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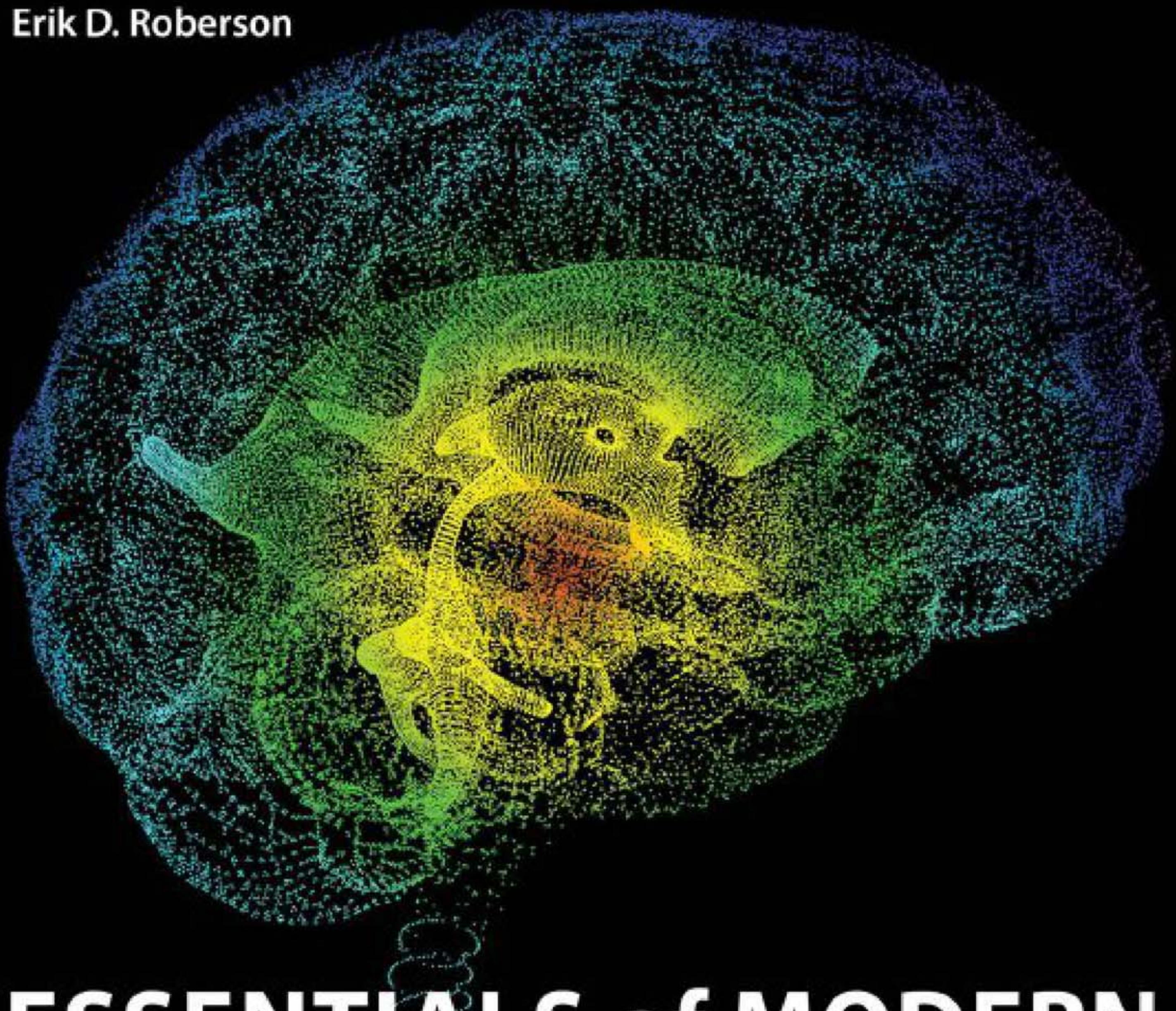

ESSENTIALS of MODERN NEUROSCIENCE

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Essentials of Modern Neuroscience

