

more neuronal tracts developed between the spinal cord and brain.

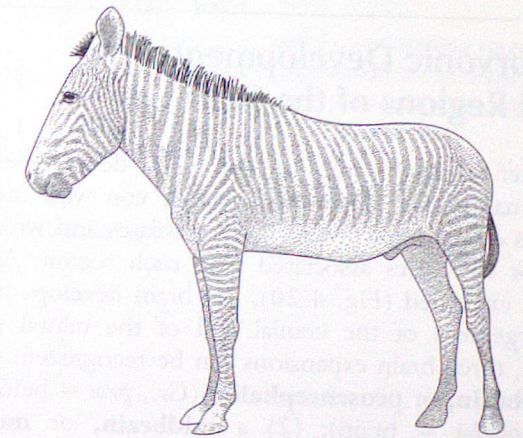
12. The dorsal and ventral roots of spinal nerves form separate nerves in lampreys, but these unite in all gnathostomes. Sensory neurons always enter through dorsal roots of spinal nerves, and somatic motor ones always leave through the ventral roots. Visceral motor neurons leave through the dorsal roots of lampreys but have shifted during evolution, so all lie in the ventral roots of amniotes.
13. The cranial nerves of gnathostomes, such as sharks, can be sorted into three groups, each with distinctive characteristics: (1) the terminal, olfactory, and statoacoustic nerves and lateral line nerves are unique to the head and contain only special somatic sensory neurons; special visceral sensory (= gustatory) fibers from taste buds may constitute what were phylogenetically separate cranial nerves but that now travel with other nerves; (2) the oculomotor, trochlear, abducens, and occipital nerves supply somatic motor neurons to the extrinsic ocular, epibranchial, and hypobranchial muscles; they rarely contain other types of neurons and appear to be serially homologous to the ventral spinal nerves of lampreys; and (3) the trigeminal, facial, glossopharyngeal, and vagus nerves supply somatic motor neurons to the branchiomic muscles, and they also contain a variety of sensory neurons; they appear to be serially homologous to dorsal spinal nerves of lampreys.
14. The heads of ancestral vertebrates probably contained eight segments. The nerves we have interpreted as serially homologous to ventral and dorsal cranial nerves can be related to these segments.
15. The optic nerve does not properly belong to any of the groups of cranial nerves because it is a brain tract.
16. During the course of gnathostome evolution, few changes occurred in the ventral cranial nerves other than the emergence of the occipital nerves from within the skull as the hypoglossal nerve (XII). Major changes occurred in other cranial nerves. For example, amniotes lost the lateral line nerves. The facial and glossopharyngeal nerves evolved visceral motor neurons (autonomic) to tear, salivary, and other glands of the head. The vagus nerve lost most of its somatic motor neurons apart from those to the larynx. The accessory branch of the vagus nerve also became separated as a distinct nerve, known as the accessory nerve (XI).
17. The autonomic nervous system is the motor system for gut, heart, and other visceral muscles and for exocrine glands. It is characterized by motor relays located in peripheral ganglia, where some divergence and integration (i.e., processing) of impulses occur.
18. The autonomic nervous system of amniotes consists of separate sympathetic and parasympathetic divisions and an enteric division, which is confined to the gut wall. Most visceral organs, including the enteric system, receive both sympathetic and parasympathetic innervation. In general, sympathetic innervation prepares an animal for fight or flight, whereas parasympathetic innervation prepares an animal to rest and digest. The sympathetic and parasympathetic divisions exit from different parts of the CNS and relay at different sites. The autonomic nervous system is poorly developed in hagfishes, lampreys, and chondrichthyans, but it is more evident in bony fishes and amphibians.

REFERENCES

All references on the nervous system are collected at the end of Chapter 14.

14

The Nervous System II: The Brain



PRECIS

After examining the development of the brain and its meninges, we will consider the structure and organization of a fish brain as an example of a craniate brain that displays the basic organizational features of all craniates. We will then summarize the major evolutionary changes seen in amphibians and amniotes before considering some important mammalian pathways.

OUTLINE

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- Focus 14-2** *Brain Size*

Craniates differ from early chordates in having a markedly enlarged brain; however, a brain is not a completely new craniate feature. We find a well-developed brain in many protostomes, including the octopus and arthropods. Although cephalochordates, the sister group of craniates, do not have a grossly visible brain, cell groups have been identified in the cranial end of their neural tube that appear to be homologous to groups of cells found in the craniate forebrain, midbrain, and hindbrain. Moreover, the embryonic development of these cell groups in cephalochordates and craniates is regulated by homologous genes. Indeed, homologues of these same genes regulate brain development in protostomes (see Butler, 2000, for a review). Although an incipient brain was present in the early chordate ancestors of craniates, it does enlarge greatly during craniate evolution—a process called **encephalization**.

We may never be certain as to all of the factors that led to this enlargement, but increasing activity certainly played a major role. The front of the body of an active animal (and we believe that ancestral craniates were far more active than their early chordate ancestors) is the first part of the body to encounter environmental changes.

Ancestral craniates probably evolved or increased the concentration of olfactory receptors, gustatory receptors, photoreceptors, neuromasts of the lateral line and ear, and probably electroreceptors on their heads. Processing the input from these receptors and directing the activity of segmental and branchial structures would require a larger aggregation of neurons and the enlargement of the rostral end of the neural tube.

Embryonic Development and Regions of the Brain

A brief consideration of the embryonic development of the mammalian brain will acquaint you with the regions of the brain found in all craniates and with the major structures associated with each region. As we have explained (Fig. 4-20), the brain develops by an enlargement of the cranial end of the neural tube. First, three brain expansions can be recognized: (1) a **forebrain**, or **prosencephalon** (Gr., *pros* = before + *enkephalos* = brain); (2) a **midbrain**, or **mesencephalon** (Gr., *mesos* = middle); and (3) a **hindbrain**, or **rhombencephalon** (Gr., *rhombos* = lozenge).

The prosencephalon first gives rise to the **optic vesicles**, which will form the retina of the eye (Fig. 4-20), and to a midventral **infundibulum**. The pituitary gland, or **hypophysis**, attaches to the infundibulum (Fig. 14-1A); and its posterior portion, the **neurohypophysis**, develops as an outgrowth of the infundibulum. Another brain region, the **telencephalon** (Gr., *telos* = end), develops soon after as a pair of rostralateral extensions from the prosencephalon (Fig. 14-1B). These differentiate into the paired **cerebral hemispheres**, which together constitute the **cerebrum**, and into the paired **olfactory bulbs** (Fig. 14-1C). Paired chambers known as the **lateral ventricles** lie in the cerebral hemispheres and may extend into the olfactory bulbs (Fig. 14-2). Brain ventricles are lined by the **ependymal epithelium**, as are all cavities within the central nervous system.

The rest of the prosencephalon remains in the midline and differentiates as the **diencephalon** (Gr., *dia* = between). Its cavity, the **third ventricle**, remains connected to the lateral ventricles by the paired **interventricular foramina of Monro** (Fig. 14-2). The lateral walls of the diencephalon thicken to form the **thalamus** (Gr., *thalamos* = inner chamber); the floor becomes the **hypothalamus**; and the roof, most of which remains very thin, is the **epithalamus**. As they enter the brain, the optic nerves partially decussate, forming an **optic chiasm**¹ just rostral to the hypothalamus. The median eye complex, which is present in some craniates, develops from a part of the epithalamus called the **epiphysis**.

The mesencephalon remains undivided. A narrow **cerebral aqueduct of Sylvius** passes through it and

connects the third ventricle with the **fourth ventricle** in the rhombencephalon. The dorsal part of the mesencephalon, known as the **tectum** (L., *tectum* = roof), enlarges as a pair of **optic lobes** in nonmammalian vertebrates (Fig. 14-2) and a more deeply situated and more caudal pair of auditory lobes called the **tori semicirculares**. The tectum often contains an extension of the cerebral aqueduct called the **optic ventricle**. The mesencephalic tectum of mammals similarly differentiates into the paired **superior colliculi** (visual) and **inferior colliculi** (auditory; Fig. 14-1C). The ventral part of the mesencephalon is known as its **tegmentum** (L., *tegmentum* = covering).

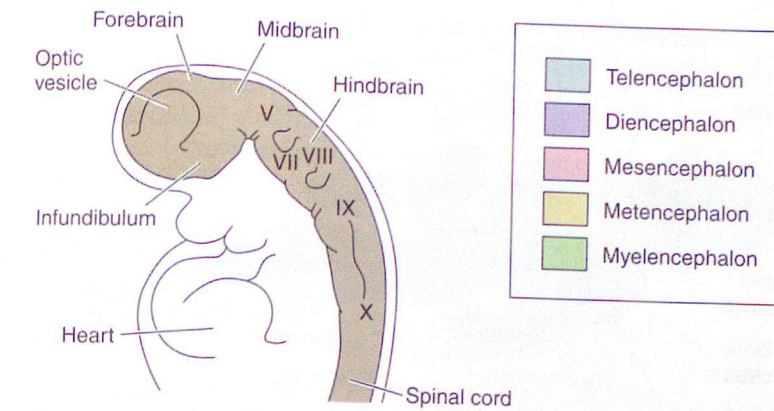
The rostral one third of the roof of the rhombencephalon differentiates into a **metencephalon** (Gr., *meta* = after), of which the most conspicuous part is the **cerebellum**. During the embryonic development of birds and mammals, neuroblasts migrate from the cerebellum into the ventral part of the rhombencephalon and differentiate into pontine and other nuclei, which relay information between the cerebrum and cerebellum, and a conspicuous band of transverse fibers. This region is known as the **pons** (L., *pons* = bridge; Fig. 14-1C). A pons does not differentiate in reptiles and anamniotes, so all of the rhombencephalon, except for the cerebellum, forms the fifth brain region, the **myelencephalon**, which leads to the spinal cord (Gr., *myelos* = marrow, or spinal cord). The myelencephalon forms the adult **medulla oblongata** and contains the fourth ventricle.

The major divisions of the brain lie along the same horizontal plane in most adult vertebrates (Fig. 14-2). Brain regions become folded on one another in birds and mammals because the head extends forward from an upward-curving neck. **Mesencephalic**, **cervical**, and **pontine flexures** develop sequentially in the positions shown in Figure 14-1B.

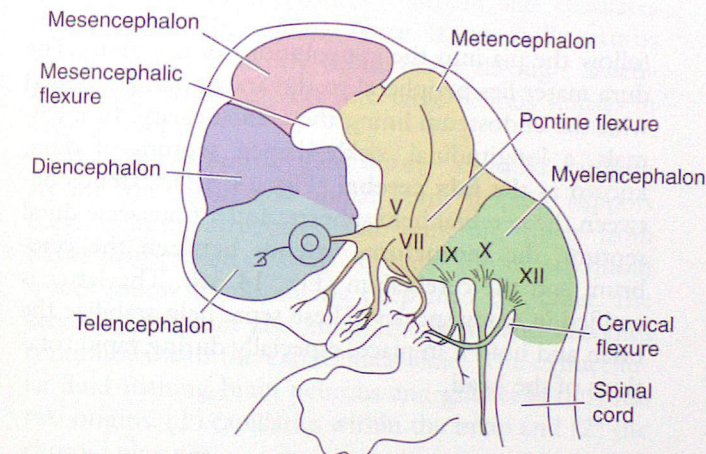
The Meninges and Cerebrospinal Fluid

The brain and spinal cord become covered by one or more layers of connective tissue that develop partly from mesoderm and partly from neural crest cells. These are the **meninges** (sing., *meninx*; Gr., *meninx* = membrane). Fishes have a single layer, the **primitive meninx**, which closely invests the central nervous system. Strands of connective tissue extend from it to a layer of connective tissue that lines the cranial cavity and vertebral canal. A gelatinous material fills the space between the primitive meninx and the surrounding cartilage and bone. Cerebrospinal fluid circulates

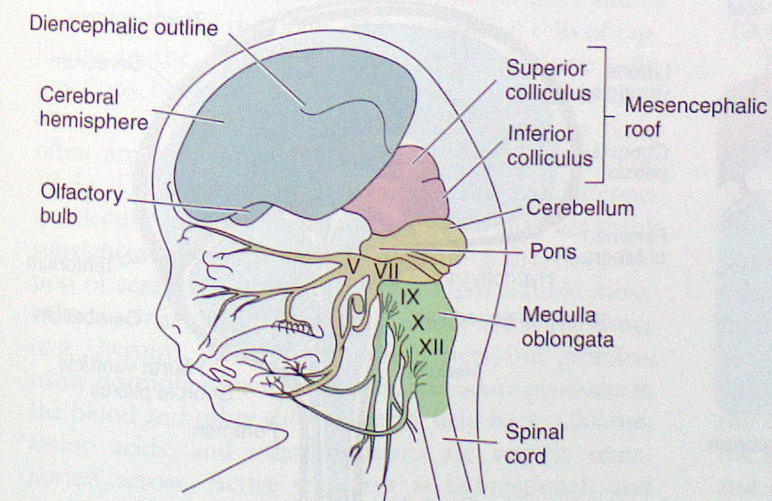
¹The Latin term for this structure is *chiasma opticus*. This often is partly anglicized as "optic chiasma"; "optic chiasm" is the full anglicization of the term.



A. Human brain at 3 mm long



B. Human brain and cranial nerves at 7 weeks' gestation



C. Human brain and cranial nerves at 3 months' gestation

FIGURE 14-1

A-C, Diagrams in lateral view of three stages in the development of the human brain, showing the differentiation of the principal brain regions. (After Corliss.)

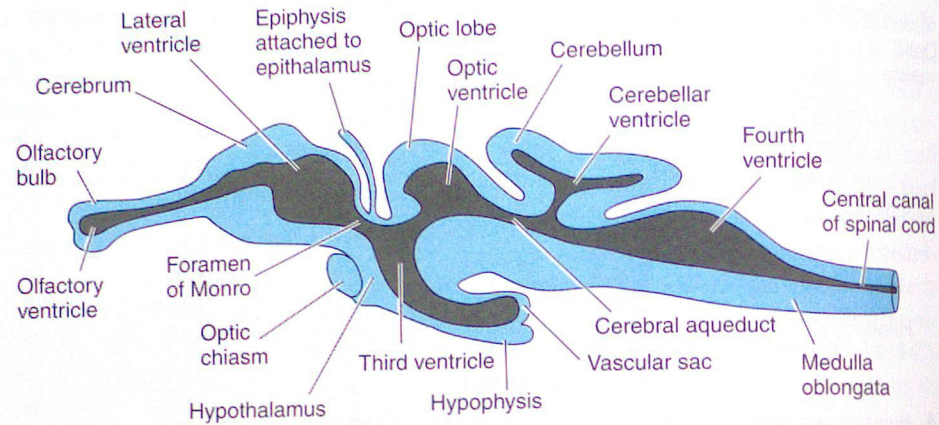
in the cavities within the central nervous system, and some is secreted into spaces around it. In amphibians and reptiles the primitive meninx is divided into a dense **dura mater** (L., *dura mater* = hard mother), which unites with the connective tissue lining the cranial cavity, and a more delicate and vascular **sec-**

ondary meninx, which covers the brain and spinal cord.

