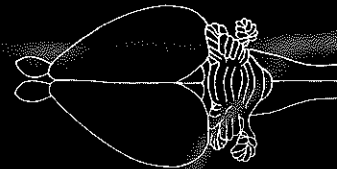
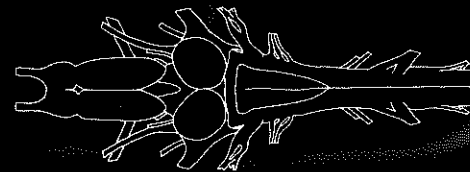
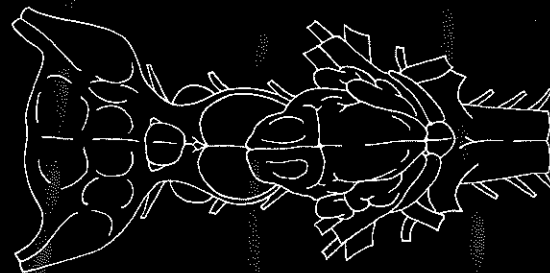


COMPARATIVE VERTEBRATE NEUROANATOMY

Evolution and Adaptation



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ANN B. BUTLER

I. T. N. I.
Arlington, Virginia

and

Krasnow Institute for Advanced Study
George Mason University
Fairfax, Virginia

WILLIAM HODOS

Department of Psychology
University of Maryland
College Park, Maryland

Ford, H. and Wiltschko, R. (1993) Red light
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The Vertebrate Central Nervous System

INTRODUCTION

The brain evolved in ancestral chordates in conjunction with the evolution of the head as a specialized body region. One of the principal evolutionary events that preceded the sequences of head and brain evolution was a novel embryological event: the development of the mouth as a distinct body opening separate from the gut opening, which eventually becomes the anus. Animals that possess these characteristics are known as **deuterostomes**, which means "second mouth." Deuterostomes comprise a number of groups of which the three major ones are echinoderms (starfishes and sea urchins), hemichordates (pterobranchs and acorn worms), and chordates. The latter include tunicates (sea squirts), cephalochordates (*Branchiostoma*, previously called *Amphioxus*), and vertebrates. Because some of the key evolutionary events in deuterostome and chordate evolution have been ones that occur relatively early in embryological development, we will begin this chapter with some of the early aspects of the embryological development of the brain in vertebrates.

In vertebrates, the process of gastrulation [Fig. 3-1(B and C)] follows the blastula stage, with continued cell proliferation and the specification and arrangement of specific groups of cells relative to the parts of the body that they will eventually form. The **gastrula** initially consists of two cell layers: an outer layer of cells, the **ectoderm**, from which the skin and nervous system will form, and an inner layer, which consists initially of **endoderm**. The endoderm surrounds the cavity, called the **archenteron**, that will become the lumen of the gut. The archenteron expands during gastrulation, obliterating the blastocoel. The opening of the gut cavity is the **blastopore**.

As gastrulation proceeds, the roof of the archenteron, formed by the dorsal part of the inner layer of cells, differentiates to form mesodermal tissue, which in turn gives rise to a midline structure called the **notochord**, as well as to lateral sheets of tissue that will form muscle. The rest of the inner layer remains endoderm, the tissue of the gut. During the later stages of gastrulation, the ectoderm overlying the archenteron roof thickens to form the **neural plate**. A pair of folds develops along this plate and grows dorsally to meet and then fuses to form a