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A LANGE medical book

Essentials of Modern Neuroscience

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Franklin R. Amthor, PhD, is a professor of Psychology at the University of Alabama at Birmingham (UAB). Dr. Amthor's research interests evolved from his undergraduate electrical engineering background at Cornell University into artificial intelligence simulations involving Perceptrons, and then visual neuroscience. His Ph.D. work was done at Duke University in Biomedical Engineering on quantitative analysis of retinal ganglion cell responses. He did a postdoctoral fellowship at the School of Optometry at UAB, and then was an NEI R01 funded principal investigator who led a team determining the relationship between mammalian ganglion cell physiology, morphology, and central projections. More recently, he has worked on retinal circuitry underlying the responses of different retinal ganglion cell classes, and on assistive devices for the blind.

Anne B. Theibert, PhD, is a professor of Neurobiology at the University of Alabama at Birmingham (UAB). Dr. Theibert is a researcher, teacher, and course director in both the UAB College of Arts and Sciences and School of Medicine (SoM). She received her B.A. in Chemistry from Goucher College, and Ph.D. in Biological Chemistry from Johns Hopkins University. Following a postdoctoral fellowship in the Neuroscience Department at Johns Hopkins, she was recruited to the SoM faculty at UAB in 1991, and directed an NIH-funded basic research program for 17 years, concentrating on cell signaling during neuronal development, with a focus on understanding pathways disrupted in neurodevelopmental disorders. In 2008, Dr. Theibert cofounded the UAB Undergraduate Neuroscience Program (UNP) and served as Director of the UNP during its first decade. She currently teaches neuroscience and nervous system development to UAB professional and graduate students, and directs and teaches undergraduate courses in cellular, molecular, systems and cognitive neuroscience.

David G. Standaert, MD, PhD, is a professor and chair of the Department of Neurology at the University of Alabama at Birmingham (UAB), where he holds the John N. Whitaker Endowed Chair in Neurology. He is a physician-scientist with interests in Parkinson disease and other disorders of movement. He received his A.B. with high honors from Harvard College, and M.D. and Ph.D. degrees from Washington University in St. Louis. He was a resident in neurology at the Hospital of the University of Pennsylvania, and a fellow in movement disorders at Massachusetts General Hospital. He joined the faculty of Harvard Medical School in 1995, and relocated to UAB in 2006. Currently he directs the NIH-funded Alabama Morris K. Udall Center of Excellence in Parkinson's Disease Research. He is Chairman of the Scientific Advisory Board of the American Parkinson Disease Association, Deputy Editor of the journal *Movement Disorders*, a Fellow of both the American Neurological Association and the American Academy of Neurology, a Councilor of the Association of University Professors of Neurology, and a member of the NIH/NINDS Board of Scientific Counselors. His lab has a long-standing interest in the basic mechanisms underlying Parkinson disease as well as the complications of therapy.

Erik D. Roberson, MD, PhD, is the Rebecca Gale endowed professor of Neurology and Neurobiology at the University of Alabama at Birmingham (UAB). Dr. Roberson is a physician-scientist whose research is dedicated to reducing the impact of age-related cognitive disorders. He received his A.B. with highest honors from Princeton University and then earned his M.D. and Ph.D. in neuroscience at Baylor College of Medicine. He was a resident and chief resident in neurology at the University of California San Francisco, where he also completed a clinical fellowship in behavioral neurology. In addition to his laboratory focused on understanding mechanisms and identifying new treatments for dementia, Dr. Roberson directs the Alzheimer's Disease Center and the Center for Neurodegeneration and Experimental Therapeutics at UAB. He also cares for patients in the UAB Memory Disorders Clinic and leads clinical trials testing new dementia treatments.

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Preface

Why does the world need another neuroscience text? Students study neuroscience for a variety of purposes that range from molecular basic science, to systems, to clinical. Although there are many neuroscience texts that cover some of these areas well, few attempt to cover the entire range. Moreover, texts that attempt to cover such a broad range of neuroscience content are often too large to be tractable, or differentiate poorly between basic science and clinical sections.

