With the restriction of CCK cells to the intestine and the appearance of gastrin cells in the stomach, the gastric and intestinal phases of digestion could be controlled separately.

Mammalian CCK is chemically similar to that of fishes, so there has been little evolution of the hormone. However, there have been significant alterations in the endocrine control of gastric and intestinal digestion. Gastrin arose, and bombesin-secreting cells changed their routes of action from delivery via the blood to direct neural stimulation.

In some instances, evolution has involved important changes in hormonal structure, or old molecules have been co-opted for new hormonal roles. For example, epinephrine is modified from a single amino acid (tyrosine). Epinephrine is placed in service as a neurotransmitter that is released locally by axons into synaptic spaces. Extending this, the adrenal gland deploys epinephrine as hormone, releasing it into the blood for dispersed effects on distant target tissues. In the endocrine system, chemical messages coordinate internal activities by traveling long distances through the circulatory system. In the nervous system, chemical messages travel short distances across the spaces between neurons and responding cells. Thus, the nervous system, like the endocrine system, regulates activities of the body, and its functional basis is much the same—the release of chemical messages that affect responses. Therefore, we turn next to the nervous system (see chapter 16).

Overview

The endocrine system initiates and coordinates the internal activity of the organism. It is comprised of ductless glands, endocrine glands, that release hormones into the blood vessels that carry these chemical messengers to the target tissues they affect. In general, each major endocrine gland may regulate a diversity of body activities—at different times in the development of the individual, and in different ways in different phylogenetic groups. The thyroid gland presides over metabolic rate, metamorphosis, growth, and reproduction. The ultimobranchial body and parathyroid gland act antagonistically to build bone matrix or to remove bone matrix, respectively, by their affects on calcium deposition/resorption. The adrenal gland is composed of two tissue types: Adrenocortical tissue produces corticosteroid hormones that affect water retention, metabolism, and reproduction; chromaffin tissue produces catecholamines that prepare the organism for strenuous activity. Pancreatic islets primarily produce insulin, which is involved in glucose and fat metabolism. The pituitary gland develops from the merger of embryonic neural (infundibulum) and ectodermal (Rathke's pouch) contributions, producing in the adult, respectively, the neurohypophysis, which influences, via neurosecretory neurons, the adenohypophysis. Pituitary hormones affect smooth muscle contractions and water conservation (neurohypophysis), as well as growth, reproduction, and melanophores (adenohypophysis). The digestive activity of the alimentary canal is regulated by hormones released from its walls to coordinate food passage and release of digestive chemicals. Hormones released from the kidney participate in blood pressure regulation and red cell production.

Hormones are signaling compounds released by dedicated organs, carried in the blood, and targeting specific organs. Sometimes, the endocrine "glands" are spread more diffusely throughout the body. For example, as adipose cells (adipocytes) throughout the body fill, they release leptin, which travels in the bloodstream to hypothalamic receptors serving as a chemical signal to reduce food consumption.

Generally, the endocrine system regulates the activity of internal organs such as the digestive system. It helps to initiate and pace developmental events such as metamorphosis or the onset of secondary sexual characteristics. The endocrine system also adjusts the organism to its environment. Immediate challenges are met with internal adjustments in metabolic rate, water balance, and alertness. Seasonal changes are matched by preparations for migration or hibernation, or by preparation for reproductive activity.

Evolution of the endocrine system of vertebrates includes the appearance of new molecules that participate in hormonal roles. Molecules that are by-products of normal physiological activities are often co-opted for service as chemical messengers. Endocrine glands have evolved, mostly by anatomical changes in association with each other and with other organs. By evolving responsiveness to circulating hormonal signals, target tissues are the most active evolutionary part of the endocrine system.

WEB LINK

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CHAPTER 16

The Nervous System

Introduction

The nervous system is divided into the **central nervous system (CNS),** which includes the brain and spinal cord, and the **peripheral nervous system (PNS),** which consists of all nervous tissue outside the CNS. The nervous system *receives* stimuli from one or more **receptors** and *transmits* information to one or more **effectors** that respond to stimulation. Effectors include **mechanical effectors,** such as muscles, and chemical effectors, such as glands. Thus, responses of the nervous system involve muscle contractions and glandular secretions. The nervous system regulates an animal's performance by integrating immediate incoming sensory information with stored information, the results of past experience, and by then translating past and present information into action through the effectors.

The nervous system includes millions of nerve cells, each of which establishes thousands of contacts with other nerve cells, so the total number of interconnections is astronomical. That is why analysis of the function of the nervous system often includes as much philosophy as it does science. The task is formidable, but not hopeless. Let us begin by looking at the fundamental cellular components of the nervous system.

Types of Cells within the Nervous System

There are two types of cells within the nervous system: **neurons** and **neuroglial cells,** or **glia.**

Neuroglia

Neuroglial ("nerve" and "glue") cells do not transmit impulses. They support, nourish, and insulate neurons. All neuroglia bind together nervous tissue, and they can be specialized (figure 16.1). **Microglia** engulf foreign material and bacteria; **oligodendroglia** and **Schwann cells** insulate the axons of neurons; **ependymal cells** line the central canal of the brain and spinal cord; and **astrocytes** pass nutrients between blood capillaries and neurons. Additionally, they guide neuron development, regulate levels of chemical communication between cells (synapses), and control blood flow to active neurons.

Neurons

Neurons are specialized for long-distance transmission of electrical stimuli throughout the body. The neuron is the structural and functional unit of the nervous system. It consists

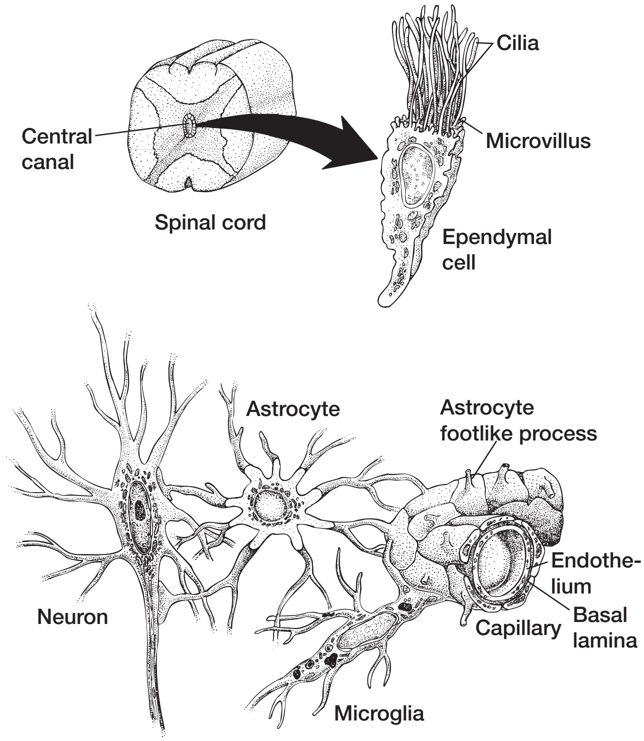


FIGURE 16.1 **Four types of neuroglia found within the central nervous system.** Astrocytes form cytoplasmic connections to transport nutrients between blood capillaries and neurons. Phagocytic microglia engulf stray or foreign materials. Ependymal cells line the central canal of the central nervous system. Oligodendroglia insulate axons within the central nervous system (not shown).

of the nerve cell body, the **perikaryon,** the **body** or **soma** of the neuron, and thin cell processes called **nerve fibers** (or neurites) if they are long (figure 16.2). The processes are of two types. There usually is one **axon** per neuron and one or many **dendrites.** Dendrites transmit incoming electrical impulses toward the perikaryon. Axons carry impulses away from the perikaryon. Neurons are grouped by the number of their processes. **Unipolar neurons** have a single stem that divides into a dendrite and axon. **Bipolar neurons** have two processes, usually at opposite ends. **Multipolar neurons** have many processes associated with the cell body (figure 16.3a–h).

Neurons and their processes are often known by different terms, depending on whether they occur in the CNS or the PNS. For example, a collection of nerve fibers traveling together is a nerve **tract** in the CNS and a **nerve** in the PNS. A collection of nerve cell bodies is a **nucleus** in the CNS and a **ganglion** in the PNS. Neuroglial cells wrap some axons in a thick **myelin** sheath. Such fibers are called **myelinated nerves,** and those without sheaths are **unmyelinated nerves** (figure 16.4a,b). A neuroglial cell that produces the myelin sheath is an oligodendroglial cell in the CNS and a Schwann cell in the PNS. The **nodes of Ranvier** are indentations between adjacent neuroglial cells in the myelin sheath.

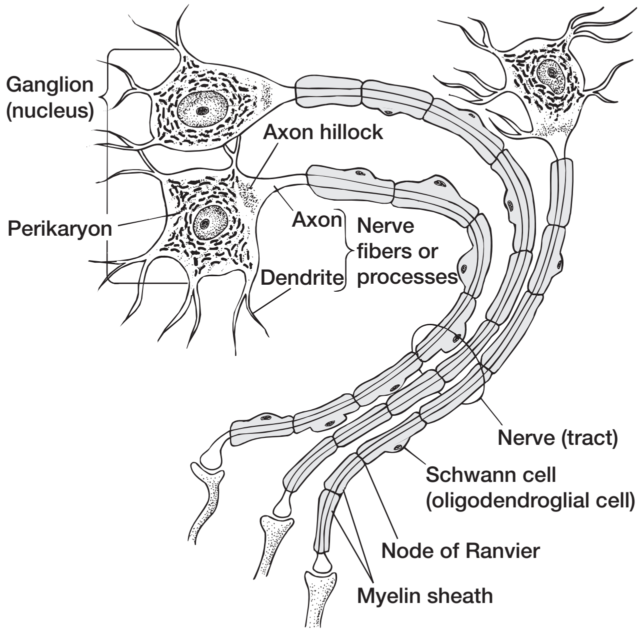


FIGURE 16.2 **Structure of a neuron.** The cell nucleus and surrounding cytoplasm form the cell body of a neuron (perikaryon). Nerve fibers or processes are cytoplasmic extensions from the perikaryon. Axons carry impulses away from the perikaryon and dendrites carry impulses toward it. The same structures are given different names in the peripheral and the central nervous systems. Central nervous system terms are given in parentheses.

Some peripheral nerves, if not damaged too severely, can regrow, sprouting a new axon from the severed axonal stump or from the perikaryon that slowly grows down the Schwann cell tube to reestablish innervation of the effector organ. Once formed, nerves of the central nervous system were thought to lack the ability to replace themselves. More recent evidence now suggests otherwise. In fact, across vertebrates so far studied, neurons of the CNS are replaced regularly. Even in the adult mammalian brain, thousands of new neurons are added daily. Although such new neurons are a tiny proportion of the total population, over a lifetime of addition this can be considerable. Additional neurons in adults are especially evident in parts of the brain important for learning and memory. In birds, new neurons are added seasonally to areas concerned with courtship.

Transmission of Information

Information traveling through the nervous system is transmitted in the form of electrical and chemical signals. Electrical signals are **nerve impulses** that travel within the plasma membrane of the neuron and are of two kinds: graded potentials and action potentials. A **graded potential** is a wave of electrical excitation proportional to the magnitude of the stimulus that triggers it. The graded potential declines in magnitude as it travels along a nerve fiber. An **action**

BOX ESSAY 16.1 Brain Gain

Late in the 1990s, it was known that a process termed "neurogenesis" (neuron + producing) added new neurons to the brains of rats, cats, and singing canaries. But what of human brains? Could humans add back brain neurons lost to age or injury? To answer this would require invasive experimentation and, in humans, that of course raised special ethical limitations. About that time, cancer researchers were using special dyes that were picked up preferentially by rapidly dividing cells, such as cancer cells, thus aiding detection of the disease. Fred Gage, a neuroscientist, realized that if new brain cells were being added, these too would pick up the dye in chronically ill cancer patients. When patients eventually died, Gage examined their donated brain tissue and found, in fact, that the human brain was making new neurons, even in these patients who were sick and tended to be elderly.

Turning to animal studies, subsequent work has found that exercise, injury, stroke, estrogen, and high social status stimulate neurogenesis; but neurogenesis is inhibited with aging, stress, loss of sleep, boring environments, and falling asleep in lecture (just kidding). Most promising is that these new neurons come from dormant stem cells stashed away in different regions of the brain, ready to be activated. One region is near the hippocampus, which plays a key role in memory. New neurons seem to be especially adaptable in forging new connections, perhaps the anatomical basis for establishing new stores of information.

See also Vastag, B. 2007. Brain gain: Constant sprouting of neurons attracts scientists, drugmakers. Sci. News *171:376–77, 380.*

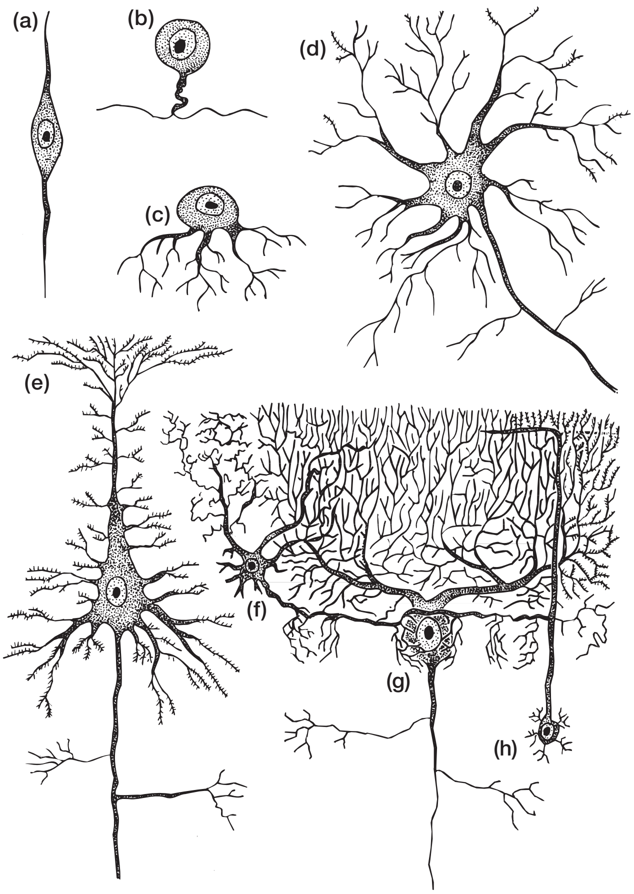


FIGURE 16.3 Types of neurons. (a) Bipolar neuron. (b) Unipolar neuron. (c–h) Multipolar neurons.

From R. V. Krstić. General Histology of the Mammal. *© 1984 Springer-Verlag. Reprinted by permission.*

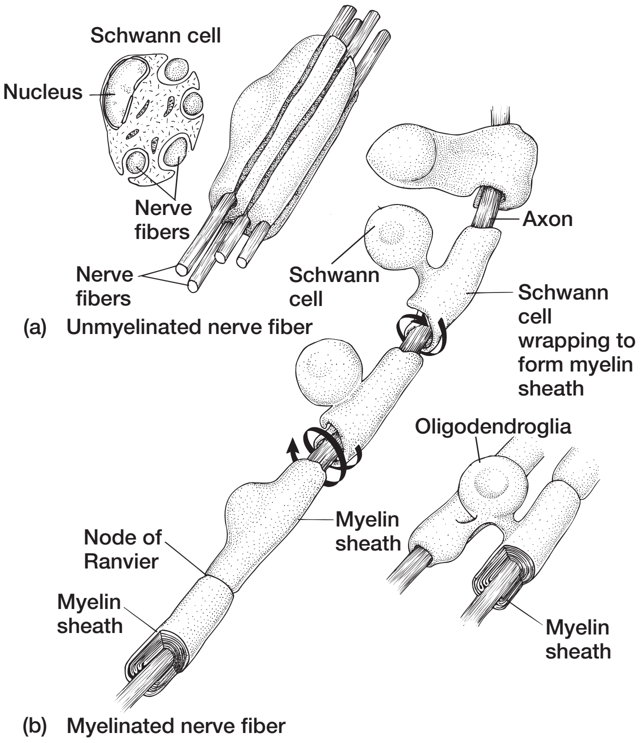


FIGURE 16.4 Myelinated and unmyelinated nerve fibers. (a) Despite their name, unmyelinated nerve fibers are associated with neuroglial cells. Usually there are several fibers per neuroglial cell, but these neuroglial cells are not wrapped repeatedly around the fibers as they are in myelinated nerves. (b) The myelin sheath is formed by a neuroglial cell that is repeatedly wrapped around a section of the nerve fiber. In the peripheral nervous system, the neuroglial cell is a Schwann cell. In the central nervous system, it is an oligodendroglial cell. Successive neuroglial cells collectively form the myelin sheath. The boundaries between them are termed nodes of Ranvier.

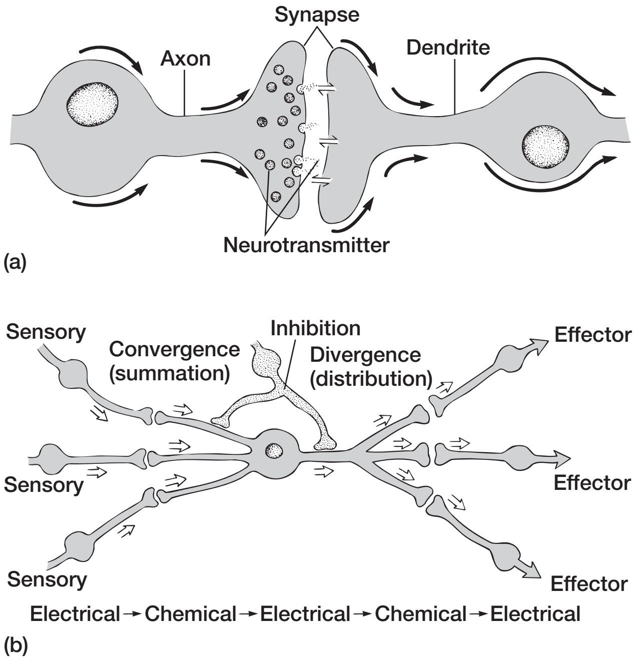


FIGURE 16.5 Transmission of information within the nervous system. (a) Neurons transmit and receive stimuli as electrical impulses along their fibers. Synapses are junctions between nerve cells. Axons release chemical messengers (neurotransmitters) that diffuse across the synapse. When they arrive at the dendrite in sufficient concentration, the neurotransmitter molecules initiate an electrical impulse in the next neuron. (b) Synapses assist in processing information. Electrical input can converge or diverge. Inputs of some neurons inhibit or reduce the sensitivity of other neurons.

potential is an all-or-none phenomenon. Once initiated, it propagates without decrement along a nerve fiber. Action potentials are often used for long-distance signaling in the nervous system. Within the dendrites and the perikaryon, nerve impulses are usually graded potentials, but they become action potentials as they travel out the axon.

Chemical signals are generated at **synapses,** gaps between the junctions of neurons (figure 16.5a). These gaps occur between the processes of one neuron and the next, and between axons and perikarya. Upon arrival at the terminus of an axon, an electrical impulse stimulates the release of stored **neurotransmitters** into the tiny space between processes. Neurotransmitters diffuse across this synaptic junction and settle on the associated cellular process of the next neuron. When collected in sufficient concentration, neurotransmitters initiate an electrical impulse in the next neuron. Excess and spent neurotransmitter molecules are rapidly inactivated to prevent prolonged effects. Neurotransmitters must quickly reach a threshold level to initiate an electrical impulse in the next neuron. Thus, passage of information through chains of connected neurons includes alternating events of electrical and chemical transmission involving nerve impulses and neurotransmitters, respectively (figure 16.5b).

Synapses introduce control into the processing of information transfer. If synapses were absent and neurons were in direct contact with each other, excitation in one neuron might spread inevitably throughout an entire network of interconnected neurons like ripples on a pond, without any local control. Synapses break up a network of neurons into information-processing units. Whether an impulse is transmitted to the next neuron in a sequence depends on whether or not there is a sufficient concentration of neurotransmitters at the synapse. Where neurons converge, transmission of a single impulse from one neuron might be insufficient. Several impulses might need to arrive simultaneously in order to release enough neurotransmitter molecules to trigger an electrical impulse in the next neuron. Convergence promotes **summation** of information. Conversely, if a neuron sends branches to several circuits, information diverges and is distributed to appropriate areas. Branches of a single axon are called **collateral branches.** Inhibition also affects the flow of information by decreasing the responsiveness of neurons to incoming information. Convergence, divergence, and inhibition are modes of information processing that take advantage of the character of the synapse (figure 16.5). Furthermore, the structure of neurons at a synapse ensures that transmission across the gap occurs in only one direction.

Neurosecretory Cells

Neurosecretory cells are specialized neurons. Most neurons release neurotransmitters at the ends of their axons. Neurosecretory cells also release secretions at the ends of their axons, but these secretions are delivered into a blood capillary and transported to a target tissue. Neurosecretory cells are thus endocrine in function.

Peripheral Nervous System

The terms used to describe the components of the peripheral nervous system refer to the anatomical or functional properties of the nerves (figure 16.6). Peripheral nerves serve either somatic or visceral tissues and carry sensory or motor information. **Somatic nerves** pass to or from somatic tissues—skeletal muscle, skin, and their derivatives. **Visceral nerves** pass to or from viscera—involuntary muscles and glands. Nerves carrying information from tissues *to* the central nervous system are **afferent,** or **sensory, neurons.** Nerves carrying information *away* from the CNS to effectors are **efferent,** or motor, neurons. Thus, a somatic sensory nerve might carry information about touch, pain, or temperature from the skin to the central nervous system. A somatic motor nerve carries impulses from the CNS to a striated muscle to stimulate its contraction. A visceral sensory nerve delivers information about the condition of internal viscera to the CNS. A visceral motor nerve innervates visceral effectors (cardiac muscle, smooth muscle, or glands). The components of the PNS that control visceral activity constitute the **autonomic nervous system (ANS).**

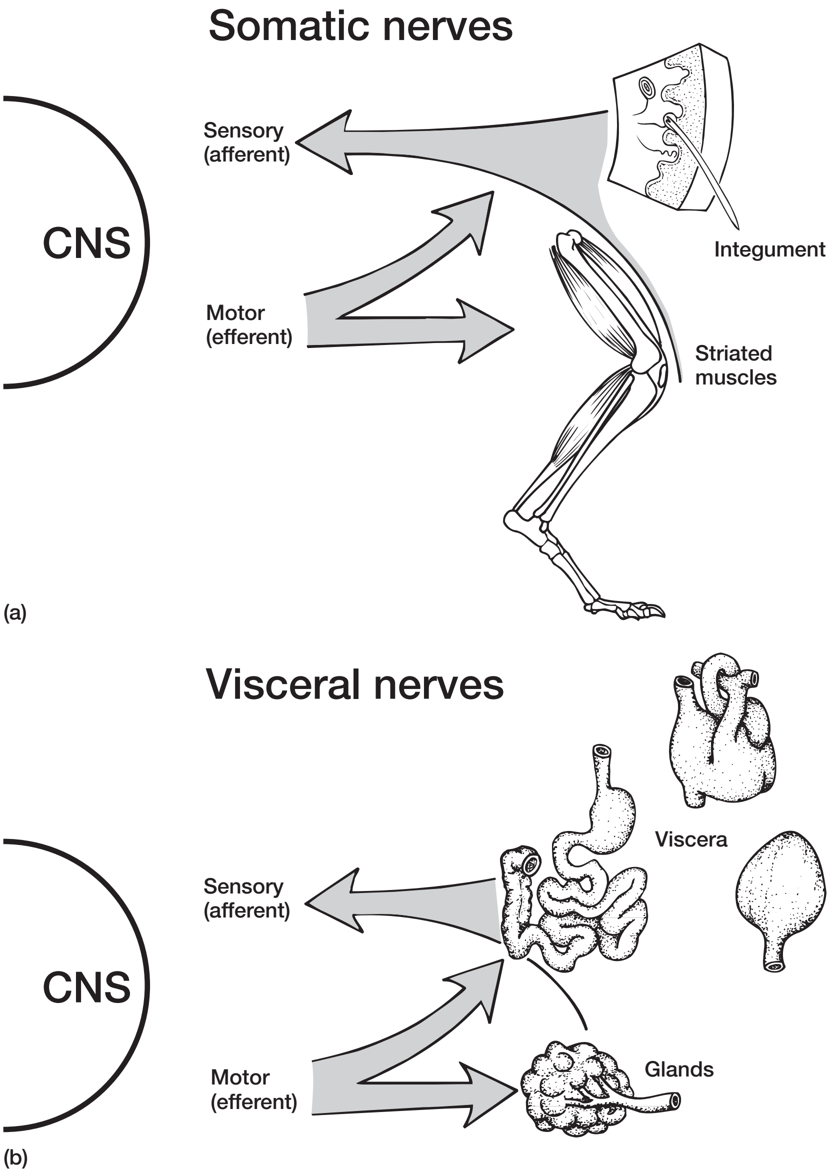


FIGURE 16.6 Functional categories of neurons of the peripheral nervous system. Some neurons supply somatic tissues, others visceral tissues. They can be sensory and respond to stimuli from these tissues, or they can be motor and deliver stimuli to these tissues.

Nerves have two additional properties based on their distribution. Neurons are termed *general* if the innervated tissues are widely distributed, or *special* if the tissues are restricted in location. Thus, general somatic neurons innervate sense organs or supply effectors to the integument and most striated muscles. Special somatic neurons are associated with somatic sense organs (e.g., eyes, olfactory organs, inner ears) or effectors (e.g., branchiomeric muscles, ciliary eye muscles, extrinsic ocular muscles) that are limited in distribution. General visceral neurons innervate sensory organs or supply effectors in glands or smooth muscles of the digestive tract, heart, and other viscera. Special visceral neurons concerned with sensory input innervate the taste buds and olfactory epithelium.

From anatomical criteria, the peripheral nervous system can be divided into **spinal nerves** emanating from the spinal cord and **cranial nerves** emanating from the brain. We begin by looking at these anatomical divisions of the peripheral nervous system.

Spinal Nerves

Spinal nerves are sequentially arranged and numbered (C-1, T-1, L-1, S-1) according to their association with regions of the vertebral column (cervical, thoracic, lumbar, sacral). Early anatomists recognized **dorsal** and **ventral roots** of each spinal nerve. Afferent fibers enter the spinal cord via the dorsal root, and efferent fibers leave by way of the ventral root. The dorsal root ganglion, a swelling in the dorsal root, is a collection of neuron bodies whose axons contribute to the spinal nerve. Parallel to the spinal cord and attached to each spinal nerve through the **ramus communicans** is the **sympathetic chain** of ganglia (paravertebral ganglia), a paired series of linked ganglia adjacent to the vertebral column or notochord (figure 16.7a,b). Other peripheral ganglia form the **collateral ganglia** (prevertebral ganglia). The paired **cervical, coeliac,** and **mesenteric ganglia** are examples of the collateral ganglia. The **visceral ganglia** occur

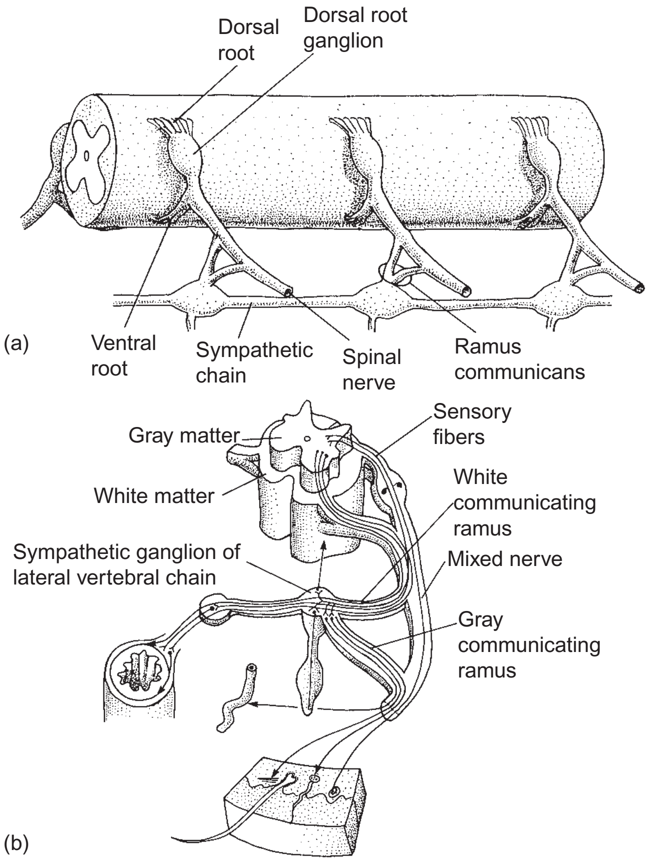


FIGURE 16.7 **Spinal nerve anatomy.** (a) Dorsal and ventral roots connect spinal nerves to the spinal cord. A dorsal root is enlarged into a dorsal root ganglion. Spinal nerves join with the sympathetic chain through communicating rami. (b) Configuration of sensory and motor neuronal routes in an adult mammal.

(b) After Tuchmann–Duplessis et al.

within the walls of visceral effector organs (figure 16.7b). Thus, there are three types of ganglia: sympathetic, collateral, and visceral.

Peripheral nerves in the trunk arise during embryonic development from two sources (figure 16.8a–c). One source is the neurons that differentiate within the spinal cord. Axonal processes sprout from these neurons and grow outward to the ganglia or to the effectors they supply (figure 16.8b). The other source is the neural crest. Cells migrate from the neural crest to specific locations and sprout processes that grow back to the central nervous system and out to the tissues they innervate (figure 16.8a). The ventral roots arise from neurons in the spinal cord that send fibers out from the spinal cord. The dorsal root arises from cells of neural crest origin that send fibers into the spinal cord. In gnathostomes, the two roots usually merge to form the composite spinal nerve and attached sympathetic chain.