Mammals and birds have three meninges because the secondary meninx has differentiated into two layers (Fig. 14-3A). A **pia mater** (L., *pia mater* = tender mother) closely invests the surface of the central ner-

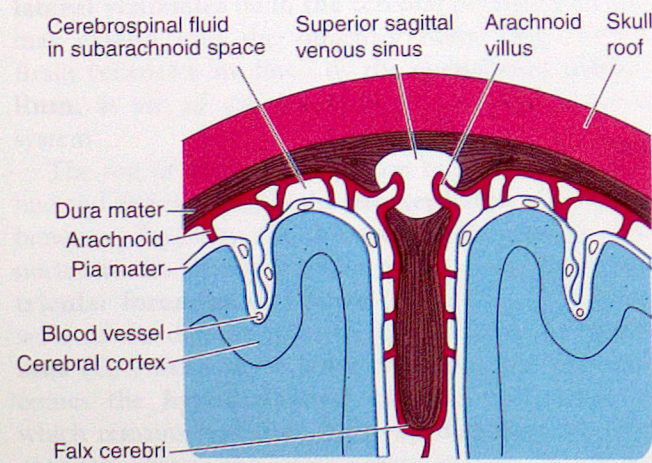
FIGURE 14-2

A sagittal section of the brain of a dogfish, showing the major parts of the brain and its ventricular system. (After Walker and Hemberger.)



vous system and follows all of the convolutions of the brain. An **arachnoid** (Gr., *arachne* = spider + *eidōs* = form) lies peripheral to the pia mater and crosses many of the crevasses on the brain surface. Strands of connective tissue extend like spider webs from the arachnoid across a **subarachnoid space** and attach to the pia mater. The cerebrospinal fluid that circulates around the central nervous system of birds and mammals is confined to the subarachnoid space and cavities of the brain. Many small blood vessels lie in the strands of the arachnoid and over the pia mater and

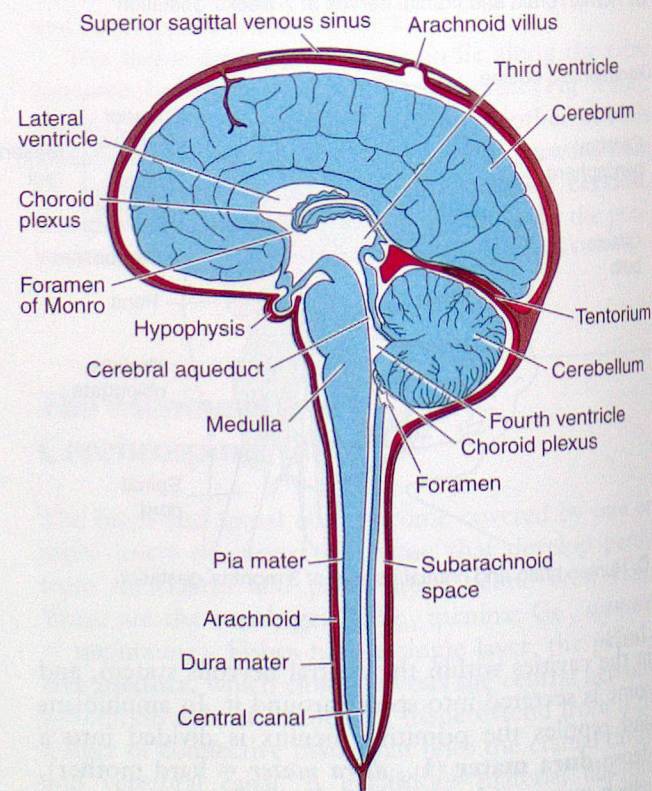
follow the pia into the convolutions of the brain. The dura mater lies peripheral to the arachnoid. It is fused with the endosteum lining the cranial cavity. In mammals, a longitudinal, sickle-shaped septum of dura, known as the **falx cerebri** (Fig. 14-3A), extends between the cerebral hemispheres, and a transverse dural septum, the **tentorium**, extends between the cerebrum and the cerebellum (Fig. 14-3B). The latter is ossified in many species. These septa help stabilize the brain and hold it in place, especially during rapid rotations of the head.



A. Transverse section through skull roof, meninges, and cerebrum

FIGURE 14-3

The meninges and cerebrospinal fluid in the mammalian central nervous system. A, The meninges as seen in a transverse section through the center of the dorsal part of the cerebrum. B, A sagittal section of the central nervous system showing the choroid plexuses, the meninges, and the circulation of the cerebrospinal fluid. (From Walker and Hemberger.)



B. Sagittal section of central nervous system

Part of the wall of many ventricles is very thin, consisting only of the ependymal epithelium and the adjacent vascular meninx. An area of this type is known as a **tela choroidea**. Vascular tufts extending from the tela choroidea form **choroid plexuses**, which secrete the cerebrospinal fluid. The choroid plexuses extend into the ventricles in mammals, but in anamniotes and reptiles, some balloon into the space around the brain. Mammals have choroid plexuses in the floor of the lateral ventricles and in the roofs of the third and fourth ventricles (Fig. 14-3B). Cerebrospinal fluid flows toward the fourth ventricle, partly by secretion pressure and partly by the action of cilia on the ependymal cells. Cerebrospinal fluid escapes through several pores in the thin roof of the fourth ventricle and circulates slowly in the subarachnoid space. It eventually returns to the blood, primarily by diffusion through **arachnoid villi**, which project into large venous sinuses in the dural septa.

The cerebrospinal fluid forms a liquid cushion around the brain and spinal cord, helping support these delicate structures and buffering them from blows to the head or body. Because the subarachnoid spaces follow blood vessels deep into the brain, the cerebrospinal fluid also enters the brain and becomes continuous with the extracellular fluid. The extracellular fluid bathing brain neurons and glial cells thus has two origins: (1) capillaries within the brain and (2) the choroid plexuses.

Blood-brain barriers exist between the extracellular fluids and the blood in the choroid plexuses and in the capillaries of the brain. The endothelial cells of capillaries in the choroid plexuses and brain have tight junctions between them and are less permeable than are other capillaries, and the capillaries in the brain often are surrounded by feet of astrocyte cells (Fig. 13-5). The choroid plexuses and cerebral capillaries act as selective barriers and active transport sites for many substances, thereby carefully regulating the composition of cerebral extracellular fluid. Lipid-soluble molecules, such as oxygen, carbon dioxide, and some drugs (e.g., heroin), easily cross these barriers; but proteins, many hormones, many enzymes, and waste products in the blood and other substances are held back. Glucose, amino acids, and other nutrients are actively transported across. Active transport is bidirectional, and many waste products and metabolites are removed in this way.

Because the brain has no lymphatic system, the cerebrospinal fluid also acts as a subsidiary drainage system for the brain, carrying off excess water, carbon dioxide, and metabolites, which are discharged into the blood at the arachnoid villi. The cerebrospinal fluid makes an important contribution to brain nutrition and drainage.

The Fish Brain: A Prototype for Vertebrates

Neurons are the functional and structural units of the nervous system, so their organization within the brain and their interconnections are of considerable importance. Many techniques to trace neurons and to determine functions of parts of the brain are now available (Focus 14-1). Although less is known about the organization and functions of the brains of fishes than of the brains of mammals, neuroanatomists have learned a great deal in recent years. We begin by discussing the structure and organization of the brains of fishes. Fish brains are far less complex than are those of amniotes, so you can become acquainted with the basic organization of the brain that is common to all craniates. This will serve as a point of departure for tracing major trends in the evolution of the brain.

The Hindbrain

The Medulla Oblongata and Reticular Formation

The hindbrain of fishes consists of the medulla oblongata and the cerebellum (Fig. 14-4). The medulla oblongata is essentially a forward extension of the spinal cord. It contains nuclei that receive the sensory input of cranial nerves attaching to it and gives rise to the axons of motor neurons leaving via these nerves (the trigeminal nerve, V, through the vagus nerve, X; Fig. 13-8).

The sensory nuclei of the hindbrain receive fibers from general cutaneous receptors, taste buds, the lateral line receptors (including electroreceptors), vestibular receptors (equilibrium and acceleration), and sound receptors. In carp, minnows, and catfish, which have extensive taste receptors on the body surface, the sensory nuclei that receive this information are enormous and form large **facial** and **vagal lobes** on the medulla oblongata (Fig. 14-4D). The **octavolateralis nuclei**, which receive sensory input from the lateral line organs and ear, also may form a pair of bumps on the dorsal surface of the medulla near the entrance of the statoacoustic or octaval nerve (cranial nerve VIII) and lateralis nerves. Most of the somatic motor nuclei supply the branchiomeric muscles of the jaws and branchial arches, but some supply epibranchial and hypobranchial muscles. Visceral motor nuclei of fishes send preganglionic parasympathetic fibers through the oculomotor nerve to the eyeball and through the vagus nerve to postcranial organs.

Although some of the integration of medullary functions occurs through direct connections between the sensory and motor nuclei, most occurs through the

FOCUS 14-1

Determining Central Nervous System Pathways and Functions

The spinal cord and brain are vital and complex organs. Investigators can see gross changes that have occurred during evolution by dissecting the CNS of representative vertebrates, but these changes tell us little about functions. To begin to understand function, it is first necessary to make a "road map," or "wiring diagram," of neuronal organization within the CNS. This will show us the pathways neurons take and give us some indication of which parts of the CNS may influence other parts. Many techniques have been used. Particularly important ones involve the injection into parts of the spinal cord or brain of isotopically labeled amino acids (e.g., tritiated thymidine), horseradish peroxidase, or other materials. These are taken up by neurons at synapses or other sites such as the cell body. Depending on the nature of the material, or proteins incorporating the labeled amino acids, the injected material will travel forward along an axon to its termination (**anterograde tracing**) or backward into the cell body (**retrograde tracing**), or both. Some substances will cross one or more synapses and label an entire pathway. At a later time the experimental animal is sacrificed, microscopic sections are made through parts of the spinal cord and brain, and neuronal tracts or nuclei containing the markers can be identified.

One of the most exciting developments in neuroanatomy in recent decades has been the introduction of dyes sometimes called intercalating dyes because they intercalate into the cell membrane of neurons. Examples include the materials known as Dil and DiO, which are fluorescent and thus can be detected using fluorescence

microscopy even when they are present in very small concentrations. The methodology for tract tracing with Dil is very straightforward and can be used on preserved specimens. A small crystal of the dye is placed adjacent to the neurons to be traced at either their terminal arborizations or their cell bodies. The specimen is left for some period of time during which the dye intercalates into the neuronal cell membranes and becomes distributed throughout the length of the neurons. At a later time, sections of any part of the pathway can be studied using fluorescent microscopy to visualize the neurons carrying the dye. This method has made it possible to investigate neuronal tracts in preserved specimens, or those species that cannot be easily maintained for laboratory study. This opens up the possibility of collecting neuroanatomical information for a much wider selection of vertebrates.

Neurobiologists can refine the "wiring diagrams" and gain some indications of function by electrophysiological experiments. In one type of experiment, a stimulating electrode activates a nerve or brain center. A recording electrode is used to penetrate the brain in regions likely to be activated, stopping at approximately 100- μm intervals to determine whether neurons in that region can be driven by the stimulus, that is, to detect **evoked potentials**. In another type of experiment, a stimulating electrode is rigidly mounted to the skull and is advanced in small steps into the region being investigated, a stimulus is given, and the response of the animal is monitored.

Neurologists first learned a great deal about human brain function by observing the changes in behavior

caused by trauma or pathological lesions and then locating the damaged area in postmortem examination. The French surgeon Pierre Paul Broca, as an example, performed an autopsy in 1861 on a patient with a severe speech defect. The patient could speak isolated words but could not speak grammatically or in full sentences. A lesion was found in a cerebral area that is now known as Broca's area (p. 493). Neurosurgeons have determined other functions during surgical procedures, which often are done with the patient under local anesthesia because the brain contains no pain receptors. As a surgeon probes for a tumor, he or she can observe a twitch of a muscle or other changes in behavior, and the patient can comment on sensations.

Many additional brain functions have been determined by neurobiologists in experimental animals by observing the changes in behavior that result from the microsurgical destruction of areas by cautery, and the local administration with micropipets of neurotransmitters and other drugs. Immunocytological procedures also are being used to localize neurons containing particular neurotransmitters.

Many procedures for neuronal tracing and for studying functions are of necessity invasive and lead to the sacrifice of experimental animals. As we discussed above, tract tracing can now be done on preserved material.

Recently, advancements in imaging techniques have allowed neurologists to explore the structure and function of a living brain without using disruptive invasive procedures. A particularly interesting example is

positron emission tomography (PET), which produces computer-generated images of a series of planes or sections through a brain. Unlike X-ray computerized tomography (CT scans), which identifies different densities in the brain, positron emission tomography shows the distribution of isotopes that emit radiation in the form of positrons. A positron-emitting isotope can be bound to an important biological compound and given to a subject, and various biological processes can be explored. For example, an analogue of glucose, which can be taken up by cells but not leave them, can be labeled with a radioactive isotope and given to a subject. Because particularly active cells take up the analogue of glucose, investigators can compare the sites and degree of glucose utilization of a person at rest and then performing various tasks. In this way, investigators have determined which parts of the brain become active when the subject is viewing an object, listening to a sound, memorizing something, or doing other things. Neurologists are learning a great deal about the internal organization of the central nervous system and its functions, but our knowledge is far from complete.

As humans, we have benefited tremendously from the insights that tract tracing and studies of CNS functions have brought to the study of human health and disease; as biologists, we benefit by understanding more completely the nervous system and biology of other vertebrates. Studies of tract tracing and CNS functions promise to continue to reveal important new insights about comparative vertebrate anatomy.

reticular formation. The reticular formation is essentially a rostral extension into the medulla oblongata and mesencephalic tegmentum of the deeper layers of the dorsal horn of the spinal cord (Fig. 14-5). It performs the same functions in the brainstem that these layers do in the spinal cord, namely receiving sensory inputs and serving to integrate complex intersegmental reflexes.

For descriptive purposes, the reticular formation often is divided into ascending and descending parts. The ascending reticular system receives sensory or afferent impulses from the lower parts of the body via **spinoreticular tracts** and sends them forward to higher brain centers, including the cerebellum, optic tectum, and hypothalamus (Fig. 14-5A). Other parts of the ascending reticular formation, at least in mammals, reach the cerebrum and affect processes such as sleep, arousal, and attention. Attention is the ability to focus on a particular task by eliminating extraneous signals.

Descending or efferent impulses reach the reticular system from the striatum, tectum, and cerebellum (Fig. 14-5B). Descending pathways from the reticular system are the **reticulobulbar tract** to motor neurons in the brainstem and the **reticulospinal tract** to motor centers in the spinal cord. Through these tracts, the reticular formation coordinates the activity of neuron pools, which are called **central pattern generators**, in the brainstem and spinal cord that control rhythmic motor patterns. These patterns involve eye movements, feeding and swallowing, breathing, heart rate, swimming, and generating electric discharges in electric fishes. Swimming and eye movements, for example, can be directed toward food. In fishes and many nonmammalian vertebrates, the reticulospinal tract is the major pathway by which the brain can affect lower parts of the body because no direct pathways from the cerebrum exist.

The descending reticular formation of lampreys, teleosts, and many amphibians includes a single pair of

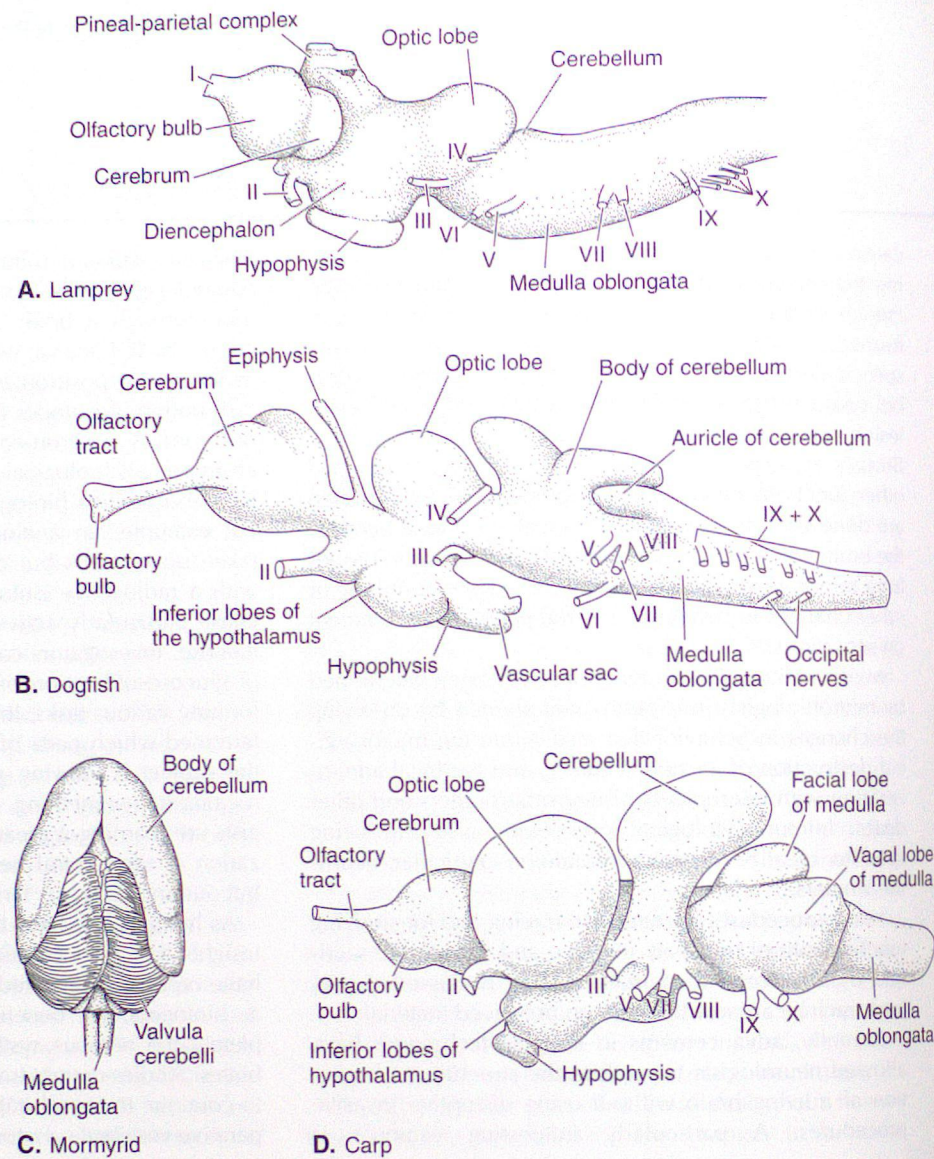
giant **Mauthner cells**, the large, myelinated axons of which decussate and descend the full length of the spinal cord, giving off numerous branches to the motor neurons. Because the speed of a nerve impulse is proportional to axon diameter, transmission on Mauthner axons is very rapid. The system mediates rapid escape reactions, such as rapid flexion of the trunk in aquatic species or rapid extension of the hind legs in frogs.