Essentials of Modern Neuroscience has been written for students in the medical and other health professions with the goal of being accessible, coherently organized, and universal in its coverage of basic science and clinical neuroscience. It is thus divided into two main parts, the first being a thorough treatment of the basic science of the anatomy and function of the nervous system, and the second comprising an extended treatment of nervous system disorders and therapeutics.

Part I, Anatomy & Function of the Nervous System, was written with two goals: (1) It stands alone as a concise introductory text for neuroscience, and could be used as such, and (2) its organization allows it to be used as a good reference for the clinical sections when basic science background is needed. Section I gives a systematic explanation of the layout of the central and peripheral nervous systems, concentrating on their role in nervous system function. Section II then covers modern molecular neuroscience, starting with a complete treatment of the cellular biophysics underlying the resting and action potentials, then covering synaptic transmission, neurotransmitter systems, and synaptic plasticity. Section III, Systems Neuroscience: Sensory & Motor Systems, considers all the sensory systems from transduction to central processing. It then moves to motor systems, covering the pyramidal and extrapyramidal cortical-spinal pathways, and then the autonomic and enteric nervous systems. Section IV is Cognitive Neuroscience, investigating the neural basis of consciousness, learning and memory, language, emotion, and circadian rhythms.

Part II, Nervous System Disorders & Therapeutics, introduces students to the major disorders of the nervous system and commonly used therapeutics, building on the foundation laid down in Part I, and is organized by clinical specialty. Section V is comprised of 12 chapters surveying disorders treated by neurologists and neurosurgeons. Section VI covers otological, vestibular, and ophthalmological disorders. Finally, Section VII covers the world of psychiatric disorders with seven chapters ranging from thought and mood disorders to addiction and functional disorders. Written by clinicians, the chapters of Part II are intended to prepare students for initial clinical encounters in each of these specialty areas. Each chapter begins with a description of disease prevalence and burden to help students understand which disorders they are most likely to encounter and which have the biggest impact. Discussions of the diagnosis, key features, and treatment of these disorders are aimed at preparing students for board-type examinations. Case studies help consolidate the presentation of classic diseases.

Acknowledgment

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PART I
ANATOMY & FUNCTION OF THE NERVOUS SYSTEM

SECTION I

Organization & Structure of the Nervous System

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CHAPTER 1

Organization & Cells of the Nervous System

Anne B. Theibert

OBJECTIVES

After studying this chapter, the student should be able to:

- Outline the major anatomic components of the central nervous system (CNS) and peripheral nervous system (PNS).
- Diagram the functional areas of the brain and spinal cord.
- Describe the types of nerves and ganglia in the PNS and their structure.
- Distinguish the different categories of neurons.
- Identify the neuronal organelles and their biochemical functions.
- Diagram the specialized neuronal processes and their functions.
- Describe the main CNS and PNS glial cells and their functions.

OVERVIEW: THE NERVOUS SYSTEM

The nervous system mediates a wide range of functions, from detection of environmental stimuli, to control of muscle contraction, to problem solving, language, and memory. The nervous system is divided into 2 main parts, the central nervous system (CNS) and the peripheral nervous system (PNS) (**Figures 1–1** and **1–2**). Anatomically, the CNS is divided into the brain and spinal cord, whereas the PNS is composed of ganglia and nerves, including cranial and spinal nerves and their branches. Functionally, the PNS can be divided into the somatic, autonomic (visceral), and enteric nervous systems. In the overall flow of information, the PNS detects and relays sensory information about the external and internal environments to the CNS. The CNS receives, integrates, and stores information and controls the output to the PNS to generate responses and behavior.