The fibers of each spinal nerve innervate restricted structures at that level of the cord. This is especially pronounced with spinal nerve innervation of somatic tissues. Each growing spinal nerve tends to accompany its adjacent embryonic **myotome,** the source of somatic muscles, and its **dermatome,** the source of dermal connective tissue and muscle, as they spread and differentiate during development (figure 16.9a–c). Once it is differentiated, a spinal nerve supplies the skeletal muscles derived from its adjacent myotome and receives somatic sensory input from the restricted area of the body surface differentiated from its dermatome. Strictly speaking, a **dermatome** refers to an embryonic structure, but the term is often used to denote the region of the adult body derived from it. The fidelity between a dermatome and its spinal nerve permits mapping of the body surface in terms of the corresponding spinal nerves that supply each region. Loss of sensation in a dermatome can be diagnostic for the particular specific spinal nerve involved.

Cranial Nerves

Cranial nerves have roots enclosed in the braincase. Most are named and numbered by Roman numerals from anterior to posterior. The conventional system for numbering these nerves is sometimes inconsistent. For instance, most anamniotes are said to have ten numbered cranial nerves plus six pairs of unnumbered, lateral line cranial nerves. A few anamniotes and all amniotes are said to have 12. In fact, there is an additional terminal nerve at the beginning of this series. If counted at all, it is numbered 0 to avoid renumbering the conventionally numbered sequence. Further, the second cranial nerve (II) is not a nerve at all but an extension of the brain. Nevertheless, by convention it is called the optic "nerve." The eleventh cranial nerve (XI) represents the merger of a branch of the tenth cranial nerve (X) with elements of the first two spinal nerves (C-1 and C-2). Despite its composite structure, it is called the spinal accessory nerve and designated by Roman numeral XI. In addition to these numbered cranial nerves, up to six pairs of unnumbered, lateral line cranial nerves are present in jawed fishes and many amphibians.

Phylogenetically, the cranial nerves are thought to have evolved from dorsal and ventral nerves of a few anterior spinal nerves that became incorporated into the braincase. Dorsal and ventral nerves fuse in the trunk but not in the head, and they produce two series: dorsal cranial nerves (V, VII, IX, and X) and ventral cranial nerves (III, IV, VI, and XII). Like spinal nerves, the cranial nerves supply somatic and visceral tissues and carry general sensory and motor information. Some cranial nerves consist of only sensory or only motor fibers. Other nerves are **mixed,** containing both types. Cranial nerves concerned with localized senses (e.g., sight, hearing, lateral line, olfaction, taste) are called **special cranial nerves** to distinguish them from those concerned with the sensory or motor innervation of the more widely distributed viscera, **general cranial nerves.**

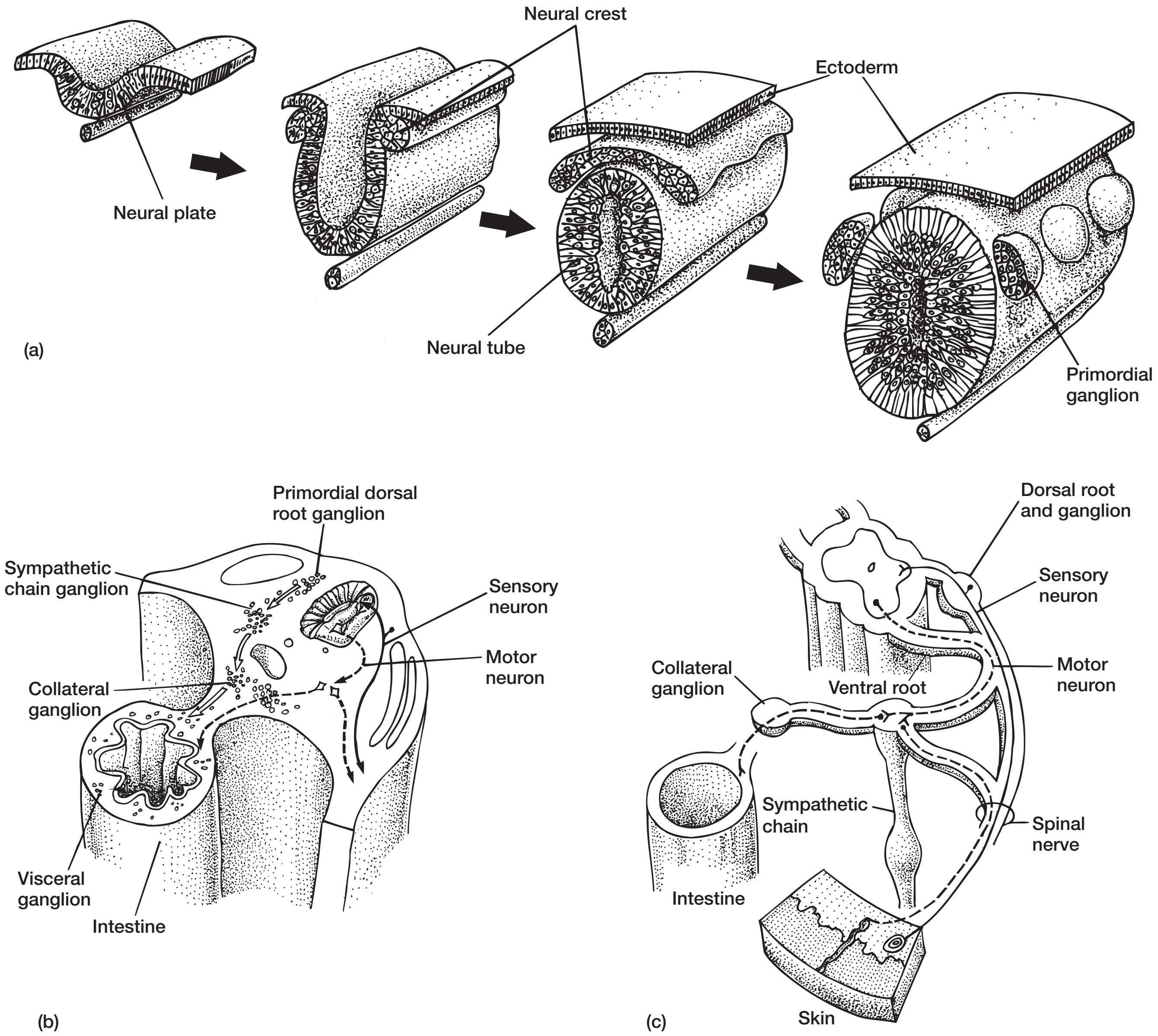


FIGURE 16.8 **Embryonic development of afferent and efferent spinal nerves.** (a) The neural crest forms from ectoderm during neurulation and becomes organized as segmental populations of cells arranged dorsally along the neural tube. (b) From this dorsal location, some cells migrate (open arrows) to specific sites within the body, forming distinct populations of neural cells at these sites. Neurons differentiating within the primordial dorsal root sprout cell processes that grow back to the neural tube and out to both somatic and visceral tissues. Neuronal bodies that remain in position constitute the dorsal root ganglion. Neurons differentiating within other populations grow cell processes to effectors, and their bodies constitute ganglia. Motor neurons differentiate within the neural tube and grow cell processes to these peripheral ganglia or directly to effectors. (c) Diagrammatic representation of established afferent and efferent neurons within spinal nerves.

(a) After Krstić; (b,c) after Tuchmann–Duplessis et al.

Primitively, all cranial nerves serving the branchial pouches formed three branches per pouch: **pretrematic, posttrematic,** and **pharyngeal** (figure 16.10). In amniotes, these tend to be lost or their homologies become uncertain.

Most anamniotes possess 17 cranial nerves. The first few spinal nerves behind the braincase become housed in the skull of later derived groups. But in anamniotes, these anterior spinal nerves are still partially outside the skull. In cyclostomes, these anterior spinal nerves outside the skull are called **occipitospinal nerves.** In other fishes and amphibians, the anterior spinal nerves become partially incorporated into the braincase. They exit via foramina in the occipital region of the skull and are called **occipital nerves.** Occipital nerves unite with the next few cervical spinal nerves to form the composite **hypobranchial nerve** that supplies hypobranchial muscles in the throat (figure 16.11a,b).

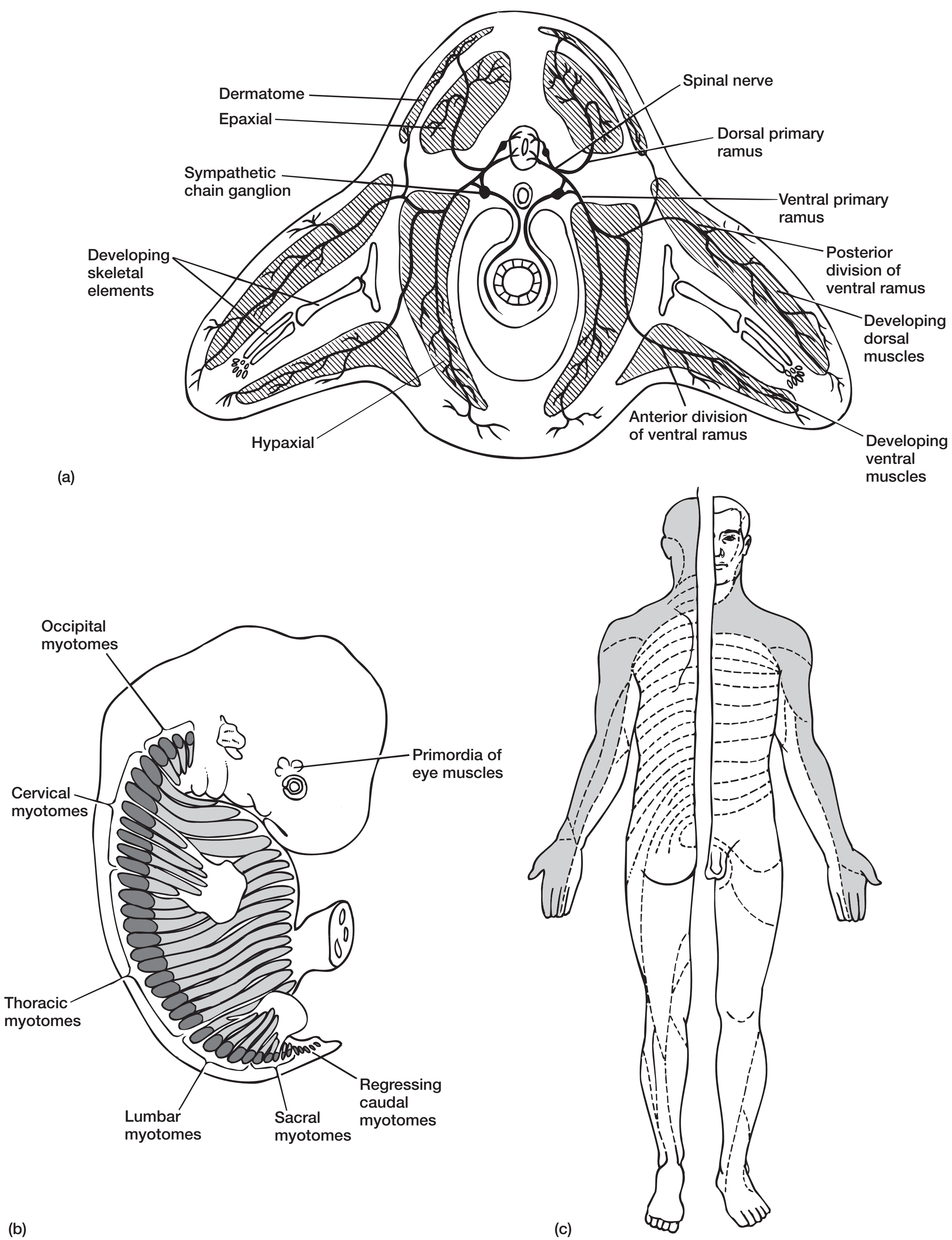


FIGURE 16.9 Spinal nerves supply vertebrate limbs and body walls. (a) Cross section of a generalized vertebrate. Note the distribution of spinal nerves to axial and appendicular muscles. (b) Sagittal section of human embryo illustrating the distribution of myotomes served by segmental spinal nerves. (c) Split image showing dorsal and ventral distribution of dermatomes within the human body.

After Patten and Carlson.

BOX ESSAY 16.2 Shingles

Shingles is the common name for a disease caused by the virus *Herpes zoster,* the same virus that produces chicken pox. Shingles is characterized by a line of blisters that usually radiate out along one side of the body following one of the spinal or cranial nerves to a dermatome.

For most people, chicken pox is a childhood disease that lasts several weeks. It causes itchy blisters over the body and also provides a few days of respite from school. Eventually, the immune system forces the virus into remission. Subsequent events are not well known, but it is thought that the virus retreats to the perikarya of neurons and is held in check there by the immune system. For most people, that is the end of *Herpes zoster.* But in some, the immune system lets down a bit and the virus proliferates, except that during this second flare-up, its spread is more restricted. The virus migrates along a nerve to the dermatome it supplies (see figure 16.9b,c). The tissue along this pathway reacts by forming the characteristic but very painful blisters. When the immune system responds again, the virus is beaten back, usually but not always, for the last time, and the symptoms of the disease abate.

Our knowledge of nerve anatomy and corresponding dermatome associations aids in the diagnosis of shingles. In most cases, it is possible to determine from the pattern of blisters which spinal or cranial nerve the virus spreads along.

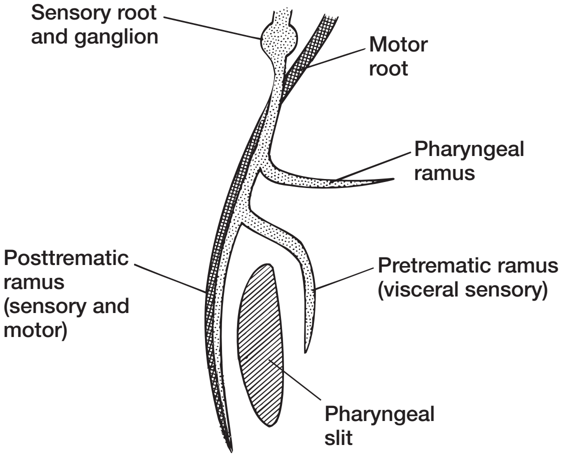


FIGURE 16.10 Components of a cranial nerve in a fish. The pharyngeal ramus, to the lining of the pharynx, and the small pretrematic ramus, to the front of the pharyngeal slit, both carry visceral sensory fibers. The dorsal ramus from the skin is composed of somatic sensory fibers. The posttrematic ramus running down the back of the pharyngeal slit includes both sensory and motor fibers. Rostral is to the right of the figure.

Latimeria (coelacanth) and many amphibians have 17 cranial nerves. In amniotes, the lateral line nerves are lost and the occipitospinal nerves are incorporated into the skull and modified. Their roots shift from the spinal cord forward into the medulla. In this way, amniotes derive the eleventh and twelfth cranial nerves. The 12 numbered cranial nerves are illustrated in figures 16.12 through 16.15. They are described in more detail next, and their functions are summarized in table 16.1.

Nervus Terminalis (0) The **terminal nerve** may be testimony to an ancient anterior head segment that has been lost. The terminal nerve is a nerve, or perhaps a complex of nerves, that arises from olfactory placodes. It is present in all classes of gnathostomes except birds. It runs to blood vessels of the olfactory epithelium in the olfactory sac and carries visceral sensory and some motor fibers. A role in reproduction is suspected.

Olfactory Nerve (I) The **olfactory nerve** is a sensory nerve concerned with the sense of smell. Olfactory cells lie in the mucous membrane of the olfactory sac. A short axon leads from each cell to the olfactory bulb. Each axon constitutes an olfactory fiber. Collectively, the olfactory fibers form the short olfactory nerve, which is the only cranial nerve composed of the axons of the receptor cells themselves.

Optic Nerve (II) Strictly speaking, the **optic nerve** is not a nerve but a sensory tract. That is, it is not a collection of peripheral axons; it is a collection of fibers in the CNS. Embryologically, it develops as an outpocketing of the brain. However, once it is differentiated, it lies outside the brain. Its fibers synapse in the thalamus and midbrain.

Oculomotor Nerve (III) The **oculomotor nerve** primarily supplies extrinsic eye muscles (superior rectus, medial rectus, inferior rectus, and inferior oblique muscles) derived from preotic myotomes. It is a motor nerve that also carries a few visceral motor fibers to the iris and ciliary body of the eye. Fibers arise in the oculomotor nucleus in the floor of the midbrain.

Trochlear Nerve (IV) The **trochlear nerve** is a motor nerve that supplies the extrinsic, superior oblique eye muscle. Fibers arise in the trochlear nucleus of the midbrain.

Trigeminal Nerve or **Trigeminus (V)** The **trigeminus** is so named because it is formed of three branches: **ophthalmic (V_1), maxillary (V_2),** and **mandibular (V_3)** in amniotes (figures 16.12c and 16.15). The ophthalmic nerve, sometimes called the deep ophthalmic (= profundus) nerve to distinguish it from a more superficial nerve, usually merges with the other two branches. However, in anamniotes, the ophthalmic nerve often emerges from the brain separately. This

TABLE 16.1 Functional Components of Cranial Nerves in Amniotes

		Somatic Sensory		Visceral Sensory		Visceral Motor		Somatic Motor	
Cranial Nerve		**General**	**Special**	**General**	**Special**	**General**	**Special**	**General**	**Special**
0	Terminal	X		X					
I	Olfactory				X				
II	Optic		X						
III	Oculomotor					(X)		X	
IV	Trochlear							X	
V_1	Trigeminal	X							
$V_{2,3}$	Trigeminal proper	X							X
VI	Abducens								
VII	Facial	(X)		X	X	X			X
VIII	Auditory		X						
IX	Glossopharyngeal	(X)		X	X	X			X
X	Vagus	X		X		X			X
XI	Spinal accessory								X
XII	Hypoglossal							X	
	Lateral line		X						

Note: Parentheses indicate variable or negligible function in the category indicated.

independent emergence was once taken as evidence that it anciently supplied an anterior branchial arch that had since been lost. However, the ophthalmic nerve (V_1) arises embryologically from a placode, unlike the maxillary (V_2) and mandibular (V_3) that arise from neural crest, suggesting an independent origin for the ophthalmic altogether without the need to postulate an association with a lost branchial arch. The other two branches, the maxillary ramus (V_2) to the upper jaw and the mandibular ramus (V_3) to the lower jaw, presumably represent pretrematic and posttrematic rami of a typical branchial nerve to the mandibular arch.

The mixed trigeminus includes sensory fibers from the skin of the head and areas of the mouth and motor fibers to derivatives of the first branchial arch. Sensory fibers of the trigeminus return to the brain from the skin, teeth, and other areas through each of the three branches. The mandibular branch also contains somatic motor fibers to muscles of the mandibular arch.

Abducens Nerve (VI) The **abducens** is the third of the three cranial nerves that innervate muscles controlling movements of the eyeball. It is a motor nerve that supplies the extrinsic, lateral rectus eye muscle. Fibers arise in abducens nucleus located in the medulla.

Facial Nerve (VII) The mixed **facial nerve** includes sensory fibers from taste buds as well as motor fibers that service derivatives of the second (hyoid) arch. This nerve also carries a substantial number of somatic sensory fibers to the skin. In fishes, the skin of the entire opercular complex is innervated by the facial nerve.

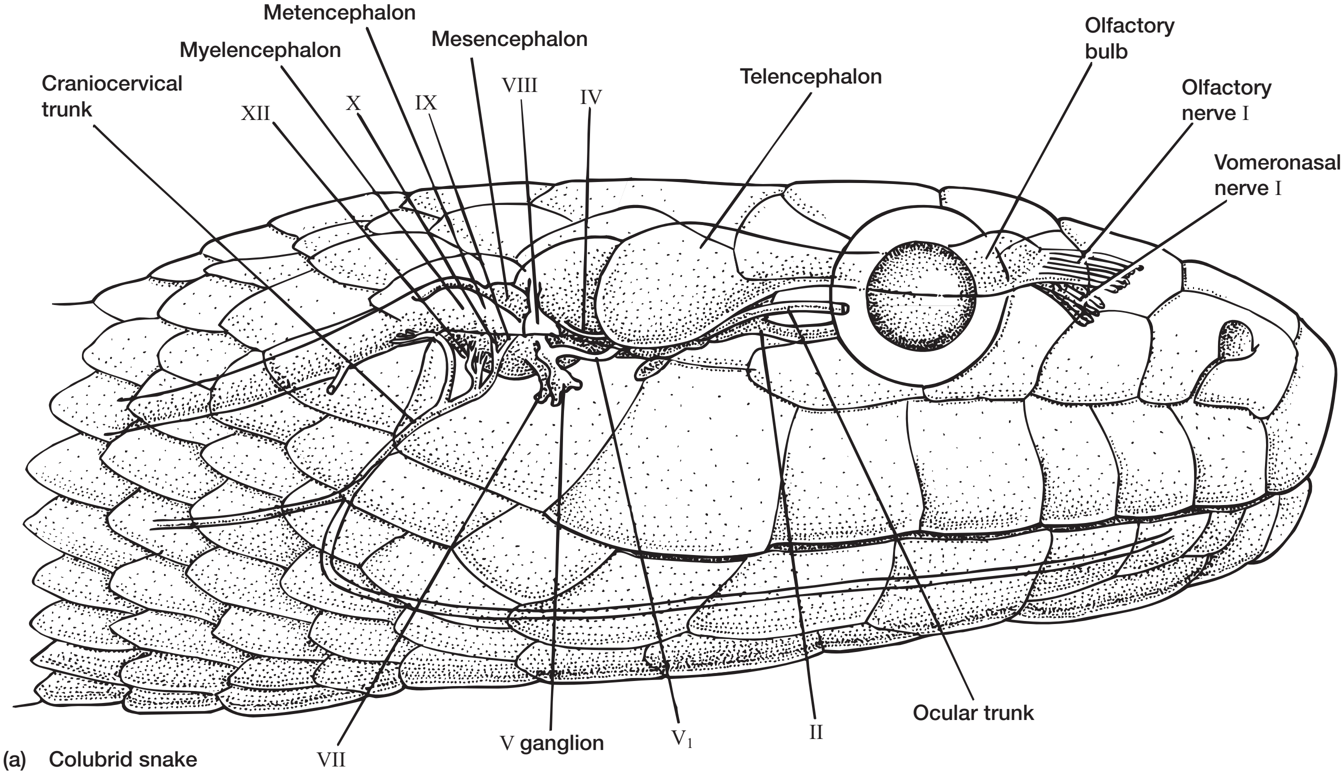
Octaval (= Auditory) Nerve (VIII) The sensory **octaval nerve** (acoustic, vestibulocochlear, statoacoustic) carries sensory fibers from the inner ear, which is concerned with balance and hearing. The nerve synapses in several regions of the medulla.

Glossopharyngeal Nerve (IX) The mixed **glossopharyngeal nerve** supplies the third branchial arch. It contains sensory fibers from the taste buds, the first gill pouch, and the adjacent pharyngeal lining. Motor fibers innervate muscles of the third branchial arch.

Vagus Nerve (X) The term **vagus** is Latin for wandering and aptly applies to this mixed nerve. The vagus meanders widely, serving areas of the mouth, pharynx, and most of the viscera. It is formed by the union of several roots across several head segments. Occasionally, additional nerves of the lateral line merge with the vagus.

Spinal Accessory Nerve (XI) In anamniotes, the **spinal accessory nerve** is probably composed of a branch of the vagus nerve and several occipitospinal nerves. In amniotes, especially in birds and mammals, it is a small but distinct motor nerve that supplies derivatives of the cucullaris muscle (cleidomastoid, sternomastoid, trapezius). A few of its fibers accompany the vagus nerve to supply part of the pharynx and larynx and perhaps the heart. Fibers arise from several nuclei within the medulla.

Hypoglossal Nerve (XII) The **hypoglossal nerve** is a motor nerve of amniotes that innervates hyoid and tongue muscles. Fibers originate in the hypoglossal nucleus within



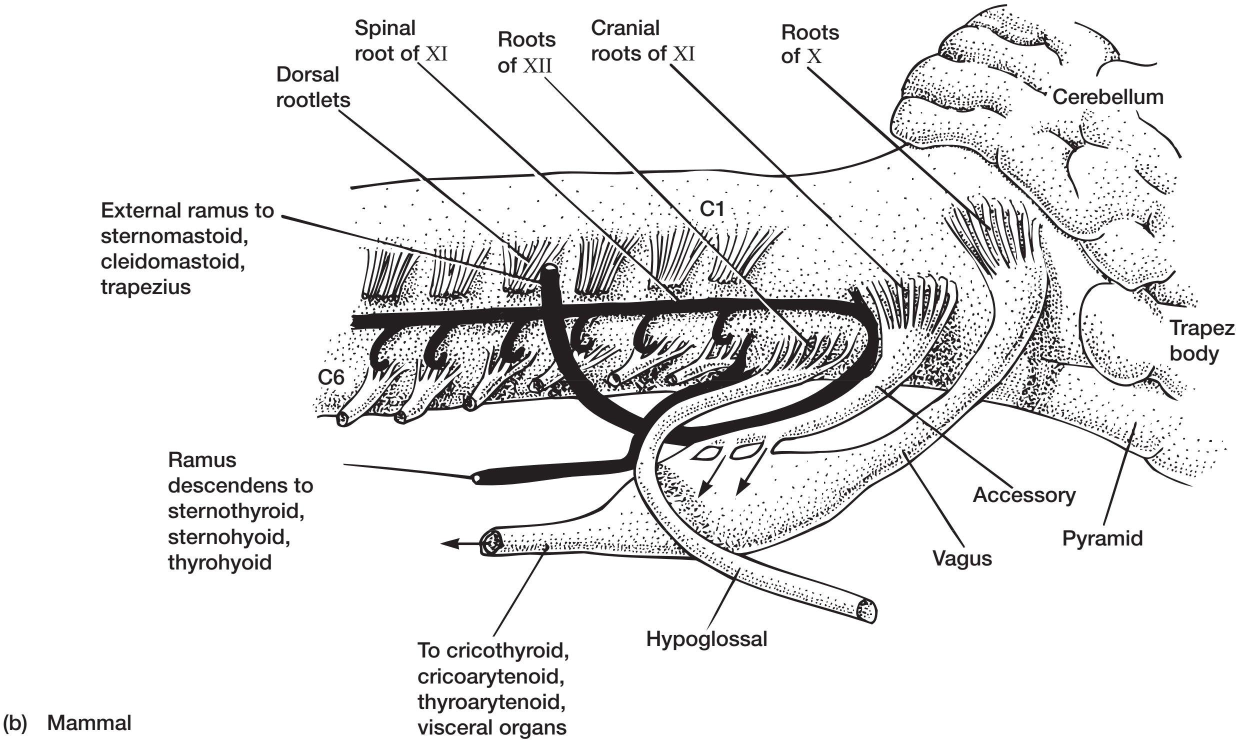


FIGURE 16.11 **Posterior cranial nerves.** (a) Colubrid snake. The glossopharyngeal (IX), vagus (X), hypoglossal (XII), and one of the spinal nerves join to form the craniocervical trunk. Unlike most other amniotes, snakes appear to lack a spinal accessory nerve (XI). (b) Mammal. The roots of the hypoglossal nerve are in series with the ventral roots of the preceding spinal nerves. Spinal nerve contributions to the accessory (XI) and hypoglossal (XII) nerves are shown in solid black. The vagus receives contributions from the accessory nerves (arrows).

(b) After Kent.