The Cerebellum Hagfishes have no trace of a cerebellum, and that of lampreys is rudimentary at best, consisting primarily of part of the octavolateralis nucleus. It probably is comparable to part of the auricles of the cerebellum of sharks (see subsequent discussion). The cerebellum of other fishes is quite large and can be divided into a median **body of the cerebellum** and a pair of lateral **auricles of the cerebellum** (Fig. 14-4B). Actinopterygian fishes have in addition an expanded part of the body of the cerebellum called the

valvula cerebelli (Fig. 14-4C). The auricles receive input primarily from the vestibular parts of the ear and the lateral line; the body of the cerebellum receives inputs from all sensory systems throughout the body, with the exception of olfactory and possibly gustatory receptors. Proprioceptive input is extensive. The body of the cerebellum also has connections with other parts of the brain, including visual and auditory centers. Considerable integration occurs among the three layers of cells that form the cerebellar surface. Its efferent fibers go first to deep neurons within the cerebellum (Fig. 14-5B). Efferents from these cells connect with the reticular formation, which, in turn, affects motor centers in the brainstem and spinal cord.

The connections of the cerebellum allow it to monitor the position and movements of the body; muscle activity; and the visual, auditory, spatial, and electric "landscape" about the fish. It plays an important role in coordinating muscle activity, including eye movements, ensuring that the degree, duration, and timing

FIGURE 14-4
Representative fish brains.
A, A lamprey (lateral view).
B, A dogfish (lateral view).
C, A mormyrid (dorsal view).
D, A carp (lateral view).
(C, After Hopkins;
D, after Bond.)



of muscle contraction occur with reference to the position and movements of the fish. The cerebellum also participates in learned motor behaviors.

The cerebellum is enormous in mormyrid fishes, which have highly developed electroreceptive and electrolocation systems. The cerebellum is so large that in a dorsal view, it covers the entire brain except for a portion of the medulla oblongata (Fig. 14-4C). Its valvula cerebelli is highly folded, providing a large surface for an increased number of neurons. If unfolded, it would be over ten times the length of the fish.

The Midbrain

The Tegmentum Because the floor or **tegmentum** of the midbrain is a part of the brainstem, much of its structure and many of its functions are similar to those of the medulla oblongata. The tegmentum contains the midbrain part of the reticular formation, part of the nucleus of the trigeminal nerve, and the nuclei of the oculomotor and trochlear nerves (see Fig. 13-8).

Beyond this, the tegmentum includes nuclei in lampreys and all jawed fishes that act as a **midbrain locomotor region**, or **command generator**. These initiate coordinated, purposeful sequences of locomotor movements, particularly of the paired fins, or limbs in tetrapods, that are sent to central pattern generators in the spinal cord. Although lacking in lampreys, the tegmentum of some fishes also contains a **red nucleus**, which receives projections from the cerebellum. The red nucleus connects with the spinal cord by a **rubrospinal tract** and is another way by which the cerebellum affects locomotor movements. The red nucleus and rubrospinal tract are better developed in tetrapods (see Fig. 14-12).

The Midbrain Roof Most of the midbrain roof of fishes forms a conspicuous pair of bulges called the **optic tectum** or **optic lobes** (Fig. 14-4B and D). Caudally, the roof contains a second pair of deeply seated centers, each called a **torus semicircularis** (L., *torus* = knot, bulge), which comprise the **auditory tectum**. The torus semicircularis receives ascending auditory,

lateral line, and electroreceptive fibers and relays impulses forward (Fig. 14-6). The size of the torus semicircularis correlates closely with the importance of auditory and both the mechanoreceptive and electroreceptive components of the lateral line system in the lifestyle of the fish.

The optic tectum is a very important integrating center in fishes, comparable in some respects to the cerebrum of amniotes. Excepting galeomorph sharks and rays, which have a large cerebrum, the optic lobes are usually the largest part of the brain. Its neurons are arranged in layers. Most of the fibers from the retina terminate here in the most superficial layers of neurons (Fig. 14-6); a few end in the dorsal thalamus. The inputs form a precise (although inverted) spatial map of the visual field. Although the primary input is visual, the optic tectum is multisensory and also receives fibers in deeper layers from the auditory, somatosensory, and electroreceptive systems. These too form spatial maps, which are in register with the visual map. That is, a location of the visual map would correspond to one in the auditory map. Descending fibers lead to tegmental motor centers and to the reticular formation (Fig. 14-5B). The connections of the tectum allow a fish to localize stimuli in space, a falling food particle, for example, and direct eye and locomotor movements toward it.

The Diencephalon

The Epithalamus The diencephalon is the caudal part of the forebrain, and it can be subdivided into an **epithalamus** dorsally, a **thalamus** laterally, and a **hypothalamus** ventrally (Fig. 14-2). The epithalamus contains a small center, the **habenula**, which has connections to the telencephalic limbic system (see subsequent discussion). The habenula appears to serve as an interface for limbic and motor system pathways. The **pineal-parietal complex** consists of the photoreceptive median eyes discussed earlier (Chapter 12), or an epiphyseal stalk, or the pineal endocrine gland (Chapter 15). The major function of this complex is the regulation of cyclic behaviors in reference to the diurnal and seasonal cycles of day length.

FIGURE 14-5
Lateral views of important neuronal pathways in the brain of fishes, based on a shark. In this and similar diagrams, nuclei and other areas of gray matter are shaded. A, Afferent pathways from sensory centers and the reticular formation to higher brain centers. B, Efferent pathways from higher brain centers to the reticular formation and motor centers.

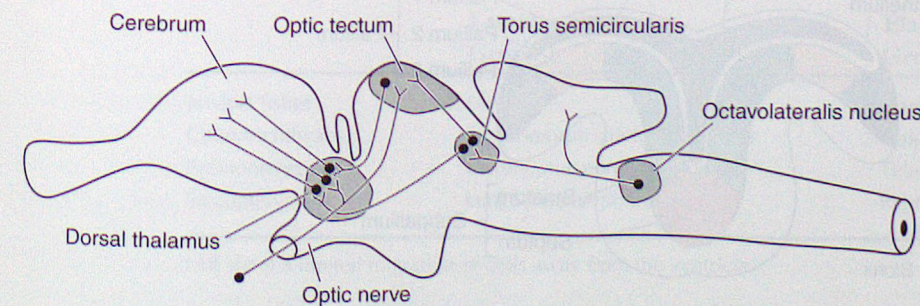
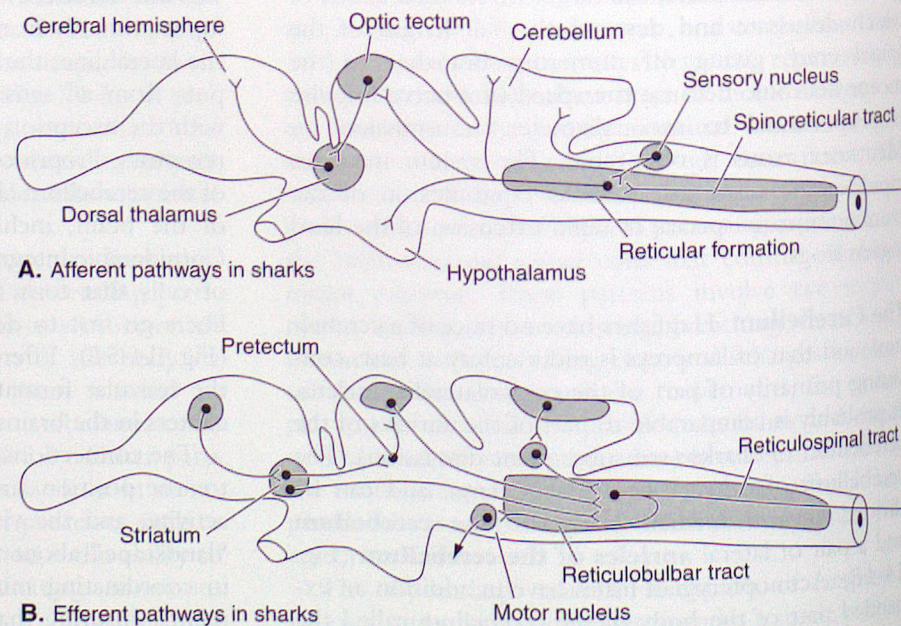


FIGURE 14-6
Lateral view of major optic and auditory pathways in a shark.

The Thalamus The thalamus is the wall of the brain lateral to the third ventricle. Most of it forms a group of **dorsal thalamic nuclei**, but a small ventral thalamus, or **subthalamus**, is closely associated with a cerebral motor center called the striatum (see subsequent discussion). Dorsal thalamic nuclei relay ascending somatosensory, visual, and auditory and lateral line information to the telencephalon, and they also have other reciprocal interconnections with the telencephalon (Figs. 14-5A and 14-6). The evolution of the dorsal thalamus is closely linked to that of the telencephalon. Dorsal thalamic nuclei occur in all vertebrates, but they are not as large and complex in fishes and amphibians as in amniotes. Uniquely, fishes have additional diencephalic nuclei that relay ascending sensory information to the telencephalon, including ventral parts of the thalamus, the hypothalamus, and a more caudal region called the posterior tuberculum.

The Hypothalamus Heart rate, respiratory rate, and some other visceral activities are coordinated in the reticular formation, but the hypothalamus is the major center for visceral integration. It is particularly important for activity mediated through the autonomic nervous system and through many of the endocrine glands. The structure and function of the hypothala-

mus are best known from studies on amniotes, but many of these features and activities have been identified in fishes. Although the hypothalamus has connections that enable it to receive most types of sensory information, its primary sensory inputs are gustatory and other visceral sensory inputs relayed from the reticular formation (Fig. 14-5A), and special somatic sensory olfactory signals relayed from parts of the telencephalon. Some of its cells also respond directly to the levels of glucose, water, salts, hormones, and other factors in the blood. Interacting with the limbic system (see subsequent discussion), the hypothalamus of all vertebrates affects behaviors essential for the survival of the individual and the species. Individual survival includes finding and obtaining the appropriate amount of food and water and regulating gut movements and digestion, blood sugar levels, and water and salt balance. The hypothalamus also regulates periods of rest and activity. Species survival includes many reproductive behaviors, such as courtship, mating, and parental care. Some parts of the hypothalamus have a stimulating, and others an inhibitory, effect. It controls many functions directly via efferent neurons to motor centers in the thalamus, reticular formation, and spinal cord. Other functions are controlled indirectly via its influence over the secretion of the hypophysis (Chapter 15).

FIGURE 14-7

Transverse sections through the cerebral hemispheres showing the two types of hemispheres found in vertebrates. Dorsal to top. A, The evaginated hemispheres as seen in a cartilaginous fish with a laminar distribution of gray matter. B, The everted hemispheres as seen in an actinopterygian fish (Bichir) with a laminar distribution of gray matter. Different regions of gray matter are shown in color.

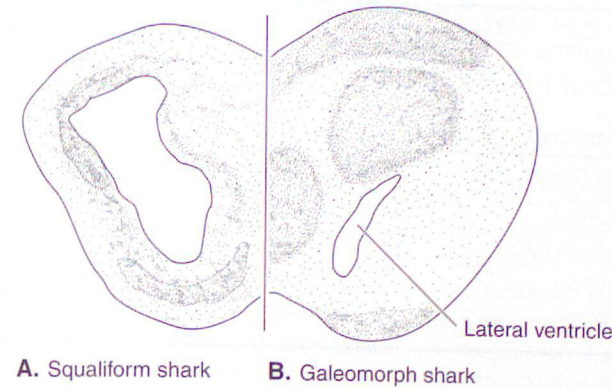
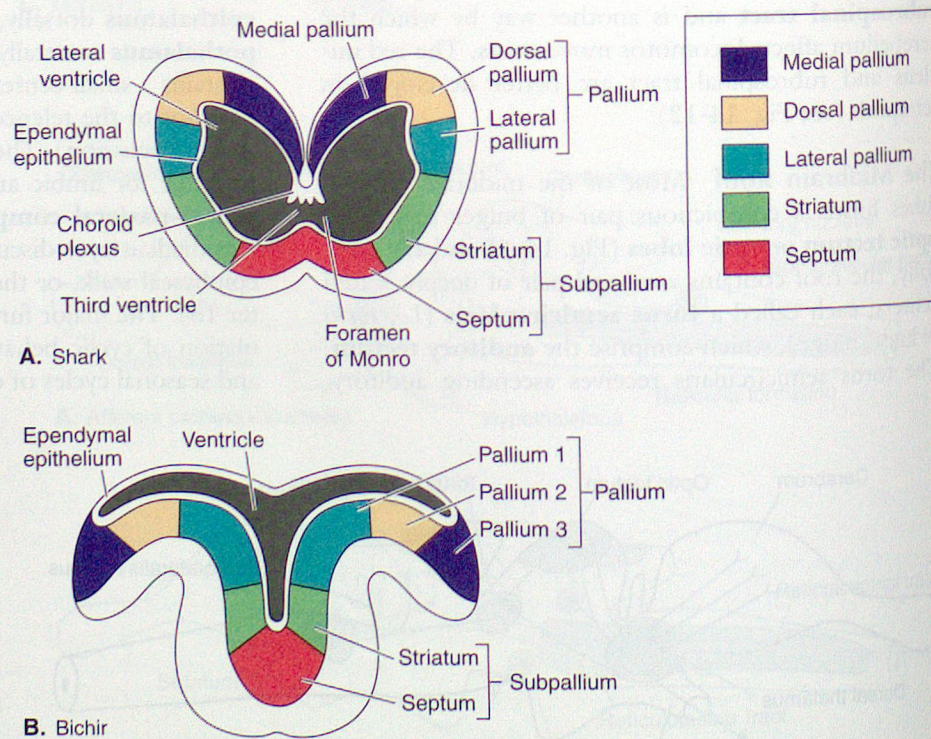


FIGURE 14-8

Transverse sections through the cerebral hemispheres of two types of sharks, showing the relative abundance and distribution of neuron cell bodies. A (left), In the laminar, or group I, hemisphere of an early shark (a squaliform shark), cell bodies have migrated only a short distance from their embryonic position close to the lateral ventricle. B, In the elaborated, or group II, cerebrum of a galeomorph shark, cell bodies are more numerous and are dispersed throughout the hemisphere. (Modified after Butler and Hodos.)

The Telencephalon

Organization of the Telencephalon As we pointed out earlier, the cerebral hemispheres of the telencephalon arise as outgrowths from the rostral end of the neural tube. In all vertebrates, except for actinopterygian fishes, the cerebral hemispheres **evaginate** as a pair of outgrowths, each containing a lateral ventricle (Fig. 14-7A). The telencephalon of actinopterygians develops as a pair of **eversions** that grow laterally and curve ventrally. The central canal of the neural tube enlarges to form a single median ventricle covered dorsally only by the ependymal epithelium and primitive menix (Fig. 14-7B).

TABLE 14-1

Types of Cerebral Hemispheres in Vertebrates

| | Laminar Cerebrum Group I | Elaborated Cerebrum Group II |
|------------------|-----------------------------------|---------------------------------|
| Jawless fishes | Lamprey | Hagfishes |
| Chondrichthyans | Squalomorph sharks, chimaeras | Galeomorph sharks, skates, rays |
| Actinopterygians | Bichirs, sturgeons, gars, bowfin* | Teleosts |
| Sarcopterygians | Lungfishes, amphibians | Reptiles, birds, mammals |

*All show a limited migration of cells away from the ventricle.

Within each of the major craniote radiations (i.e., jawless fishes, chondrichthyans, actinopterygians, and sarcopterygians) early species in the radiation retain cerebral hemispheres in which the cell bodies of the neurons have not migrated far from their embryonic position close to the ventricle (Fig. 14-8A and Table 14-1). This pattern is called **laminar**, or **Group I**, by Northcutt (1978) and Butler and Hodos (1996). The number of neurons has increased greatly in derived members of each radiation, and the cell bodies have migrated extensively through the wall of the cerebral hemispheres, forming a more complex **elaborated**, or **Group II**, pattern (Fig. 14-8B).