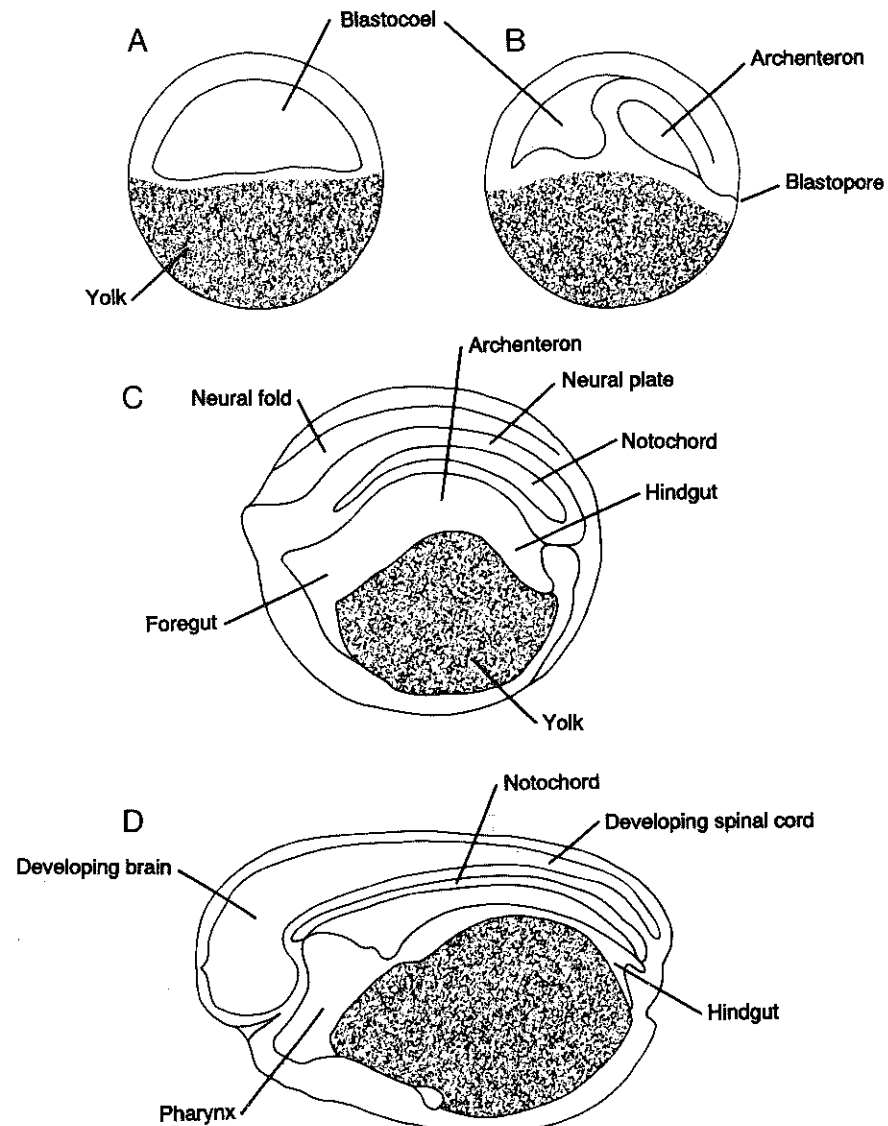


FIGURE 3-1. Drawings of sections through a gastrula (A) and stages of blastulation (B and C) to form a 3 mm embryo (D) in a frog.

to components of the developing nervous system, as do specific areas of neurogenic ectoderm in the head, called **placodes**.

THE BRAIN AND SPINAL CORD

In the head region of the earliest vertebrates, the neural

The central nervous system consists of the brain and the spinal cord. Figure 3-2 illustrates the location of the brain and the rostral end of the spinal cord in the head of an adult vertebrate, a lizard in this example, and demonstrates some of the standard terms of orientation (also see the Appendix). The central nervous system traditionally has been divided into two great regions: the brain and the spinal cord. While this distinc-

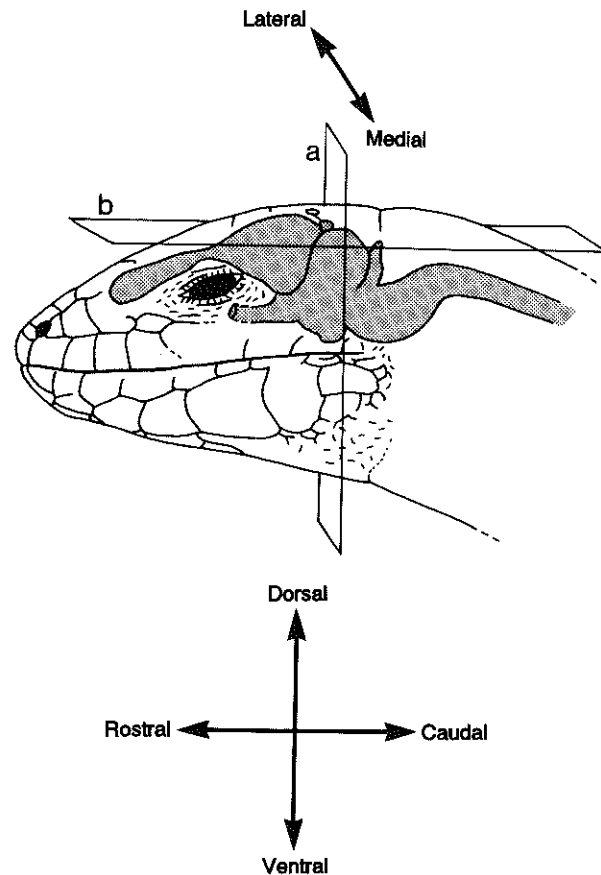


FIGURE 3-2. Lateral view of the head of a lizard (*Lacerta sicula*) with the position of the brain and the rostral part of the spinal cord (indicated by shading) shown *in situ*. Rectangle "a" represents the transverse plane, which runs from dorsal to ventral and medial to lateral. Rectangle "b" represents the horizontal plane, which is approximately parallel to the line of the mouth and runs from rostral to caudal and medial to lateral. The sagittal plane is parallel to the lateral view shown in the figure and runs from rostral to caudal and dorsal to ventral. Adapted from Senn (1979). Used with permission of Academic Press Ltd.

protects the spinal cord. Although a substantial portion of the brain consists of unique structures that have no counterpart in the spinal cord, much of the brain, especially its caudal region, is actually a continuation of the structures and general organization of the spinal cord.

The spinal cord is organized for the control of the body's limbs and trunk; similarly, the caudal brain is organized for the control of specialized structures in the head, such as the jaws, tongue, eye muscles and lids, and vocal organs. Moreover, the caudal brain and spinal cord share the task of control and

neurons and wrap around parts of neurons, and the neurons themselves. The neurons can be categorized into three broad categories. The first category is composed of Golgi Type I cells (see Chapter 2) that are the **afferent neurons**, which are cells that bring information about the internal and external environments into the central nervous system. The second category is composed of Golgi Type I cells that are **efferent neurons**, which are motor or effector cells that bring instructions from the central nervous system to the body's effector organs, that is, the muscles and glands. The third category consists of both Golgi Type I and II cells that are **interneurons**; these neurons account for the greatest proportion of the mass of the central nervous system (Fig. 3-3).

