase in number with subsequent reversals. Similarly, Cranny and Powers (1983) found that lesions of dorsal cortex in turtles produced a deficit in the animal's ability to perform visual reversal tasks or to shift the basis of the discrimination from a pattern to color or to reverse go/no-go discriminations. For example, turtles were first trained to respond to a horizontal stripe and then required to respond to a vertical stripe. Or, turtles might be trained to respond to a vertical stripe regardless of its color (red or green) and then to shift to a response made on the basis of color.

9. Reptilian and Mammalian Patterns of Cortical Organization

As noted in section 1, it has been clear for over 100 years that reptiles and mammals are the two groups of vertebrates with complex, laminated cerebral cortices. This apparent similarity prompted considerable and sustained interest in the cortex of reptiles because of the possibility that an understanding of the cortex of reptiles would provide clues to the evolution of the mammalian cortex. Until quite recently, reptiles were believed to lack the direct thalamocortical projections that seemed the hallmark of mammalian cortex, and the progressive establishment of such projections in early mammals was seen as a key step in the evolution of the mammalian brain. However, it now appears that reptiles do have direct thalamocortical projections and that cortex in both reptiles and mammals receives projections from a large list of subcortical structures. The cortices of reptiles and mammals may then be more alike than previously

suspected. This last section briefly summarizes what now seem to be the most important similarities and differences between the cortices of reptiles and mammals.

The forebrains of both reptiles and mammals are similar in that the dorsal surface of their cerebral hemispheres is formed by a pallium that extends from the septum, medially, to the striatum laterally. In contrast to the situation in other groups of vertebrates whose forebrains develop by a process of evagination, the pallium in reptiles and mammals consists, at least partially, of a laminated cortex in which neurons have migrated away from the ventricle to form at least three layers of cell bodies. The pallium can be divided into three major segments in both groups (Fig. 37).

The first is an "olfactory cortex"—lateral cortex or pyriform cortex—which is situated on the lateral wall of the hemisphere and receives direct projections

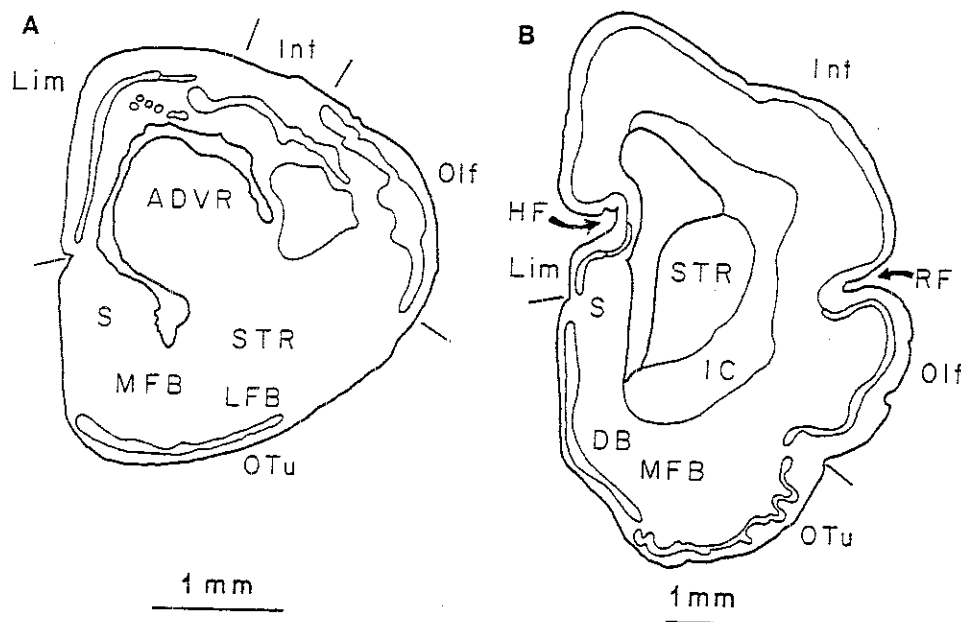


Figure 37. Comparison of pallial organization in reptiles and mammals. This figure shows transverse sections through the telencephalon of (A) a tegu lizard, *Tupinambis*, and (B) an opossum, *Didelphis*. Unlike placental mammals, marsupials (and monotremes) lack a corpus callosum, thereby simplifying comparisons with the lizard brain. Both telencephalons have a lateral ventricle and are divided into three major parts. The septum (S) makes up the ventromedial face of the telencephalon. The striatum (STR) makes up the ventrolateral wall of the telencephalon. Olfactory structures such as the diagonal band (DB) or olfactory tubercle (OTu) are present on the ventral surface. The forebrain bundles run rostrally into the telencephalon. They consist of the medial forebrain bundle (MFB) and the lateral forebrain bundle (LFB) or internal capsule (IC). The pallium or roof of the telencephalon has two components in reptiles: a cortex and the anterior dorsal ventricular ridge (ADVR). The pallium in mammals has only a single component: the cortex. In both groups the pallium can be divided into three functional segments. The olfactory cortex (Olf) is situated laterally. The intermediate segment (Int) is present dorsally. It includes part of dorsal cortex and ADVR in reptiles and the cortex between the rhinal fissure (RF) and the hippocampal formation (HF) in mammals. The limbic cortex (Lim) occupies the medial wall of the pallium in both groups. It is inviolated by the hippocampal fissure in mammals. Note that the two sections are drawn to different scales.