Cerebral Regions and Functions The gray matter of the cerebrum can be divided into a dorsal portion, called the **pallium** (L., *pallium* = cloak), and a ventral **subpallium** (Fig. 14-7 and Table 14-2). Three pallial regions can be recognized in most craniates, but their presence in hagfishes is questionable. In craniates with evaginated cerebral hemispheres, these regions are described by their relative positions: **medial pallium**, **dorsal pallium**, and **lateral pallium**. In actinopterygians with everted hemispheres, the medial pallium lies most laterally, but, because homologies are unclear, pallial regions are simply numbered (Fig. 14-7B). Subpallial regions are a medial **septum** and a more lateral **striatum** (Fig. 14-7).

The lateral pallium is the **primary olfactory center**. It receives fibers directly from the olfactory bulbs via olfactory tracts and sends this information to other pallial areas. At one time, zoologists believed that the cerebral hemispheres of fishes were nearly exclusively olfactory centers. Olfactory input is extensive, and the cerebral hemispheres are the primary centers for olfactory integration and motor responses to olfactory stimuli. However, it is now recognized that the cerebrum of fishes has other functions as well.

TABLE 14-2

Terminology for Regions of Gray Matter in Evaginated Cerebral Hemispheres

| Cerebral Gray Matter | Current Terms | Mammalian Structures | Former Terms |
|----------------------|-----------------|----------------------|--------------|
| Pallium | Medial pallium | Hippocampus | Archipallium |
| | Dorsal pallium | Isocortex | Neopallium |
| | Lateral pallium | Piriform lobe | Paleopallium |
| Subpallium | Striatum | Striatum | Striatum |
| | Septum | Septum | Septum |

The medial pallium, which is called the **hippocampus** in mammals, is a major part of the **limbic system**. Other telencephalic parts of the limbic system are nuclei in the septum and the **amygdala**, which is a deep part of the lateral pallium and striatum (Gr., *amygdale* = almond). The limbic system also includes parts of the hypothalamus and the habenula within the diencephalon. The limbic system has an extensive sensory input from all of the sensory systems. Olfactory impulses come directly from the olfactory bulbs and also from the lateral pallium; most of the other sensory inputs are relayed from the dorsal thalamus or other pallial regions. Its major efferent pathways go back to other pallial regions and to the septum, habenula, and hypothalamus. Acting with the hypothalamus, the limbic system of mammals influences many aspects of behavior, especially motivational and emotional behaviors related to self-preservation and species preservation. These behaviors include fighting, fleeing, sexual behavior, and care of the young. It also has a role in memory and learning. Although the limbic system of amniotes has not been studied as extensively, homologues of all of the major components are present, and studies that have been made suggest that it has the same functions as in mammals.

Receiving somatosensory, visual, auditory, and other sensory input from the dorsal thalamus, and not receiving direct projections from the olfactory bulbs, are defining features of the enlarged amniote dorsal pallium. Whether the relatively small pallial area tentatively identified as the dorsal pallium in fishes and other amniotes is homologous to the amniote dorsal pallium is unresolved. Supporting the hypothesis of a homology is the fact that the dorsal pallium receives some visual, auditory, lateral line, and electrosensory projections from the dorsal thalamus, and olfactory input, when present, is not extensive. In contrast to amniotes, most ascending sensory information in amniotes goes to the medial pallium. Integration of some sensory information occurs in the dorsal pallium, and efferents project through the

striatum to the brainstem (Fig. 14-5B). The striatum of all vertebrates is involved with the regulation of body movements.

Major Trends in Tetrapod Brain Evolution

The brains of fishes and tetrapods vary enormously in size and in complexity of organization (Focus 14-2). But the brain regions of tetrapods, the structures they contain, and their basic organizational features are the same as in fishes. In discussing the evolution of the tetrapod brain, we need only consider the major differences between them and fishes. The cerebrum, thalamus, mesencephalic tectum, and cerebellum were the regions most affected as vertebrates adapted to terrestrial life and became more active and inquisitive creatures with a wide range of behavioral responses.

The Amphibian Brain

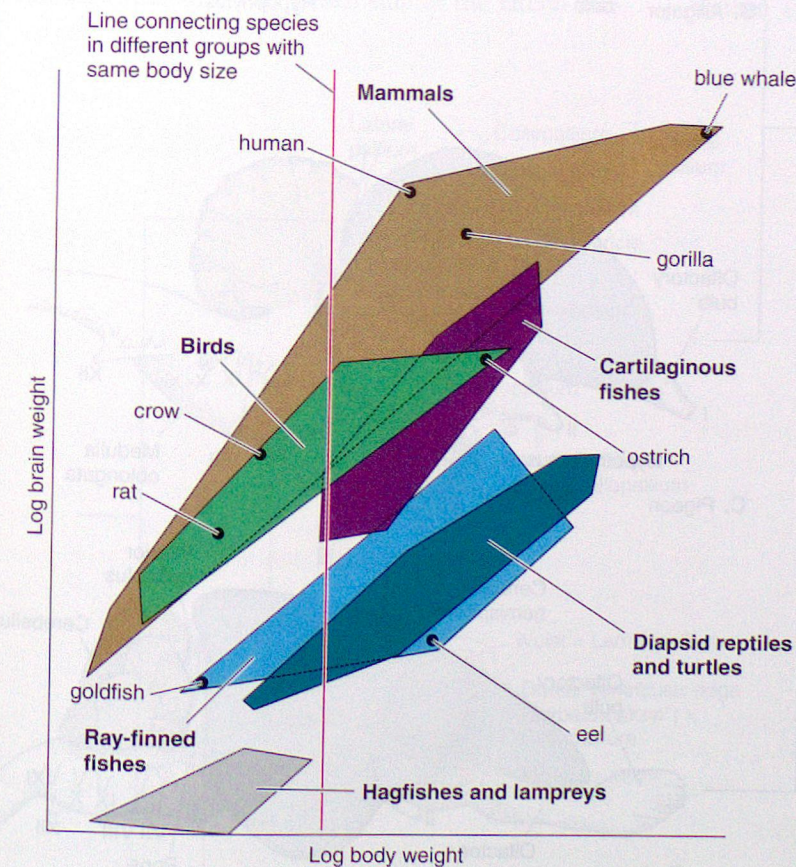
The amphibian brain is little different from the brain of many fishes (Fig. 14-9A). The major sensory input into the cerebrum continues to be olfactory, although some somatosensory, visual, auditory, lateral line, and probably other sensory stimuli are projected to it from dorsal thalamic nuclei. A few sensory impulses from caudal parts of the body reach the thalamus directly on **spinthalamic tracts**, but most continue to be relayed to the dorsal thalamus through the reticular formation. The small dorsal pallium projects to the lateral and medium pallium from where cerebral efferents extend to the hypothalamus, tectum, and reticular formation. None go directly to the spinal cord. The cerebrum of amphibians is Group I, or laminar, so its organization is simpler than in many fishes with a Group II, or elaborate, cerebrum. The amphibian cerebrum certainly mediates responses to olfactory stimuli, but we know little about its other functions. A decre-

FOCUS 14-2 Brain Size

Large vertebrates tend to have larger sensory and motor surfaces on and in the body, so they naturally have more neurons and larger brains than do smaller vertebrates. Brain size alone is a meaningless figure, but comparing brain size as expressed by weight with body weight gives a useful figure. Because body weight of vertebrates ranges from 1 g or less to many tons, weights are expressed on a logarithmic scale (Fig. A). Data points for species in each major group of vertebrates cluster, and the clusters have been outlined in the figure by polygrams. Notice the tremendous variation even within a single vertebrate group, such as mammals, and the considerable overlap of groups. The most significant comparisons are among species with the same body weight. Any vertical line connects species with the same body size, and the line shown in the figure comes close to intersecting all groups that are shown.

Brain size is largely a function of the number of neurons it contains. As the number of neurons increases, so

does the potential for more complex repertoires of behaviors. One might expect, therefore, that derived species and groups would have larger brains than early groups and their species. To some extent, this is true. Hagfishes and lampreys have the smallest brains, and birds and mammals, which have evolved the most complex behaviors, have the largest brains relative to their body size. Although many birds and mammals of the same size have similar-sized brains, some mammals have larger brains than do birds of the same size. Cartilaginous fishes, which we usually regard as an early group, have larger brains than do the ray-finned fishes of the same size. Moreover, the brain size of some cartilaginous fishes overlaps that of birds and mammals of the same size. Turtles and diapsid reptiles have brains that are no larger than those of ray-finned fishes of the same size.



A. The logarithm of brain weight plotted as a function of body weight in approximately 200 species representing major craniate clades. (Modified from Butler and Hodos, after Northcutt.)

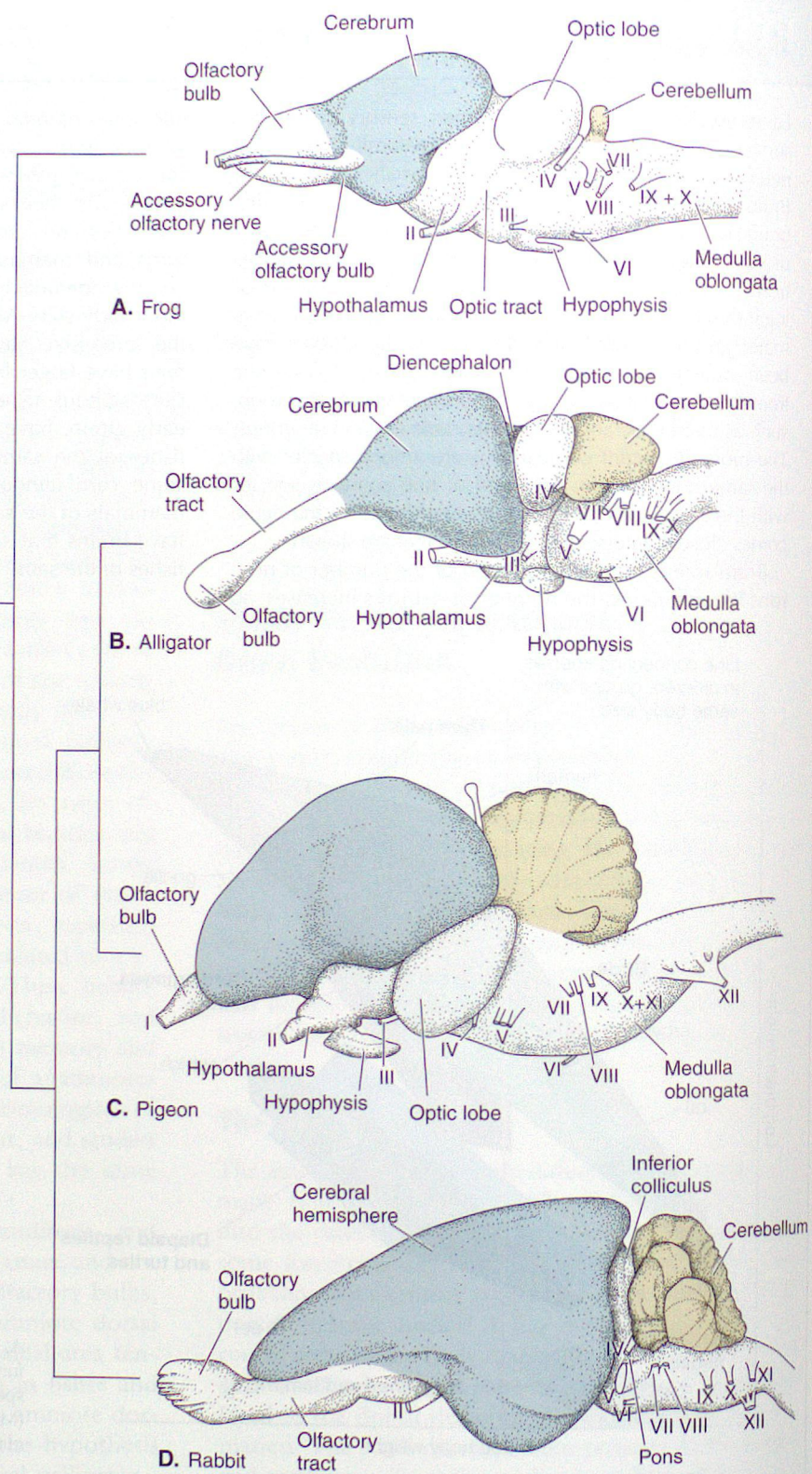
brated frog does not seek shelter or feed spontaneously.

The optic tectum remains the primary integration center of the body. It continues to project to the reticular formation, but **tectospinal tracts** have evolved

that extend directly to motor columns in the rostral part of the spinal cord and are involved with neck movements. As in fishes, electrical stimulation of parts of the tectum elicits many coordinated locomotor and feeding movements. Stimulation of certain parts of the

FIGURE 14-9

The evolution of the brain in tetrapods, as seen in lateral view, emphasizing the changes in size of the cerebrum, optic lobes, and cerebellum. Four stages are shown: amphibian (frog, A); diapsid reptile (alligator, B); bird (pigeon, C); and mammal (rabbit, D). (A, After Gaupp; B, after Weidersheim; C, after Pettingill; D, after Barone et al.)



tectum also inhibits certain activities, including the clasping reflex in a male frog.

Locomotor movements in amphibians are not as complex as in many fishes, and the cerebellum is smaller than in most fishes. Its connections are essentially the same as in fishes. Adult amphibians that

spend most of their adult lives on land have lost the lateral line system and, with it, brain centers that process this information. Interestingly, ambystomid and some other salamanders redevelop the lateral line system when reentering ponds to reproduce. Paedomorphic species, such as the salamander, *Necturus*,

and highly aquatic frogs, such as *Xenopus*, retain the system.

The Brain of Amniotes

The Cerebrum, Dorsal Thalamus, and Optic Tectum We will consider major sensory and motor pathways in the mammalian brain in the next section. At this time, we present an overview of the evolution of the brain in amniotes. The evolution of the cerebrum, dorsal pallium, and tectum are closely linked. The cerebrum of all amniotes is greatly enlarged compared with that of amphibians, for it has the elaborated, or Group II, pattern of neurons. The expanded cerebral hemispheres have grown caudally, partly (reptiles and birds) or nearly completely (mammals) covering the dorsal and lateral surfaces of the diencephalon (Fig. 14-9B-D). This enlargement results primarily from the growth and expansion of the dorsal pallium. The medial (limbic) pallium is “pushed” medially and, in mammals, rolls into the medial side of the lateral ven-

tricle to form the **hippocampus** (Fig. 14-10D). The lateral pallium is “pushed” laterally and ventrally. In mammals, it forms the **piriform lobe** (primary olfactory cortex), which is separated from the dorsal pallium by a longitudinal **rhinal sulcus** (Gr., *rhin* = nose + *L.*, *sulcus* = furrow; Figs. 4-10D and 14-11B). These regions of the brain have essentially the same functions in amniotes as they have in anamniotes.