We should note that the terms "afferent" and "efferent" can be used in conjunction with the primary sensory and the motor or effector neurons, respectively, or in reference to the direction of information relay in the central nervous system. These terms refer to the direction of conduction and are also used in talking about interneurons. Afferent means "coming into," and efferent means "going out of." A long-axon interneuron coming into and terminating within a specified local-circuit population, which we will call A, is afferent to A. Another long-axon interneuron going from A to a different local-circuit population, which we will call B, is efferent from A and afferent to B.

The interneurons form the neural chain between the primary sensory afferent neurons and the efferent motor or effector neurons. Rarely does a primary sensory neuron make direct contact with a motor neuron. Rather, a few or many thousands of interneurons typically receive the flow of information from sensory neurons into the central nervous system, process that information, and send the resultant outflow of instructions to muscles or glands via the motor neurons. The interneurons determine whether the instructions will be for action or for inaction, whether a response will be rapid or leisurely, vigorous or delicate, towards an object or away from it.

As described in Chapter 2, interneurons form discrete neuronal populations, called **nuclei** (singular: **nucleus**). In addition to **nuclei**, there are also areas of layered sets of interneurons in the brain. Some of these layered areas are called **cortex**. Cortices are present in some of the more dorsal, or roof, areas of the brain. A number of cortical areas are present in the rostral part of the brain in some vertebrates, and cortex is also present in the roof of the middle part of the brain (midbrain) and of the hindbrain.

This general description of central nervous system organization applies to both the spinal cord and brain. The rostral-most parts of the brain have fewer primary sensory, afferent components and fewer effector, efferent components than are present in the brainstem. The rostral brain consists mostly of

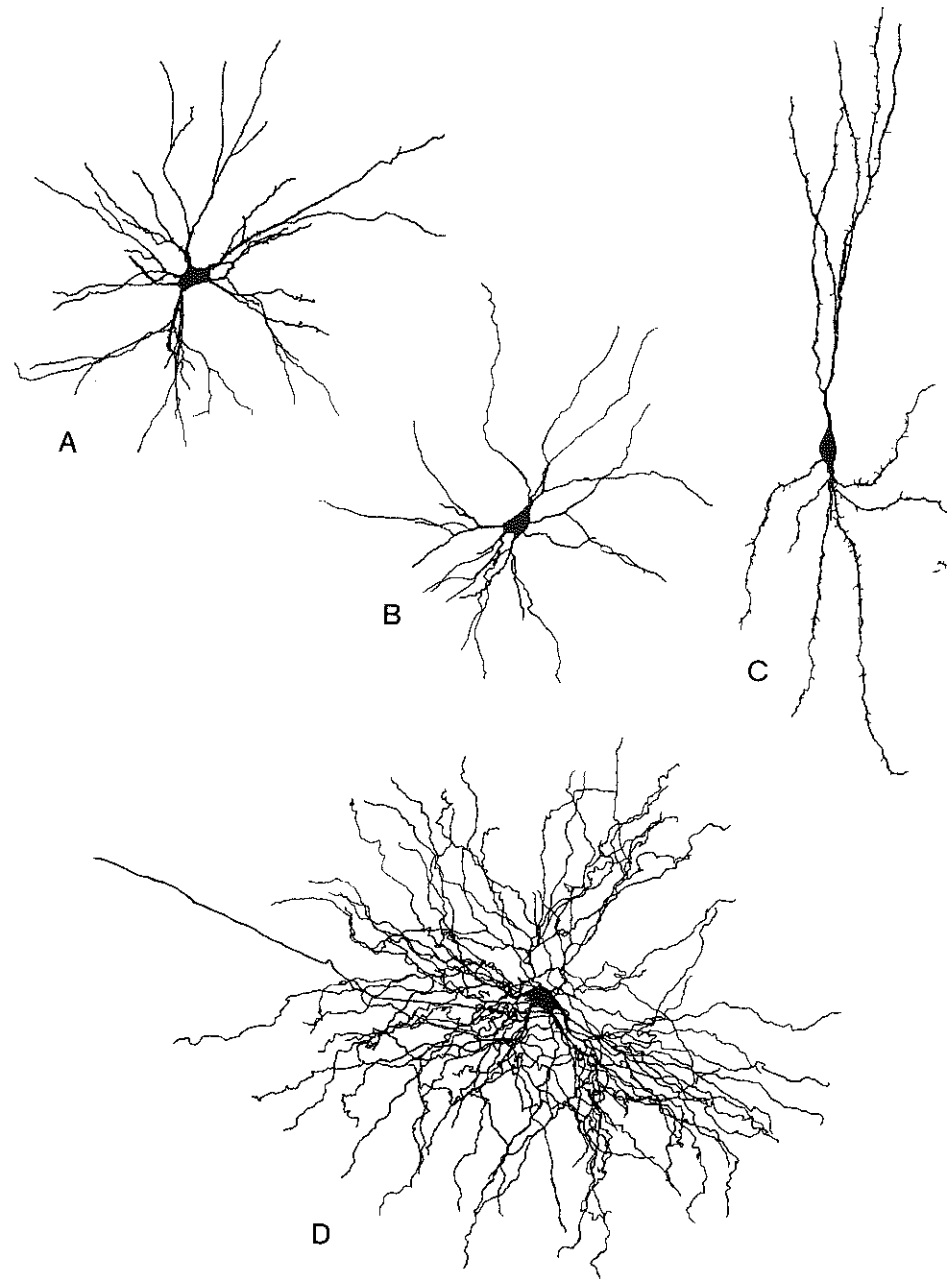
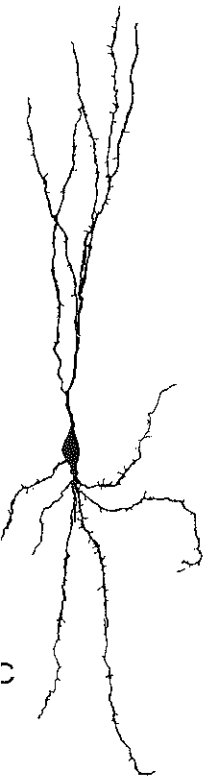