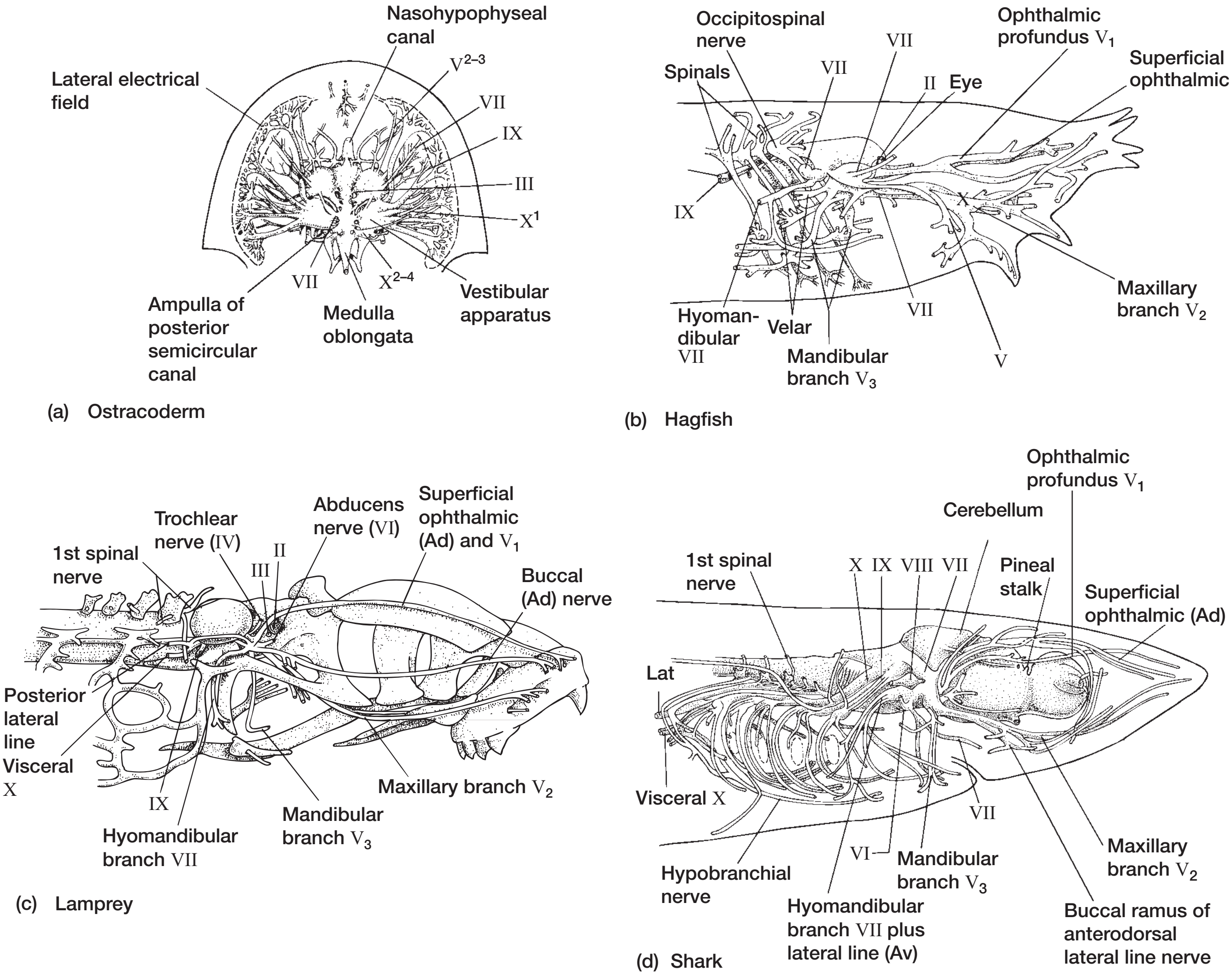
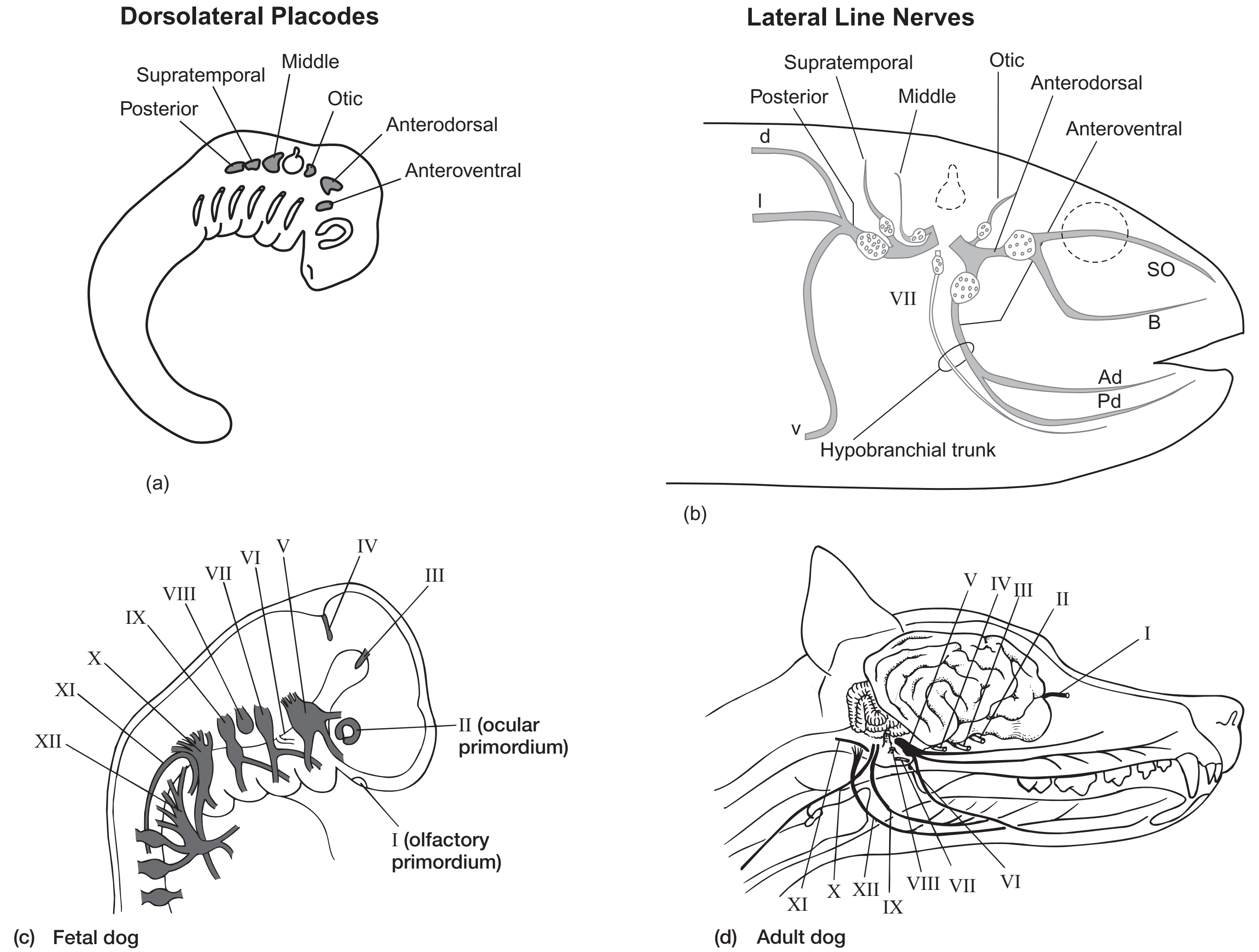


FIGURE 16.12 **Cranial nerves of vertebrates.** (a) Ostracoderm, *Kiaeraspis*. (b) Hagfish, *Myxine*. (c) Lamprey. (d) Lateral view of cranial nerves in the shark, *Squalus*. Abbreviations: anterodorsal lateral line nerve (Ad), anteroventral lateral line nerve (Av).

(a) After Stensiö; (b–d) after Jollie.

the medulla. In fishes and amphibians, the confluence of one or several occipital nerves (ventral roots of original spinal nerves) and often modified spinal nerves form the hypobranchial nerve. In amniotes it is incorporated into the skull and therefore more appropriately recognized as a cranial nerve, the hypoglossal nerve.

Lateral Line Nerves In addition to formally numbered cranial nerves, fishes possess preotic and postotic **lateral line cranial nerves** that are rooted in the medulla and supply the lateral line system. They were once thought to be components of the facial, glossopharyngeal, and vagal nerves, but they are now recognized as independent cranial nerves, derivatives of the dorsolateral placodes (octavolateralis placodes) (figure 16.13a). Unfortunately, this late recognition as distinct cranial nerves has left them without an identifying Roman numeral. In most jawed fishes and some amphibians, up to six pairs of lateral line nerves are present. Three are preotic (rostral to the otic vesicle, future inner ear): the anterodorsal, anteroventral, and otic lateral line nerves; three are postotic: the middle, supratemporal, and posterior lateral line nerves (figure 16.13a,b). Each of the dorsolateral placodes initially gives rise to a distinct sensory ganglion whose distal fibers innervate the lateral line receptors (neuromasts and ampullary organs) that themselves also arise from the same placode. Only rarely are any of the ganglia of the lateral line nerves fused with cranial nerves V, VII, IX, and X, but all preotic and all postotic lateral line nerves converge, entering the brain rostral and caudal to the otic vesicle, respectively. Frequently each converged nerve divides into a dorsal and ventral root. If present, the dorsal root only carries fibers that innervate ampullary organs and the ventral root only carries fibers that innervate the neuromast organs. Because



(c) Fetal dog

(d) Adult dog

FIGURE 16.13 Embryonic development of cranial nerves. (a) The lateral line cranial nerves arise from the dorsolateral placodes. (b) Generalized number and innervation pattern of lateral line nerves in jawed fishes. Ganglia are represented by expanded areas with small circles inside. Relative position of eye (dashed circle) and otic vesicle (dashed pear-shape) are indicated. Hypobranchial trunk includes the lateral line nerve and the facial cranial nerve VII. (c) Fetal dog. (d) Adult dog. The posterior lateral line nerve has three rami: dorsal (d), lateral (l), and ventral (v). The anterodorsal lateral line nerve has two major rami: the superficial ophthalmic (SO) and buccal (B). The anteroventral lateral line nerve produces two major rami: the anterior (Ad) and posterior (Pd) divisions.

(b) After Northcutt.

the lateral line and the octaval nerves share organizational similarities, they are often spoken of as the **octavolateralis system** (= acouticolateralis).

Mechanoreceptors, neuromasts (p. 693); electroreceptors, ampullary organs (p. 709); lateral line system (p. 694)

Evolution

In early vertebrates, each head segment may have been innervated by anatomically separate dorsal and ventral roots in much the same way that separate dorsal and ventral spinal nerves supply each trunk segment in lampreys. Each segment was perhaps innervated by a mixed dorsal nerve and a motor ventral nerve. It has been suggested that the cranial nerves are derived from losses or mergers of these separate dorsal and ventral nerves. But complex fusions and losses make it difficult to determine the distribution of ancient nerves to their respective head segments. The mandibular arch incorporates the deep ophthalmic nerve into its own dorsal root branches (the maxillary and mandibular branches), forming the composite trigeminal nerve. Other persisting dorsal nerves include the facial, glossopharyngeal, vagus, and accessory nerves. Ventral nerve derivatives include the oculomotor, trochlear, abducens, and occipital nerves.

When associated with a branchial arch, each cranial nerve exhibits fidelity to that particular arch and its muscles. Consistently throughout vertebrates, the first arch, the mandibular, is innervated by the trigeminal nerve (V); the

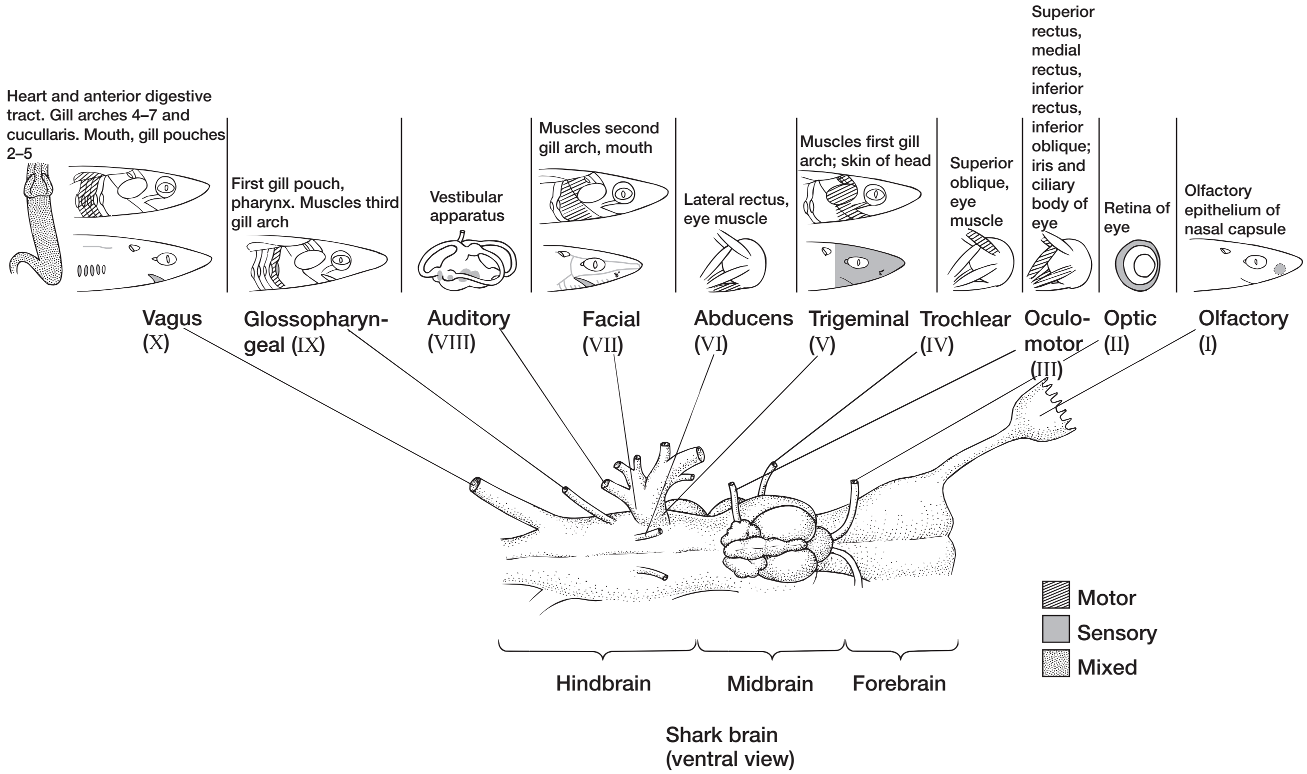


FIGURE 16.14 **Distribution of cranial nerves in the shark *Squalus*.** Enlarged views of the innervated structures of cranial nerves II, III, IV, VI, and X. Lateral views of the head with and without skin indicate the location of the first ten cranial nerves.

After Gilbert.

second, the hyoid, by the facial nerve (VII); the third, by the glossopharyngeal (IX); and the remaining arches by the vagus (X) and spinal accessory (XI) nerves (table 16.2 and figure 16.16a,b).

The olfactory (I), optic (II), and auditory (VIII) nerves and the lateral line cranial nerves are believed to be derived separately in conjunction with their respective special sense organs rather than in association with ancient head segments.

The shift from aquatic to terrestrial life is reflected in the cranial nerves. The lateral line system, devoted to detecting water currents, is completely lost in terrestrial vertebrates, as are the cranial nerves that served it. Pre- and posttrematic branches associated with the gills are modified as well. The spinal accessory and hypoglossal nerves enlarge or emerge as separate cranial nerves. The spinal accessory separates from the vagus nerve. It supplies the branchiomeric muscles that become more prominent in holding and rotating the head. The hypoglossal nerve to the tongue and hyoid apparatus becomes prominent as the role of these structures in terrestrial feeding and manipulating food in the mouth expands.

Functions of the Peripheral Nervous System

Spinal Reflexes

Spinal reflexes exhibit the simplest level of control within the nervous system. Although reflexes can disperse information to higher centers, all of their necessary and functional components reside or are rooted in the spinal cord. The **spinal reflex** is a circuit of neurons from a receptor to the spinal cord and out to an effector. Incoming sensory and departing motor information travels in circuits laid down by neurons in the spinal nerves. Within the spinal cord, **association neurons (interneurons, internuncial neurons)** connect these sensory and motor neurons to complete the circuit between them. There are two types of spinal reflex arcs, somatic and visceral (figure 16.17). The neuronal circuitry for each type of arc is distinctive, at least in mammals, where it has been most widely studied (table 16.3). The role of the central nervous system in modifying spinal reflexes is discussed later in this chapter.

Most **somatic reflex arcs** at the level of the spinal cord include three neurons: somatic sensory and somatic motor neurons, with an association neuron connecting them. The body of the somatic sensory neuron is located in the dorsal root. Its nerve fibers travel through the spinal nerve and synapse with an association neuron within the spinal cord. The association neuron may transmit impulses in several possible directions. It may synapse with a somatic motor neuron on the same side of the cord, on the opposite side of the cord, or travel up or down the cord to motor neurons at different levels. The motor neuron then transmits the impulse through the ventral root to a somatic effector. A somatic reflex arc may be even more simple. Spinal reflexes controlling posture involve only two neurons. The sensory neuron synapses

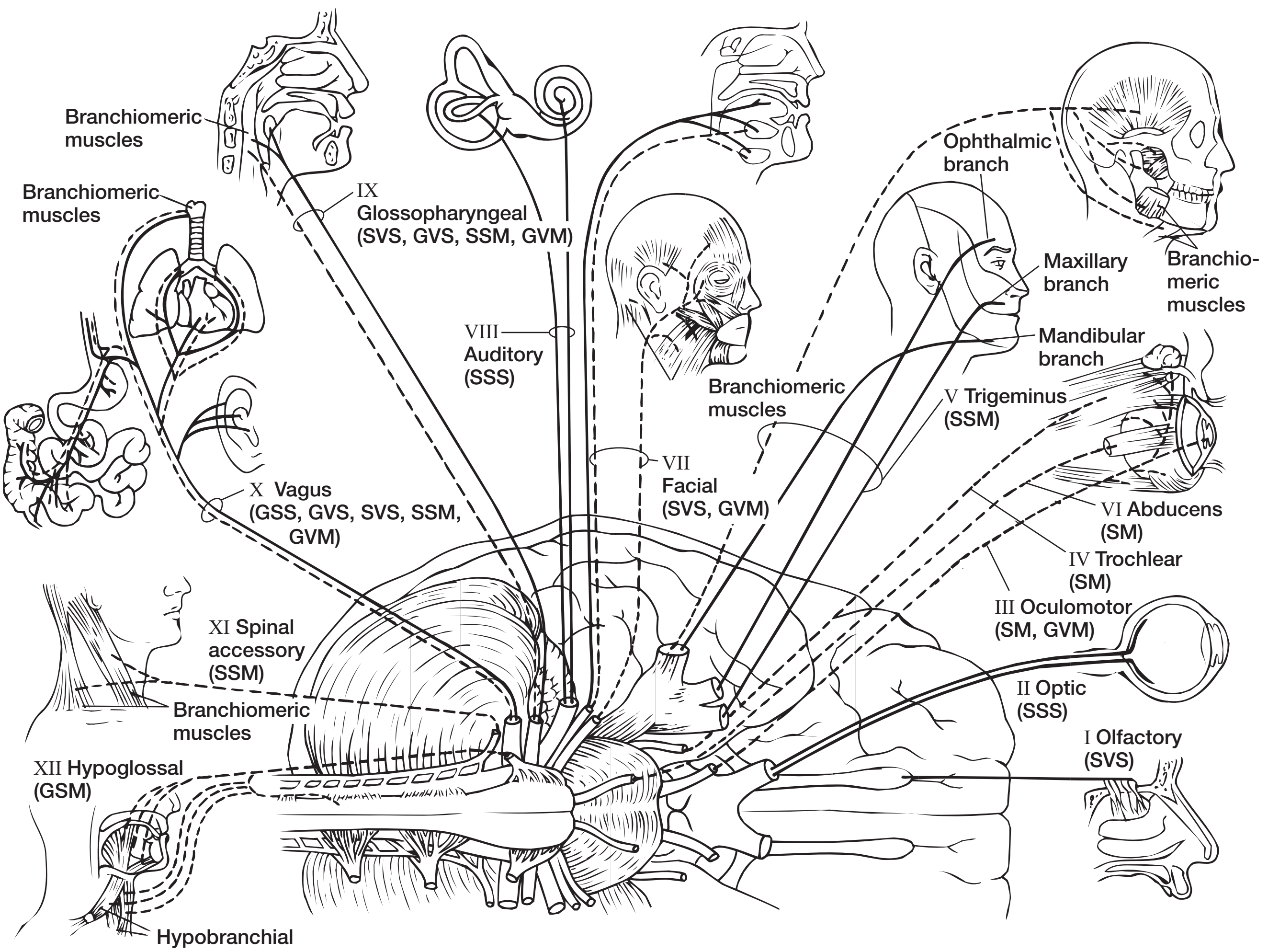


FIGURE 16.15 **Distribution of cranial nerves in a mammal, *Homo sapiens*.** Sensory (solid lines) and motor (dashed lines) nerve fibers are indicated. Enlarged views of innervated structures of cranial nerves are shown around the human brain in ventral view. Abbreviations: general somatic sensory (GSS), general visceral sensory (GVS), general somatic motor (GSM), general visceral motor (GVM), special somatic sensory (SSS), special somatic motor (SSM), special visceral sensory (SVS).

After H. M. Smith.

TABLE 16.2 Cranial Nerves and Their Associated Branchial Arches

Ancient Segment	Current Arch	Dorsal Root Representative	Ventral Root Representative
?		Terminal (0)	
0		Deep ophthalmic (V)	Oculomotor
—	Mandibular		
1		Superficial ophthalmic (skin; V) maxillary (pretrematic; V) mandibularis (posttrematic; V)	Trochlear
2	Hyoid	Facial (VII)	Abducens
3	Branchial 3	Glossopharyngeal (IX)	
4	Branchial 4	Vagus (X)	
5	Branchial 5	Vagus (X)	Hypoglossal
6	Branchial 6	Vagus (X)	Hypoglossal
7	Branchial 7	Spinal accessory (XI)	Hypoglossal

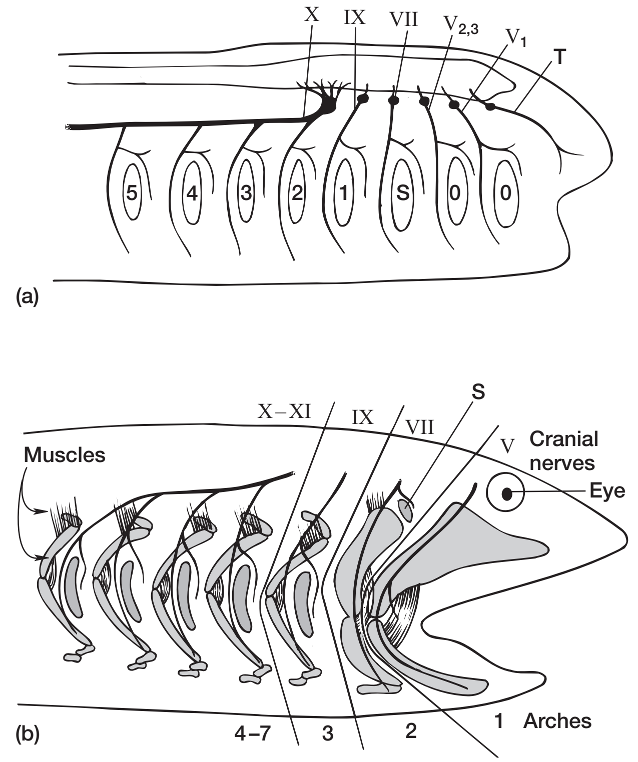


FIGURE 16.16 Phylogenetic derivation of cranial nerves. (a) Hypothesized primitive condition. Each pharyngeal slit was supplied by a nerve. The first, or terminal (T), nerve supplied an anterior arch that was lost early in vertebrate evolution. (b) Nerve supply to associated branchial arches. Cranial nerves V, VII, IX, and X–XI supply the following arches: mandibular (1), hyoid (2), third (3), and fourth–seventh (4–7), respectively. These associations between cranial nerves and their derivatives remain stable throughout teleosts and tetrapods. Abbreviations: gill slits lost in gnathostomes (0, 0′), gill slits usually present in gnathostomes (1–5), spiracular slit (S).

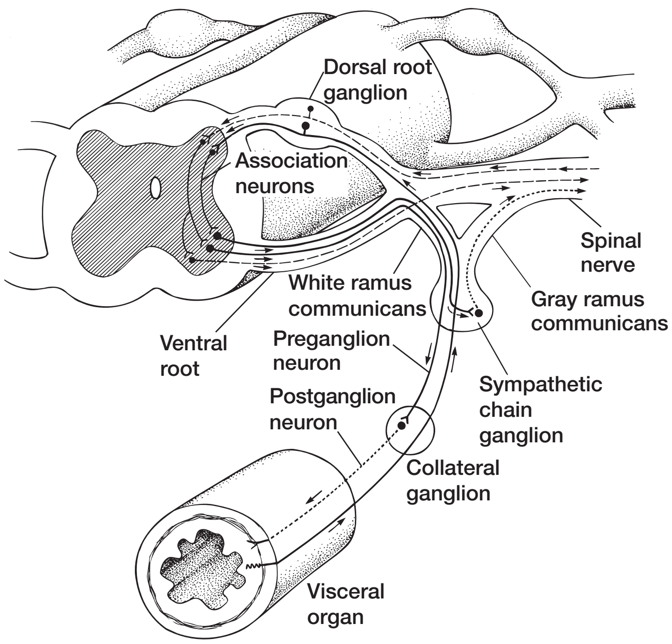


FIGURE 16.17 Somatic and visceral reflex arcs of mammals. Sensory input arrives in fibers of the dorsal root that synapse in the spinal cord. Motor output departs in fibers of the ventral root. An association neuron usually connects input and output within the spinal cord. Somatic sensory fibers reach the dorsal root via a spinal nerve. Visceral sensory fibers travel from the visceral organ through one or more ganglia and then through the ramus communicans and the dorsal root finally to synapse in the spinal cord. The somatic motor outflow includes a single neuron that sends its fiber out from the spinal nerve to the effector. The visceral motor outflow includes two neurons in series: a preganglionic neuron (solid line) and a postganglionic neuron (dotted line). The synapse between them can occur in a sympathetic chain ganglion, in a collateral ganglion, or in the wall of the innervated organ. If they synapse in the sympathetic chain, postganglionic fibers usually reach the effector via the spinal nerve.

TABLE 16.3 Reflexes in Mammals

Components of a Reflex Circuit	Somatic Arc	Visceral Arc
Effector	Skeletal muscle	Cardiac and smooth muscle, glands
Number of neurons in circuitry	Three (or two) neurons: sensory (association) and motor	Four neurons: sensory (association), preganglionic motor, postganglionic motor
Neurotransmitters	Acetylcholine	Acetylcholine, norepinephrine

directly with the motor neuron. If an animal should start to deviate inadvertently from its normal posture, its muscles are stretched. These stretched muscles elicit a somatic reflex that causes the appropriate muscle to contract and restore the animal to its original posture (figure 16.18a,b).

The **visceral reflex arc** is structurally more complex. The body of a visceral sensory neuron also resides in the dorsal root, but its nerve fibers travel through one or more sympathetic chain ganglia and then through the ramus communicans. Its axons eventually synapse within the spinal cord with an association neuron (figure 16.17). Unlike with the somatic arc, the motor output of the visceral reflex arc includes two neurons in sequence. The first is the **preganglionic neuron,** which extends out the ventral root and synapses in the sympathetic ganglion, in a collateral ganglion, or in the wall of a visceral organ with a second neuron, the **postganglionic neuron.** The postganglionic neuron travels on to innervate the effector visceral organ. Thus, at its simplest, the visceral arc includes four neurons: one visceral sensory neuron, two visceral motor neurons in series, and an interconnecting association neuron.

In summary, the somatic arc includes somatic afferent neurons that carry sensory impulses to the CNS from skin, voluntary muscles, and tendons. Somatic efferent neurons

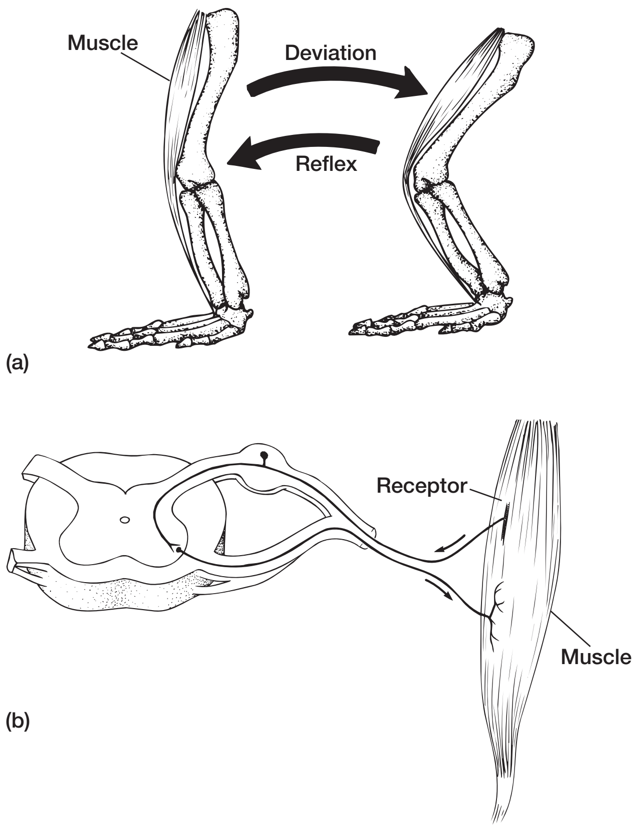


FIGURE 16.18 Somatic reflex arc. (a) Posture can be maintained through a spinal reflex involving a single sensory and single motor neuron connected directly within the spinal cord. When a tetrapod begins to deviate from its normal posture, sensory receptors within joints and muscles detect the deviation. (b) Sensory fibers that carry this impulse to the spinal cord synapse with appropriate motor neurons that stimulate skeletal muscle motor units to contract, straighten the limb, and restore normal posture.

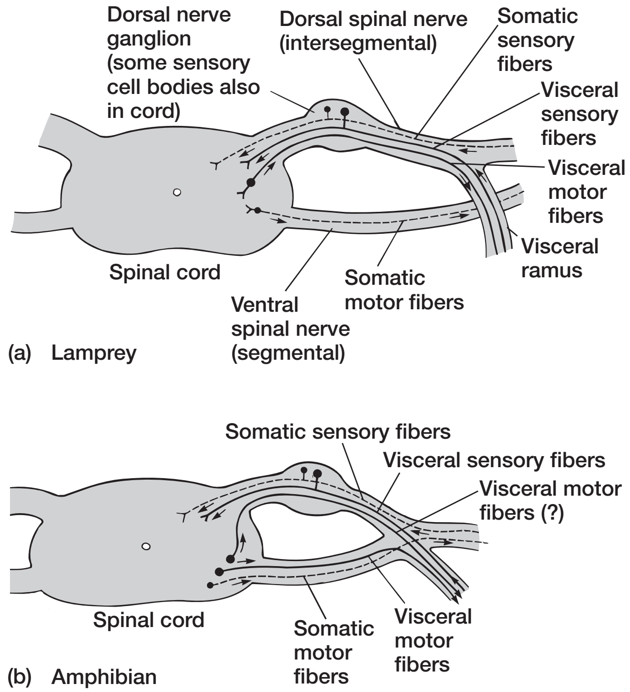


FIGURE 16.19 Somatic and visceral circuits in anamniotes. (a) Lamprey. (b) Amphibian. It is unclear whether the amphibian dorsal root carries visceral motor output.