The enlargement of the dorsal pallium in amniotes is closely linked to an expansion of the dorsal thalamus, which relays more somatosensory, optic, and auditory impulses forward to parts of the dorsal pallium. The evolution of the dorsal thalamus and dorsal pallium among different groups of amniotes is controversial. We follow a hypothesis put forward by Butler (1994) and elaborated by Butler and Hodos (1996). Butler recognizes two distinct groups of nuclei in the dorsal thalamus and two recipient regions in the dorsal pallium. A **collopalium** receives visual, auditory, and some somatosensory information from the midbrain tectum (which forms the colliculi in mammals) and

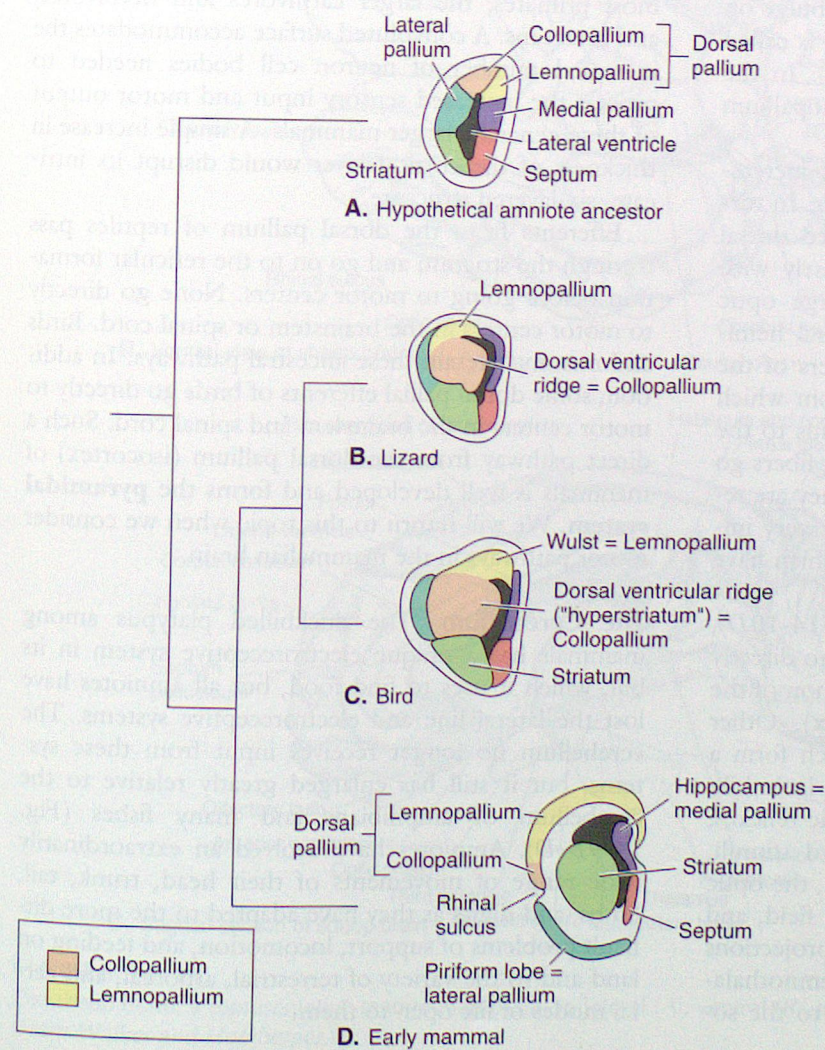


FIGURE 14-10 A-D, The Butler-Hodos hypothesis of the evolution of the cerebrum in amniotes as seen in transverse sections through the left cerebral hemisphere. Lateral is toward the left. Colors are as in Figure 14-7, with the addition of colors for the collopalium and lemнопallium. (After Butler and Hodos.)

sends it forward to a **collopallium** (Fig. 14-10). A **lemnothalamus** predominantly receives somatosensory and visual fibers more directly from primary sensory centers. These fibers bypass the midbrain tectum by travelling along ribbon-like fiber tracts, such as the **lateral lemnisci** (Gr., *lemniscus* = ribbon) and part of the **optic tract**, which go directly to the lemnothalamus. The lemnothalamus relays this information to the **lemnopallium**.

Butler further hypothesizes that the dorsal pallium of ancestral amniotes already had differentiated into a lateral collopallium and a medial lemnopallium (Fig. 14-10A). In the line of evolution to turtles, diapsids, and birds, an enlarged **dorsal ventricular ridge** evolved that pushed into the lateral ventricle (Fig. 14-10B and C). This ridge lies above the striatum and often is named the **hyperstriatum, neostriatum, and ectostriatum** in birds in the mistaken belief that it was a part of the striatum. Neurobiologists generally agree that the dorsal ventricular ridge evolved from the pallium. Butler believes that it represents an expanded collopallium; others argue that it arose from the lateral pallium. The lemnopallium also expands, but not as much. In birds, it forms a conspicuous dorsal bulge on the medial side of a cerebral hemisphere that is called the **Wulst** (German, *Wulst* = bulge, hump). In the line of evolution to mammals, it is the lemnopallium that expands the most (Fig. 14-10D).

The dorsal pallium of amniotes becomes increasingly important as a sensory integration center. In turtles, diapsids, and birds, the greatly expanded dorsal ventricular ridge (collopallium) interacts closely with the optic tectum, which in birds forms large optic lobes that protrude from beneath the cerebral hemisphere (Fig. 14-9C). For example, most fibers of the optic nerve terminate in the optic lobes, from which impulses are relayed through the collothalamus to the dorsal ventricular ridge (collopallium). Other fibers go directly to the lemnothalamus, from which they are relayed to the lemnopallium (Wulst). Vision is very important in birds and other amniotes, all of which have at least two interacting systems.

In the line of evolution to mammals (Fig. 14-10D), most fibers in the optic nerve, for example, go directly to the lemnothalamus and on to an optic region of the lemnopallium (i.e., **primary visual cortex**). Other optic fibers still go to the optic lobes, which form a pair of **superior colliculi** (L., *colliculus* = little hill; Fig. 14-11C). These remain centers for optic reflexes, such as directing eyeball movements toward stimuli, and in spatial orientation. In most mammals, the optic tectum also localizes an object in the visual field, and the visual cortex identifies the object. Most projections of somatosensory impulses also go to the lemnothalamus by the medial lemniscus and then on to the so-

matosensory cortex within the lemnopallium. Auditory impulses related to auditory reflexes (e.g., turning your head toward a sound) are mediated in the torus semicircularis, which in mammals becomes a pair of small **inferior colliculi** on the surface of the mesencephalic roof. Most auditory impulses are relayed to the collothalamus and on to the auditory part of the collopallium (**primary auditory cortex**).

The lateral pallium and medial pallium are characterized by containing three neuronal layers. Such a pattern is called an **allocortex**. The more complex mammalian dorsal pallium forms a six-layered **isocortex**, or **neocortex**, on the surface of the cerebral hemispheres. The surface of the isocortex remains relatively smooth in many mammals, including the duckbilled platypus, opossum, rabbit (Fig. 14-9D), and many rodents. A smooth surface probably was the ancestral condition of the isocortex. As mammals increased in size in many evolutionary lineages, the isocortex became highly convoluted, forming surface folds called **gyri** (Gr., *gyrus* = circle), which are separated by grooves, the **sulci** (Fig. 14-11A). A convoluted surface is found in such diverse species as kangaroos, the spiny anteater, most primates, the larger carnivores and herbivores, and cetaceans. A convoluted surface accommodates the increased number of neuron cell bodies needed to process the increased sensory input and motor output of these generally larger mammals. A simple increase in thickness of the cortical layer would disrupt its intricate, six-layered structure.

Efferents from the dorsal pallium of reptiles pass through the striatum and go on to the reticular formation before going to motor centers. None go directly to motor centers in the brainstem or spinal cord. Birds and mammals retain these ancestral pathways. In addition, some dorsal pallial efferents of birds go directly to motor centers in the brainstem and spinal cord. Such a direct pathway from the dorsal pallium (isocortex) of mammals is well developed and forms the **pyramidal system**. We will return to this topic when we consider motor pathways in the mammalian brain.

The Cerebellum The duckbilled platypus among mammals has a unique electroreceptive system in its bill, which it uses to find food, but all amniotes have lost the lateral line and electroreceptive systems. The cerebellum no longer receives input from these systems, but it still has enlarged greatly relative to the cerebellum of amphibians and many fishes (Fig. 14-9B-D). Amniotes have evolved an extraordinarily wide range of movements of their head, trunk, tail, limbs, and digits as they have adapted to the more difficult problems of support, locomotion, and feeding on land and to the variety of terrestrial, arboreal, and aerial modes of life open to them.

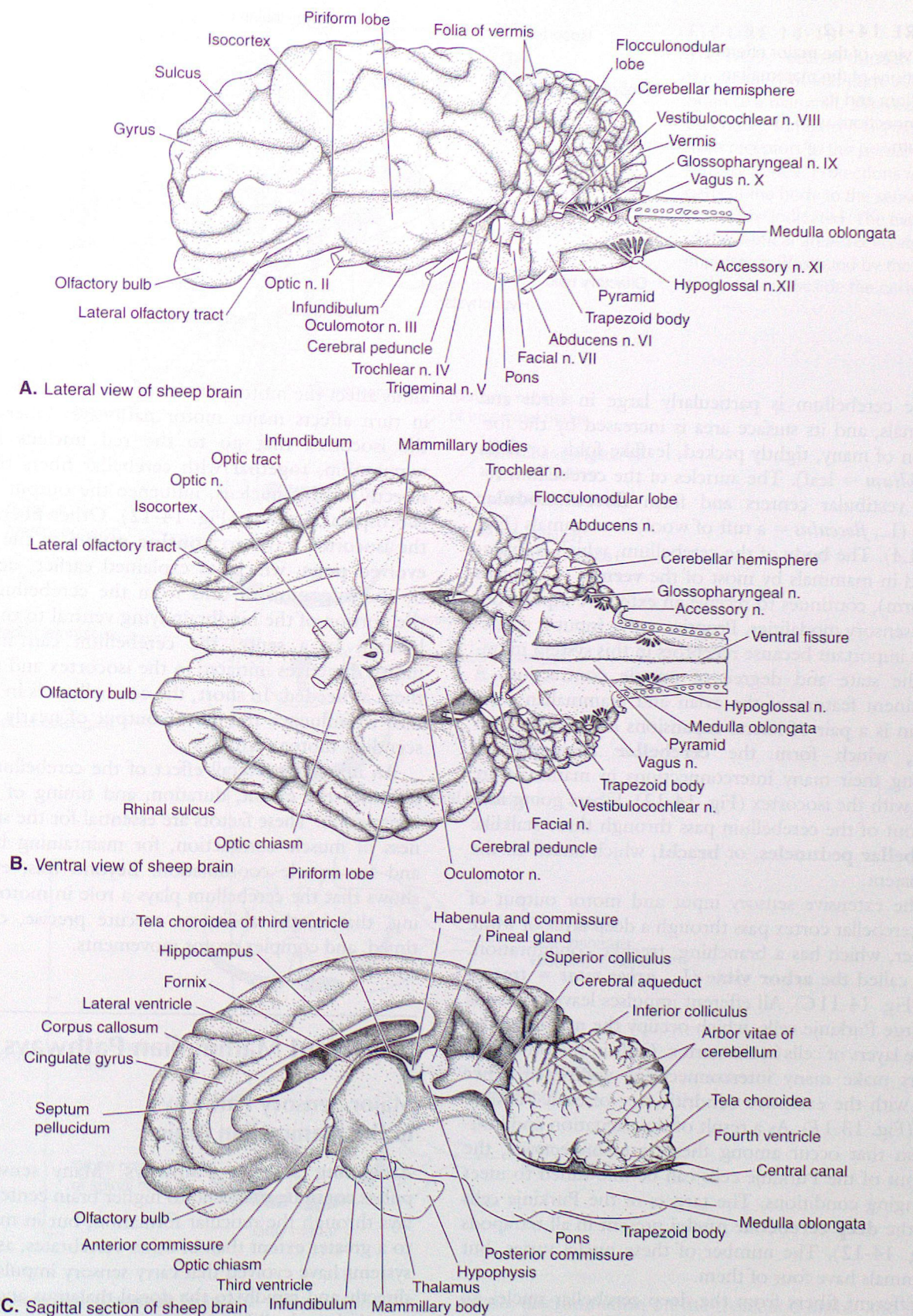
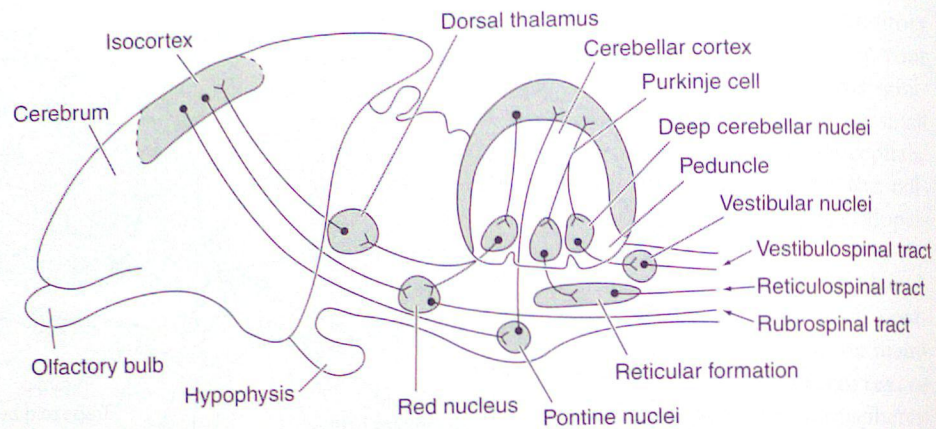


FIGURE 14-11

The sheep brain, a representative mammalian brain, in lateral (A), ventral (B), and sagittal (C) views. (From Walker and Homberger.)

FIGURE 14-12

Lateral view of the major efferent connections of the mammalian cerebellum and its interconnections with the cerebrum.



The cerebellum is particularly large in birds and mammals, and its surface area is increased by the formation of many, tightly packed, leaflike folds, or **folia** (L., *folium* = leaf). The auricles of the cerebellum remain vestibular centers and form **flocculonodular lobes** (L., *flocculus* = a tuft of wool) in mammals (Fig. 14-11A). The body of the cerebellum, which is represented in mammals by most of the **vermis** (L., *vermis* = worm), continues to receive an extensive input from most sensory modalities. Proprioceptive input is particularly important because receptors in this system monitor the state and degree of muscle contraction. A prominent feature of the avian and mammalian cerebellum is a pair of lateral expansions of the cerebellar body, which form the **cerebellar hemispheres**. Among their many interconnections in mammals are ones with the isocortex (Fig. 14-12). Fibers going into and out of the cerebellum pass through three stalklike **cerebellar peduncles**, or **brachi**, which attach to the brainstem.

The extensive sensory input and motor output of the cerebellar cortex pass through a deep layer of white matter, which has a branching, treelike configuration. It is called the **arbor vitae** (L., *arbor vitae* = tree of life; Fig. 14-11C). All efferent impulses leave on axons of large Purkinje cells, which occupy the middle of the three layers of cells in the cortex. Cells in the other two layers make many interconnections with each other and with the extensive dendritic tree of each Purkinje cell (Fig. 13-1E). As a result of the excitation and inhibition that occur among these interconnections, the output of the Purkinje cells can be fine-tuned to meet changing conditions. The targets of the Purkinje cells are the **deep cerebellar nuclei** present in all tetrapods (Fig. 14-12). The number of these nuclei varies, but mammals have four of them.

Efferent fibers from the deep cerebellar nuclei go to brainstem motor nuclei, especially the ones that control eye movements (not shown in Fig. 14-12), to vestibular centers, and forward to the red nucleus and dorsal thalamic nuclei. Projections from the thal-

amus affect the motor activity of the isocortex, which in turn affects major motor pathways. Fibers from the isocortex that go to the red nucleus in the tegmentum, together with cerebellar fibers that go directly to this nucleus, influence the output of the rubrospinal pathway (Fig. 14-12). Other fibers from the isocortex travel to **pontine nuclei** in the newly evolved **pons**, which, as explained earlier, develops by the migration of cells from the cerebellum into the portion of the hindbrain lying ventral to the cerebellum. In a sense, the cerebellum can monitor motor directives initiated in the isocortex and modify them as needed. In short, the cerebellum is in a position to influence the motor output of nearly all descending motor pathways.

An important overall effect of the cerebellum is to influence the extent, duration, and timing of muscle contraction. These factors are essential for the smoothness of muscle contraction, for maintaining balance, and for muscle coordination. Beyond this, evidence shows that the cerebellum plays a role in motor learning, that is, the ability to execute precise, carefully timed, and complex motor movements.