FIGURE 3-3. Examples of interneurons found in the forebrain in various mammals. (A and B) Both are from the dorsal thalamus of a cat, after Robson (1993); (C) is from the cerebral cortex of a monkey, after Lund and Lewis (1993); and (D) is from the dorsal thalamus of a monkey, after Havton and Ohara (1993).



spinal nerves exit on their way to the various parts of the body. Thus, the region of the cord from which nerves exit through the cervical (neck) bones is called the **cervical cord**. This is the most rostral division of the cord and is continuous with the most caudal region of the brain.

Proceeding caudally within the spinal cord, the remaining divisions are the **thoracic** (chest) **cord**, the **lumbar** (abdominal) **cord**, and the **sacral** (pelvic) **cord**. In addition to receiving primary somatic, afferent fibers from the skin, muscles and joints of the neck, body, limbs (if any) and tail (if any), the spinal cord also sends out motor, efferent fibers (axons) that control the muscles of these body parts. The latter are known as somatic efferent fibers.

From the thoracic and lumbar regions of the cord, a special group of efferent neurons sends its axons to innervate the smooth muscles of the digestive system and other internal organs and glands. These are known as **visceral efferent fibers**. The visceral efferents originating in the thoracic and lumbar spinal cord are known as the **sympathetic nervous system**. They function to provide a rapid activation of various internal organ systems such as the cardiovascular and respiratory systems when severe demands are placed on these systems or in times of emergency when quick action is required. This system serves "fight or flight" and related responses.

The sympathetic nervous system is complemented by another visceral efferent system, the **parasympathetic nervous system**, which is composed of visceral efferent neurons from the sacral division of the spinal cord and from the caudal regions of the brain. The parasympathetic system controls the same organs as does the sympathetic system, but it does so under normal conditions, when no special stresses are present. This system functions in promoting the digestion of food, allowing urination to occur, and other, related, normal functions of the organs. Thus, when a high-demand situation arises, the sympathetic system takes control; when the high-demand situation ceases, control returns to the parasympathetic system. The sympathetic and parasympathetic systems together are known as the **autonomic nervous system**.

The Brain

Figure 3-4 is a drawing of the brain and rostral spinal cord of a vertebrate, in this case a ray-finned fish, which will serve

as an example for the general organization of vertebrate brains. Each of the lobes and other swellings of the brain surface has a specific name, such as the optic lobe (tectum) or cerebellum. Groups of lobes or swellings are known by regional names, such as the mesencephalon (midbrain). Still more-encompassing regional names are forebrain and brainstem.

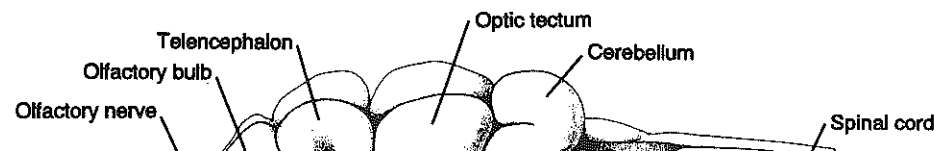
The nerves entering and leaving the brain are the **cranial nerves**. Like the spinal nerves, the cranial nerves carry primary sensory afferent neurons (in this case from the head rather than the body) into the central nervous system and motor or effector efferent neurons to control the muscles and glands of the head and neck. Although these nerves are given special names, such as trigeminal nerve and oculomotor nerve, the organization of at least some of them is essentially the same as that of the spinal nerves. Moreover, some of the interneuron networks of the more caudal cranial nerves are directly continuous with equivalent cell populations in the spinal cord.

Hindbrain. The caudal-most region of the brain is the **rhombencephalon** or **hindbrain**, which consists of the **medulla** and **pons**. The cranial nerves of this area include components that comprise most of the cranial division of the parasympathetic nervous system. However, a number of what have traditionally been called "special senses" are also represented by cranial nerves that enter the brain at this level. Such special senses are those that are unique to the head region, such as hearing and the sense of balance and acceleration. Other special senses, not present in all vertebrates, include the lateral line system for the detection of water displacement over the body surface and of electric fields in the aquatic environment and the infrared (IR) sense for the detection of body heat radiated by other animals. The cell bodies of the efferent neurons that control the muscles of the jaws and the superficial facial muscles, such as those of the lips and eyelids, are also located in this region of the brain.