After Hildebrand.

deliver motor impulses to somatic effectors. The visceral arc includes visceral afferent neurons that carry sensory impulses to the CNS from the digestive tract and other internal structures. The visceral efferent neurons carry motor impulses to visceral organs; this part of the circuit includes two neurons: preganglionic and postganglionic.

In amniotes, the dorsal root carries predominantly sensory information, which can be somatic or visceral. The ventral root almost exclusively carries motor information, which can be somatic or visceral. In anamniotes, there is considerable variation in both the structure of the spinal nerve pathways and the information they carry. In lampreys, the dorsal and ventral roots do not join. The ventral root carries only somatic motor information transmitted to striated muscles at that level of the spinal cord. The dorsal root carries somatic and visceral sensory information as in amniotes, but it also carries visceral motor fibers (figure 16.19a). In fishes and amphibians, dorsal and ventral roots are joined, but visceral motor fibers depart via both the dorsal root, as in lampreys, and the ventral root, as in amniotes (figure 16.19b).

The Autonomic Nervous System

Early anatomists noticed that visceral activity did not appear to be under voluntary control. The peripheral nerves and ganglia associated with visceral activity seemed to be autonomous, or independent of the rest of the nervous system. Collectively, they were considered to constitute the autonomic nervous system, a functional division of the peripheral nervous system that presides over visceral activity. Both sensory and motor fibers are included. Autonomic sensory fibers monitor the internal environment of the organism—that is, blood pressure, oxygen and carbon dioxide tension, core and skin temperature, and activity of the viscera. Motor fibers are general visceral motor neurons that innervate cardiac muscle, smooth muscle, and glands. Thus, they control the digestive tract, blood vessels, respiratory tree, bladder, sex organs, and other general body viscera. Because the autonomic nervous system includes the general visceral motor circuit, pre- and postganglionic neurons in series characterize the motor innervation to each organ.

Conscious centers also can affect visceral activity controlled by the autonomic nervous system. For instance, through practiced meditation or through deliberate effort that brings a chilling thought to mind, it is possible to affect the heartbeat or the release of sweat. But, for the most part, the autonomic system operates subconsciously and is not under voluntary control. Reflexes control activities maintaining the internal environment. In its simplest form, the neuronal circuitry of the autonomic nervous system includes four neurons linked in a reflex loop: a sensory neuron that synapses with an association neuron that synapses with a preganglionic motor neuron in series with a postganglionic motor neuron.

Functional Divisions of the Autonomic Nervous System In mammals, the autonomic nervous system is divided into two contrasting, antagonistic systems of control over visceral activity: the sympathetic system and the parasympathetic system.

The **sympathetic nervous system** prepares the body for strenuous action by increasing activity of the viscera, although it slows digestive processes. Stimulation of the sympathetic system inhibits activity of the alimentary canal but promotes contraction of the spleen (causing it to release extra red blood cells into the general circulation), increases heart rate and blood pressure, dilates coronary blood vessels, and mobilizes glucose from glycogen storage in the liver. It is often said that the sympathetic nervous system prepares the individual to **fight or flee**, perhaps indicative of an organism's quotient of courage or wisdom (table 16.4).

The general visceral motor nerves that participate in sympathetic activity depart from the thoracic and lumbar regions of the mammalian spinal cord. This activity is referred to as the **thoracolumbar outflow.** The sympathetic preganglionic neuron is usually short and synapses in the sympathetic chain ganglion or in a ganglion located away from the vertebral column. The postganglionic fiber is usually long (figure 16.20).

The **parasympathetic nervous system** restores the body to a restful or vegetative state by lowering its activity level, although digestion is stimulated. The effects of the parasympathetic system are antagonistic to those of the sympathetic system. It enhances digestion, slows heart rate, drops blood pressure, constricts coronary vessels, and promotes glycogen formation.

Participating visceral motor neurons include cranial nerves VII, IX, and X together with spinal nerves departing from the sacral region. This is referred to as **craniosacral outflow.** Parasympathetic preganglionic fibers are long and reach to the wall of the organ they innervate and synapse with very short postganglionic fibers (figure 16.20).

Adrenergic and Cholinergic Control The sympathetic system is said to be **adrenergic** because the neurotransmitters released during stimulation are **adrenaline** or **noradrenaline** (also termed **epinephrine** and **norepinephrine**). The parasympathetic system is said to be **cholinergic** because the neurotransmitter released is **acetylcholine.** Acetylcholine is also released between pre- and postganglionic fibers in both systems (figure 16.20) and at junctions between nerves and skeletal muscles.

In mammals, almost every visceral organ has sympathetic and parasympathetic innervation (figure 16.21 and table 16.4). Exceptions to this double innervation include

TABLE 16.4 Functional Divisions of the Autonomic Nervous System

Organ/ Activity	Sympathetic Stimulation	Parasympathetic Stimulation
Eye		
Ciliary muscle	Relaxation	Contraction
Pupil	Dilation	Constriction
Glands		
Salivary	Vasoconstriction Slight secretion	Vasodilation Copious secretion
Gastric	Inhibition of secretion	Stimulation of secretion
Pancreas	Inhibition of secretion	Stimulation of secretion
Lacrimal	None	Secretion
Sweat	Sweating	None
Digestive tract		
Sphincters	Increase tone	Decrease tone
Walls	Decrease motility	Increase motility
Liver	Glucose release	None
Gallbladder	Relaxation	Contraction
Bladder		
Smooth muscle	Relaxation	Contraction
Sphincter	Contraction	Relaxation
Adrenal gland	Secretion[a]	None
Heart		
Muscle	Increase rate and force	Slowed rate
Coronary arteries	Dilatation	Constriction
Lungs (bronchi)	Dilatation	Constriction
Spleen	Contraction	Relaxation
Blood vessels		
Abdomen	Constriction	None
Skin	Constriction	None
Sex organs		
Penis	Ejaculation	Erection
Clitoris	?	Erection
Metabolism	Increased	None

[a] *Preganglionic neuron innervation.*

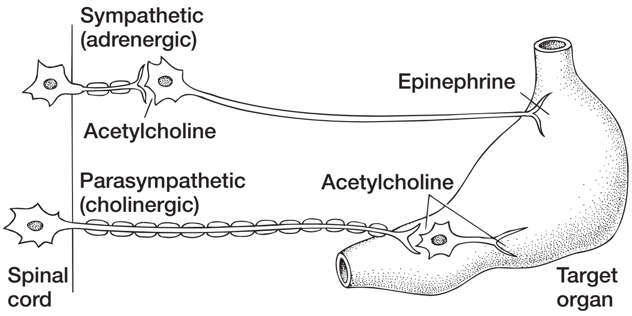


FIGURE 16.20 Neurotransmitters of the autonomic nervous system. Adrenergic and cholinergic neurotransmitters are released at the ends of the sympathetic and parasympathetic circuits, respectively. This is the basis for differential organ response.

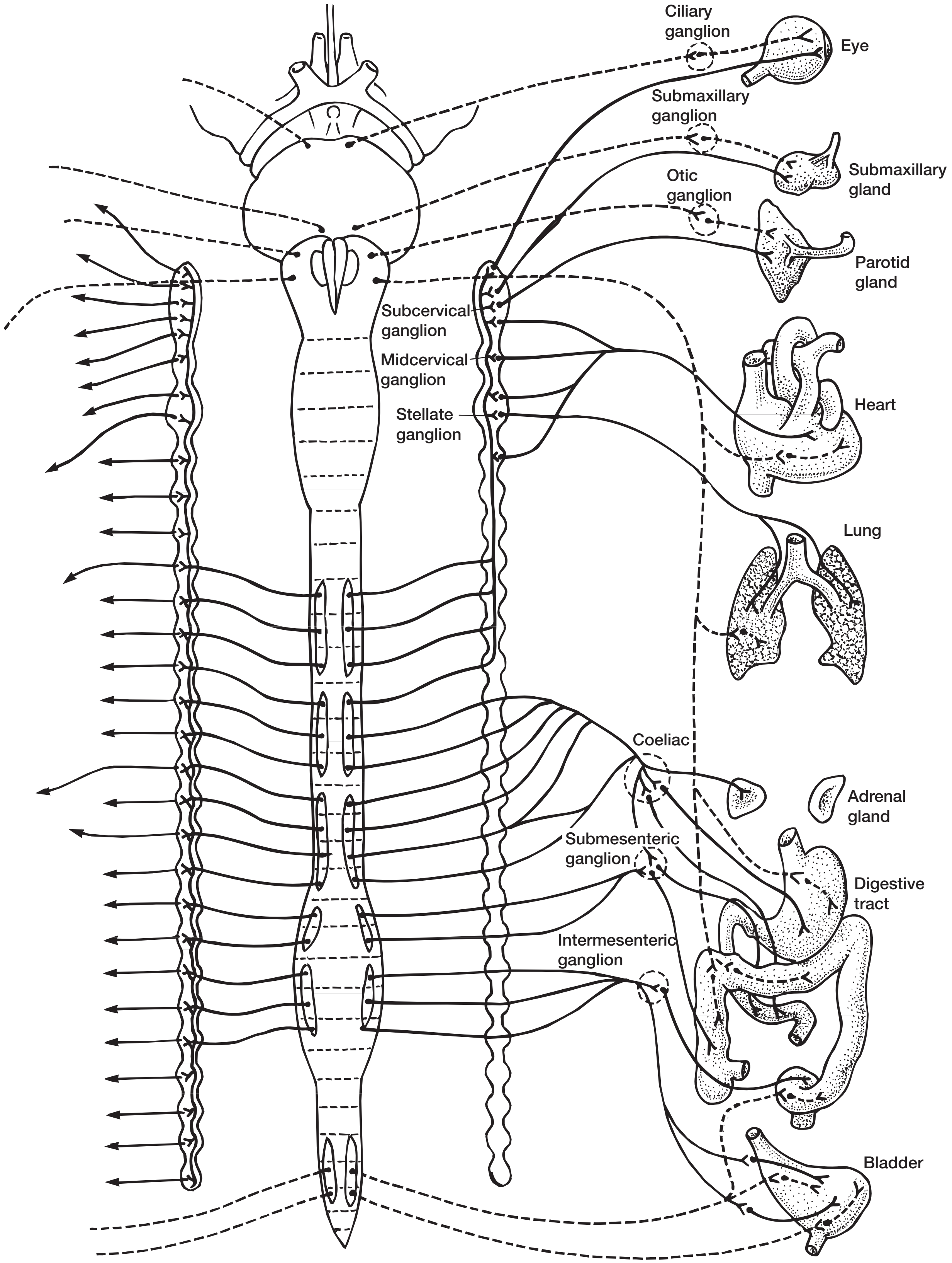


FIGURE 16.21 **Sympathetic (solid lines) and parasympathetic (dashed lines) systems in a mammal.** Note the double innervation of most organs. Preganglionic and postganglionic fibers are indicated.

Redrawn from H. Tuchmann-Duplessis et al., 1974. Illustrated Human Embryology, *Vol. III, Nervous System and Endocrine Glands. © 1974 Springer-Verlag, NY. Reprinted by permission.*

the adrenal gland, peripheral blood vessels, and sweat glands, all of which receive only sympathetic innervation. Cessation of sympathetic stimulation allows these organs to return to a resting state.

The adrenal gland is also exceptional in that it is innervated by the preganglionic fiber only; the postganglionic fiber is absent. Because epinephrine and norepinephrine serve both as adrenergic chemical signals of the sympathetic circuit and as hormones produced by the adrenal gland (see chapter 15), there is a possibility for chemical confusion. But the preganglionic neuron releases acetylcholine rather than adrenaline or similar chemicals, so direct innervation of the adrenal gland by preganglionic fibers removes the possibility of chemical ambiguity between parasympathetic innervation and hormonal stimulation by the gland.

Anatomical Divisions of the Autonomic Nervous System

The division of the autonomic nervous system into sympathetic and parasympathetic functional components holds reasonably well for mammals; however, in other vertebrates, the comparative anatomy of the autonomic nervous system is poorly understood. Most viscera receive contrasting sympathetic and parasympathetic innervation, but these functional divisions do not always correspond to thoracolumbar and craniosacral outflow, respectively. Often, in nonmammalian vertebrates, the autonomic nerves departing from these regions have a mixed function. When examining the location of autonomic nerves of anamniotes, we cannot safely infer function from anatomical position. Therefore, we prefer anatomical distinctions alone, without implied functional significance, when describing the autonomic nervous system of nonmammalian vertebrates.

There are three anatomical divisions of the autonomic nervous system: cranial autonomic, spinal autonomic, and enteric autonomic systems (table 16.5). The **cranial autonomic system** includes the cranial nerves leaving the brain. The **spinal autonomic system** consists of all autonomic fibers departing from the central nervous system in the spinal segments, specifically all thoracic, lumbar, and sacral autonomic fibers.

The **enteric autonomic system** includes intrinsic sensory and motor neurons residing in the wall of the digestive tract. The enteric system consists of large numbers of neurons, probably as many neurons as there are in the central nervous system. Nerves formed from these neurons interconnect and mingle to form woven patches of nerve processes, termed **plexuses,** within the wall of the digestive tract. The **myenteric plexuses** (Auerbach's plexuses) are situated within the outer wall of smooth muscles, and the **submucosal plexuses** (Meissner's plexuses) are located deep within smooth muscles near their lumen. The enteric autonomic system is responsible for coordination of digestive tract activity. It is independent from but can be modified by the spinal and cranial autonomic systems. Food distending the smooth muscles of the digestive tract mechanically stimulates enteric neurons. These neurons, in turn, activate contractions of the circular and longitudinal smooth muscles in the wall of the digestive tract, resulting in synchronized **peristaltic waves** that propel food through the tract. The enteric autonomic system seems to be present in all classes of vertebrates, although it may be poorly developed in some.

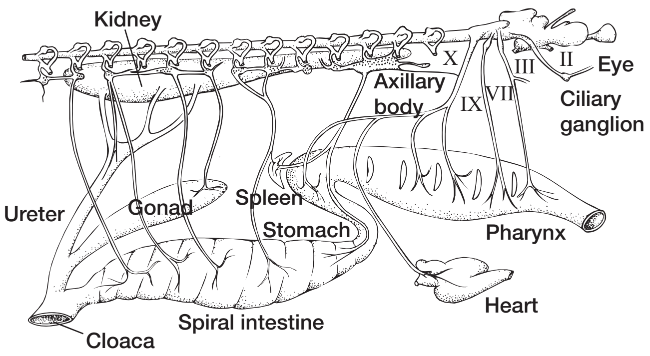
TABLE 16.5 Relationship between Functional and Anatomical Divisions of the Autonomic Nervous System

Location	Function (Mammals)	Anatomical Designation
Cranial	Parasympathetic	Cranial autonomic
Thoracic	Sympathetic	Spinal autonomic
Lumbar	Sympathetic	Spinal autonomic
Sacral	Parasympathetic	Spinal autonomic
Intrinsic digestive tract	Enteric	Enteric autonomic

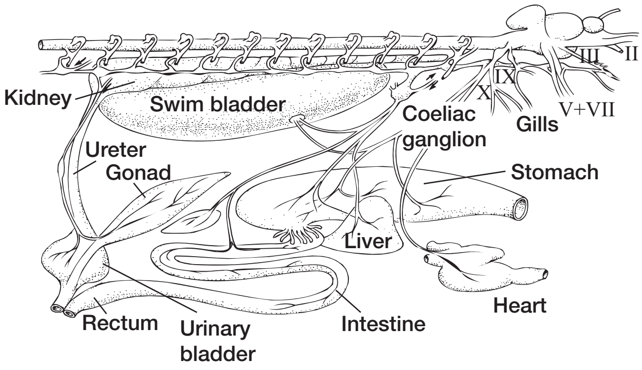
Fishes In cyclostomes, the autonomic nervous system is fragmentary. Sympathetic chains are absent, but collateral ganglia, presumably part of the autonomic system, are scattered throughout the viscera. In hagfishes, cranial autonomic fibers apparently occur only in the vagus (X). However, in lampreys, in addition to the vagus (X), the facial (VII) and glossopharyngeal (IX) nerves include autonomic fibers that mediate events in the gills. In hagfishes, spinal autonomic fibers pass through the ventral roots of spinal nerves, but their subsequent distribution is poorly known. In lampreys, spinal autonomic fibers depart through dorsal roots of the spinal nerves to supply the kidneys, gonads, blood vessels, posterior digestive tract, cloaca, and other viscera.

In chondrichthyan and osteichthyan fishes, the autonomic nervous system is well represented. A sympathetic chain of ganglia is present within the spinal autonomic system. Nerves of the cranial autonomic system pass to the viscera. However, in elasmobranchs, collateral ganglia are absent and sympathetic chains apparently do not contribute fibers to the cranial nerves. The vagus is well developed with branches to the stomach and heart, but the heart apparently lacks a sympathetic counterpart to the inhibitory vagal innervation (figure 16.22a). Further, the sympathetic ganglia of elasmobranchs are associated with populations of chromaffin cells, neural crest derivatives that in teleosts and most tetrapods (except urodeles) become separated from the ganglia. In most teleosts, collateral ganglia occur, and some spinal nerve fibers are shared with cranial nerves (figure 16.22b).

Tetrapods The autonomic nervous system is well developed in tetrapods. The paired sympathetic chain is present, collateral ganglia are dispersed among the viscera, and cranial and spinal nerves are well delineated. Autonomic outflow in amphibian spinal nerves passes through the ventral roots, but it is still unclear whether motor fibers also occur in the dorsal root (figure 16.23a). In reptiles, birds, and mammals, the autonomic systems are quite similar in basic construction.



(a) Elasmobranch



(b) Teleost

FIGURE 16.22 Autonomic nervous system of fishes. (a) Elasmobranch (shark). Notice that the vagus nerve (X), which supplies the pharynx, stomach, and heart, does not carry fibers from any of the spinal nerves. (b) Teleost. The vagus (X), which supplies most of the same viscera as in the shark as well as contributes to innervation of the swim bladder, is connected to the sympathetic chain.

Redrawn from S. Nilsson, 1983, "Autonomic nerve function in the vertebrates," in Zoophysiology. Ed. By D.S. Farmer, Springer-Verlag, NY, based on Young 1933, and Nilsson 1976. Reprinted by permission.

Spinal autonomic motor fibers depart via the ventral roots of spinal nerves (figure 16.23b,c).

Overview With the exception of cyclostomes, the anatomical organization of the autonomic nervous system is similar in all vertebrate classes. The spinal autonomic outflow includes a paired sympathetic chain (except in cyclostomes and elasmobranchs), with some fibers contributing to cranial nerves. The cranial autonomic outflow includes the facial (VII), glossopharyngeal (IX), and vagus (X) cranial nerves, although the facial and glossopharyngeal can be reduced in fishes. In vertebrates with eyes, the oculomotor (III) nerve may send fibers to the iris and ciliary muscles in the eyes.

In mammals, especially in humans, the autonomic nervous system is better known, and the circuits for motor outflow can be traced with greater confidence. The human autonomic nervous system includes a sympathetic thoracolumbar outflow and a parasympathetic craniosacral outflow. The existence of a sacral parasympathetic system in other vertebrates is still uncertain. The pelvic nerves of amphibians arising from the posterior end of the spinal cord and supplying the urinary bladder and rectum have traditionally been regarded as parasympathetic sacral outflow. However, even in mammals, sacral parasympathetic fibers mingle with thoracolumbar sympathetic fibers in the pelvic plexus, making it difficult to trace the posterior circuitry of these two systems on their way to visceral effectors. Until the comparative features of the autonomic nervous system are better known in vertebrates, the functional roles of autonomic nerves in nonmammalian classes must be inferred.

To summarize, somatic and visceral effectors receive motor information. Effectors and receptors are linked through the central nervous system. Control of much of the body's activity involves simple reflexes. The somatic reflex arc is primarily involved in controlling skeletal muscles. The visceral reflex arc is the basic component of the autonomic nervous system, which is responsible for monitoring internal visceral activity. We turn next to the central nervous system to examine its role in processing information.

Central Nervous System

The central nervous system primarily coordinates activities that enable an organism to survive and reproduce in its environment. In order to do this, the central nervous system must receive incoming information from several sources. Sensory receptors known as **interoceptors** gather information and respond to general sensations of organs within the internal environment. **Proprioceptors** are a type of interoceptor that inform the central nervous system about the position of the limbs and the degree to which joints are bent and muscles are stretched. This information-processing component of the nervous system is referred to as the **somatosensory system,** which includes proprioceptors and surface receptors within the skin. Sensations gathered by the somatosensory system are especially important in coordinating limb and body positions during locomotion. **Exteroceptors** gather information from the external environment. Sensations of touch, pressure, temperature, sight, hearing, smell, taste, and other stimuli from the external environment are transmitted via exteroceptors to the brain and spinal cord. A third source of information comes from memory, which allows an organism to adjust its activity on the basis of past experiences.

The central nervous system processes incoming information and returns instructions to the effectors (figure 16.24). These constitute the response of the organism. Entering information **diverges** to inform various areas of the brain and spinal cord about the state of affairs at that point. When a decision is made, instructions **converge** to the appropriate effectors. The spinal cord and brain carry the pathways through which this information travels and form the association areas where it is evaluated.

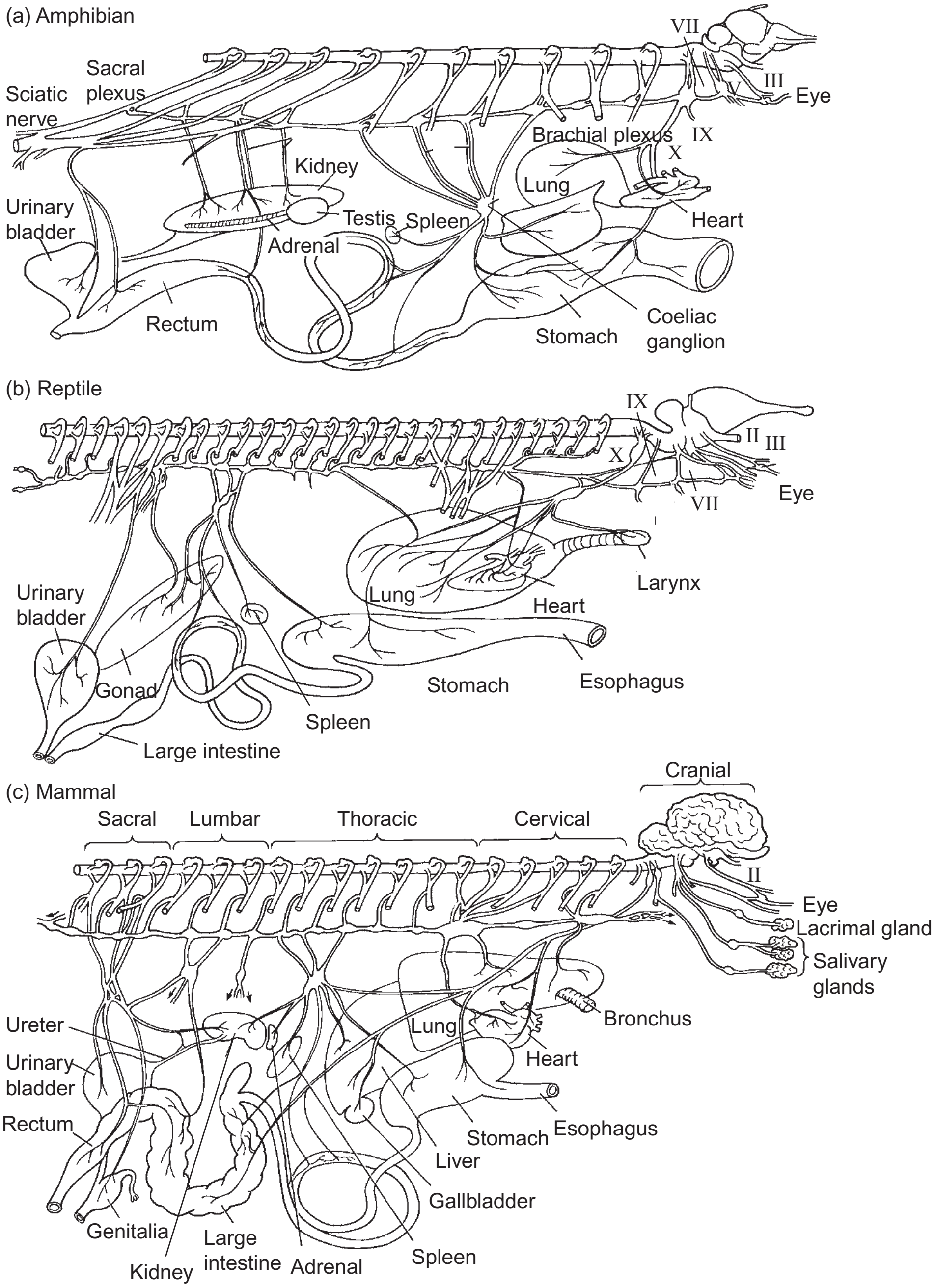


FIGURE 16.23 Autonomic nervous system of various tetrapods. (a) Amphibian (anuran). (b) Reptile (lizard). (c) Mammal (eutherian).

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Embryology

The vertebrate central nervous system is hollow, a result of the fusion of two raised neural folds within the ectoderm. In the brain, the central canal enlarges into fluid-filled **ventricles** that are connected spaces located within the center of the brain. Within the anterior neural tube, three embryonic regions of the brain differentiate into the **prosencephalon, mesencephalon,** and **rhombencephalon** (figure 16.25a–c). These give rise to three regions of the adult brain: **forebrain, midbrain,** and **hindbrain** (figure 16.25f).

The brain and spinal cord are wrapped in **meninges** (sing., *meninx*) derived in part from neural crest. In mammals, the meninges consist of three layers: the tough outermost **dura mater,** the weblike **arachnoid** in the middle, and the innermost **pia mater** (figure 16.26a). The pia mater contains blood vessels that supply the underlying nervous tissue. **Cerebrospinal fluid (CSF)** is a slightly viscous fluid that flows slowly through the ventricles of the brain, the subarachnoid space beneath the arachnoid, and the central canal. The **choroid plexus,** small tufts of blood vessels associated with ependymal cells, projects into the ventricles at specific sites and is the primary source of cerebrospinal fluid. This fluid is reabsorbed into venous sinuses. Although cerebrospinal fluid is derived from the blood and returns to it, it is devoid of red blood cells or any other large formed elements. When a person is injured and trauma to the central

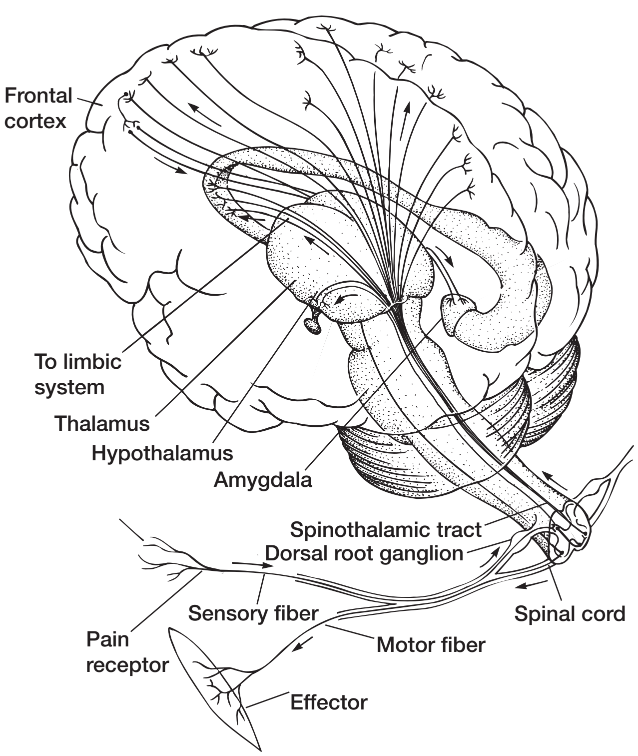


FIGURE 16.24 **Sensory and motor circuits.** Sensory receptors in the skin respond to stimuli by generating an electrical impulse that travels to the spinal cord and synapses in the thalamus. This impulse is relayed by other neurons to other areas of the brain, which produces a response that travels down the spinal cord to a motor neuron and out to an effector.

nervous system is suspected, a procedure called a spinal tap is done to sample the cerebrospinal fluid. If it contains red blood cells, then the brain or spinal cord may be damaged. Cerebrospinal fluid forms a cushion of fluid around the brain and spinal cord to support the delicate nervous tissues and absorb shocks from concussions. The average human has about 150 ml of cerebrospinal fluid, less than a cup, that is replaced several times per day, flushing the central nervous system. Recent speculation suggests that it might carry chemical messages important in regulating the organism's daily circadian rhythms.

In fishes, the meninges consist of a single membrane, the **primitive meninx,** wrapped around the brain and spinal cord (figure 16.26b). With the adoption of terrestrial life, the meninges doubled. In amphibians, reptiles, and birds, the meninges include a thick outer dura mater derived from mesoderm and a thin inner **secondary meninx** (figure 16.26c). With a double meningeal layer, cerebrospinal fluid may circulate more effectively and absorb shocks from the jolts sustained during terrestrial locomotion. In mammals, the dura mater persists, but division of the secondary meninx yields both the arachnoid and the pia mater from ectomesoderm (figure 16.26d).