At the cellular level, the nervous system is composed of neurons and glial cells (**Figure 1–3**). Neurons (also called nerve cells or neuronal cells) are the main signaling cells that communicate with other neurons, muscles, or glands. Neurons can be categorized by their function as sensory neurons, motor neurons, or interneurons or by their morphology or neurotransmitter. Glial cells (also called neuroglia or glia) are the support cells in the nervous system. Astrocytes and satellite cells provide structural and metabolic support, oligodendrocytes and Schwann cells furnish myelination of axons, pericytes regulate capillaries, ependymal cells synthesize cerebrospinal fluid (CSF), microglia are immune cells, and enteric glia are part of the gastrointestinal (GI) tract. Neurons have a cell body where the nucleus and majority of cellular organelles are located and many biochemical activities occur. Neurons also contain specialized processes and regions that allow them to send and receive signals rapidly and precisely. The axon is a process by which electrical signals are conducted and where signals are sent to other neurons or target cells. The dendrites are branched processes that receive signals from other neurons. The synapse is a structure where signals are transmitted, via synaptic transmission, from the axon to its target. Neurons can receive thousands of synaptic inputs, can form neural circuits, and function in networks that underlie sensations, cognitive functions, and the generation of responses and behavior.

CNS COMPONENTS, COVERINGS, & VASCULATURE

The brain and spinal cord compose the CNS. The brain is enclosed within the cranial cavity and is protected by the cranium (skull) and meninges (**Figure 1–4**). The meninges are a 3-membrane system that covers, protects, and nourishes the brain and spinal cord. The outer dura mater is a thick tough membrane that is connected to the cranium and protects the brain. The middle membrane, called the arachnoid mater,