In addition to the nuclei associated with some of the cranial nerves, the medulla and pons contain other nuclei and a number of fiber tracts. Many of the fiber tracts are long pathways between the spinal cord and the more rostral parts of the brain, while others are shorter and run between nuclei within this area. Some of the cell populations in the medulla and pons are more widely scattered and diffuse than most other nuclei in the brain. These scattered populations are collectively referred

(A and B) Both are from monkey, after Lund and Nara (1993).

ation to the outgoing, motor or effector

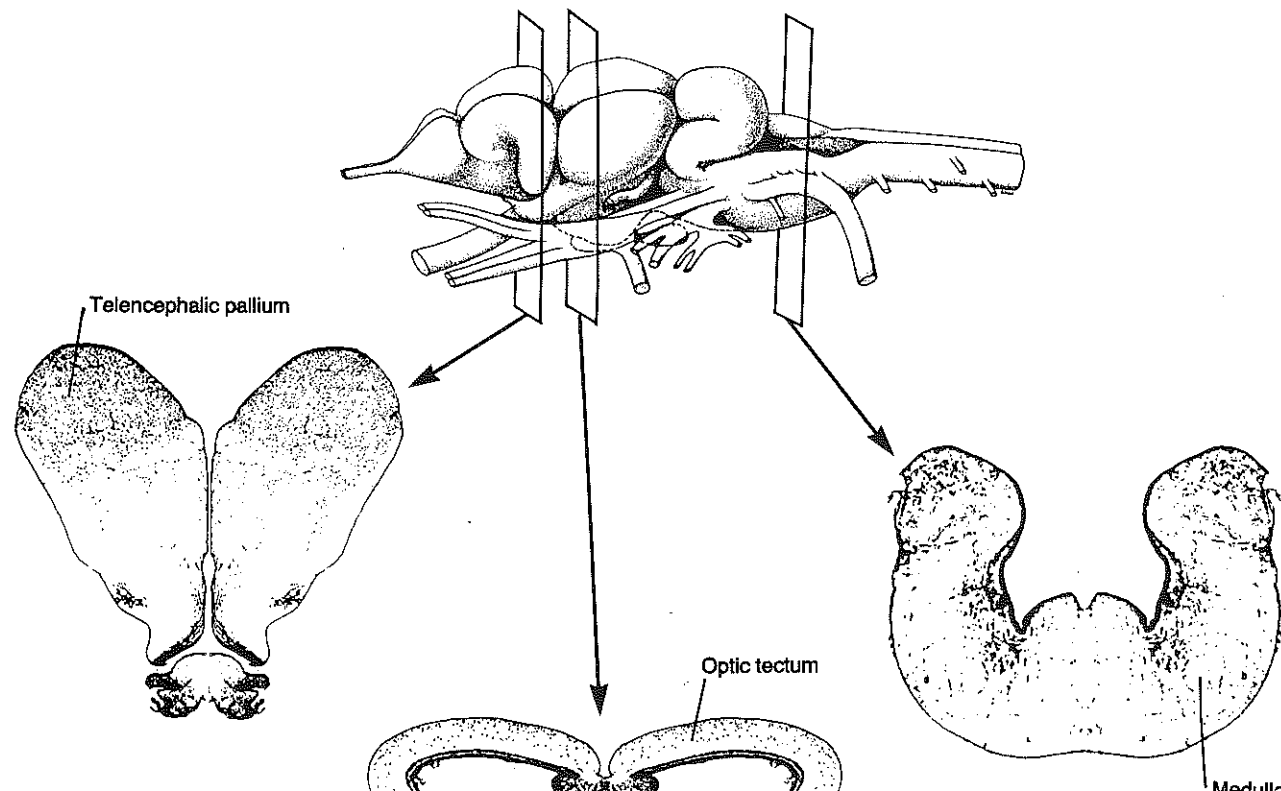


to as the **reticular formation**. The nuclei of the reticular formation are involved in integrating inputs from a variety of sources, including the cranial nerve nuclei and more rostral parts of the brain. The reticular formation regulates and modulates activities elsewhere in the brain on the basis of the incoming information. A transverse section through the hindbrain in a fish (Fig. 3-5) illustrates the distribution of nerve cell bodies within the brain. Fiber tracts run in the areas in which there are few or no cell bodies. Closely related to the pons, both geographically and functionally, is the **cerebellum** (Fig. 3-4). The cerebellum is a cortical structure in the roof of the hindbrain. Among its other functions, the cerebellum is involved in balance, coordination, and the smooth execution of rapid movements.

Midbrain. The next major subdivision of the brain is the **mesencephalon** or **midbrain** (Figs. 3-4 and 3-5). The most prominent external feature of this area in most vertebrates is the **optic lobe**, or **optic tectum**, so named because of the large number of neurons of the optic nerve that terminate in it. The ventral portion of the mesencephalon, the region underneath the optic tectum, is known as the **tegmentum**. The

mesencephalic tegmentum contains a number of nuclei and fiber tracts, including the nuclei of two of the cranial nerves that control the movements of the eyes. The operation of the intraocular eye muscles, which control the pupil and the focus of the lens, are controlled from this region as well.

Forebrain. The **prosencephalon** or **forebrain** is the most rostral division of the brain. It contains two major parts: the **diencephalon** and the **telencephalon**. The diencephalon (= interbrain) lies rostral to the midbrain, caudal-ventral to the telencephalon, and medial to the axons that form the optic tract, the central nervous system continuation of the optic nerve. The diencephalon is a large division composed of six principal areas. The caudal part of the diencephalon contains a dorsal area called the **pretectum** and a more ventral area called the **posterior tuberculum**. More rostrally, four areas are present. In dorsal to ventral sequence, these areas are the **epithalamus**, the **dorsal thalamus**, the **ventral thalamus**, and the **hypothalamus**. Each of these areas are composed of a number of nuclei, and there are also major fiber tracts that pass through this region.



um contains a number of nuclei and the nuclei of two of the cranial nerves (the optic nerves) of the eyes. The operation of the muscles which control the pupil and the focus of the eye is directed from this region as well.