Spinal Cord

The vertebrate spinal cord, like the brain, is organized into two regions and named because of their appearance in fresh preparations (figure 16.27a–f). The **gray matter** of the spinal cord includes nerve cell bodies that lie within the core of the spinal cord. Dorsal and ventral extensions of the gray matter are the **dorsal horns** and **ventral horns,** respectively. The dorsal horns contain the bodies of neurons receiving incoming sensory information. The ventral horns contain the bodies of motor neurons (figure 16.17). The **white matter** of the spinal cord surrounds the gray matter. It is predominantly composed of nerve fibers linking different levels of the spinal cord with each other and with the brain. Many of these fibers are myelinated, creating their white color.

The spinal cord functions in two capacities. It establishes simple reflexes and contains pathways of diverging and converging information.

Spinal Reflexes

As you know from the discussion of somatic and visceral reflex arcs, the spinal cord completes the reflex loop between sensory input and motor output. In doing this, the spinal cord selects the effectors to be activated or inhibited. Although the spinal cord operates at the reflex level, it also contains circuits that coordinate different parts of the cord.

Arriving sensory fibers synapse in the dorsal horn of the gray matter with association neurons (figure 16.28a). Association neurons carry the impulse to the ventral horn on the same side, to the opposite side, or to a different level of the spinal cord or brain. In the ventral horn, the association neuron synapses with a motor neuron whose axon travels out the ventral root to the effector. Dispersion of information within the spinal cord can produce complex responses to stimuli without involving higher centers. For example, if an animal should inadvertently place its foot on a sharp object, the reflex to withdraw it could involve as few as three neurons (figure 16.29). The first, the afferent sensory neuron, carries the painful stimulus to the spinal cord, where it synapses with an association neuron. The association neuron transmits the stimulus to the ventral horn, where it synapses with a motor neuron whose axon conveys the impulse to appropriate retractor muscles that contract and withdraw the foot. Association neurons that connect to appropriate levels on the opposite side of the cord reach motor neurons innervating extensor muscles in the opposite leg. These muscles contract, extend the leg, and prevent the animal's collapse when it lifts its other leg from the sharp object. The circuitry involved demands a connection between painful stimulus and appropriate effectors (retractor and extensor muscles). It need not involve higher brain centers. Usually, the association neurons also convey the painful stimulus to conscious centers of the brain, where it is perceived (figure 16.28b); however, by the time the higher centers become aware of the surprise trauma to the foot, the spinal reflex to retract it is already under way.

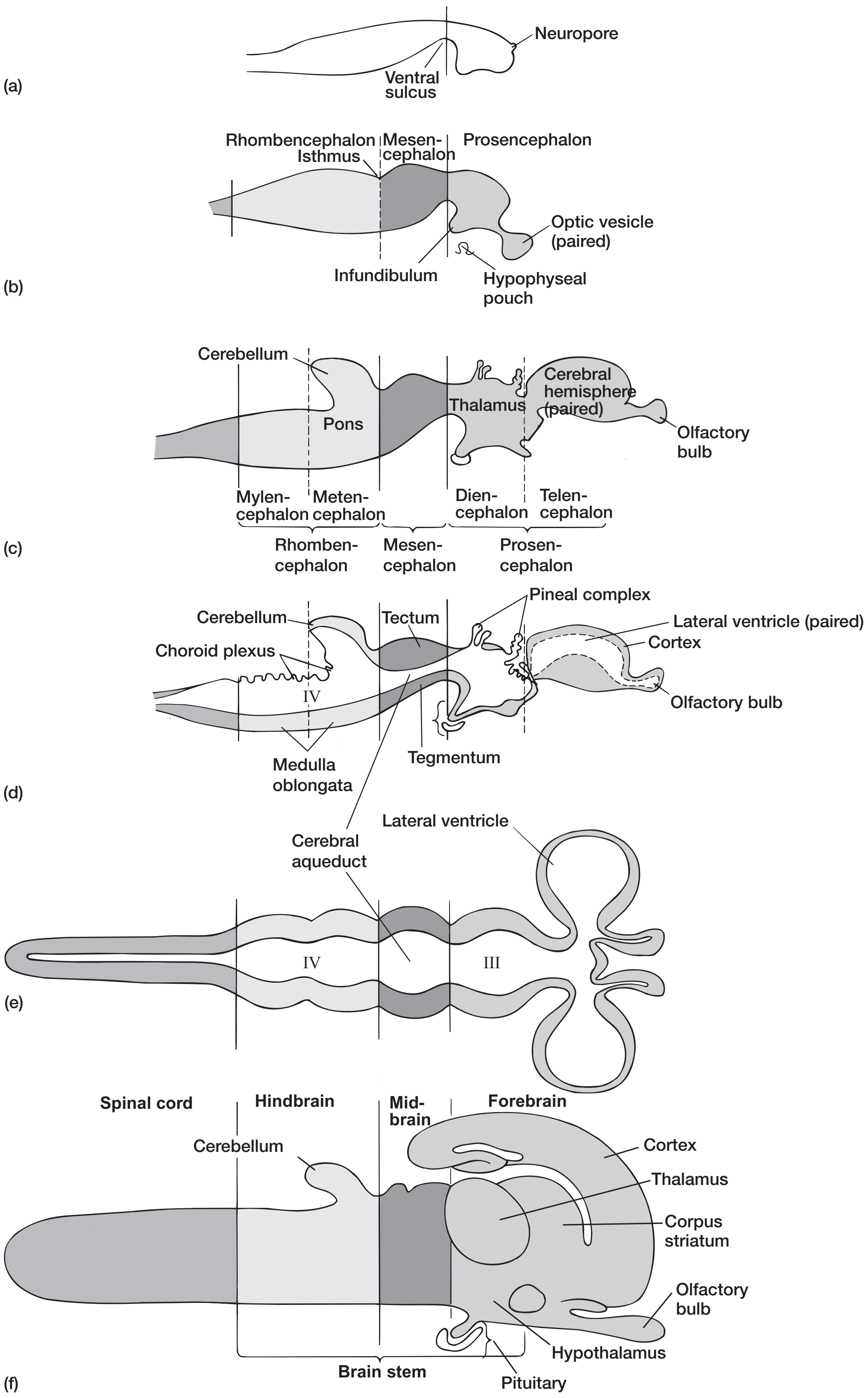


FIGURE 16.25 **Development of the central nervous system.** (a–d) Embryonic development. (e) Fluid-filled ventricles within the central nervous system. (f) Anatomical regions of the adult brain.

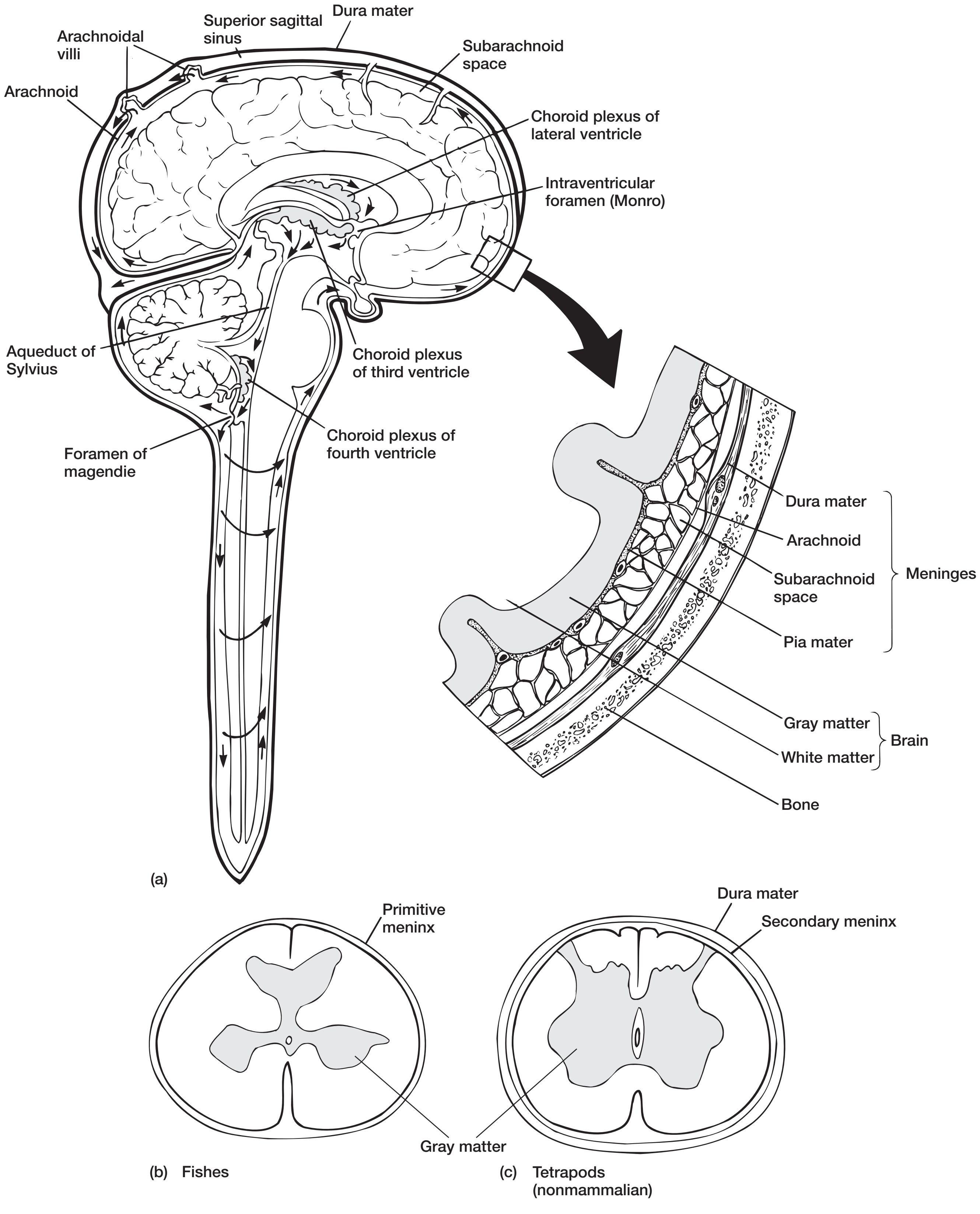
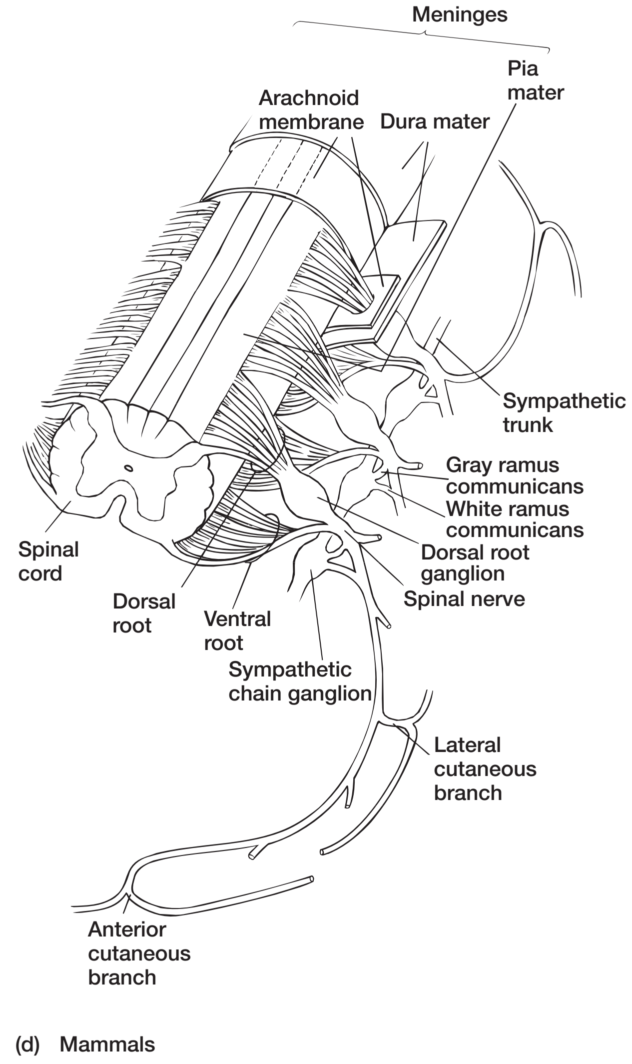


FIGURE 16.26 **Cerebrospinal fluid and meninges.** (a) Arrows trace the circulation of cerebrospinal fluid through the brain and spinal cord of a mammal. The triple-layered meninges are enlarged to the right. (b) The meninges of fishes consist of a single thin layer, the primitive meninx. (c) In all tetrapods except mammals, the meninges are double layered and consist of an outer dura mater and inner secondary meninx. (d) Cutaway section of the spinal cord in a mammal illustrates the three meningeal layers: dura mater, arachnoid, and pia mater. Branches of the spinal nerve are shown along with their connections to the sympathetic chain. (*Continued on next page.*)

(a–c) After H. M. Smith; (d) after R. T. Woodburne.



(d) Mammals

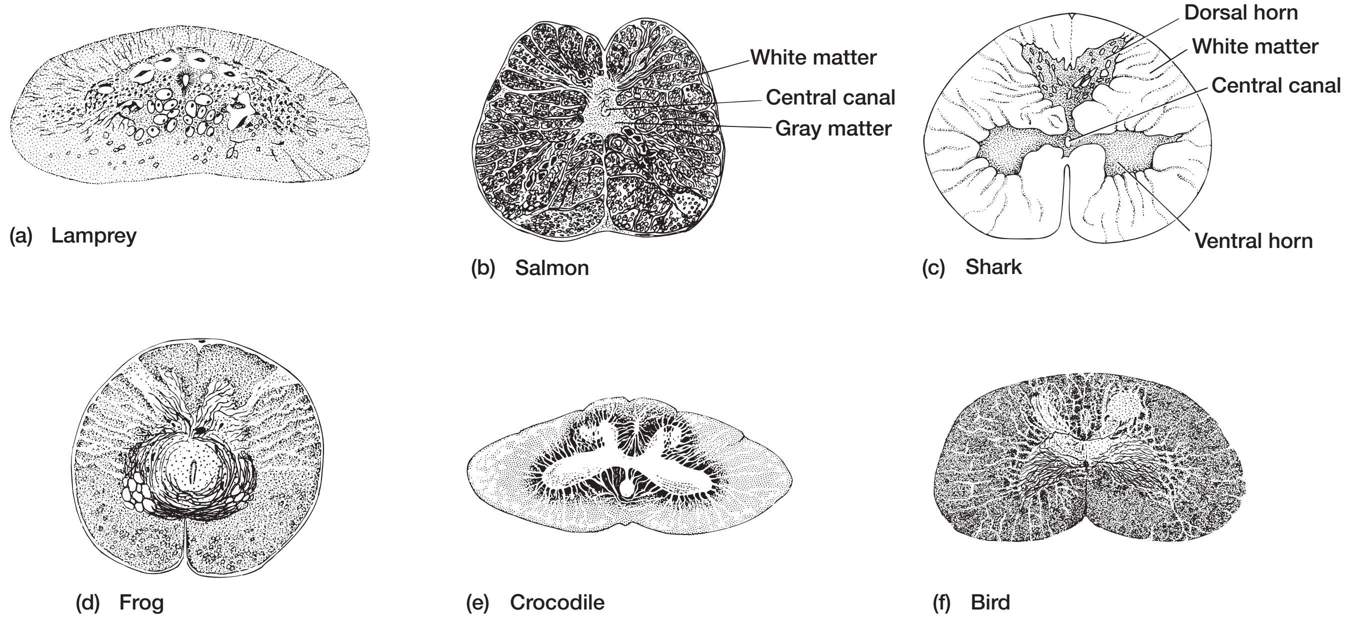
FIGURE 16.26 continued

Spinal Tracts

Not all information is processed at the level of the spinal cord. Much, perhaps most, information is carried to higher levels of the nervous system for evaluation. The resulting decisions are carried down the spinal cord to appropriate effectors. Nerve fibers carrying similar information tend to travel together in nerve tracts, bundles of similar fibers that occupy a specific region of the spinal cord. Nerve tracts may be ascending or descending tracts, depending on whether they convey information up or down the cord, respectively (figure 16.30). They are usually named for their source and their destination. For example, the spinothalamic tract begins in the spinal cord and extends to the thalamus (table 16.6).

Wars, accidents, and diseases can lead to localized wounds of the spinal cord that sever the ascending or descending flow of information. In humans, such losses of function have been correlated with the specific region in which the wound occurred and used to map the positions of these nerve tracts. More precise information from animal studies has added to our understanding of spinal cord organization. For convenience, these mapped tracts are drawn in discrete locations. In practice, their precise positions may change slightly at different levels of the cord, and there is some overlap of tracts as well.

Ascending tracts carry sensory impulses from the spinal cord to the brain. Among the most prominent are the **fasciculus gracilis** and **fasciculus cuneatus,** located in the dorsal region of the spinal cord. Both carry proprioceptive stimuli and sensations associated with posture to the medulla. As each tract ascends, more axons are added. For instance, the gracilis is supplemented laterally to produce the cuneatus (figure 16.31). Thus, at higher levels of the cord, the more medial fasciculus gracilis carries sensations from the lower limb and the more lateral fasciculus cuneatus carries sensations from the upper limb.



(a) Lamprey (b) Salmon (c) Shark (d) Frog (e) Crocodile (f) Bird

FIGURE 16.27 Cross sections of vertebrate spinal cords.

After Bolk.

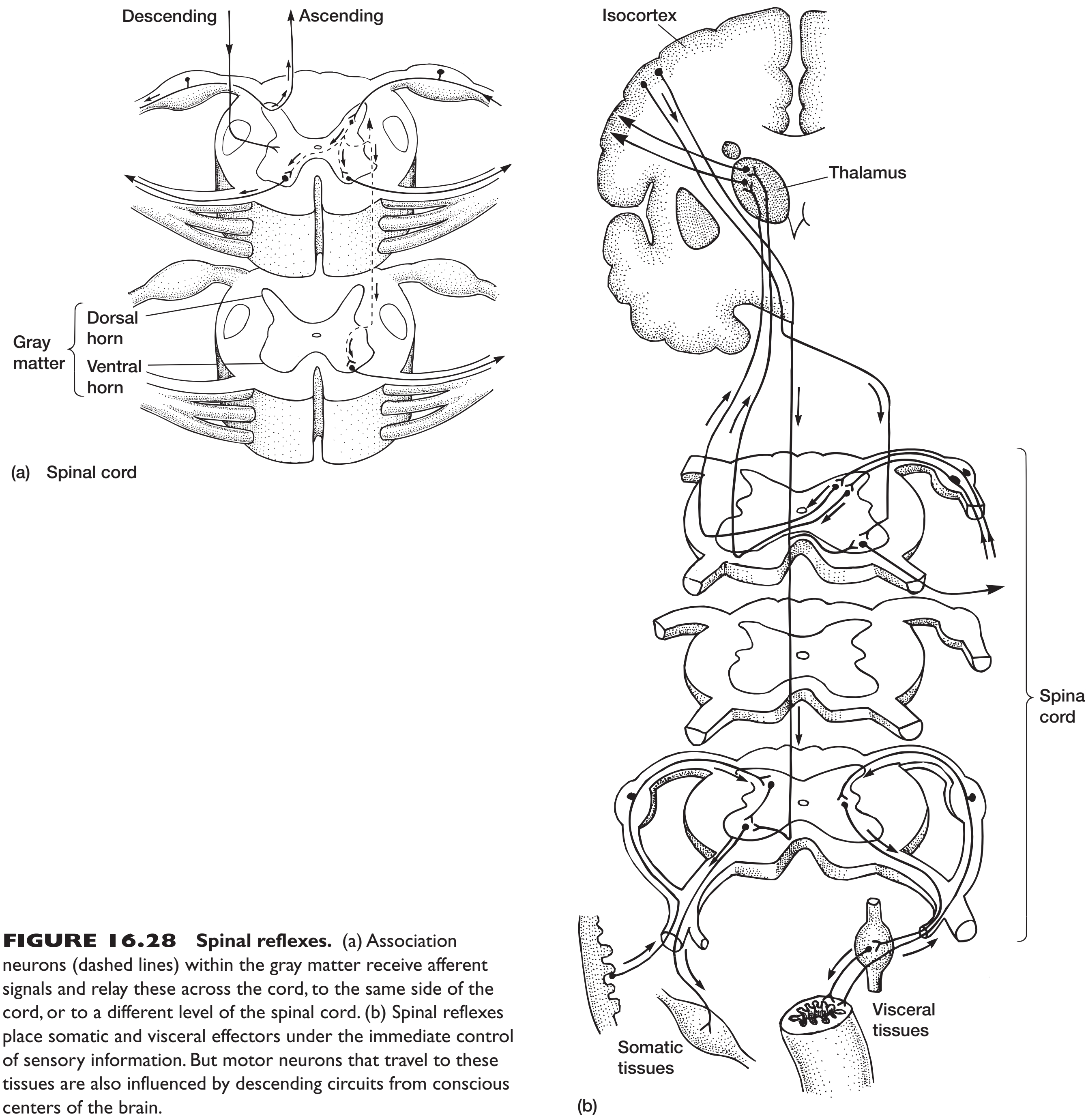


FIGURE 16.28 Spinal reflexes. (a) Association neurons (dashed lines) within the gray matter receive afferent signals and relay these across the cord, to the same side of the cord, or to a different level of the spinal cord. (b) Spinal reflexes place somatic and visceral effectors under the immediate control of sensory information. But motor neurons that travel to these tissues are also influenced by descending circuits from conscious centers of the brain.

The **spinocerebellar tracts** carry proprioceptive information concerning positions of the limbs and body to the cerebellum. This information is not consciously perceived, but it enables the cerebellum to coordinate movements of different parts of the body. The **lateroventral** (= anterolateral) **spinothalamic tract** transmits information to the thalamus concerned with sensations of pain and temperature.

Descending tracts transmit impulses from the brain to the spinal cord. One of the most important is the **corticospinal tract,** which runs directly from the cerebral cortex to motor neurons going to the limbs; thus, it places skeletal muscles under cerebral control. The **tectospinal tract** is associated with optic and auditory stimuli. It does not go through conscious centers, but extends a short distance directly down the spinal cord to cervical levels, where it ends on somatic motor neurons that innervate neck muscles. Its function is to turn the head quickly toward threatening or surprising visual or auditory stimuli. The **rubrospinal tract** conveys impulses from the midbrain to the spinal cord and is involved in initiating coordinated movements.

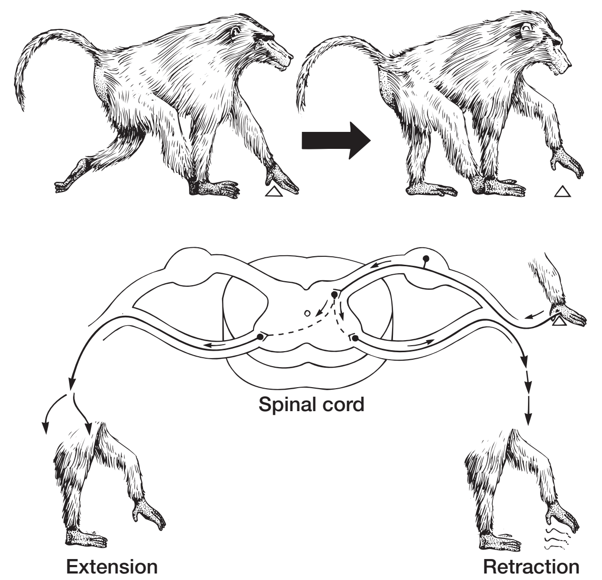


FIGURE 16.29 **Spinal reflex.** Association neurons (dashed lines) within the spinal cord deliver stimuli to motor neurons, causing the retractor muscles of this animal to lift its foot from a harmful object. These stimuli also spread to motor neurons in other areas of the cord that innervate extensor muscles of the opposite limb to contract and support the weight of the body.

Brain

The brain forms embryologically from the neural tube anterior to the spinal cord. It includes three anatomical regions (figures 16.25a–f and 16.32). The most posterior region is the hindbrain, which includes the **medulla oblongata, pons,** and **cerebellum.** Next is the midbrain, which includes a sensory **tectum** and a motor **tegmentum.** The **brain stem** includes all regions of the hindbrain and midbrain except for the cerebellum and colliculi. The most anterior region of the brain, the forebrain, includes the **telencephalon,** or **cerebrum,** and the **diencephalon,** which is the source of the **thalamus.**

Phylogeny

Independently, the forebrain tends to enlarge in various vertebrate groups, including hagfishes, some sharks, rays, teleost fishes, and tetrapods (figure 16.33). Some of this is correlated with the increased importance of olfactory (smell) information, as occurs, for example, in hagfishes. Forebrain enlargement also accompanies increasingly complex behaviors and muscle control. In amniotes, limb posture and body carriage change as terrestrial modes of locomotion become predominant. The limbs move from a sprawled position to one in which they are carried more directly under the weight

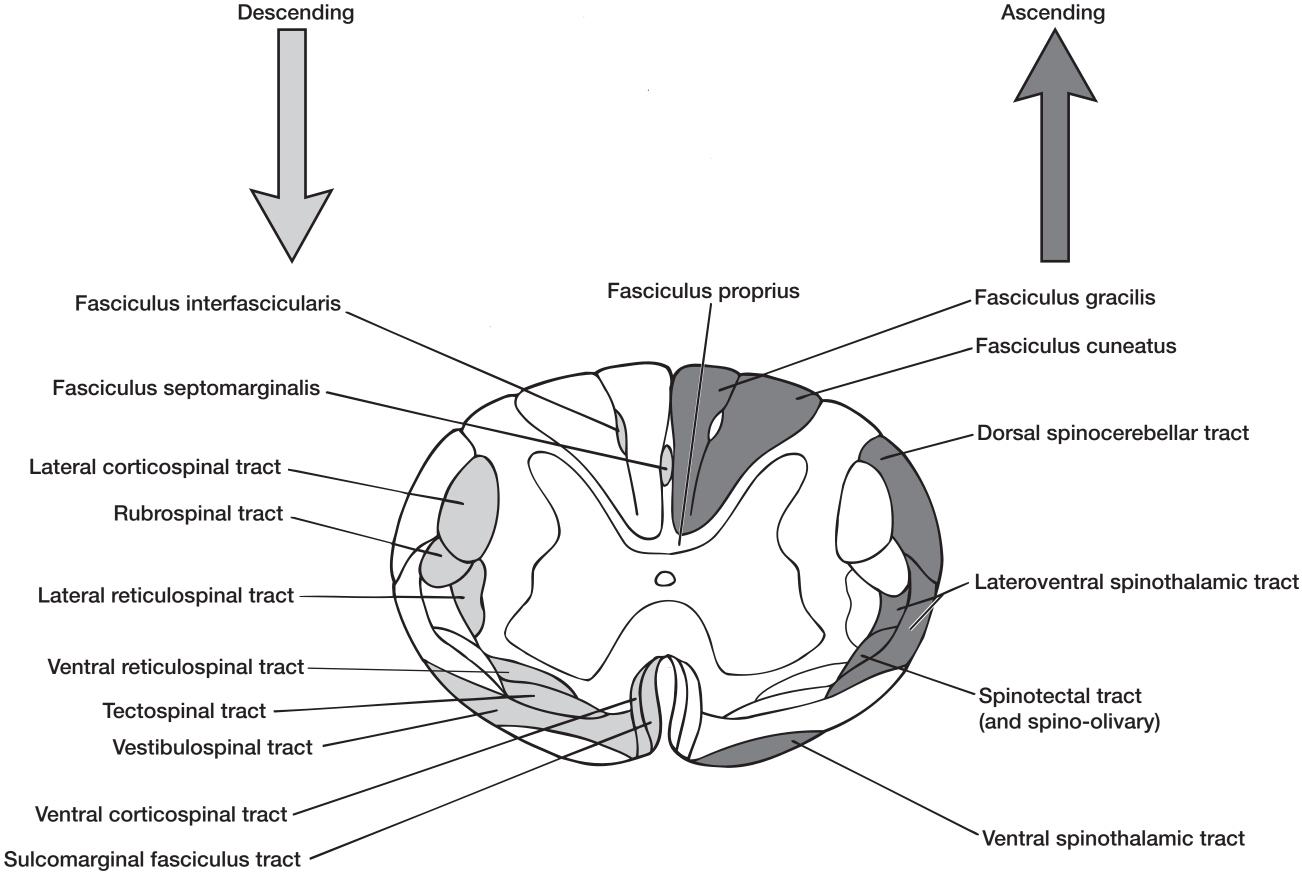


FIGURE 16.30 **Cross section of the human spinal cord showing approximate locations of ascending (right) and descending (left) nerve tracts.**

After Netter.