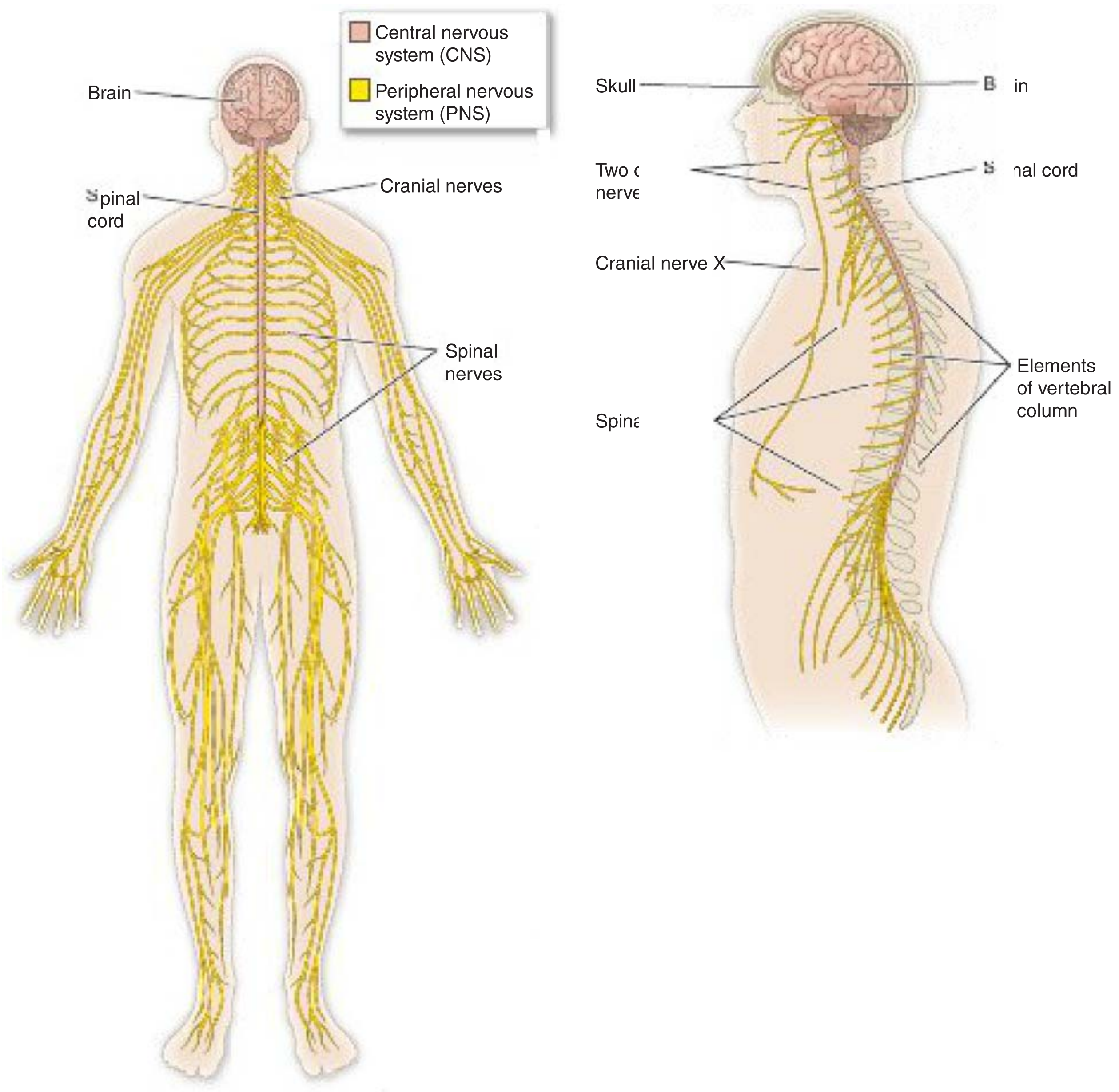

FIGURE 1–1 Anatomic divisions of the nervous system and their structures: CNS and PNS. Forming the CNS, the brain (encased in the skull) is continuous with the spinal cord (encased in the spinal column). Forming the PNS, cranial nerves emerge from the brainstem, while spinal nerves emerge from the spinal cord. In the PNS, nerves are associated with spinal, cranial or autonomic ganglia, which are not shown.

cushions the brain. Below the arachnoid is the subarachnoid space, which contains CSF and where specialized regions called arachnoid granulations resorb CSF. The innermost layer, the pia mater, is a thin layer that adheres to the surface of the brain and follows its contours, forming a barrier but with many capillaries that nourish the brain and spinal cord.

The brain has 3 main regions: the forebrain, brainstem, and cerebellum. The inner spaces of these regions form the ventricles, which produce and circulate CSF and are connected to form the ventricular system (**Figure 1–5**). Both the meninges and brain are highly vascularized. Two main pairs of arteries supply blood to the brain (**Figure 1–6**). The internal carotid arteries, which are branches from the common carotid artery, supply the anterior brain, whereas the vertebral arteries, which are branches from the subclavian artery, supply the posterior brain and brainstem. The main venous blood outflow from the brain is via the jugular veins.

CNS capillaries are specialized in that their vascular endothelial cells form tight junctions and are enveloped in glial cells, together producing the blood–brain barrier (BBB). The BBB is a selective permeability barrier that prevents the direct movement of unwanted molecules, immune cells, and pathogens into the brain. The BBB allows the passage of water, oxygen, carbon dioxide, and lipid-soluble molecules, including