The **telencephalon** or **forebrain** is the most rostral part of the brain. It contains two major parts: the **telencephalon**. The diencephalon is located caudal to the midbrain, caudal-ventral to the telencephalon. It contains the axons that form the optic system and a continuation of the optic nerve. A large division composed of six principal parts of the diencephalon contains a dorsal **thalamus** and a more ventral area called the **hypothalamus**. More rostrally, four areas are present. In vertebrates, these areas are the **epithalamus**, the **ventral thalamus**, and the **hypothalamus**. These areas are composed of a number of nuclei and also major fiber tracts that pass through

An additional neuroanatomical term frequently encountered is **brainstem**. This term sometimes refers to the more ventral parts of the brain except for any part of the telencephalon, that is, to the medulla and pons, the midbrain tegmentum, and the diencephalon. It is alternatively used to refer only to the medulla, pons, and midbrain tegmentum (and sometimes the midbrain tectum) without including the diencephalon. Context must be used to determine the specific sense in which this somewhat loose term is being used.

A number of the nuclei in the pretectum receive visual input from the retina and are involved in visuomotor behaviors. Pretectal nuclei and other visually related nuclei in the tegmentum influence eye movements in relation to prey and predator detection and to orientation of the body within space. The posterior tuberculum consists in part of a medially lying nucleus that contains neurons involved in regulating motor functions. In ray-finned fishes, more laterally lying nuclei of the posterior tuberculum are also present. These nuclei relay sensory inputs to the telencephalon. Similar nuclei may be present in cartilaginous fishes, but migrated posterior tubercular nuclei have not yet been identified in amphibians or land vertebrates.

The nuclei in the dorsal thalamus receive information via long-axon interneurons from the various sensory systems, which they transmit to various parts of the telencephalon. The nuclei in the dorsal thalamus constitute a gateway to the sensory areas of the telencephalon. A number of different parts within the telencephalon are involved in integrating the incoming sensory information for learning, memory, emotional responses, and motor responses.

Nuclei in the ventral thalamus are involved in modulating the activity of dorsal thalamic nuclei and also play a role, in concert with telencephalic structures, in motor control of the body and limbs. The epithalamus contains the **epiphysis** (pineal gland and related structures), which is located at the end of a stalk, the epiphyseal stalk. In some animals, such as reptiles, the pineal is a structure very similar to the eye. It contains light receptors and gives rise to primary sensory afferent neurons, which terminate in the epithalamus. In mammals and birds, the pineal is a glandular structure.

The hypothalamus is very much involved in the activities of the autonomic nervous system and the endocrine system. It controls the endocrine system's production of hormones by means of the **hypophysis** or **pituitary**, which is directly connected to the hypothalamus. The pituitary is located at the end of a stalk, the **infundibulum**, which is a direct outgrowth of the base of the hypothalamus. The hypothalamus thus is able to control and regulate behavior patterns that depend on the levels of hormones in the blood, such as sexual behavior, parental behavior, territoriality, migration, and hibernation, to name but a few. The hypothalamus also is concerned with feeding and drinking, as well as with the regulation of body temperature.

which the sense of smell is not especially important for survival, the bulb is relatively small in comparison. The olfactory bulb projects to the **olfactory pallium** in the telencephalon via **olfactory tracts**, which can be short if the olfactory bulb lies adjacent to the telencephalon (as in the brain of the fish shown in Fig. 3-4) or elongated.

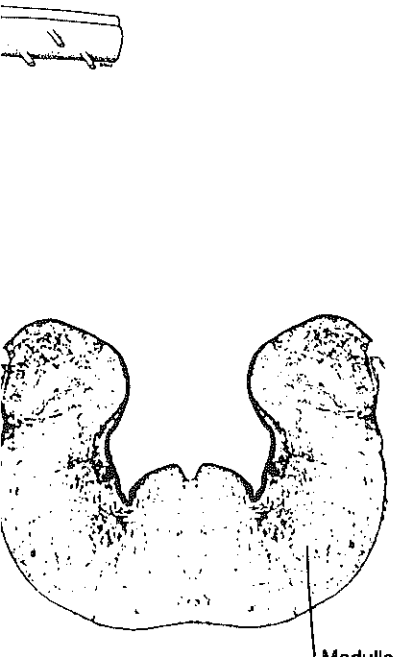
The cerebrum itself has a relatively smooth surface in most vertebrates. It is composed of nuclear areas in some vertebrate groups, such as cartilaginous and ray-finned fishes; in other vertebrate groups, particularly tetrapods, it is composed of both nuclei and cortex. In some animals, mostly among the mammals, although there are other instances as well, the surface of the cerebrum develops deep ridges and valleys known as convolutions. The ridges are called **gyri** (singular = **gyrus**) and the valleys are called **sulci** (singular = **sulcus**). The deepest of the sulci are known as **fissures**.

The telencephalon also includes several other major areas. The **limbic pallium** comprises a set of structures that include a cortical area known as the **hippocampus**, which is necessary for memory and is also involved in emotion. The hippocampus and some nuclei related to it, including the **septal nuclei** and **amygdala**, receive olfactory information from other telencephalic areas, which is integrated with other inputs. Several additional major areas lie in the more ventral part of the telencephalon and are involved with motor functions. These areas are collectively called the **striatum**, or **striatal nuclei**. They are interconnected with motor areas of the dorsal pallium and with nuclei in the more caudal parts of the brain.