TABLE 16.6 Locations and Functions of Descending and Ascending Nerve Tracts of the Spinal Cord

Tract	Source	Destination	Function
Descending			
Lateral and ventral corticospinal tracts	Cerebral cortex	Spinal cord	Motor connections direct from cortex to primary motor neurons of arms and legs (places motor neurons under direct voluntary cortical control)
Rubrospinal tract	Midbrain (red nucleus of tegmentum)	Spinal cord	Motor connections in spinal cord
Lateral and ventral reticulospinal tracts	Medulla reticular formation	Spinal cord (dorsal horn)	Postural reflexes
Tectospinal tract	Midbrain (colliculus, roof)	Spinal cord	Visual and auditory stimuli to limbs and trunk
Vestibulospinal tract	Medulla (vestibular nucleus)	Spinal cord	Postural reflexes accomplished by axial and limb musculature
Ascending			
Fasciculus gracilis and fasciculus cuneatus	Spinal cord	Medulla	Fine tactile information, Golgi tendon organs, Pacinian corpuscles in joints
Dorsal and ventral spinocerebellar tracts[a]	Spinal cord	Cerebellum via peduncle	Proprioceptive information from muscles to cerebellum, intrafusal muscle fibers
Lateroventral spinothalamic tract	Spinal cord	Thalamus	Pain and temperature sensations to thalamus
Spinotectal tract	Spinal cord	Midbrain (tectum)	Proprioceptive information from neck and shoulders
Spinoreticular tract	Spinal cord	Medulla (reticular formation)	Pain and sensations from internal organs

[a] *May be single tract.*

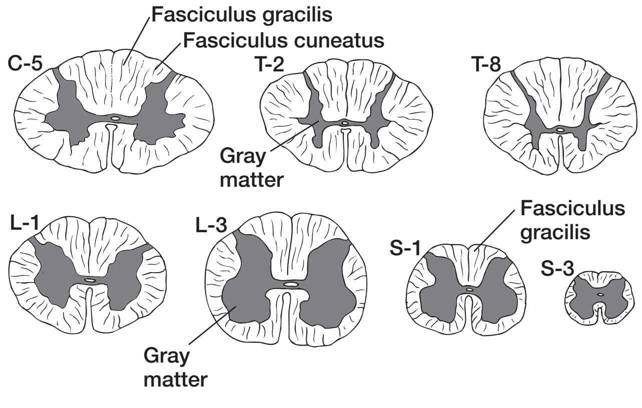


FIGURE 16.31 Gray and white matter at various levels of the human spinal cord. Sections are identified by their region—cervical (C), thoracic (T), lumbar (L), sacral (S)—and by specific vertebrae numbered (Arabic number) within each of these regions from which they came. At the level of the arms (C-5) and legs (L-3), additional sensory and motor fibers enter and leave the spinal cord. This is reflected in the more extensive gray matter compared to other regions of the cord (e.g., T-2, T-8). Note the addition of the fasciculus cuneatus at the highest level on the cord. Primarily, this carries sensory information from the arms.

After Netter.

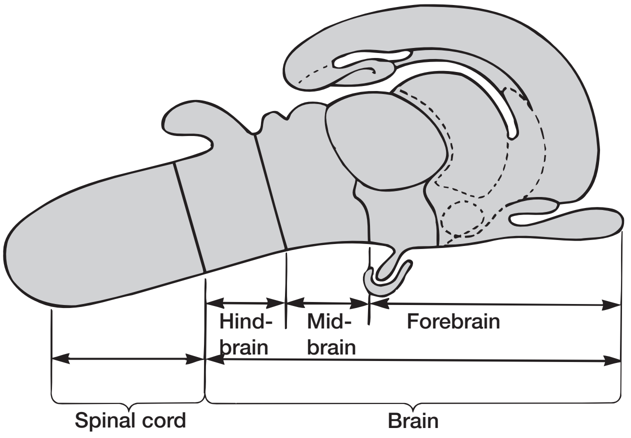


FIGURE 16.32 Regions of the vertebrate brain represented diagrammatically.

After Nauta and Feirtag.

of the body, increasing the ease and efficiency of limb oscillation (see chapter 8). Coordination of limb oscillation and placement during rapid locomotion becomes especially complicated in bipedal archosaurs and birds. Increased input of somatosensory information and increased output of motor

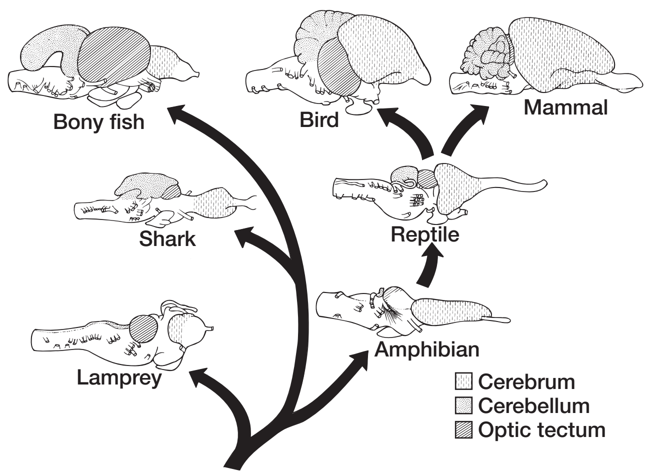


FIGURE 16.33 **Evolution of the vertebrate brain.** Note the phylogenetic enlargement of the cerebrum and cerebellum.

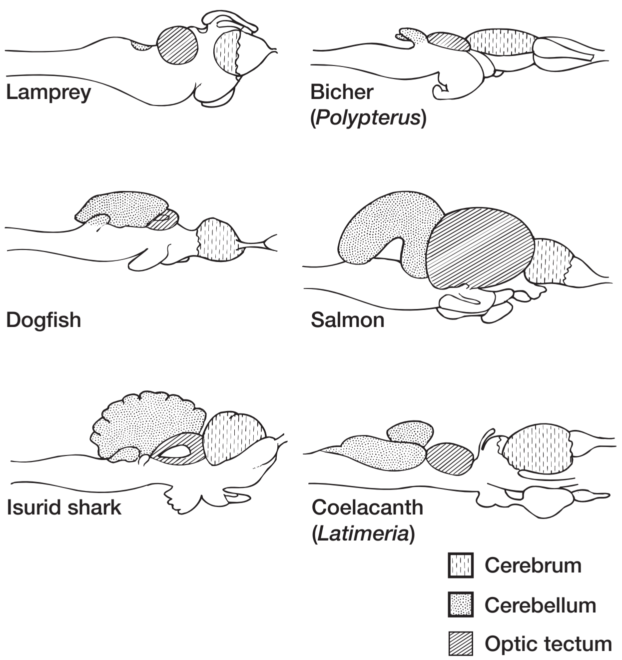


FIGURE 16.34 **Brains of fishes.** Note variations in the sizes of different regions of the brain. These reflect differences in the role that each region plays in processing information important to different species.

After Ebbesson and Northcutt; Roberts and Kremers.

responses to skeletal muscles requires mediation. The enlargement of the amniote forebrain reflects its increasing role in this mediation within the locomotor system.

In advanced teleost fishes, the midbrain tends to enlarge rather than the forebrain. This seems to be correlated with the processing of visual information, as well as the increasing importance of sensory input from the lateral line system, and with greater movement of teleosts in the three-dimensional space of their aquatic environment.

Within these general patterns, the brain of each species reflects the demands of information processing required by its habitat and mode of life (figure 16.34). Cavefish, for instance, have reduced eyes and live in caves, a permanently dark subterranean environment. Correspondingly, the tectum of the midbrain, which normally receives visual input, is reduced as well. On the other hand, when visual information constitutes a large part of the brain's sensory input, as in salmon, the tectum is enlarged. Thus, reduction or loss of sensory input from an exteroceptor or interoceptor results in a corresponding reduction or loss of brain nuclei that receive and process this information, whereas increased sensory input leads to increased prominence of the appropriate association.

Form and Function

Representative vertebrate brains are shown in figures 16.35 through 16.37.

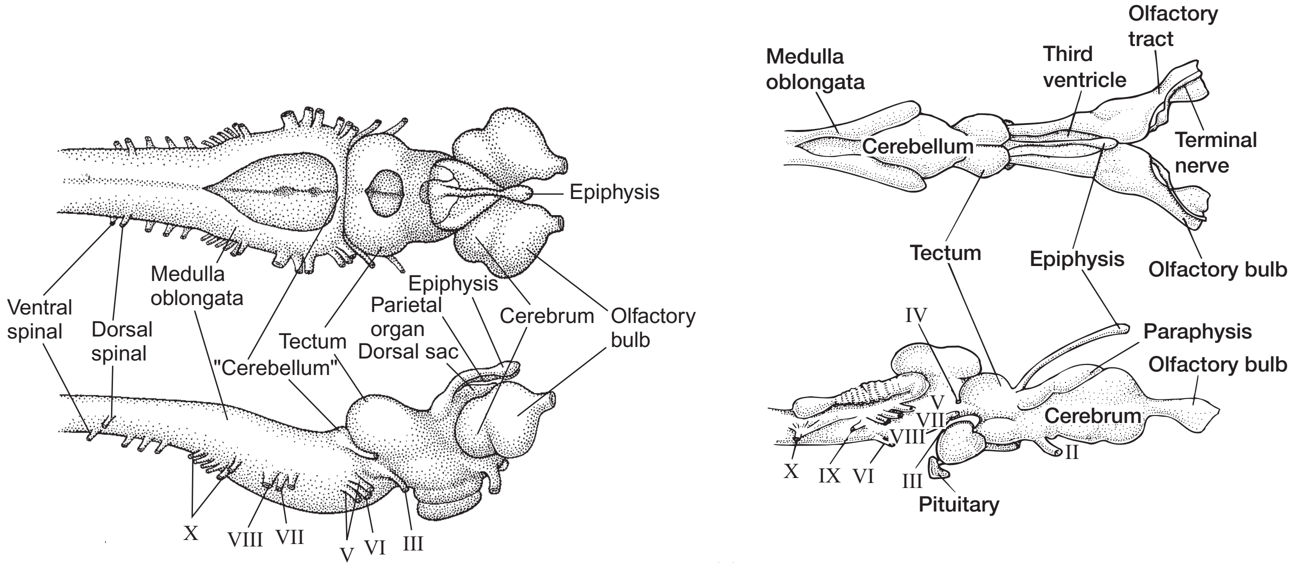
Hindbrain The **medulla oblongata** operates primarily at the reflex level. It has three major functions. First, it houses the primary nuclei of cranial nerves (figure 16.36a–c). In sharks, the primary nuclei or roots of cranial nerves V through X are contained in the medulla, whereas in mammals, the primary nuclei of cranial nerves VII through XII reside in the medulla. Second, the medulla serves as a major route through which ascending and descending pathways run to and from higher centers of the brain. Third, the medulla contains centers for visceral, auditory, and proprioceptive reflexes, including reflex centers for respiration (figure 16.38), heartbeat, and intestinal motility. Damage to the medulla can be life-threatening because these centers control vital functions.

Medullary nuclei receive afferent signals from spinal and cranial sensory nerves as well as descending signals from higher centers such as the hypothalamus. All branchiomeric cranial nerves—trigeminal (V), facial (VII), glossopharyngeal (IX), vagus (X)—arise in the medulla. Within these medullary centers, arriving information is processed and efferent output is initiated to adjust visceral activity as well as rhythmic feeding and respiration patterns.

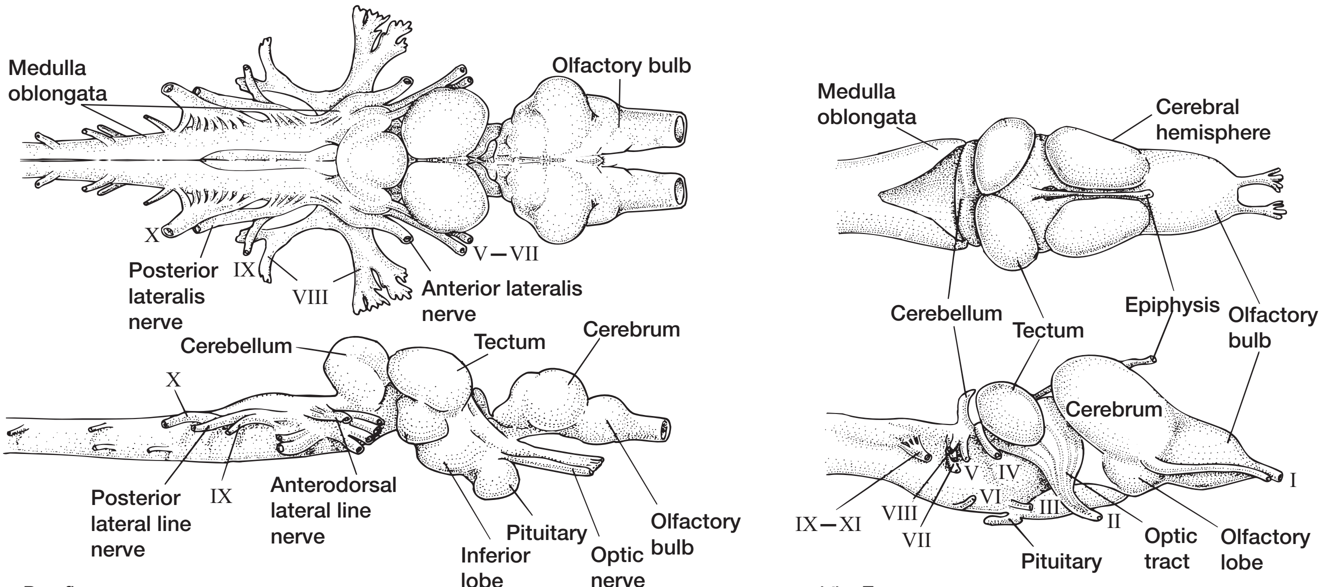
The floor of the hindbrain in amniotes becomes a crossroads of increasing importance for the flow of information. In mammals, it develops into a distinct enlargement, the **pons** (figure 16.37e). The pons is primarily formed by the pontine nuclei, which convey information to the cerebellar cortex from the cerebral cortex.

The **cerebellum** is present in gnathostomes, and is even quite large in some, but is apparently absent in cyclostomes and ostracoderms, although some uncertainties remain. In lampreys, a raised neural lip defines the anterior, dorsal wall of the medulla oblongata ("cerebellum"; figure 16.35a), once proposed to be a modest cerebellum. However, its cell types differ from cerebellar cells and it is more likely part of the medulla oblongata. In most gnathostomes, the cerebellum is a dome-shaped extension of the hindbrain. Its surface is often highly convoluted and folded. The cerebellum can be divided into a medial **corpus** (body) and a paired lateral **auricle.** The sides of the corpus expand into the cerebellar hemispheres in birds and mammals. The **flocculus,** or flocculo-nodular lobe, of tetrapods is homologous to the dorsal half of the auricle of fishes. The ventral auricle of fishes receives lateral line input.

The cerebellum modifies and monitors but does not initiate motor output. It operates at an involuntary level and has two primary functions. First, it is important in maintaining equilibrium (figure 16.39). Information pertaining to touch, vision, hearing, proprioception, and motor input from higher centers is processed in the cerebellum. Integration of these incoming sensations results in the maintenance of



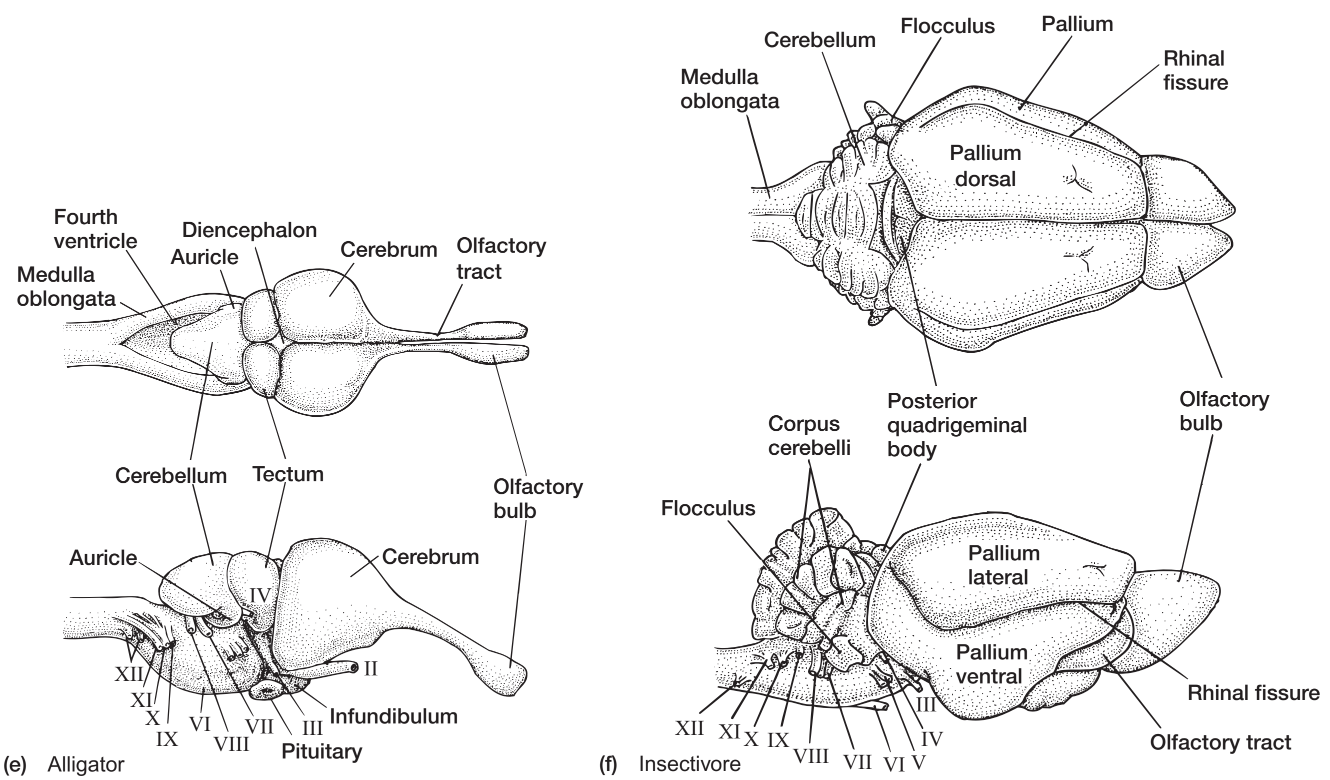
(a) Lamprey **(b)** Shark



(c) Bowfin **(d)** Frog

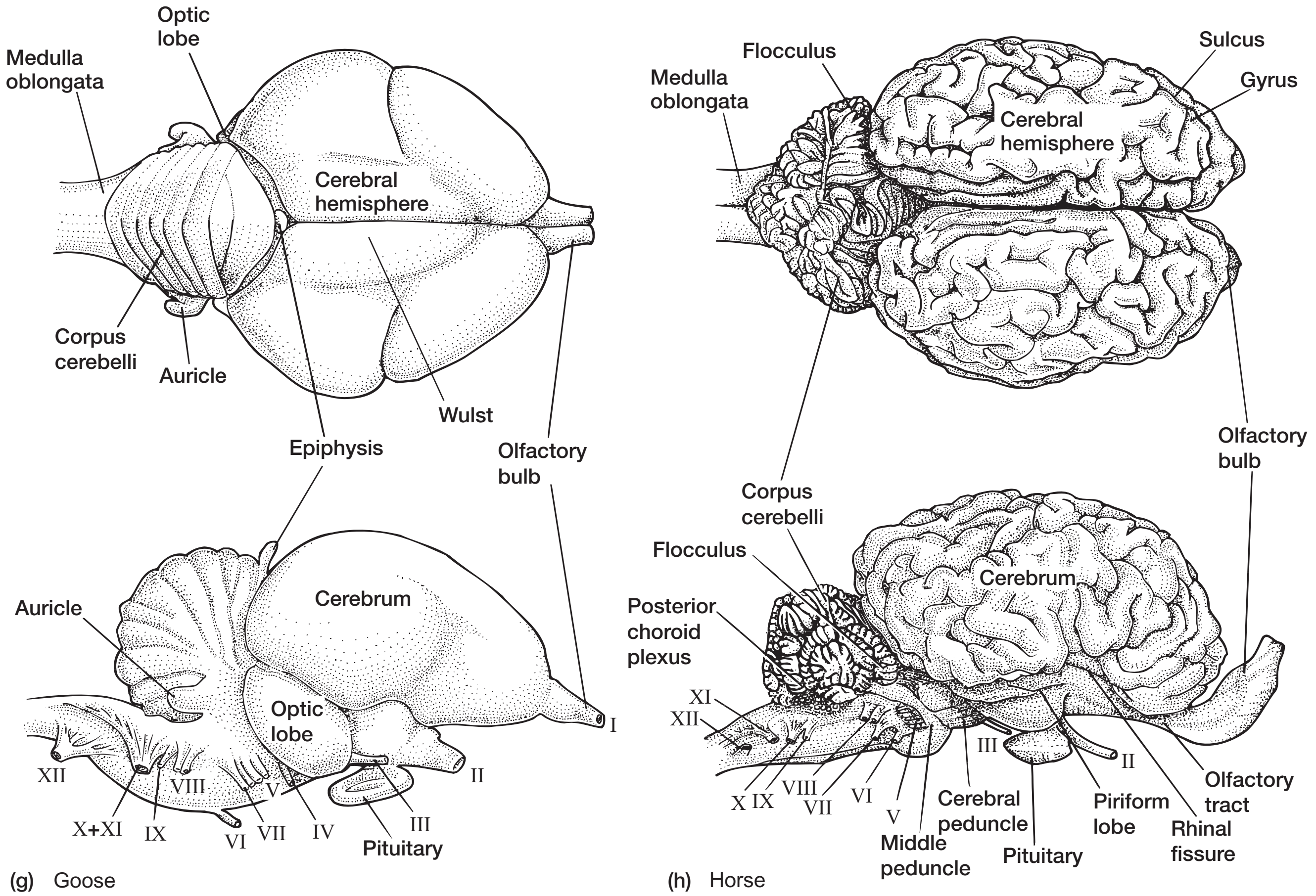
FIGURE 16.35 Vertebrate brains. Dorsal views are shown above, lateral views below. (a) Lamprey (*Lampetra*). (b) Shark (*Scymnus*). (c) Bowfin (*Amia*). (d) Frog (*Rana*). (e) Alligator (*Alligator*). (f) Insectivore (*Gymnura*). (g) Goose (*Anser*). (h) Horse (*Equus*).

(a,b) (d–g) After Romer and Parsons; (c) after Davis and Northcutt; (h) after Getty.



(e) Alligator

(f) Insectivore (mammal)



(g) Goose

(h) Horse

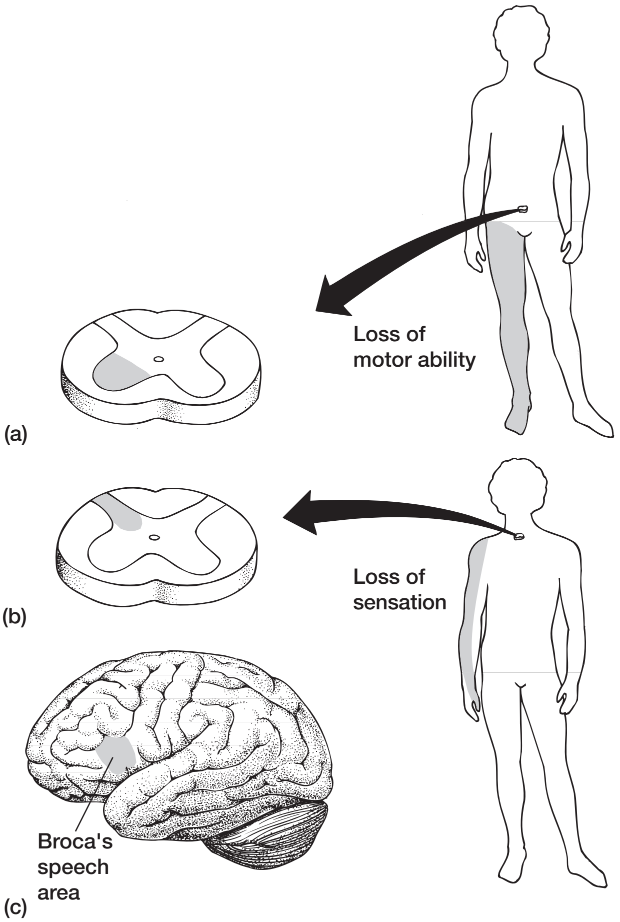
FIGURE 16.35 continued

BOX ESSAY 16.3

Disease, War, Barroom Brawls—The Early Science of Neurology

Some of the first insights into the functioning of the nervous system came from the results of damage to it. Distribution of information in the nervous system is very orderly in mammals. Sensory information arrives via the dorsal root, motor responses depart via the ventral root, and association neurons intervene between them (see figure 16.29). Anatomical structure and functional activity are closely matched. Because form and function are closely matched in the nervous system, disruption of function can be used to identify the location of an anatomical injury. Because the spinal cord and brain are organized into discrete functional areas, damage to a part results in selective impairment of function. The earliest indication of this came from battle wounds that soldiers survived, but with persistent deficits in function (box figure 1a). Stab or bullet wounds causing restricted damage to the dorsal horn of the gray matter leave patients with more or less normal motor ability but impair their ability to feel sensations from the level of the body where a wound was inflicted (box figure 1b).

Other pathologies affect motor output rather than sensory input. In 1861, the German neurologist P. P. Broca performed a postmortem examination of the brain of a patient who suffered from a speech defect following injury to his head. While still alive, the patient's lips, tongue, and vocal cords were fully functional, but he could not speak intelligibly. His speech was slow, and many nouns and verbs were deleted. A lesion was found in a restricted area of the forebrain, a region still known as Broca's motor speech area (box figure 1c).



BOX FIGURE 1
Clinical evaluation of injuries to the nervous system. (a) Loss of motor control to right leg muscles can imply selective injury to the ventral horn of the spinal cord at the level where motor neurons to the skeletal muscles of the leg reside. (b) Loss of sensation to the right arm can result from loss or injury to the dorsal horn of the cord at that level. (c) Injury to Broca's area of the brain leaves a person with an understanding of language but results in impaired speech.

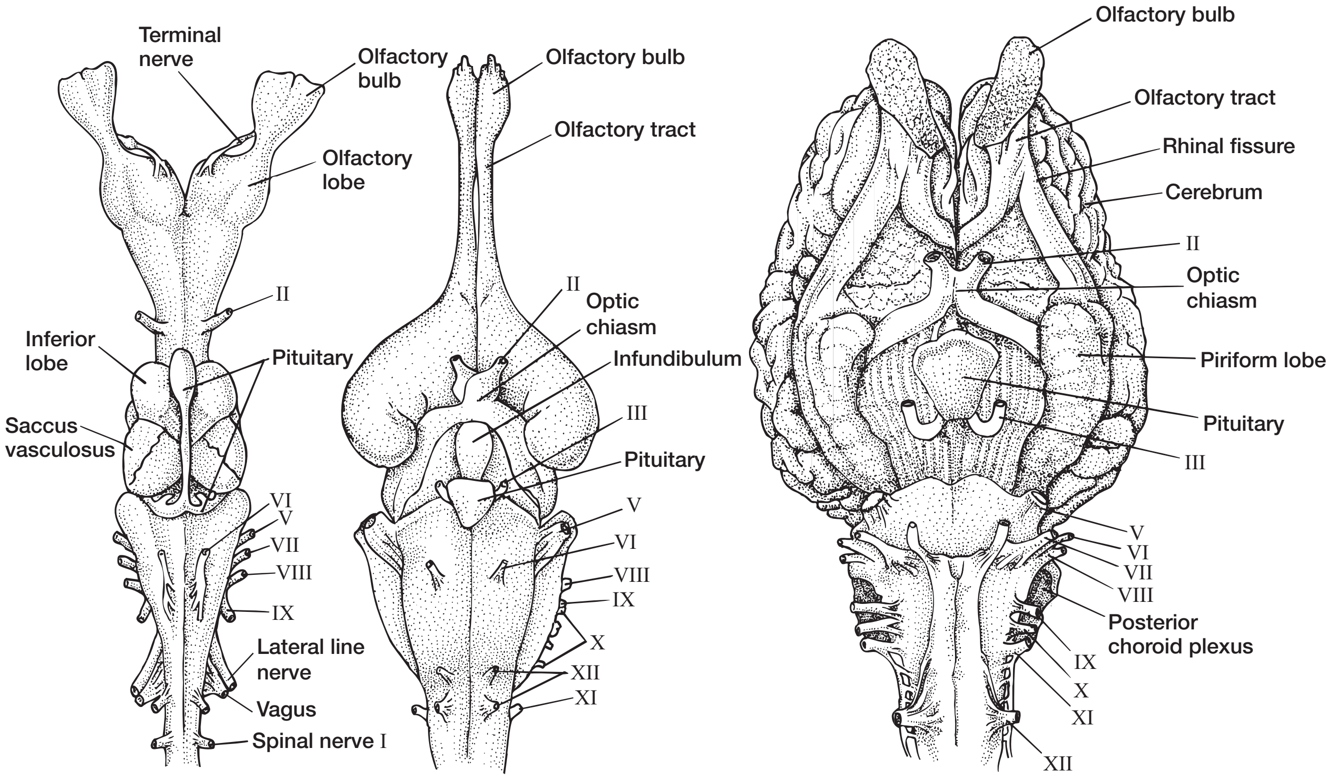
Poliomyelitis, once a common disease primarily afflicting children, struck motor neurons in the ventral horns of the spinal cord. If the disease settled low in the spinal cord, the lesion would likely cause paralysis in the leg on the same side.

In the twentieth century, car accidents were added to the list of events that inflict this type of damage. Experiments with animals have augmented our knowledge of the functional organization of the central nervous system.

muscle tone and balance. For an organism to run, jump, fly, or swim in a three-dimensional world, it must be able to keep itself upright and orient itself in space relative to gravity. The cerebellum is involved in processing information that results in maintaining positional equilibrium of the organism.