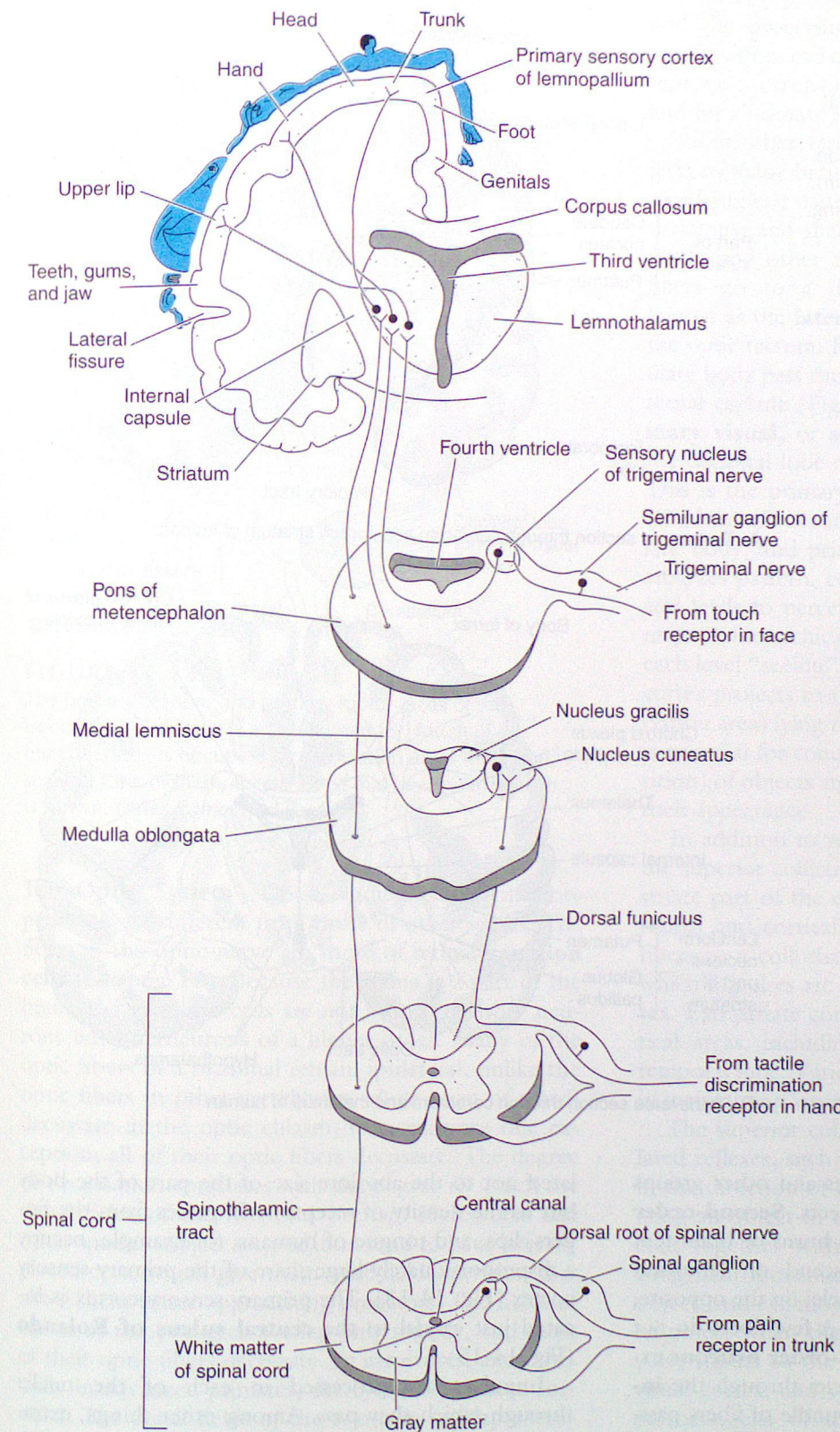
Important Mammalian Pathways

Major Sensory Pathways in the Mammalian Brain

Ascending Sensory Pathways Many sensory impulses continue to ascend to higher brain centers by relays through the reticular formation, but in mammals, to a greater extent than in other vertebrates, ascending systems have evolved that carry sensory impulses more directly and rapidly to the dorsal thalamus and isocortex. Although different sensory stimuli have different pathways, those coming from pain, temperature, pressure, touch, and taste receptors have several common features. Impulses ascend on three neuron chains. The

FIGURE 14-13

Transverse sections through the spinal cord and parts of the brain of a mammal, showing the ascending somatosensory pathways from receptors to the primary sensory cortex. Projections from parts of the body to the sensory cortex are indicated. The extent of the cortical areas receiving impulses is illustrated by the size of the figures beside the cortex.

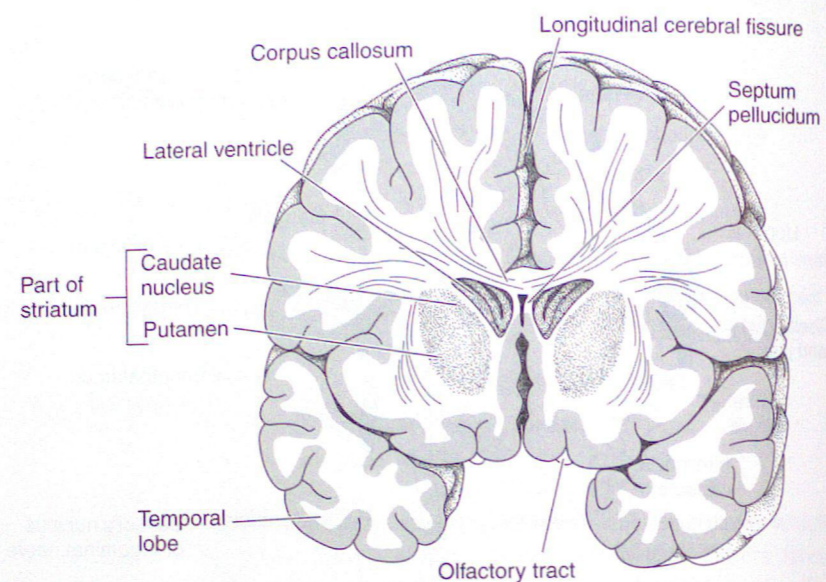


primary sensory neurons from the receptors usually terminate on interneurons in the dorsal horn of the spinal cord, or sensory nuclei of cranial nerves, at the level at which they enter the central nervous system (Fig. 14-13). The sensory neurons from receptors for

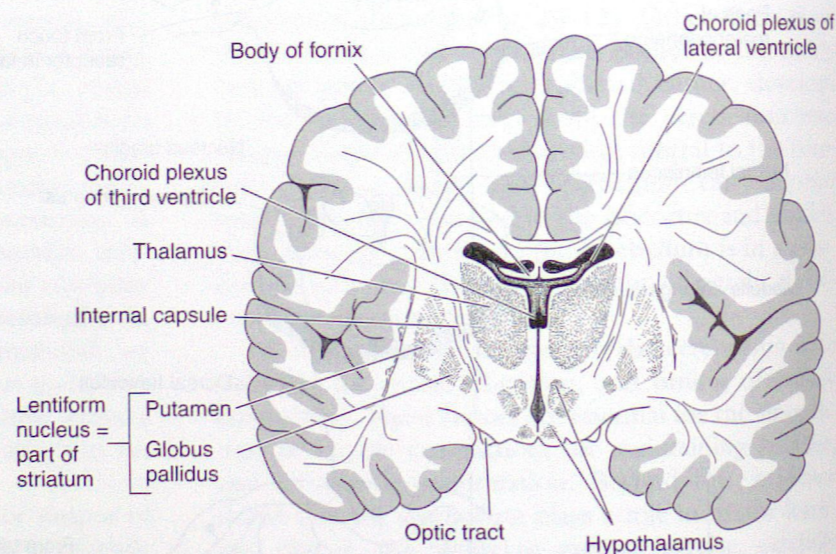
tactile discrimination on the trunk and limbs, and from proprioceptors, are an exception to this generalization because they ascend in the dorsal funiculi of the spinal cord all the way to the **cuneate** and **gracile nuclei** in the medulla. Tactile discrimination pathways are par-

FIGURE 14-14

Two transverse sections through the human brain, showing the positional relationships to each other of the cerebral hemispheres, striatum, internal capsule, thalamus, and hypothalamus. *A*, A section through the cerebrum and corpus striatum. *B*, A section slightly posterior to *A*, passing through parts of the cerebrum and thalamus. (After Noback et al.)



A. Transverse section through cerebrum and corpus striatum of human



B. Transverse section through cerebrum and thalamus of human

ticularly well developed in primates and other groups that use their hands to handle objects. **Second-order neurons** continue from the dorsal horns or brainstem nuclei, usually decussate, and ascend on lemniscal tracts to specific dorsal thalamic nuclei on the opposite, or contralateral, side of the body. A few fibers do not cross and remain ipsilateral. **Third-order neurons** extend from the dorsal thalamic nuclei through the **internal capsule** (Fig. 14-14*B*), a bundle of fibers passing between the striatum and thalamus, to terminate in very specific parts of the **primary sensory cortex**. In general, sensory information from different parts of the body is projected topographically upside down in the primary sensory cortex. The amount of this cortex that receives signals from different parts of the body is re-

lated not to the absolute size of the part of the body but to the density of receptors. Impulses from the fingers, lips, and tongue of humans, for example, occupy a disproportionately large share of the primary sensory cortex (Fig. 14-13). The primary sensory cortex is located just caudal to the **central sulcus of Rolando** (Fig. 14-15).

Impulses are processed in each of the nuclei through which they pass. Among other things, extraneous information ("noise") tends to be suppressed, and the important information ("signal") is enhanced. Except for pain and certain combinations of signals that are interpreted as pleasurable, which are centered in the thalamus, consciousness of stimuli is attained when the impulses reach the cerebral cortex.

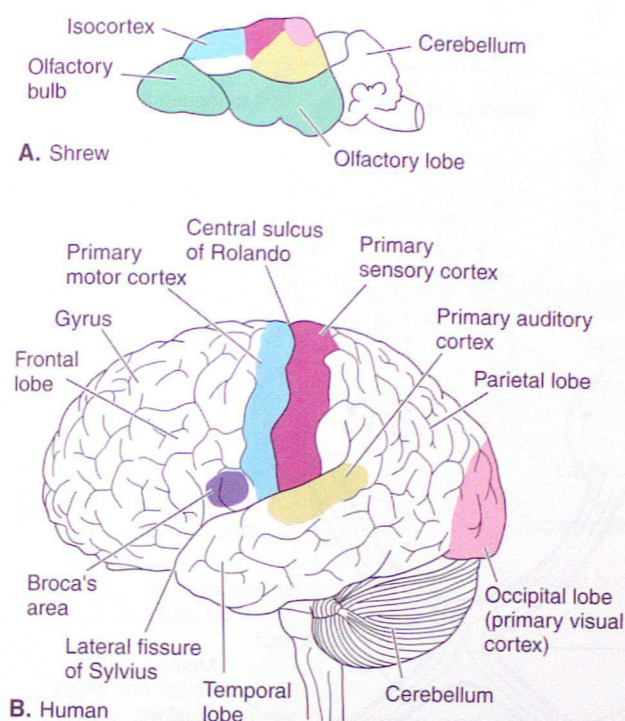


FIGURE 14-15

The primary sensory and primary motor areas of the isocortex of a shrew (*A*) and a human (*B*). Much of the human cortex is occupied by association areas (the blank spaces). One of them, Broca's area that deals with speech, is shown. (After Romer and Parsons.)

The Optic System Optic, auditory, and olfactory pathways are different from those of other senses. The fibers in the optic nerve are those of retinal **ganglion cells** (Chapter 12). Because the retina is a part of the brain, the ganglion cells are not primary sensory neurons but interneurons of a higher order. Many of the optic fibers of a mammal remain ipsilateral, unlike the optic fibers in other vertebrates, all or most of which decussate in the optic chiasm. Cetaceans are one exception; all of their optic fibers decussate. The degree of decussation correlates with the degree to which the visual fields of the two eyes overlap. Herbivores and other species subject to predation tend to have laterally placed eyes, which give them wide fields of vision that allow them to see approaching predators. The fields of vision of the two eyes overlap only slightly, and most of their optic fibers decussate. In carnivores, and especially in advanced primates, the eyes have rotated forward. The visual fields of the two eyes overlap extensively, and many optic fibers are ipsilateral (Fig. 14-16). As many as 50% of the optic fibers project ipsilaterally in some primates; the others continue to decussate. Objects in the center of the visual field are seen by each eye but from slightly different angles. The image in each eye projects to both sides of the brain,

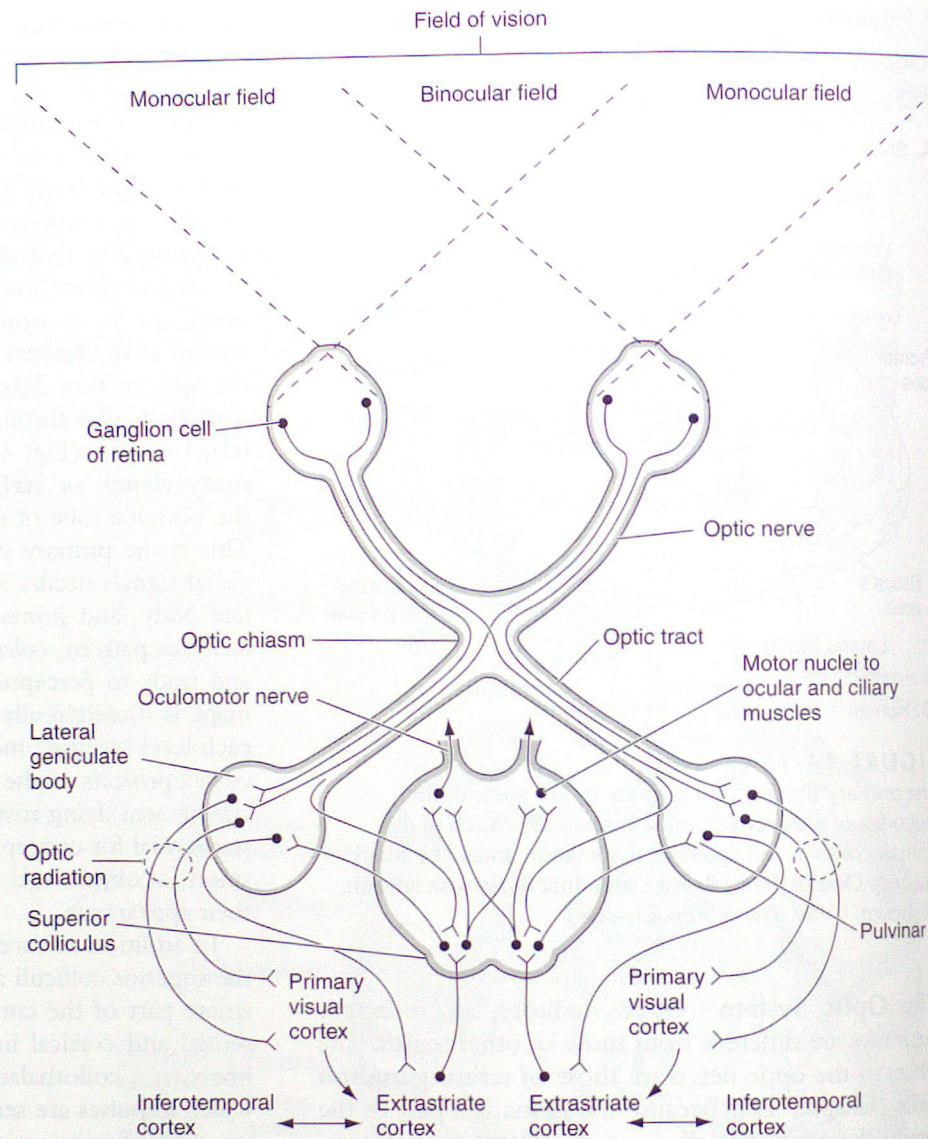
and the processing of these images permits stereoscopic vision and depth perception. This is very important for a carnivore, which must judge prey distance, and for a primate that scampers through the trees.

As in other vertebrates, the mammalian retina projects to many brain areas: the tectum, a small pretectal area lying just rostral to the tectum; tegmentum; hypothalamus; and thalamus. Mammals differ from anamniotes and other amniotes in that most of their optic fibers go to a dorsolateral lemnthalamic nucleus known as the **lateral geniculate body**, rather than to the optic tectum. Fibers beginning in the lateral geniculate body pass through the **optic radiation** of the internal capsule (Fig. 14-16) and terminate in the **primary visual**, or **striate**, **cortex**, which is located in the occipital lobe of the dorsal pallium (Fig. 14-15*B*). This is the primary visual pathway. Processing of the visual signals occurs at all levels: retina, lateral geniculate body, and primary visual cortex. This processing analyzes pattern, color, and depth of the visual image and leads to perception. The processing of the visual maps is hierarchically organized, with the neurons at each level "seeing" more and more. The primary visual cortex projects to the **extrastriate cortex** (visual association area) lying rostral to the striate cortex. This area is essential for conceptualizing visual relationships (position) of objects and for learning to identify objects by their appearance.

In addition to receiving fibers from the optic tract, the superior colliculi also receive input from the extrastriate part of the cortex. Following processing of the retinal and cortical inputs, the superior colliculi send fibers to a collothamic nucleus, the **pulvinar**, from which impulses are sent directly to the extrastriate cortex. Extrastriate cortices project to multiple visual cortical areas, including the inferotemporal area in the temporal lobe. Various visual cortical areas are involved in maintaining visual attention and analyzing motion.

The superior colliculi also participate in visually related reflexes, such as movements of the head and eye in the direction of an unexpected stimulus, and localizing an object in the visual field. The superior colliculi, together with the pretectal area, also mediate congruent movements of the eyes to follow a moving object, and eye movements that keep the eyes fixed on an object when the head moves. Eye movements involve inputs to the superior colliculi from the retina, visual cortex, and vestibular system. Output is to the motor nuclei of the extrinsic ocular muscles (Fig. 14-16). The superior colliculi and pretectal area also mediate pupillary and accommodation reflexes through their effect on autonomic nuclei. A few tectal fibers go to a small nucleus that sends efferent fibers back to the retina through the optic nerve. These fibers, which also are present in some other verte-

FIGURE 14-16
Dorsal view of the major
mammalian optic pathways.



brates, may modulate retinal sensitivity and may affect image processing in the retina.