The Meninges and the Ventricular System

The brain and spinal cord are covered by one or more layers of connective tissue, which are called the **meninges**, from the Greek word **meninx**, which means membrane. In fishes, only a single layer, the **primitive meninx**, is present. Amphibians and reptiles have two meningeal layers, an outer **dura mater** (meaning "hard mother") and an inner thin layer, the **secondary meninx**. In mammals and birds, three meningeal layers are present. The layer closest to the brain is a thin, vascular layer called the **pia mater** (meaning "tender mother"). The middle layer is a thin, avascular layer called the **arachnoid** due to its spider web-like appearance. The space between the pia mater and the arachnoid is the **subarachnoid space**. The outermost layer is the **dura mater** and is actually composed of two layers: an inner layer enclosing the central nervous system and an outer layer that lines the inside of the skull. The use of the word "mother" to describe these membranes comes from an ancient notion that they were the origin, or mother, of all membranes in the body.

Embryologically, the central nervous system develops from



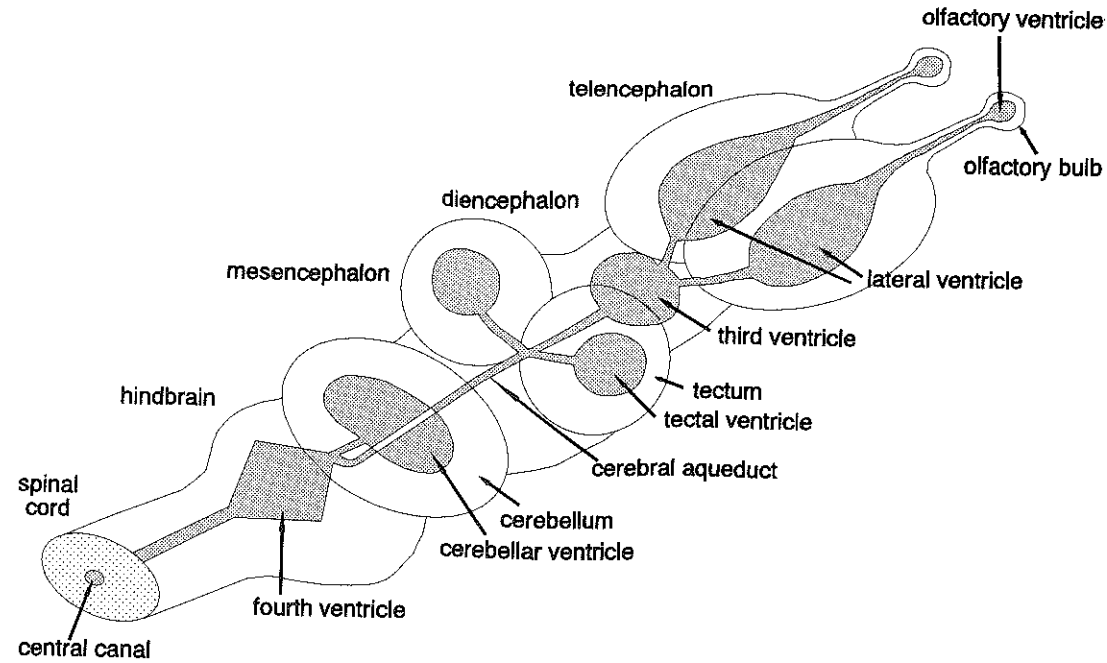


FIGURE 3-6. Dorsolateral schematic drawing of a vertebrate brain with the ventricular system, indicated by shading, projected onto it. Rostral is toward the upper right.

and this pair of laterally extending spaces are called the **lateral ventricles**. The lateral ventricles are in continuity, through paired openings called the **foramina of Monro**, with the unpaired, medial ventricular space of the diencephalon, called the **third ventricle**. The caudal continuation of the third ventricle is a narrow canal called the **cerebral aqueduct of Sylvius**, which in turn opens into the **fourth ventricle**, the unpaired, medial ventricular space of the hindbrain. The fourth ventricle is caudally continuous with the **central canal** of the spinal cord.

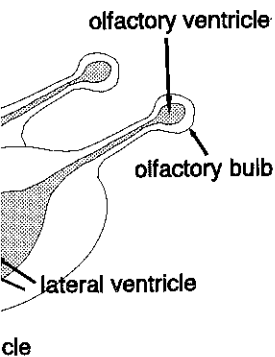
Parts of the ventricular walls consist of a thin ependymal epithelial layer and an inner, vascular meningeal layer, which together form the **tela choroidea**. A network formed by the blood vessels of the inner meningeal layer, called the **choroid plexus**, secretes **cerebrospinal fluid** into the ventricular spaces. The cerebrospinal fluid circulates in the ventricular system and also in the subarachnoid space; it reaches the latter by passing through three openings that connect the fourth ventricle with an enlarged part of the subarachnoid space, the **cisterna magna**. The three openings are a paired set, the **foramina of Luschka**, and an unpaired, medial foramen, the **foramen of Magendie**. After circulating, the cerebrospinal fluid passes out of the subarachnoid space into vascular sinuses through structures in the arachnoid called **arachnoid villi**, which act as one-way, pressure-sensitive valves. The cerebro-

is relayed through various nuclei, being modified and sorted along the way. In later chapters, which cover various parts of the brain, a general idea of the basic organization of these systems will help you to make sense of the anatomy.