The second primary function of the cerebellum is the refinement of motor action. The cerebellum compares incoming impulses and sends modified signals to motor centers. Direct electrical stimulation of the cerebellum does not produce muscle contractions. Following removal of the cerebellum, an organism can still move in space, but its movement is uncoordinated, exaggerated, or insufficient, and its motion is likely to be uneven. Thus, the role of the cerebellum is to monitor and modify rather than initiate action.

This said, we must note that much of what the cerebellum does is not well understood. It is now clear that the cerebellum is also heavily involved in forming memory related to motor events. It acquires detailed sensory information about external space and may take advantage of innate, prewired activity patterns, as well as the results of previous learned experience. Although involved in orientation, much of balance is also mediated by the vestibular and



(a) Shark (b) Alligator (c) Horse

FIGURE 16.36 **Vertebrate brains, ventral views.** (a) Shark (*Scymnus*). (b) Alligator (*Alligator*). (c) Horse (*Equus*).

After Romer and Parsons.

ocular nerves acting directly on motor nerves at lower levels of the spinal cord. In most animals, if the cerebellum is surgically removed, there are few lasting, severe effects on behavior. In humans, destruction of the midline region (vermis) results in ataxia, the loss of coordination of limbs, body, speech, or eye movements. Destruction of the lateral lobes of the cerebellum (hemispheres) results in a condition known as dysmetria, characterized by under- or overshooting a target that is reached for with either hands or feet.

As with other parts of the brain, the size of the cerebellum is proportional to its role. In fishes, the cerebellum is usually relatively large because of extensive input from the lateral line sensory system regarding water currents and electrical stimuli. Furthermore, active aquatic organisms must navigate and orient themselves in a three-dimensional medium. Equilibrium and balance are important; therefore, the cerebellum is well developed. As we would expect, in bottom-dwelling fishes (e.g., flounders) and in fishes that are not active swimmers (e.g., lampreys), the cerebellum has a reduced role and is relatively small (figure 16.35a). It should be noted that the region in fish termed the "cerebellum" is actually part of the octavolateralis nucleus, the primary target of electroreceptor fibers of the lateral line nerve.

With the advent of terrestrial life, the lateral line system is lost and sensory input to the cerebellum decreases. However, as robust limbs used in terrestrial locomotion develop, proprioceptive information and refinement of muscle action become important and place increased demands on the cerebellum. The cerebellum of terrestrial vertebrates thus remains large and prominent.

Midbrain The roof of the midbrain is the **tectum,** which receives sensory information. Specifically, the midbrain roof is divided into an optic tectum, receiving visual information, and a torus semicularis, receiving auditory and lateral line input. In mammals, the optic tectum is specialized into **superior** and **inferior colliculi.** The floor of the midbrain is the **tegmentum,** which initiates motor output usually via the trochlear (IV) and occulomotor (III) nerves, which arise in the midbrain.

In fishes and amphibians, the midbrain is often the most prominent region of the brain (figure 16.35a–e). The tectum receives direct input from the eyes. In addition, information from the octavolateralis system, the cerebellum, and the cutaneous sensors is transmitted indirectly to the tectum. The tegmentum is also prominent in anamniotes. In some fishes, it seems to be an important learning center.

In reptiles, birds, and mammals, the tectum continues to receive visual and auditory input, which it relays to the telencephalon through the thalamus. Thus, visual information in all vertebrates reaches the telencephalon via the tectum. A second route by which visual information reaches the telencephalon is through the thalamus of the forebrain, without

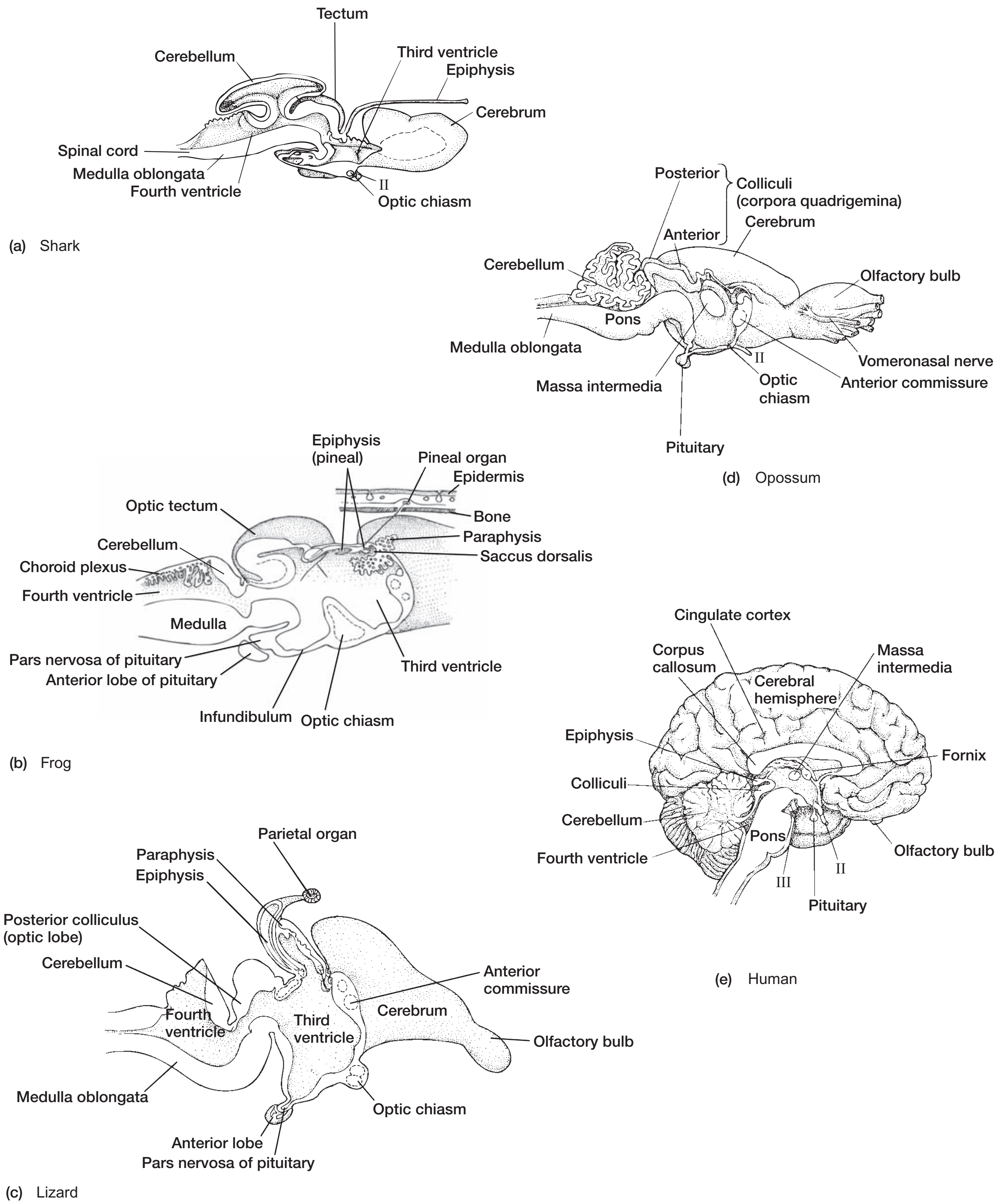


FIGURE 16.37 **Vertebrate brains, sagittal views.** (a) Shark (*Scyllium*). (b) Frog (*Rana*). (c) Lizard (*Lacerta*). (d) Opossum (*Didelphis*). (e) Human (*Homo*).

(a,d,e) After Romer and Parsons; (b,c) after Jollie.

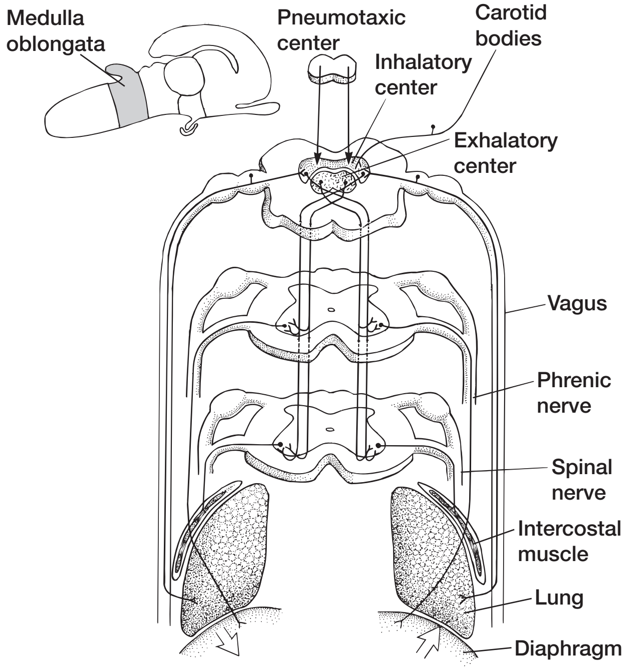


FIGURE 16.38 Coordination of breathing by the mammalian medulla. Reflex control of respiration is under the influence of three paired nuclei: the pneumotaxic center in the pons and the dorsal inhalatory center and ventral exhalatory center in the medulla. The inhalatory center receives information about gas composition and blood pH from the carotid bodies and about the degree of lung expansion from the vagus nerve. The inhalatory center excites descending neurons that terminate in motor neurons of the phrenic nerve to the diaphragm. It also stimulates a spinal nerve to the intercostal muscles. When these nerves are excited, inhalation and lung expansion result. The ventral expiratory center does not seem to function during quiet, normal breathing. This center is connected to motor neurons (not shown) serving antagonistic intercostal and accessory muscles of expiration.

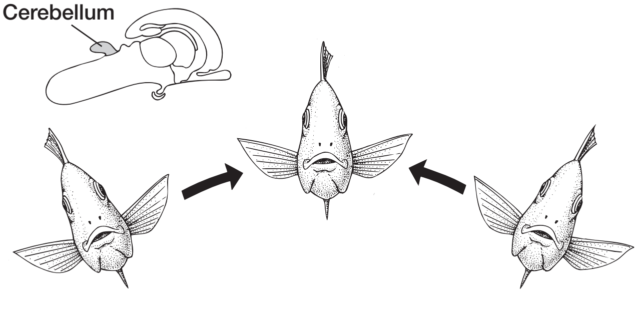


FIGURE 16.39 Function of the cerebellum. Balance and orientation are mediated through the cerebellum. As an animal changes its orientation in a gravitational field (left and right sketches), sensory organs that detect its altered position send impulses to the cerebellum. The cerebellum mediates responses that restore the animal's position (center sketch).

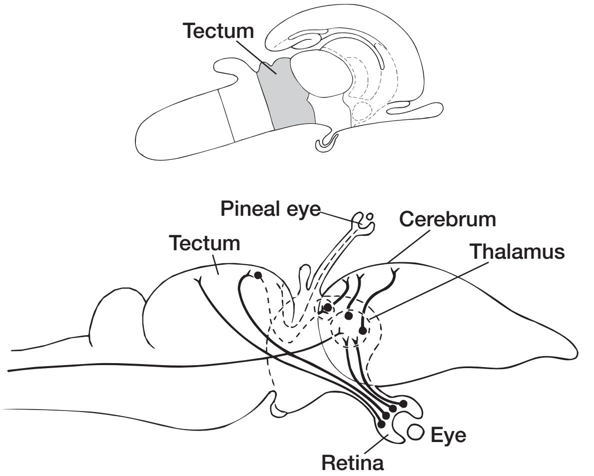


FIGURE 16.40 Function of the amniote tectum. The tectum receives visual information directly from the retina of the eye and relays this first to the thalamus and then to the cerebrum. In most vertebrates, visual information from the retina reaches the cerebrum via a second route without passing through the tectum. From the retina, visual information first reaches the thalamus and then is relayed to the cerebrum.

passing through the tectum (figure 16.40). This route is present in all vertebrates, if only modestly, but becomes enlarged and more important in tetrapods, especially mammals.

Forebrain The **diencephalon** includes four regions: epithalamus, hypothalamus, ventral thalamus, and **dorsal thalamus.** The roof of the diencephalon produces the epithalamus, which includes the **pineal gland** and the **habenular nucleus** at its base. The function of the habenular nucleus is uncertain. In anamniotes, the pineal gland affects skin pigmentation by acting on melanocytes, and it may be important in regulating photoperiod as well. In amniotes, the pineal plays a role in regulating biological rhythms (see chapter 15).

The floor of the diencephalon produces the hypothalamus. The **mammillary bodies,** which are very prominent in mammals, develop within the hypothalamus (figure 16.41). These bodies are part of the Papez circuit (figure 16.44), which is involved in reproductive behavior and short-term memory. The hypothalamus houses a collection of nuclei that regulate homeostasis to maintain the body's internal physiological balance. Homeostatic mechanisms adjusted by these nuclei pertain to temperature, water balance, appetite, metabolism, blood pressure, sexual behavior, alertness, and some aspects of emotional behavior. The hypothalamus stimulates the pituitary gland situated beneath it to regulate many homeostatic functions. The **limbic** and **reticular systems** influence the functions of the hypothalamus as well. These systems are discussed later in the chapter.

The ventral thalamus is a small area between the midbrain and the rest of the diencephalon. The largest part of the diencephalon is the dorsal thalamus, sometimes called

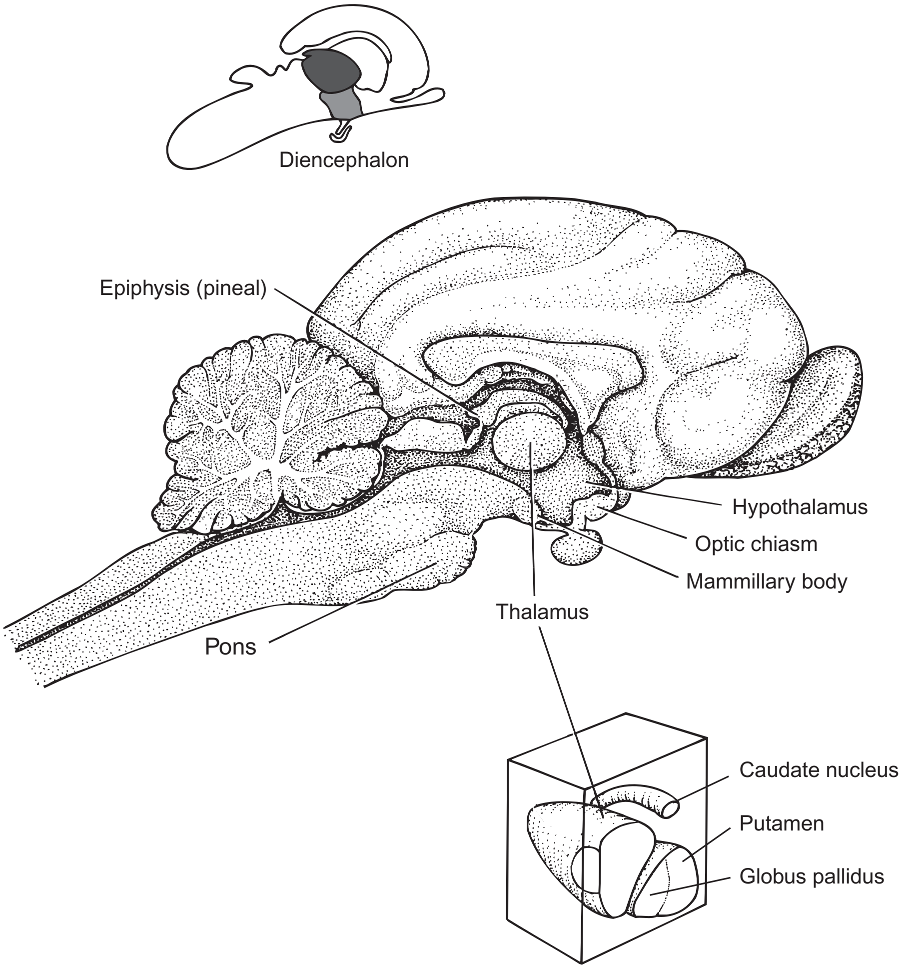


FIGURE 16.41 Hypothalamus and its relationship to adjacent regions of the brain. The region of the diencephalon is shaded in the small, top figure. The isolated dorsal thalamus in three-dimensional cutaway view is shown in the small block below the brain.

just thalamus, an area comprising nuclei that receive sensory input. The thalamus is the major coordinating center of afferent sensory impulses from all parts of the body. Except for the olfactory tracts, which transmit stimuli directly to the cerebral cortex, all somatic and visceral sensory tracts, including those relaying sensations of touch, temperature, pain, and pressure, as well as all visual and auditory fibers, synapse in thalamic nuclei on their way to the cortex. Thus, the thalamus is a relay center for sensory information going to the cerebral cortex. The thalamus integrates sensory somatic impulses into a pattern of sensations that is projected to the somatic sensory area of the cerebral cortex.

The **telencephalon,** or cerebrum, includes a pair of expanded lobes known as **cerebral hemispheres,** plus the **olfactory bulbs.** The outer wall of these hemispheres forms the **cerebral cortex,** or **cortical region.** The **subcortical region** comprises the remaining cerebral tissue. The subcortical tissue immediately surrounding the corpus callosum is the **cingulated gyrus,** part of the limbic system (figure 16.44). The hemispheres appear embryologically at the most anterior end of the neural tube. In actinopterygian fishes, the embryonic telencephalon proliferates outward to form the everted adult cerebrum. In all other fishes and tetrapods, the embryonic telencephalon forms lateral swellings, which give rise to the cerebral hemispheres of adults (figure 16.42). The reason the hemispheres are everted in ray-finned fishes, but in no other vertebrates, is not known. But it has been suggested that it is an indirect consequence of embryonic packing of the hemispheres in the crowded space between the developing large nasal capsules and eyes.

Reception of olfactory information is a major function of the telencephalon. Even in basal vertebrates, however, ascending fibers arrive from the thalamus, suggesting that the telencephalon has assisted in regulating other sensory integrative functions as well since early in vertebrate evolution. In reptiles and especially in birds and mammals, the cerebral region enlarges 5- to 20-fold compared with most anamniotes of similar body size. This phylogenetic enlargement occurs, in part, because the cerebrum must process more sensory information from the thalamus. This is accompanied by an increased number of association centers within the cerebrum. Nevertheless, within any vertebrate class, the size of the telencephalon may vary considerably among species. For example, among chondrichthyan fishes, primitive sharks and rays possess cerebrums comparable in size with those of amphibians, but in advanced sharks and skates, the relative size of the cerebral hemispheres approaches that of birds and mammals.

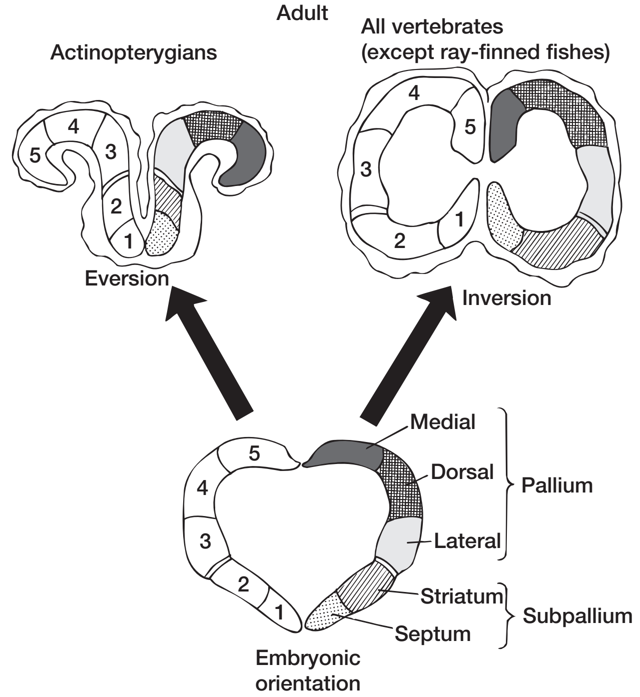


FIGURE 16.42 Embryonic development of the telencephalon. In actinopterygians, the telencephalon becomes everted during development, the pallium swings outward. In all other vertebrates, it becomes evaginated and inverted; walls of the hemispheres inflate outward (evagination) and the medial pallium and septum roll inward (inversion).

TABLE 16.7 Comparison of Recent and Former Terms Designating the Telencephalon

FORMER TERMS		
Morphological	**Descriptive**	**Recent Terms**
	Roof of Telencephalon	
Pallium		PALLIUM
Archipallium	Hippocampus	***Medial*** *pallium*
Neopallium *(Neocortex)* *(Isocortex)*	Cerebral cortex	***Dorsal*** *pallium* *Dorsomedial cortex (cingulate)* ***Lateral*** *pallium* *Dorsal ventricular ridge*
Paleopallium	Piriform cortex	***Lateral*** *cortex*
	Floor of Telencephalon	
Corpus striatum	Basal nuclei	SUBPALLIUM
Neostriatum	*Caudate nucleus,* *Putamen*	***Striatum***
Paleostriatum	*Globus pallidus*	***Pallidum***
Archistriatum	Amygdala (part)	
Septum	Septal area	***Septum***

In many mammals, the cerebral cortex is folded in a complicated fashion to accommodate its increased volume. The rounded folds are **gyri,** and the intervening grooves are called **sulci.** The term **fissure** is often used to note a deep sulcus that separates major surface regions of the cerebrum. Not all mammals show such folding. In the platypus, opossum, and many rodents, the cerebral cortex is smooth. In the echidna, kangaroos, and most primates, the degree of folding is variable. In all groups of mammals, the extent of folding seems to be more pronounced in large species. Left and right halves of the forebrain interconnect via **commissures,** bands of neurons transversely crossing the midline between respective brain regions. Most prominent of the commissures is the **corpus callosum,** found only in eutherian mammals. It communicates between left and right cerebral hemispheres. In monotremes and marsupials, all commissural fibers between the halves of the isocortex cross in the anterior commissure. In eutherian mammals, the anterior commissure contains fibers interconnecting the olfactory and piriform cortices. Other commissures connect paired regions and nuclei within the brain.

Early theories about the evolution of the cerebrum held that new regions progressively emerged out of preexisting regions. A recent "neostructure" was thought to arise from a former "archistructure" that evolved from an initial "paleostructure." The morphological terms coined attempted to express these presumed phylogenetic relationships. In addition, much early study of the brain centered on mammals, especially humans, in which descriptive terms were preferred. Instead of recognizing phylogenetic homologies, these terms expressed quaint or fanciful features. For example, *hippocampus* means horse tail, *amygdala* means almond, and *putamen* refers to a fruit pit. Some of these older terms, including *hippocampus* and *amygdala,* are still used today. However, within recent years, new experimental techniques have improved our understanding of comparative brain structure, leading to an ongoing reinterpretation of earlier ideas and introducing a new and still formative terminology. These differences in terminology are compared in table 16.7. Proliferation of terms has been especially noticeable in mammalian neuroanatomy and human medicine.

The revised view of cerebral evolution challenges not just the terminology but the assumptions on which the old terminology was based. The current view holds that the basic regions of the telencephalon did not emerge in a stepwise fashion. The pattern in which these regions are laid out is very ancient and was present in the common ancestor of all vertebrates. From this fundamental pattern, we see that the cerebrum has two regions: a dorsal **pallium** and a ventral **subpallium.** The pallium possesses **medial, dorsal,** and **lateral** divisions. The subpallium consists of a **striatum** and a **septum** (figure 16.42). All vertebrates have a cerebrum based on this basic plan. Major phylogenetic changes in the cerebrum center on loss, fusion, or enlargement of one or more of these regions.

Pallium The *medial pallium* receives a small primary olfactory input, but substantial auditory, lateral line, somatosensory, and visual inputs. The dorsal and lateral pallia receive ascending input, including visual information relayed from the thalamus. Agnathans possess a characteristic pallium (medial, dorsal, lateral) and subpallium (striatum, septum). However, in lampreys, the cerebral hemispheres incorporate only the lateral pallium and septum; the rest of the pallium (medial and dorsal) and subpallium (striatum) is located just posterior to this in the caudal telencephalon. The lamprey olfactory bulbs are large, about the same size as the cerebral hemispheres (figure 16.35a). Processing of olfactory information is an important role of the olfactory bulb, but it is unclear what additional sensory inputs reach the adjacent telencephalon from ascending tracts.

The elasmobranch pallium includes lateral, dorsal, and medial divisions, although these may in turn be subdivided. The lateral pallium receives the main olfactory input via the lateral olfactory tract. Parts of the dorsal pallium receive visual, lateral line, thalamic, and possibly auditory stimuli. Less is known about the medial pallia, but exchange of information between hemispheres is likely because they fuse across the midline. In ray-finned fishes, the characteristic pallial and subpallial regions can be recognized in a basal group, such as *Polypterus* (figure 16.43), even in the everted telencephalon (figure 16.42). However, in derived teleosts, the embryonic cells of the pallium disperse and intermingle, rather than differentiate into characteristic regions. Thus, the teleost pallium is generally homologous with that of *Polypterus* and other vertebrates, although many of its subdivisions may be unique.

The lungfish and amphibian pallia are similar to each other and to those of primitive sharks but less complex than those of reptiles. In both, the pallium consists of three regions—dorsal, lateral, and medial pallial divisions—which receive olfactory input as well as sensory input from the thalamus. In living amphibians, but not in lungfishes, the amygdala is another region of the pallium concerned with information from the vomeronasal organ.

The pallium of reptiles includes dorsal, lateral, and medial divisions as well as a hypertrophied region, the **dorsal ventricular ridge (DVR),** that dominates the central region of the cerebral hemisphere. Once thought to be part of the striatum, the DVR is now generally believed to be a derivative of the lateral pallium. In birds, the DVR expands further. It accounts for much of the relative increase in size of the cerebral hemispheres and crowds the lateral ventricle into a slit. The dorsal part of the DVR of birds hypertrophies into a region usually called the **Wulst** (figure 16.35g), containing highly organized visual information important in stereoscopic vision. The DVR receives visual, auditory, and somatosensory input from several major thalamic nuclei and projects this information to the striatum and to other parts of the pallium. Its size and central position in the flow of information suggest that the DVR may be a major higher association area in both reptiles and in birds. Both the lateral pallium (formerly termed the piriform lobe) and the medial pallium (the former hippocampus) persist as significant cortical areas in reptiles and birds, but the dorsal pallium is usually reduced in prominence, especially in birds.

Birds have a surprising number of sophisticated behaviors mediated through their enlarged forebrain. Some can memorize over 700 visual patterns (pigeons); make simple tools (crows); recall events that take place within a specific place and time (scrub-jays); have highly accurate sound localization for nocturnal hunting (owls); and exhibit vocal learning and even learn human words to communicate reciprocally with humans (parrots).

Mammals also show a dramatic increase in proportionate size of the cerebral hemispheres, but not because of an enlarged DVR as in reptiles and birds. Instead, the dorsal pallium is enlarged in mammals. In the course of this enlargement, the dorsal pallium thickens and differentiates into layers. The resulting mammalian cerebral cortex is an extensive area called the **isocortex.** In primates, approximately 70% of the neurons in the central nervous system is found in the cerebral cortex. The isocortex is devoted to deciphering auditory, visual, and somatosensory information as well as to controlling the function of the brain stem and spinal cord. All sensory areas are channeled or relayed to the cerebral cortex, bringing together sensory and recall information.

The mammalian medial pallium (hippocampus) receives sensory information and seems to initiate inquisitive or investigative behaviors. It is also concerned with memory of recent events. Olfactory information is shunted to the mammalian lateral pallium (piriform).

Subpallium As mentioned, the *subpallium* is divided into two regions: a medial septum and a more extensive lateroventral striatum. Both regions are distinct, even in the earliest fishes. In lampreys, the subpallium is split between the posterior telencephalon (striatum) and cerebral hemispheres (septum). In other fishes, including teleosts, the subpallium differentiates into homologous septal and striatal regions contained within the cerebral hemispheres. Lungfishes and all tetrapods retain this organization (figure 16.43).

The septum receives information from the medial pallium and is connected to the hypothalamus of the forebrain as well as to the tegmentum of the midbrain. It is an important part of the limbic system. The striatum has a more complicated phylogeny.