from the mitral cells of the main olfactory bulb. It is a trilaminar cortex in both groups, and there are several similarities in its neuronal organization (Ulinski and Rainey, 1980). Perhaps the major difference is that lateral cortex of reptiles receives direct, bilateral projections from the main olfactory bulbs, while in mammals there are only indirect connections between the two piriform cortices (Haberly and Price, 1978).

The second major pallial segment is a "limbic cortex" that lies dorsal to the septum and forms the dorsomedial wall of the hemisphere. This relationship is partly obscured in mammals by the formation of the hippocampal fissure, the ventral elaboration of limbic cortex that accompanies the formation of the temporal lobe in some species, and by the disruption of the medial wall of the hemisphere caused by the formation of the corpus callosum in placental mammals. Nevertheless, there are general similarities between limbic cortex in reptiles and that of mammals. These include the trilaminar organization of the medial and dorsomedial cortical areas in reptiles and the mammalian dentate gyrus and CA fields, the cytology of neurons in these areas (particularly that of the candelabra cells of medial cortex and the granule cells of the dentate gyrus), and the presence of a population of neurons that contain zinc in their axons. There is also a less obvious similarity in that limbic cortex in both groups received afferents from olfactory and nonolfactory cortical areas. These connections are direct in reptiles. Lateral cortex carries information from the main olfactory bulb to medial cortex, and dorsal cortex carries information from the dorsal lateral geniculate complex to medial cortex. The connections are indirect in mammals. Information from the main olfactory bulb reaches the dentate gyrus only after relay in both the piriform and entorhinal cortical areas. Information from thalamic sensory nuclei reaches the dentate gyrus only after passing through several cortical areas, including one or more "sensory" areas and the entorhinal cortex (Jones and Powell, 1970). However, there is a striking similarity in the organization of afferent systems within the limbic cortex of the two groups with inputs from the "olfactory" and "nonolfactory" sensory modalities terminating in a laminar fashion in the outer part of the first cortical layer and commissural and association systems terminating deeper in the most medially situated cortical areas of animals in the two groups. Finally, the connections of the limbic cortices in the two groups show a tendency toward a lamellar organization in which axon systems run roughly in the transverse plane at each level of the septotemporal axis. This is seen, for example, in the trajectory of the axons of candelabra cells that run from medial cortex to the other three cortical areas in reptiles and those that run from the granule cells of the dentate gyrus to field CA3 in mammals.

The major differences between limbic cortex in the two groups lie in the organization of their efferent systems. Both have projections to the septum, hypothalamus, thalamus and reciprocally back to those areas on the lateral surface of the hemisphere that project, directly or indirectly, to medial cortex. However, in reptiles medial cortex is the major source of efferents from limbic cortex, and dorsomedial cortex (which bears some resemblance to the CA fields of mammals in terms of its cytology) participates only in commissural and association projections, while in mammals the dentate gyrus projects almost exclusively to the CA fields which, together with the subicular complex, are the source of efferent projections from the limbic cortex.

The third segment of the pallium lies on the dorsal surface of the hemi-

sphere between limbic cortex and olfactory cortex. It is composed entirely of isocortex and adjacent areas in mammals, but in reptiles (and birds) it consists of at least part of dorsal cortex and the anterior dorsal ventricular ridge. This segment receives projections from the auditory, somatosensory, and visual sensory nuclei of the dorsal thalamus as well as a range of subpallial structures (e.g., locus coeruleus, raphe, basal telencephalon) in both reptiles and mammals. The organization of the anterior dorsal ventricular ridge appears to be very different from that of isocortex at first glance, but there are actually several similarities in organization between the two structures. These are discussed in some detail by Ulinski (1983), and will not be considered here. However, this intermediate segment of the pallium is laminated, contains modality-specific sensory areas, and gives rise to efferent projections to the striatum in both groups.

Some of the most important differences between the intermediate segment in reptiles and mammals pertain to motor systems. Isocortex of monotreme, marsupial, and placental mammals contains one or more cortical areas that elicit movements of restricted body parts following electrical stimulation, give rise to corticospinal and corticobulbar projections, and receive afferent projections from thalamic nuclei that carry information from the cerebellum and striatum to the cortex. There is no indication that such areas are present in reptiles. Thus, reptiles seem to have only corticostriate systems and lack direct projections from the pallium to the reticular formation and spinal cord. It is also the case that the striatum is relatively small in reptiles, while it is greatly expanded and bulges into the lateral ventricles in mammals. Ulinski (1986a) has speculated that these differences reflect the evolution of the ability to control complex movements of the jaws and limbs that occurred relatively late in the evolution of mammals.

10. References

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