Sensory Systems

All of the receptors for touch, radiant-energy sense, pain, lateral line (for wave displacement and electrical field detection), hearing, vestibular sense, and gustatory sense have their initial points of termination within the central nervous system either in the spinal cord or in the medulla-pons region of the brain. The target cell populations of these primary pathways then project to more rostral levels of the brain. Most of the axons in the primary sensory pathways from the eyes terminate in part of the dorsal thalamus in the diencephalon and in the optic tectum. The olfactory pathways, in contrast to the more caudal sensory pathways, project directly into part of the telencephalon. Topographic organization is an important characteristic of all of these pathways; this feature provides for orderly maps of the sensory input within particular parts of the brain that correspond to the spatial map of the external world.

Each of the ascending sensory pathways to the telencephalon terminates in its own specific region of the brain.



sensory, which includes touch and position sense from the body.

The Auditory Pathway. In the auditory pathway, axons arise from neurons in the inner ear and pass into the brain in the **eighth (octaval) cranial nerve**. These axons synapse on the dendrites of neurons in an auditory nucleus in the hindbrain [Fig. 3-7(A)]. The neurons in this nucleus give rise to axons that pass rostrally in a tract (called the **lateral lemniscus**) and synapse on the dendrites of neurons within a part of the midbrain roof called the **torus semicircularis** in most vertebrates and the **inferior colliculus** in mammals. The torus semicircularis lies ventral and/or caudal to the optic tectum. Neurons within the torus semicircularis give rise to axons that terminate on the dendrites of neurons in an auditory nucleus in the dorsal thalamus. Neurons in the dorsal thalamic auditory nucleus give rise to axons that pass into the telencephalon (via tracts called the **forebrain bundles**) and terminate on the dendrites of neurons within one or more auditory regions of the dorsal pallium.

The Visual Pathways. Neurons in the retina give rise to axons that enter the brain via the **optic nerve** [Fig. 3-7(B)] and its continuation, the **optic tract**. The retinal axons terminate on the dendrites of neurons located either in the **optic tectum** of the midbrain (called the **superior colliculus** in mammals) or in a visual nucleus in the dorsal thalamus. Visual neurons in the optic tectum also give rise to axons that terminate on the dendrites of neurons in a second visual nucleus in the dorsal thalamus. Neurons in each of the two visual dorsal thalamic nuclei give rise to axons that pass into the telencephalon via the forebrain bundles and terminate on the dendrites of neurons in two or more visual areas within the dorsal pallium.

The Somatosensory Pathways. Axons that carry somatosensory information [Fig. 3-7(C)] enter the spinal cord and pass rostrally to terminate on the dendrites of neurons within two cell groups called the **dorsal column nuclei**. These nuclei lie in the junctional area between the spinal cord and the brainstem. Neurons in the dorsal column nuclei give rise to axons that pass rostrally in a tract called the **medial lemniscus**. Some of these axons terminate on the dendrites of neurons in a somatosensory part of the midbrain tectum. Other somatosensory axons from the dorsal column nuclei bypass the midbrain and terminate on the dendrites of neurons in a somatosensory nucleus in the dorsal thalamus. Neurons in the somatosensory part of the midbrain also give rise to axons that pass rostrally and terminate on the dendrites of neurons in a second somatosensory nucleus in the dorsal thalamus. Neurons in each of the two dorsal thalamic somatosensory nuclei give rise to axons that pass into the telencephalon via the forebrain bundles and

Motor Systems

Complex control mechanisms for motor responses derive from neurons in the motor pallial areas of the telencephalon, and/or from neurons in other dorsally lying structures, such as the roof of the midbrain and the cerebellum. Motor responses are also regulated by a number of structures including the **striatum**, also known as the **basal ganglia**, in the ventrolateral part of the telencephalon [Fig. 3-7(D)] and nuclear areas within the hindbrain. Mammals have motor neurons in the dorsal pallium of the telencephalon that give rise to axons that terminate on the dendrites of neurons within the striatum. In turn, neurons within the striatum give rise to axons that pass caudally and terminate within a number of nuclei in the brainstem, including a nucleus in the diencephalon. Neurons in the latter nucleus give rise to axons that terminate on the dendrites of neurons within the midbrain tectum.

Other neurons within the motor part of the dorsal pallium (long-axon interneurons) pass caudally via the same major bundles in which sensory axons ascend: the forebrain bundles. These axons collectively form a tract that is rather like a major interstate highway. They pass caudally to synapse on the dendrites of neurons within nuclei in the midbrain and the brainstem and, in some cases, directly on the dendrites of neurons in the spinal cord. The midbrain tectum also gives rise to axons that pass caudally in a tract called the **tectospinal tract** and terminate on the dendrites of neurons in brainstem motor nuclei and in the spinal cord. Motor nuclei of the cerebellum similarly contain neurons that give rise to axons that pass ventrally to terminate on the dendrites of neurons within brainstem nuclei. Neurons in the various brainstem motor nuclei give rise to axons that pass caudally and terminate on the dendrites of neurons in the spinal cord. The reticular formation of the brainstem is composed of a number of different nuclear areas that also are involved in these descending motor pathways.

DEVELOPMENT OF THE BRAIN

During the embryological development of the brain from the neural tube, the rostral part of the brain flexes ventrally [Fig. 3-8(A)]. A transverse, ventral fold develops on the ventral surface of the tube in the position where the pituitary gland will form. A pair of lateral bulges in the rostral part of the forebrain forms the cerebral hemispheres of the telencephalon. More caudally, the eyes grow out of the diencephalon, and the pineal gland develops in the dorsal part of the diencephalon [Fig. 3-8(B)].

The midbrain lies caudal to the ventral fold in the neural tube. Paired bulges in the roof of the midbrain expand to form the optic tecti (plural of tectum), or roof of the midbrain, while