The Auditory System The primary sensory neurons of the auditory system begin in the organ of Corti of the cochlea (Chapter 12), travel in the vestibulo-cochlear nerve, and terminate in **cochlear nuclei** in the medulla (Fig. 14-17). Many second-order neurons from the cochlear nuclei decussate in the **trapezoid body**, located on the ventral surface of the medulla (Fig. 14-11B), and terminate in the **superior olivary complex of nuclei** in the medulla. Some second-order neurons remain ipsilateral. Third-order neurons that originate in the superior olivary complex, with second-order fibers from the cochlear nuclei that bypass the olivary complex, continue on a tract called the **lateral lemniscus** to the **inferior colliculi** of the midbrain tectum. Some fibers project from here to the

reticular formation and motor nuclei of the brainstem. The tectum mediates reflexes that move the head and sometimes the auricles of the ear toward the sound sources. The inferior colliculus projects to the **medial geniculate body** of the collothalamus. Thalamic fibers travel through the internal capsule to the **primary auditory cortex**, which is located in the temporal lobe of the dorsal pallium (Fig. 14-15). As is the case with the optic system, processing of signals at all levels. Two points should be emphasized. First, the cochlear nuclei and other ascending centers are **tonotopically** organized, that is, different sounds are “dissected” into their separate components, and these are finally synthesized in the primary auditory cortex and adjacent areas where the awareness and interpretation of sounds occur. Second, auditory signals from each ear ascend on each side of the brain, which enables the brain to localize the source of sounds by

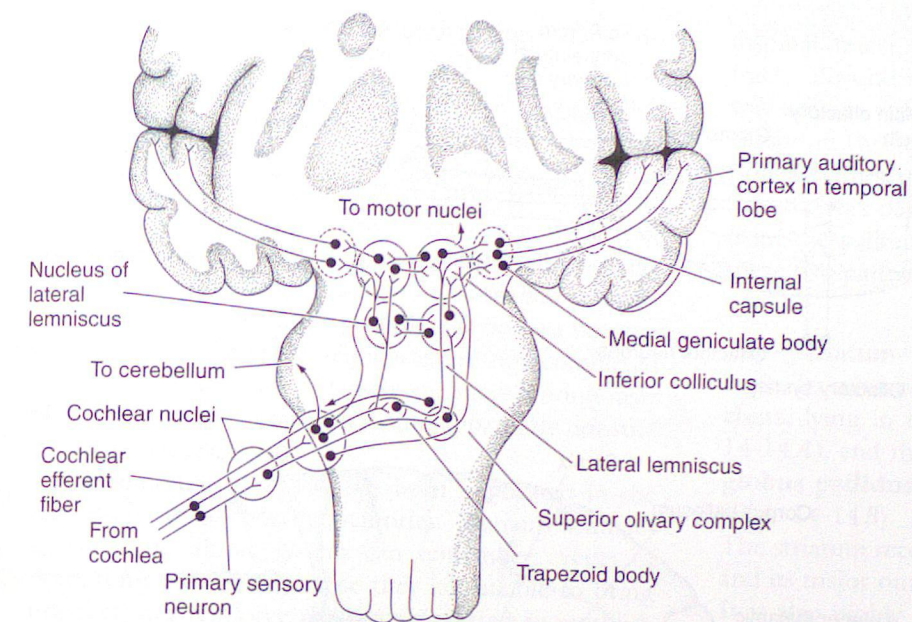


FIGURE 14-17
The major mammalian auditory
pathways projected onto a dorsal
view of the brain. (After Noback
et al.)

comparing differences in the timing and intensity of sounds arising in each ear.

A few efferent fibers return from the superior olivary nuclei through the vestibulocochlear (octaval) nerve to the organ of Corti. These fibers modulate the activity of the organ of Corti by enhancing the meaningful signal and suppressing extraneous “noise.”

The Olfactory and Limbic Systems The olfactory and limbic systems are closely integrated because the sense of smell is so important to many limbic functions. These systems include the olfactory bulbs, lateral pallium (piriform lobe of the cerebrum), medial pallium (hippocampus), amygdala, and septum. Although some of these centers have other functions, they may have evolved in early vertebrates as centers for processing olfactory impulses.

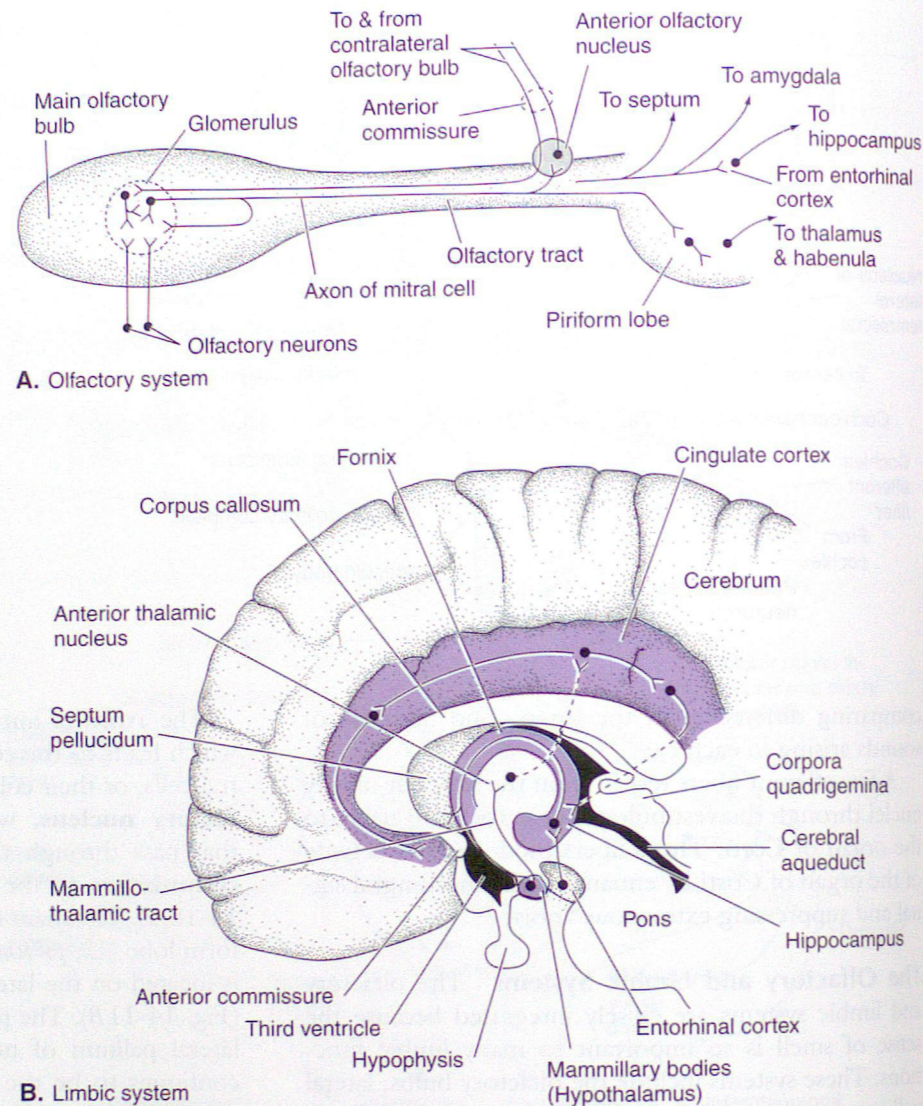
Olfactory neurons from the nasal cavities extend the short distance to the **main olfactory bulb**, where they terminate in hundreds of complex tangles of neuronal processes called **glomeruli** (Fig. 14-18A). Among other connections in the glomeruli, the olfactory neurons synapse with large **mitral cells**, the axons of which are the primary ones leaving the olfactory bulb. Each glomerulus may receive as many as 25,000 (in rabbits) olfactory neurons and the terminations of nearly 100 other neurons. Many of these are from short neurons within the glomerulus, collaterals of mitral cells that feed back to the glomerulus, and neurons coming from the contralateral olfactory bulb. Obviously a great deal of signal processing, some known to be inhibitory, occurs here. Considerable convergence also occurs because far fewer mitral axons leave the glomeruli than olfactory neurons enter.

The axons of mitral cells form the **olfactory tract**, which leads to the cerebrum (Fig. 14-11B). Some mitral cells, or their collaterals, enter a small **anterior olfactory nucleus**, where they synapse with neurons that pass through the anterior part of the **anterior commissure** to the contralateral olfactory bulb (Fig. 14-18A). The main target of the mitral cells is the piriform lobe (L., *pirum* = pear + *forma* = shape), which is located on the lateroventral surface of the cerebrum (Fig. 14-11B). The piriform lobe is homologous to the lateral pallium of nonmammalian vertebrates, and it continues to be the primary olfactory area. Olfactory discrimination and awareness probably occur here, and conditioned olfactory reflexes are lost when this area is destroyed. Olfactory learning also involves extensive parts of the forebrain. The piriform lobe projects to dorsal thalamic nuclei which, in turn, project to the isocortex immediately dorsal to the rhinal sulcus. It also projects to the habenula in the epithalamus, from where efferents lead to the reticular formation and motor nuclei.

Other mitral fibers from the main olfactory bulb project to the septal region, a small rostral part of the hippocampus, and to the amygdala (Fig. 14-18A). A different part of the amygdala receives fibers from the vomeronasal organ via the accessory olfactory bulb. The amygdala is located deeply in the ventral part of the cerebrum lateral to the optic chiasm. It evolved from part of the lateral pallium and striatum but is now a part of the limbic system. The amygdala receives other fibers from the thalamus, cerebral cortex, and reticular formation. It influences many aspects of behavior, primarily through efferent fibers that go to the hypothalamus. Among its functions are mediating

FIGURE 14-18

The major components of the mammalian olfactory and limbic systems. *A*, The major olfactory pathways in a ventrolateral view. The size of the glomerulus is greatly exaggerated; hundreds are present in an olfactory bulb. *B*, The limbic system as projected onto a dissected sagittal section of the brain. Two major parts of the limbic system are shown in purple. (Modified after Noback et al.)



sniffing, licking, and other olfactory-based reflexes. It also sends fibers to parts of the thalamus and dorsal pallium.

The **hippocampus** is an important part of the limbic system. As we have seen, it represents the medial pallium, which has been shifted medially by the expansion of the dorsal pallium. It receives olfactory fibers from the **entorhinal cortex**, which lies near the caudal part of the piriform lobe (Fig. 14-18A). The hippocampus also receives gustatory and other visceral sensory fibers from the reticular formation; fibers from the **cingulate cortex** on the medial side of a cerebral hemisphere (Fig. 14-11C); and auditory, visual, and general somatic sensory projections, which are relayed into the hippocampus via the entorhinal cortex. It retains all of the visceral integrating functions that it has in fishes. Beyond this, the hypothalamus is an important center in both birds and mammals for controlling body temperature and the high level of metabolism that characterize these endothermic vertebrates. Effer-

ents from the hippocampus aggregate to form a prominent tract known as the **fornix** (L., *fornix* = arch or vault), which makes an arc in the base of the cerebrum and then turns ventrally to the **mammillary bodies** of the hypothalamus (Figs. 14-18 and 14-11B). A small section of the fornix goes to septal nuclei, which in turn project to the hypothalamus. A prominent **mammillothalamic tract** from the mammillary bodies returns to the thalamus. Relays in anterior thalamic nuclei and the cingulate cortex return impulses to the hippocampus. The complex pathway from hippocampus to mammillary bodies, to anterior thalamic nuclei, to the cingulate cortex, and back to the hippocampus is called the **Papez circuit** (Fig. 14-18B). This circuit integrates the hypothalamus into the limbic system.

Because of their extensive connections, the hippocampus, amygdala, hypothalamus, and other parts of the limbic system influence many aspects of behavior, especially motivational and emotional behaviors related to self-preservation and species preservation. These be-

haviors include feeding, drinking, fighting, fleeing, reproduction, and care of the young. The limbic system exerts much of its influence by inhibiting the hypothalamus and tegmental part of the reticular formation. For example, electrical stimulation of parts of the limbic system causes a mammal to stop an activity in which it is engaged. Conversely, destruction of parts of the limbic system releases the mammal from normally inhibitory stimuli and leads to an overreaction to stimuli. Destruction also causes some behaviors to become repetitive, and complex sequences are not completed in an orderly fashion. A female rat may continuously pick up and drop a newborn infant, apparently not sure what to do next.

The limbic system also has been implicated in the formation of short-term memories. Humans with lesions in the limbic system can remember events of times long past, but because they are unable to bring together and reinforce the signals needed to establish new memories, they cannot recall events that occurred a few minutes ago. The formation of some memories may require an emotional input, especially of the type that is essential to survival.

Motor Control and Pathways

The motor systems allow vertebrates to maintain posture and balance and to move the body and its parts in response to sensory clues and (in many vertebrates) the desires of the animal. Pools of neurons in the brainstem and spinal cord control many reflexes, the rhythmic, stereotyped movement of body parts during locomotion, and other movements.

Pathways descending from the brain also initiate or modulate motor activity. As we have described, tracts descend from the optic tectum (tectospinal tract), red nucleus (rubrospinal tract), reticular formation (reticu-

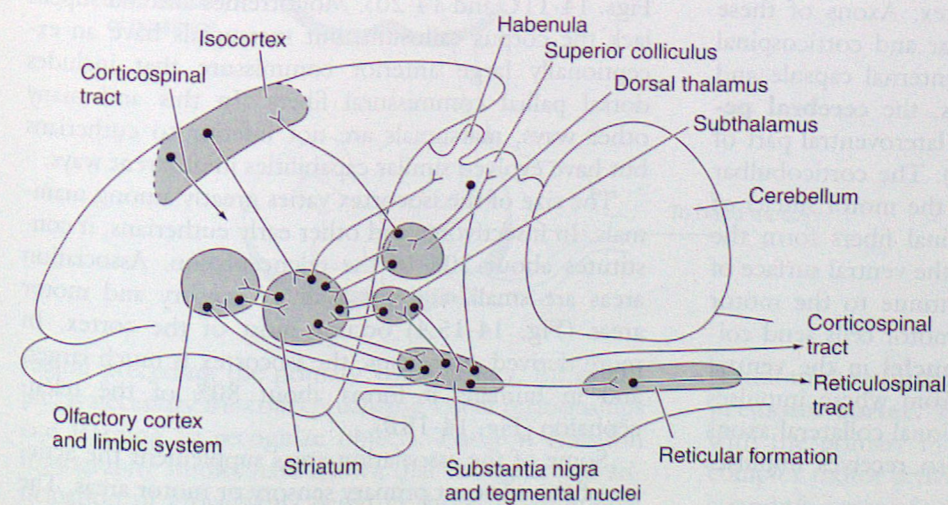


FIGURE 14-19 Lateral view of the major connections of the mammalian striatum and associated substantia nigra in the tegmentum.

lospinal tract), and vestibular nuclei (vestibulospinal tract). Beyond these, amniotes retain the motor pathway seen in other vertebrates that descends from the cerebrum through the striatum to the reticular formation and motor centers (Fig. 14-5B). Mammals also have a direct **corticospinal tract** that descends directly from the pallium to motor centers. Now we examine these two pathways from the cerebrum.

The Striatum The mammalian striatum is quite large. Its most conspicuous nuclei are the **caudate nucleus**, lying in the floor of the lateral ventricle (Fig. 14-14A), and the **lentiform nucleus** (= **putamen** + **globus pallidus**), lying lateral to the internal capsule (Fig. 14-14B). Additional, deeper nuclei also exist. The striatum receives a major input from the isocortex, and its major outflow is to part of the dorsal thalamus. It is also highly interconnected with the subthalamus (ventral thalamus) and a group of tegmental nuclei (Fig. 14-19), including a heavily pigmented nucleus called the **substantia nigra**. Neurons of the striatum and substantia nigra produce many neurotransmitter and neuromodulator substances, including acetylcholine, noradrenalin, dopamine (the pigment in the substantia nigra is associated with dopamine production), GABA (gamma aminobutyric acid), and serotonin. These substances allow for many excitatory and inhibitory reactions as the striatum processes information reaching it.

Via its many interconnections, the mammalian striatum regulates motor output from the isocortex to tegmental nuclei and the reticular formation, from which impulses are sent to motor nuclei in the brainstem and the spinal cord. In general, the striatum tends to smooth out what might otherwise be jerky muscle contractions by inhibiting undesirable movements. The importance of the striatum and substantia nigra in

motor control is evident when disease or lesions destroy parts of them or alter their complex "cocktail" of neurosubstances, for example, in Parkinson's disease or Huntington's chorea. These diseases cause changes in muscle tone, tremors in limb and body movements, and disturbances in gait and eye movements. In some cases, patients can think about and plan to make body movements, such as lifting a leg or speaking, but are unable to execute them effectively. In other cases, uncontrollable hyperactivity may occur, for example, constantly turning the head or moving a limb.