The **striatum,** together with a region termed the **pallidum,** are part of an assortment of nuclear groups at the base of the cerebral hemispheres known collectively as the **basal ganglia.** The basal ganglia have been best described in amniotes, especially mammals (table 16.7). Depending upon species, the striatum may form subdivisions, principally the **caudate nucleus** and the **putamen.** The pallidum may form several distinct subdivisions, principally the **globus pallidus.** Although homologies of some of these subdivisions have been difficult to confirm outside amniotes, basal ganglia were likely present in the brain of the ancestral jawed vertebrates. The

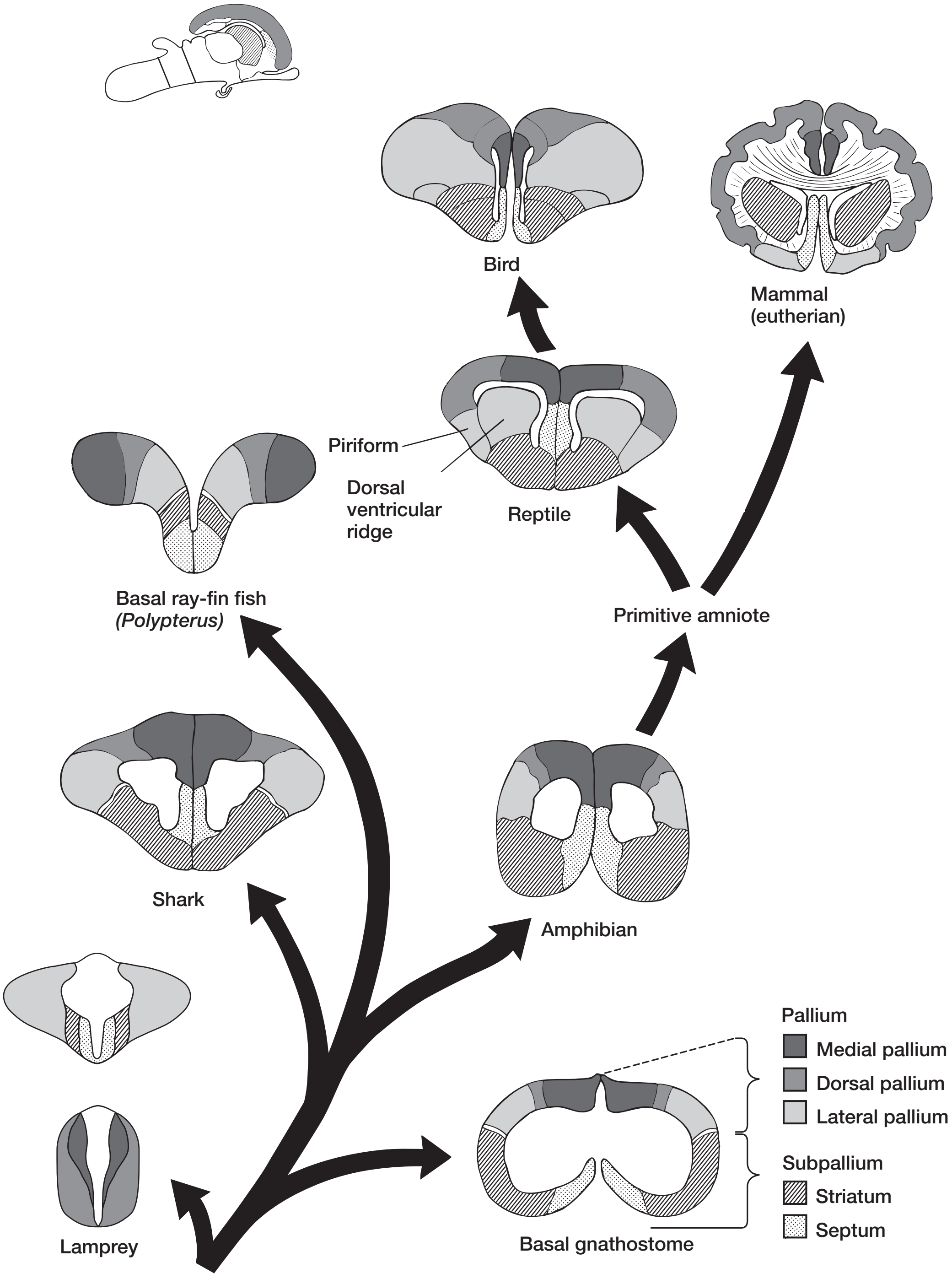


FIGURE 16.43
Evolution of vertebrate cerebral hemispheres. The cerebral hemispheres are shown in characteristic cross section. In the lamprey, the cerebral hemispheres incorporate (top) the components of the subpallium (septum, striatum), but only the lateral pallium; the rest of the pallium resides mostly in the unevaginated region of the telencephalon (bottom) posterior to the cerebral hemispheres. In basal gnathostomes, and thereafter, these five regions are within the cerebral hemispheres.

basal ganglia receive sensory input to and from a nucleus called the **substantia nigra,** located in the midbrain tegmentum. The basal ganglia participate in the control of movement. They receive information on body position and motivational state, then integrate this into suitable motor activity or suppression of unwanted movement. Disruption of the basal ganglia leads to involuntary and purposeless motions known as dyskinesias. Parkinson's disease, characterized by an involuntary tremor that is often worse when the patient is at rest, is associated with degeneration of the basal nuclei. The **amygdala** is complexly derived and functionally integrated into major regions of the brain. One part arises ontogenetically from the pallium and receives vomeronasal input; the other part arises from other regions of the subpallium. The amygdala is linked with the limbic system.

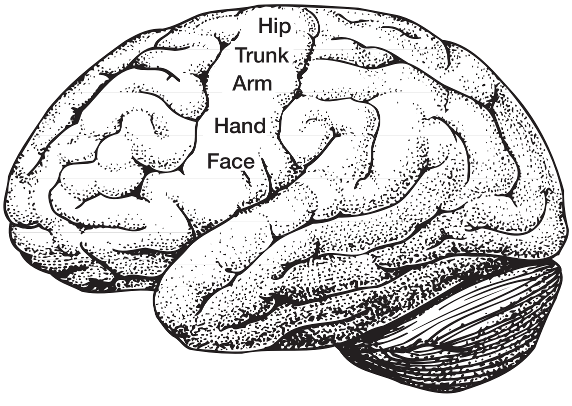
In reptiles and birds, the striatum receives information from the DVR and transmits it first to the brain stem and then to the optic region of the tectum. Neurons within the

BOX ESSAY 16.4

Phrenology to Neuroanatomy: Attempts to Decipher the Relationship between Brain Anatomy and Personality

Phrenology, popular in the nineteenth century, attempted to map moral qualities or personal appetites, which were thought to arise from specific areas of the brain. It was believed that by massaging the scalp, one could detect overdeveloped passions because the brain in that region would be enlarged and produce a swelling in the overlying skull (box figure 1a).

Careful stimulation of motor areas of the brain allows neurophysiologists to map the regions of the brain devoted to specific motor cortex functions (box figure 1b).



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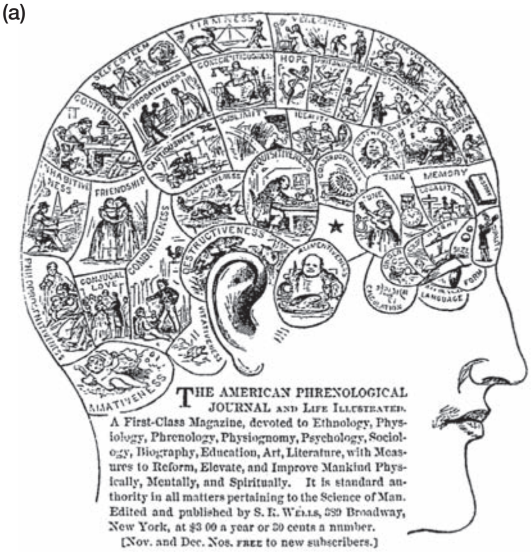

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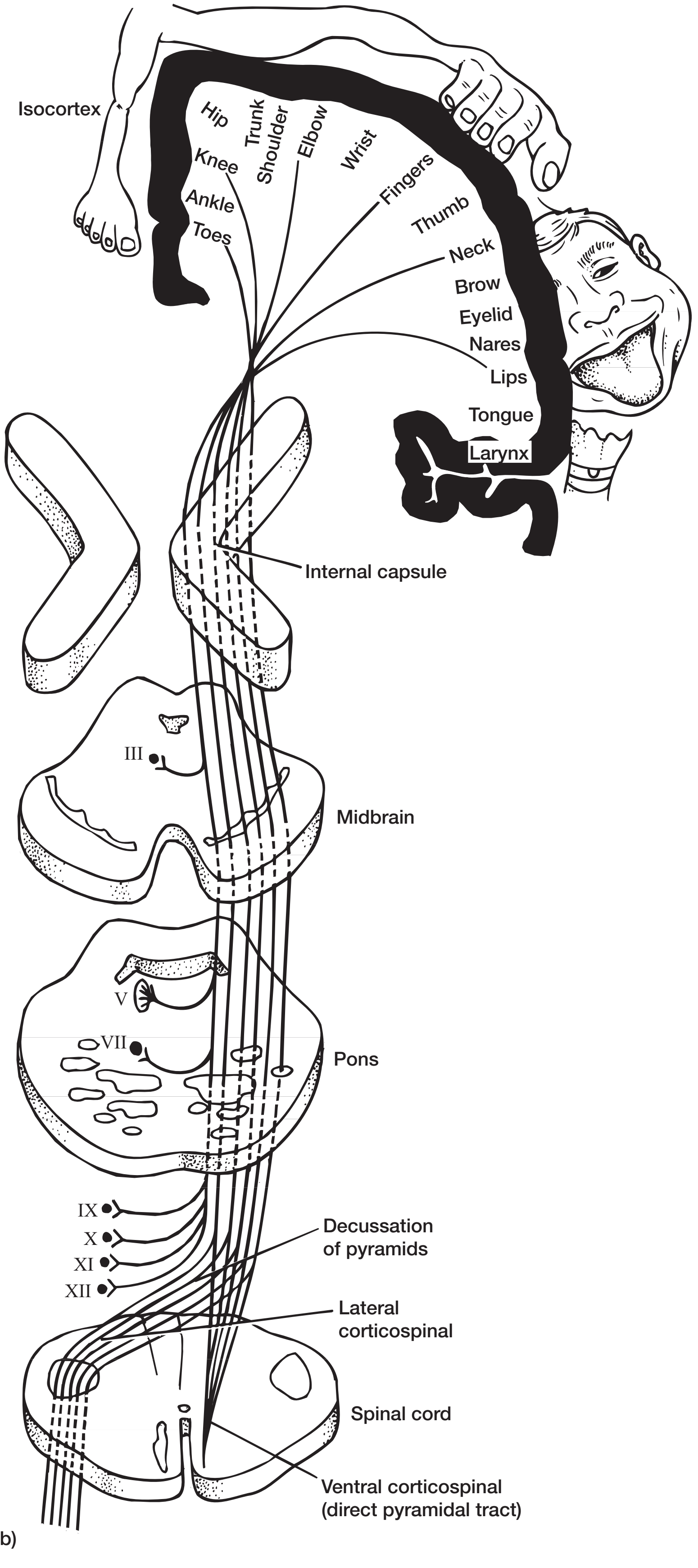


BOX FIGURE 1 Function and phrenology. (a) Map of the human skull used by nineteenth-century phrenologists. (b) In this example, areas of the motor cortex responsible for control of movements in different parts of the body are indicated.

After Netter.

avian striatum are often organized into layers or bands. Expansion of the DVR (reptiles and birds) and the isocortex (mammals) is accompanied by a corresponding expansion of the striatum.

Vomeronasal (p. 677); olfaction (p. 675)

Functional Associations of Parts of the Central Nervous System

Telencephalon The pallium receives direct sensory input, especially auditory, visual, and somatosensory information, from the thalamus, processes this information, and transmits responses to the striatum, hypothalamus, and brain stem. Thus, it indirectly controls locomotion. Major reorganization and expansion of the forebrain are correlated with changes in terrestrial locomotion and posture. In birds, upright posture and complex wing movements are served by the expanded DVR. In mammals, the isocortex enlarges to assume an increasing role in the coordination of complex locomotion.

Especially important sensory signals may be duplicated several times within the telencephalon, giving multiple representations of the same information. For example, visual input, which is important in almost all vertebrates, has two parallel routes to the telencephalon. One is from the retina to the tectum and then to the telencephalon via a relay in the thalamus. The other is from the retina to the thalamus to the telencephalon. In some eutherian mammals in which vision is a major source of information, there may be a dozen areas in the telencephalon that decipher visual stimuli. Similarly, multiple visual areas are found in cats, squirrels, bats, and primates. Duplication of centers that process stimuli apparently improves comparison of sensory input within the nervous system and helps extract information it contains. The anatomical consequence is an increase in the size of the brain area to accommodate the reception and processing of multiple sets of similar sensory information.

Limbic System

The limbic system was first described in the nineteenth century by Paul Broca, whose name is today mostly associated with speech centers of the brain (see box essay 16.3). The functional significance was unknown then, but Broca defined it anatomically. Based mostly upon human brains, Broca defined the limbic system as the cerebral cortex immediately encircling the corpus callosum and brain stem. This includes the deep parts of the cerebral cortex (cingulate gyrus) and medial surface of the temporal lobe of the cerebral cortex. It was not until the early twentieth century that James Papez realized the relationship between the limbic system and emotion. In particular, he and later scientists recognized a functional association of brain centers that include nuclei of the thalamus, hypothalamus, amygdala, hippocampus (medial pallium), **cingulate gyrus,** and septum. The **fornix** is a two-way fiber system that connects all nuclei of the limbic system (figure 16.44a,b and table 16.8). This circuit, the Papez circuit, receives stimuli from the isocortex and returns responses to the isocortex and to the autonomic nervous system. The hypothalamus contains nuclei that affect heart rate, respiration, and general visceral activity through the autonomic nervous system. Changes in these usually accompany strong emotion. The amygdala is active in the production of aggressive behavior and fear. The hippocampus (medial pallium) lies adjacent to the amygdala. Damage to it causes loss of recent memory. The cingulate gyrus and septum are other routes of input to this system. Damage to the cingulate gyrus results in disruption of the *order* of complex behaviors such as parental care. A female rat with such damage still attends to her pups but nurses, licks, repairs the nest, and so forth in no logical sequence and frequently switches randomly from one behavior to another.

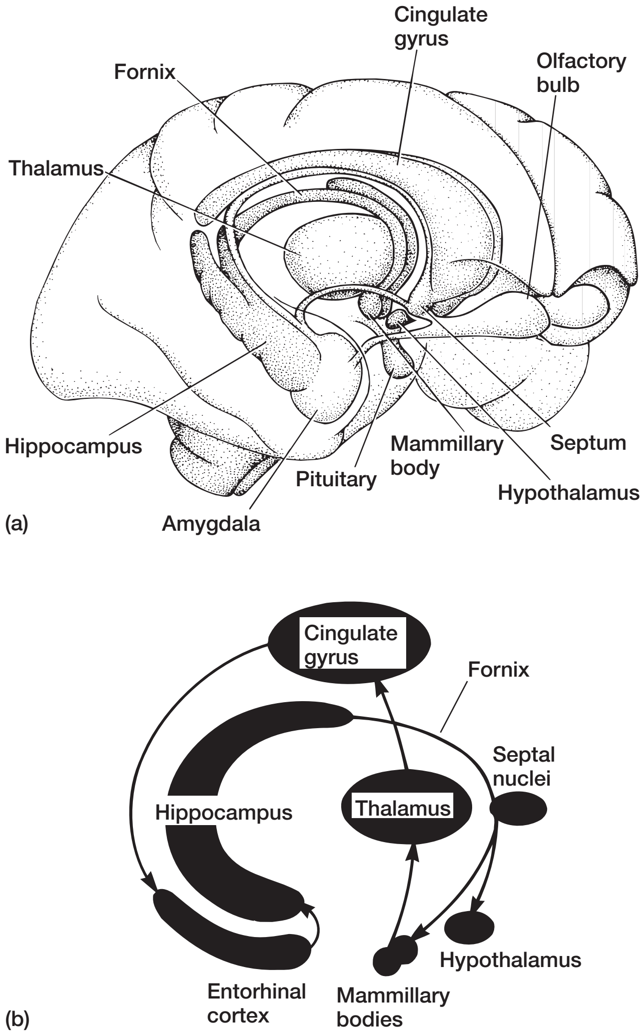


FIGURE 16.44 **Limbic system.** (a) Anatomical components of the limbic system. (b) Flow of information through the limbic system, the Papez circuit.

TABLE 16.8 Centers of the Brain Allied as the Limbic System

Cortical Centers	Subcortical Centers
Telencephalon	Telencephalon
Pallium	Subpallium
Hippocampus	*Septum*
Dentate gyrus	*Amygdala (part)*
Parahippocampus	
	Diencephalon
Cingulate gyrus	*Habenular nucleus*
Amygdala (part)	*Thalamus*
Piriform cortex	*Hypothalamus*
Entorhinal cortex	*Mammillary bodies*

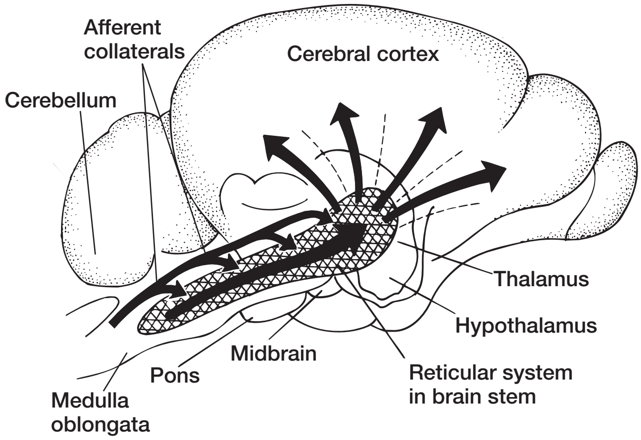


FIGURE 16.45 **Reticular formation.** The reticular formation lies in the medulla and midbrain and projects to the higher centers of the brain. When active, it seems to bring about general alertness. Sensory afferent pathways traveling to higher centers send branches, afferent collaterals, into the reticular system. Through the thalamus, the reticular system is then projected to the cerebral hemispheres, resulting in general arousal.

After T. E. Stize et al., 1951.

The limbic system is involved in two functions. First, as mentioned, it regulates the expression of emotions. Experimental or accidental removal of parts of the limbic system leads to emotional passiveness. This function is important to survival. To sustain itself, an animal must actively seek food, be alert to danger, and respond appropriately when threatened. Phylogenetically, the limbic system, or at least many of its centers, arises early in evolution even before there are many direct connections between the thalamus and the cerebral cortex. The limbic system has been called the "visceral brain" because of its substantial influence on visceral functions through the autonomic nervous system.

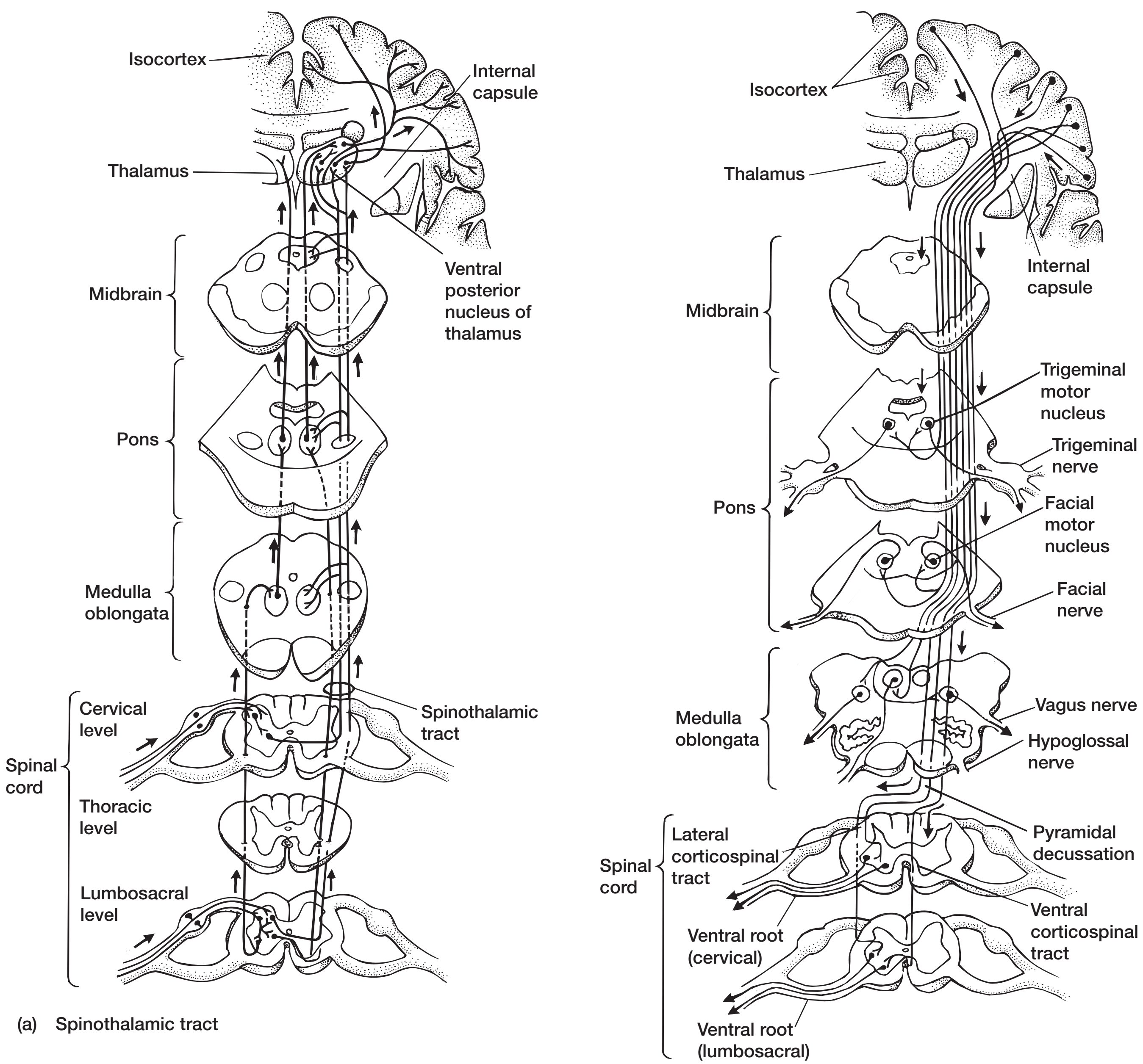
The second function of the limbic system involves spatial and short-term memory. Severe damage to the hippocampus (medial pallium) does not destroy the memory of events prior to the injury, but subsequent events are recalled only with great difficulty or not at all. Memory is probably resident in the isocortex rather than in the limbic system, but the limbic system is involved in temporarily retaining the memory of a recent experience until the experience becomes established as long-term memory in the isocortex. Destruction of the hippocampus, which is very large in food-hiding birds and mammals, severely impairs their ability to locate the hidden food items. In humans, persons with hippocampal damage retain good long-term memory (memory prior to damage), but poor short-term memory. If interrupted while speaking, they must be prompted about what they were saying. Persons they have met just a few minutes before must be reintroduced when returning to the room. One patient, who lived in his house for over 20 years, could not draw a diagram of the house because of impaired spatial and short-term memory loss due to hippocampal damage two decades earlier.

Reticular Formation The reticular formation resides in the medulla and midbrain (figure 16.45). This structure is defined in several ways, but it generally consists of enmeshed neurons and their fibers. The term *reticula* and the term *formation* referred to the microscopic appearance of this region using early methods. It seemed to lack delineated tracts or nuclei like a "center" or a "system." This diffuse arrangement of fibers resembled some parts of the nervous systems of anamniotes and thus inspired the idea that the reticular formation was a phylogenetic retention of an earlier feature. More recent methods for tracing pathways and identifying groups of neurons have turned up almost 30 nuclei, all interconnected and in turn radiating to other areas.

The reticular formation has several functions. First, it is arousal in action via its awakening or stimulation of the cerebral cortex. An alert animal is more attentive to sensory input. Some anesthetics and tranquilizers act by suppressing transmissions through the reticular formation. Damage to the reticular formation can lead to a prolonged coma. Second, the reticular formation also acts as a filter. It selects information to be relayed to higher centers or down the spinal cord. It tends to pass along information that is novel or persistent.

Finally, neurons in the reticular formation act like association neurons in the spinal cord, except here the neurons connect sensory nuclei in the brain with motor neurons in the brain stem and spinal cord. Many complex innate functions such as feeding, vocalization, posture, respiration, and locomotion involve muscles that are innervated by several different cranial centers. The neurons of the reticular formation interconnect these centers and coordinate their separate control into cooperative motor output.

Spinocortical Associations So far we have looked at regions of the central nervous system that perform local functions: reflexes of the spinal cord, association centers of the brain, and systems of alliance. But the central nervous system shows a high degree of integration. Even reflexes completed



(a) Spinothalamic tract

(b) Pyramidal tract

FIGURE 16.46 Processing of sensory and motor information. (a) The spinothalamic tract gathers sensory neurons that carry sensations of pain. The tract then courses to the thalamus, where sensations are relayed to higher brain centers. (b) Pyramidal tract. Decisions initiated in the cerebral cortex are conveyed along descending motor neurons, which form the pyramidal tract, to the appropriate level of the spinal cord. From the spinal cord, the response is passed along a motor neuron to the effector.

After Barr and Kiemm.

at the level of the spinal cord are registered at higher centers, and events in higher centers influence lower levels in the spinal cord. This flow of information tends to occur along distinctive tracts.

Sensory impulses travel up the spinal cord, but before they reach conscious centers in the cerebral cortex, they synapse in the gray matter, in the thalamus, and even in additional nuclei. Thus, information that reaches conscious centers has already been sifted and filtered (figure 16.46a). As discussed previously, all sensory fibers synapse in the thalamus on their way to the cerebral cortex except for olfactory tracts. In the thalamus, sensory impulses are coordinated into an integrated pattern of sensations that is then projected to specialized sensory areas in the cortex. In other words, the cortex receives information that has already been interpreted by subcortical centers. Information traveling down the spinal cord, even if it originated in the cerebral cortex, is modified by the cerebellum, by subcortical centers, and by reflexes at the level of the cord (figure 16.46b).

Overview

The study of nervous system function often includes as much philosophy as it does science. From its basic units, the nervous system builds into complex regions of bewildering and intricate information processing. The basic unit is the neuron, insulated and nourished by neuroglia. Chained together at synapses, neurons form circuits connecting one part of the organism to another—sensory input to motor output via effectors. Somatic and visceral organs pass sensory information to the CNS, and after processing, nerves here carry information, in the form of electrical signals, out to effectors. The peripheral nervous system consists of cranial and spinal nerves, carrying sensory (afferent) or motor (efferent) or both types of fibers. Roots of cranial nerves are usually enclosed in the braincase and supply a variety of organs. Simple reflex response to sensory input occurs at the level of the spinal cord, where arriving sensory information is distributed by association neurons to appropriate motor output. The autonomic nervous system exerts contrasting control over visceral activity to prepare an active state (sympathetic) or restore the organism to a vegetative state (parasympathetic).

The central nervous system includes the spinal cord and brain. The spinal cord is a corridor carrying similar sensory information up to higher levels and returning motor information down to motor neurons. Within the brain, nuclei, clusters of nerve cell bodies, receive ascending sensory information, pertinent to the function in which it is involved. Through association neurons (interneurons), nuclei pass this information to other nuclei involved in processing of similar information, until a response via motor output occurs. Thus, a similar, but more complex, passing of information from sensory input to motor output communicated via interconnecting neurons is established in the brain. Regions of the brain hold collections of nuclei. As functions enlarge phylogenetically, meeting adaptive demands in different environments, the nuclei responsible for processing associated information increase, and the respective brain region exhibits enlargement. The hindbrain includes the medulla oblongata, which houses the primary nuclei of cranial nerves, is a major corridor for ascending and descending tracts, and operates at a suprareflex level presiding over visceral activity. The cerebellum monitors and modifies rather than initiates motor output, thereby smoothing action of effectors. The midbrain roof includes the tectum, which receives sensory input, primarily visual, auditory, and lateral line. Its floor is the tegmentum, a site initiating motor output. The forebrain includes a variety of important regions, the thalamus being one of the most important. Except for olfactory tracts, all other ascending somatic and visceral sensory neurons synapse first in the thalamus, which organizes this input into a pattern of sensations relayed to the cerebral cortex. The cerebrum is inflated into cerebral hemispheres made up of an outer wall, the cerebral cortex, and subcortical regions beneath. The cerebrum is based in all vertebrates upon a common plan that includes a dorsal region, the pallium, and a ventral region, the subpallium. These highly interconnected regions preside over integration of information arriving from lower centers. These regions are in turn organized into systems responsible for coordination of somatic and visceral activity, and even emotional states.

One way to think about the function of the brain is to consider the vertebrate body as consisting of receptor sheets—two-dimensional layers holding sensory receptors. For example, the integumental surface of skin receives impinging points of environmental stimuli or the retinal layer of the eye responds to arriving light stimuli. Neurons from these and other receptor sheets project to corresponding regions of the brain, where this environmental information is mapped, landscaped into an organized geographic chart of the corresponding receptor sheet (e.g., box essay 16.4, figure 1b). In turn, brain maps connect with each other via extensive fiber highways. For example, the corpus callosum connects parts of your right and left brain across the midline, and contains about 200 million fibers. As modern neurobiology has discovered but not yet clarified, these parallel and reciprocal interconnections between mapped brain regions may be the basis for brain function above simple reflex responses leading to higher-order mental processes.

These maps are set up in two steps. The first is during embryonic development wherein genes direct formation of a general map of receptor sheets to brain regions. The second step occurs as the animal activates these pathways in its young life. As a consequence, the synapses between nerve cells change and shift to accommodate the neural pathways used by the active animal, with the result that these maps become modified and more refined. During this step, these connections are not precisely prespecified in the genes but arise as a consequence of the organism's activity and exposure to environmental information. This means that brain maps are not fixed, but instead their borders fluctuate over time, making each slightly different from individual to individual.

Short-term memories that initially form in the hippocampus are eventually transferred to long-term storage in other parts of the brain, residing in both areas for some time. Some of this new memory is thought to be established through addition or modification of new connecting synapses. Neurogenesis, the birth of new neurons, arising in the adult brain is also thought to participate. Within a couple of weeks, newborn neurons perish if not challenged to learn something new. If involved in learning something new with great effort, the new neurons persist. But these new neurons also weaken or boot old memories, a function thought to clear the hippocampus of old memories, making room for new memories.

The subtleties of the central nervous system are profound. We have seen that the nervous system gathers information about the body's internal status and the outside world and the results of previous experience and turns these into responses that might allow the organism to maintain itself in its environment. But there is more to this process than the mechanical processing of information. Emotions, goals, and conscious participation shape a response, at least in humans. To a large extent, our responses are shaped by our perceptions of physical stimuli, which are mediated by sensory receptors. In chapter 17, we take a closer look at these sensory receptors.

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