The Pyramidal System A new and important cortical level of motor control evolved along with the isocortex of mammals (Fig. 14-20). It is called the **pyramidal system** and consists of direct pathways from the isocortex to motor centers in the brainstem and spinal cord. These pathways are the **corticobulbar tract** and the **corticospinal tract**. The pyramidal system is the highest of the hierarchically arranged levels of motor control. The pyramidal system allows mammals to execute complex, voluntary motor activities with precision. For humans, this includes speech, manipulating tools with their hands, playing a piano, or batting a ball. These activities are purposeful and may be initiated at will. They also are learned to a large extent, so performance improves with practice.

The fibers of the pyramidal system going to motor centers begin with neuronal cell bodies located in the precentral gyrus, or **primary motor cortex**, of the dorsal pallium (Fig. 14-15). Some of these are large, pyramid-shaped cells. The amount of cortex occupied by cells supplying different parts of the body is proportional not to the size of the part but to the number of motor units it contains (Fig. 14-20). Neurons going to motor centers supplying the lips, tongue, and hands occupy a disproportionately large share of the motor cortex in humans. As with the primary sensory cortex, the body is represented more or less upside down in the primary motor cortex. Axons of these motor cells form the corticobulbar and corticospinal tracts that descend through the internal capsule and contribute to conspicuous bulges, the **cerebral peduncles**, that can be seen on the lateroventral part of the mesencephalon (Fig. 14-11B). The corticobulbar fibers decussate and terminate in the motor nuclei of cranial nerves, but the corticospinal fibers form the **pyramids** (which can be seen on the ventral surface of the medulla), decussate, and continue to the motor horns of the spinal cord. These motor cells send collateral axons into the **pontine nuclei** in the ventral portion of the metencephalon from where impulses are sent to the cerebellum. Additional collateral axons enter the red nucleus, which also receives impulses back from the cerebellum.

Cortical Integration

The isocortex of mammals is divided into **frontal, parietal, temporal, and occipital lobes**, which, in humans, underlie skull bones bearing the same names (Fig. 14-15B). The boundaries between the lobes are not well defined in many mammals, but a prominent **lateral fissure of Sylvius** separates the human temporal lobe from the others, and a **central sulcus of Rolando** separates the frontal and parietal lobes. The **primary sensory cortex** lies in the parietal lobe just posterior to the central sulcus; the **primary motor cortex** lies in the frontal lobe just rostral to the central sulcus; the **primary auditory cortex** lies in the temporal lobe; and the **primary visual cortex** is in the posterior part of the occipital lobe. Cortical regions between these sensory and motor cortices are called **association areas**. Apart from differences in their afferent and efferent connections, the cortical areas differ in cell density, thickness of their six layers, types of interconnections, and other cytological details. On the basis of these differences, Brodmann, an early 20th-century German anatomist, subdivided the cortex into nearly 50 areas. His numbering system is still used in detailed analyses.

The different areas of the cortex have many interconnections. **Short association fibers** pass from one gyrus to adjacent ones, **long association fibers** interconnect more distant lobes within one hemisphere, and **commissural fibers** pass between the two hemispheres (Fig. 14-20). The phylogenetically older olfactory and limbic parts of the two hemispheres are interconnected by the **anterior commissure** (Fig. 14-18A) and by the **commissure of the fornix**. Major parts of the temporal lobes also are interconnected by the anterior commissure. The rest of the isocortex of the two hemispheres is interconnected in eutherian mammals by a very large commissure called the **corpus callosum** (L., *corpus callosum* = hard body; Figs. 14-11C and 14-20). Monotremes and marsupials lack the corpus callosum, but marsupials have an exceptionally large anterior commissure that includes dorsal pallial commissural fibers. In this and many other ways, marsupials are not inferior to eutherians but have evolved similar capabilities in different ways.

The size of the isocortex varies greatly among mammals. In insectivores and other early eutherians, it constitutes about 20% of the telencephalon. Association areas are small, and the primary sensory and motor areas (Fig. 14-15A) occupy most of the cortex. In more derived eutherians, the isocortex is much larger, and in humans it forms about 80% of the telencephalon (Fig. 14-15B).

Some of the association areas supplement the activity of the adjacent primary sensory or motor areas. The

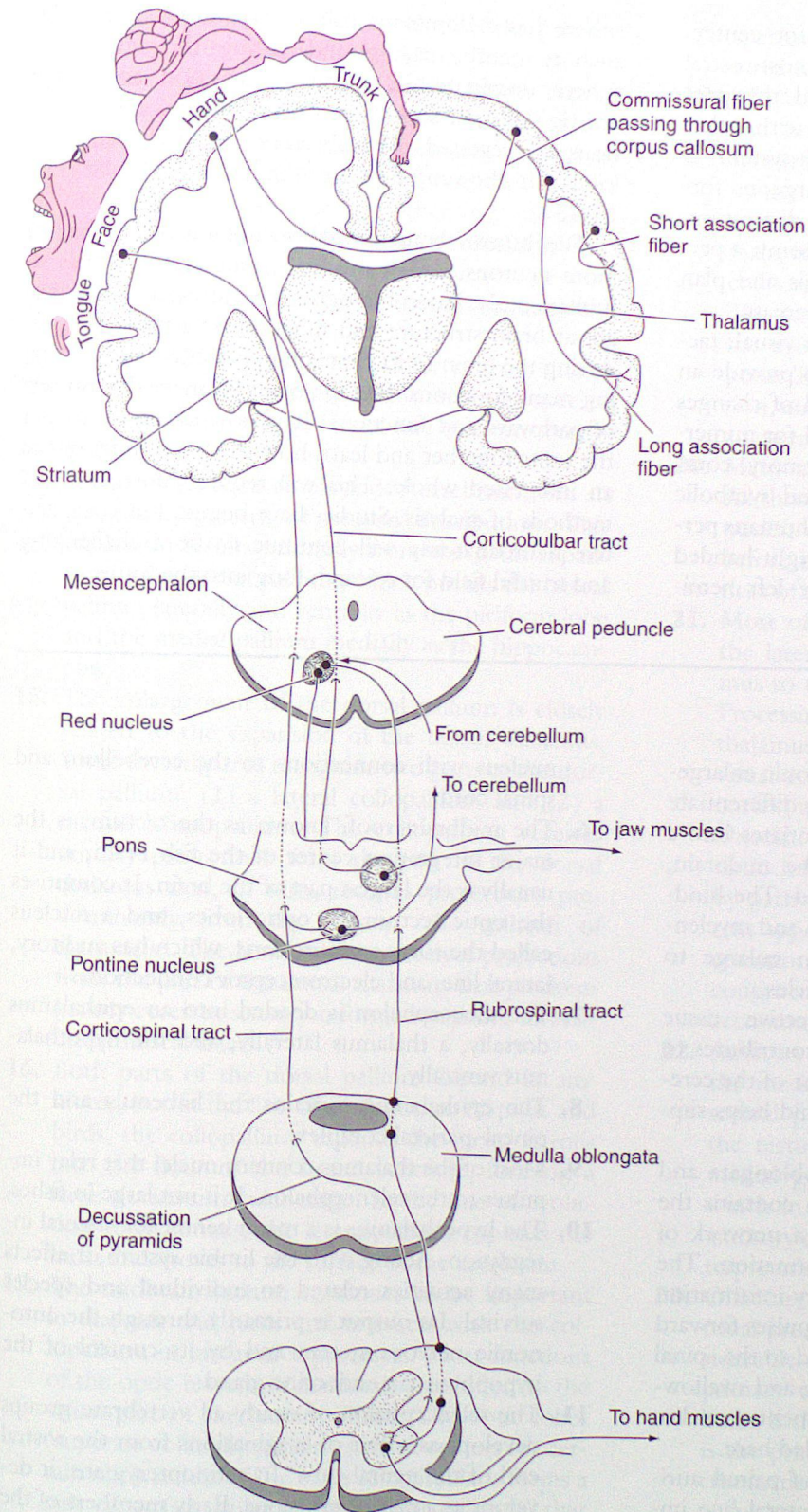


FIGURE 14-20

Transverse section through the spinal cord and parts of the brain in a mammal showing the pyramidal system, or corticobulbar and corticospinal pathways, which extend directly from the primary motor cortex to motor centers in the brainstem and spinal cord. The location in the motor cortex of motor regions for parts of the body is shown, and the approximate area devoted to each part is indicated by the size of the figures beside the cortex. Collateral fibers from the corticobulbar and corticospinal tracts enter the red nucleus and pontine nuclei, thereby establishing connections from and to the cerebellum, respectively.

region preceding the primary visual cortex, for example, is necessary for conceptualizing visual relationships and learning to recognize objects. Positron emission tomography studies have shown that thoughts and anticipation of movements begin in the association area

rostral to the primary motor cortex, which is called the **premotor cortex**. The premotor cortex also interacts with the primary motor cortex in such a way that a complex motor activity, such as playing a piano, is not a random series of movements but forms an integrated

pattern. The final motor impulses to motor centers leave from the primary motor cortex. The most rostral part of the frontal lobe, sometimes called the **pre-frontal lobe**, has extensive connections with other parts of the isocortex and with the limbic system. If these connections are severed, as neurosurgeons formerly did in treating certain cases of severe depression, by an operation known as a prefrontal lobotomy, a person's motivation, ability to formulate goals and plan for the future, and ability to concentrate decrease.

Association areas also integrate separate visual, tactile, olfactory, and other sensory signals to provide an overall perception of the environment and of changes taking place. Association areas are essential for numerous mental processes, such as learning, memory, communication, reasoning, and conceptual and symbolic thought. The two cerebral hemispheres of humans perform somewhat different functions. In right-handed people and most left-handed people, the left hemi-

sphere has a dominant role in communication skills, such as speech, reading, and writing; the right hemisphere dominates in spatial recognition and other artistic skills. In some left-handed people, these functions are reversed. **Broca's area**, a speech center, is located in the ventral part of the left frontal lobe (Fig. 14-15B).

The human brain probably contains 10 billion or more neurons, and it processes millions of signals simultaneously. Neurobiologists have learned a great deal about brain structure and function by a process of reducing the brain to its elementary pathways and localizing many functions. But the brain is far more than sets of pathways and functions. It is now necessary to put the units together and learn how the brain functions as an integrated whole. This will require more complex methods of analysis. Studies have begun, but comparative neuroanatomy will continue to be a challenging and fruitful field for research long into the future.

SUMMARY

1. The brain develops from three embryonic enlargements of the neural tube, which later differentiate into five regions. A forebrain differentiates into a telencephalon and diencephalon. The midbrain, or mesencephalon, remains undivided. The hindbrain divides into the metencephalon and myelencephalon. Cavities within the brain enlarge to form a series of interconnected ventricles.
2. The brain is covered by connective tissue meninges, the innermost of which contributes to the choroid plexuses that secrete most of the cerebrospinal fluid. The cerebrospinal fluid helps support, protect, and nourish the brain.
3. The hindbrain forms the medulla oblongata and cerebellum. The medulla oblongata contains the nuclei of many cranial nerves and a network of neurons known as the reticular formation. The reticular formation integrates sensory information received in this region and relays impulses forward to higher brain centers and backward to the spinal cord. Many eye movements, feeding and swallowing movements, respiratory movements, cardiac rate, and blood pressure are controlled here.
4. The cerebellum of fishes consists of paired auricles, which receive vestibular and lateral line impulses, and a central body, which receives tactile, proprioceptive, and electroreceptive information. The cerebellum interacts with other centers in motor coordination.
5. The tegmentum, or midbrain floor, contains an extension of the reticular formation and also a red nucleus with connections to the cerebellum and spinal cord.
6. The midbrain roof, known as the tectum, is the major integration center of the fish brain, and it usually is the largest part of the brain. It comprises the optic tectum, or optic lobes, and a nucleus called the torus semicircularis, which has auditory, lateral line, and electroreceptor connections.
7. The diencephalon is divided into an epithalamus dorsally, a thalamus laterally, and the hypothalamus ventrally.
8. The epithalamus contains the habenula and the pineal-parietal complex.
9. Most of the thalamus contains nuclei that relay impulses to the telencephalon. It is not large in fishes.
10. The hypothalamus is a major center for visceral integration. Acting with the limbic system, it affects many activities related to individual and species survival. Its output is primarily through the autonomic nervous system and by its control of the hypophysis, an endocrine gland.
11. The telencephalon of nearly all vertebrate groups develops as a pair of evaginations from the rostral end of the neural tube. In actinopterygians, it develops as a pair of eversions. Early members of the major vertebrate radiations have a laminar pattern for the distribution of neurons within the telencephalon. More advanced, derived species have an elaborated pattern.
12. Several regions can be recognized in the gray matter of a cerebral hemisphere. The lateral part of its

roof forms a lateral pallium, which is the primary olfactory area. The medial pallium (hippocampus of mammals) is part of the limbic system. Acting with the hypothalamus the limbic system regulates emotional and motivational behavior related to self-preservation and species preservation. The dorsal pallium between the other two pallial regions receives ascending sensory information from the dorsal thalamus. This is not extensive in most fishes. The floor of the cerebrum includes the striatum and septum.

13. The amphibian brain is little different from that of some fishes with laminar brains. In most species, the cerebellum has no lateral line or electroreceptive input.
14. All amniotes have an expanded cerebrum with an elaborated pattern of neuron distribution. This expansion results primarily from the great expansion of the dorsal pallium, which pushes the lateral pallium laterally and ventrally as the piriform lobe and the medial pallium medially as the hippocampus.
15. The enlargement of the dorsal pallium is closely related to the expansion of the dorsal thalamus. Some investigators recognize two parts of the dorsal pallium: (1) a lateral collopallium and (2) a medial lemnopallium. The collopallium receives sensory projections from the part of the dorsal thalamus that, in turn, receives projections predominantly from the tectum (the colliculi of mammals). The lemnopallium receives projections from the part of the dorsal thalamus that predominantly receives sensory information more directly on lemniscal tracts.
16. Both parts of the dorsal pallium expand in amniotes, but in the line of evolution to diapsids and birds, the collopallium expands the most. It rolls into the floor of the lateral ventricle, forming a large dorsoventricular ridge. In the line of evolution to mammals, the lemnopallium expands the most and moves to the surface of the cerebrum.
17. The midbrain tectum continues to be important in diapsids and birds and interacts with the collopallium in integrative processes. Most functions of the optic tectum in mammals are shifted to the visual part of the lemnopallium. The optic lobes (superior colliculi) remain as reflex centers for certain optic reflexes. The torus semicircularis forms a pair of surface bulges (the inferior colliculi) that mediates certain auditory reflexes and relays ascending auditory input to the dorsal thalamus.
18. A cortex of three cell layers characterizes the lateral and medial palliums. The isocortex of the dorsal pallium has six cell layers. The surface area of the isocortex is increased in large mammalian species by forming a series of folds, the gyri, separated by grooves, the sulci.
19. The cerebellum also has enlarged as head, body, and limb movements have become more complex. Its surface area is increased in birds and mammals by the formation of folds, the folia. The cerebellar auricles form the flocculonodular lobes in mammals, the body forms most of the vermis, and lateral expansions form the cerebellar hemispheres. The cerebellum retains its earlier connections and has evolved new ones with the isocortex via the pons. The cerebellum influences the extent, duration, and timing of muscle contractions, so it plays an essential role in motor coordination.
20. Many ascending sensory pathways have evolved. All those from lower centers go to dorsal thalamic nuclei, where some processing of signals occurs before they are sent to the primary sensory cortices of the isocortex.
21. Most of the optic fibers of mammals project via the lateral geniculate bodies of the dorsal thalamus to the primary visual cortex of the isocortex. Processing of the visual image occurs in the retina, thalamus, and primary visual cortex. The primary visual cortex, in turn, projects to the extrastriate cortex, an area essential for learning to recognize objects. Some optic fibers continue to go to the optic lobes (superior colliculi), which are linked by pathways to the extrastriate cortices. This system appears to be involved in maintaining visual attention. The superior colliculi also participate in congruent eye movements, pupillary reflexes, and accommodation.
22. Auditory fibers go first to the cochlear nuclei in the medulla. From there, they are projected on several pathways toward the inferior colliculi of the tectum. The inferior colliculi project to the medial geniculate body of the dorsal thalamus, which in turn projects to the primary and other auditory cortical areas where the awareness and interpretation of sounds occur.
23. Olfactory neurons terminate in clusters of neuronal processes in the olfactory bulbs, where considerable processing of the impulses occurs. The primary target of neurons leaving the olfactory bulbs is the lateral pallium, or piriform lobe. This is the primary olfactory center, and olfactory discrimination, awareness, and learning probably occur here.
24. The medial pallium, or hippocampus, still receives some olfactory signals. The hippocampus is a central part of the limbic system, which integrates the olfactory centers, hypothalamus, thalamus, and part of the cerebrum into a system that is important in motivational and emotional behaviors re-