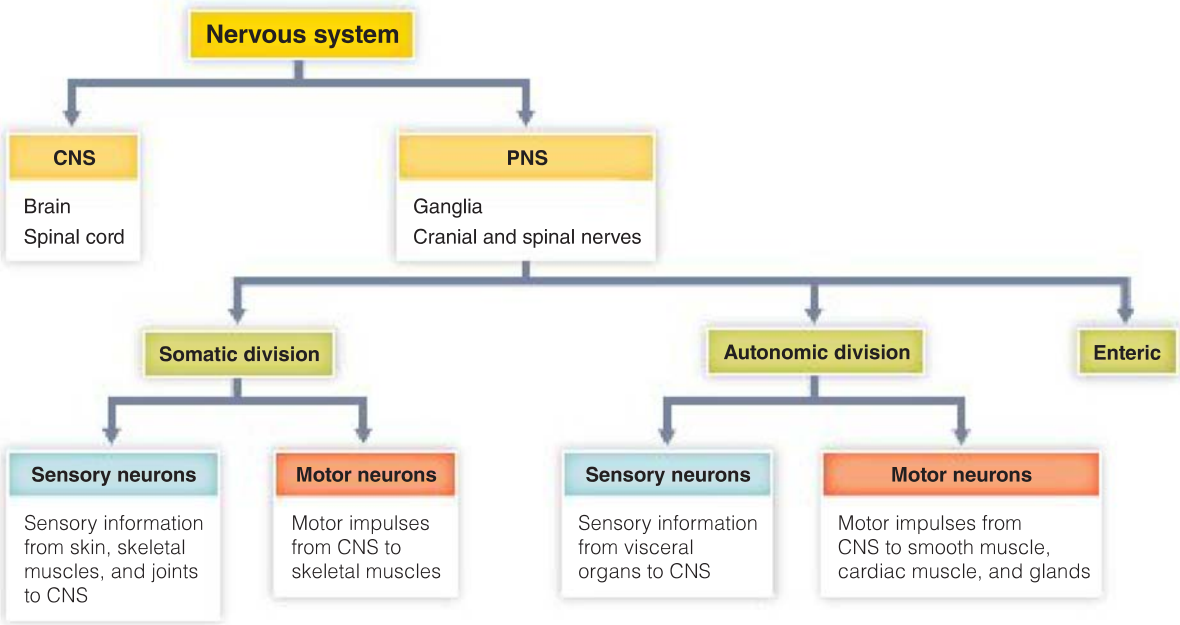

FIGURE 1–2 Functional divisions of the nervous system: CNS and PNS.

steroid hormones, by passive diffusion. Astrocytes selectively transport ions and molecules such as glucose and amino acids and release them into the extracellular fluid to supply neurons and other glia with essential nutrients.

BASIC BRAIN ANATOMY

The forebrain is the largest part of the brain and contains the cerebrum and diencephalon (**Figure 1–7**). The cerebrum is formed by the large left and right cerebral hemispheres, which are separated by the medial longitudinal fissure, and contains the outer cerebral cortex, inner cerebral white matter, and subcortical nuclei. The cerebrum encloses the lateral ventricles and overlies the diencephalon, a structure that contains the thalamus and hypothalamus and that surrounds the third ventricle. Functionally, the forebrain is involved in receiving sensory information from the PNS and generating outgoing motor information, and is where executive and cognitive functions are generated. The oldest part of the brain, the brainstem, is composed of the midbrain, pons, and medulla and serves to relay information from the spinal cord and cerebellum to the forebrain and vice versa. In addition, the brainstem regulates vital functions, such as breathing, consciousness, and control of body temperature. The cerebral aqueduct and fourth ventricle lie inside the brainstem. Connected to the pons, the cerebellum forms the posterior-most region of the brain and is involved in control and coordination of movement and some cognitive tasks.

Examination of postmortem fixed brain tissue reveals that each of these brain regions contains gray and white matter areas (**Figure 1–8**). In living tissue, gray matter appears pinkish light brown. Gray matter contains mainly neuronal cell bodies, their dendrites, and associated glial cells. In the brain, 2 types of gray matter are present. Cortical gray matter forms the outer regions of the cerebrum and cerebellum and is distinguished by its layered organization of neurons. The other type of gray matter is called a nucleus, an aggregate of cell bodies with similar morphology and function found below the cortex (subcortical nuclei) and in the brainstem and cerebellum. White matter contains predominantly myelinated axons (which, because of their fatty rich myelin membrane, produce the white appearance) and white matter glial cells. White matter contains bundles of myelinated axons that are referred to as tracts in the CNS. In the brain, the white matter tracts include projection tracts that connect neurons in the forebrain to neurons in the brainstem or spinal cord, association tracts that connect one cortical region to another, and commissural tracts, which connect areas from one side of the brain to the other.

The exterior surface of the cerebrum is distinguished by many gyri (singular: gyrus) and sulci (singular: sulcus) that produce the characteristic folded appearance of the human and many mammalian brains. A sulcus is a groove or furrow in the cerebral cortex, whereas a gyrus is a crest or ridge. The folding created by gyri and sulci facilitates a larger surface area of cerebral cortex to fit inside the skull. Deep sulci separate the cortex into 4 cortical lobes on each side, called the frontal, parietal, temporal, and occipital lobes, named for the cranial bones that overlie each (**Figure 1–9**). The central sulcus forms the division between the frontal and parietal lobe. The lateral sulcus (also called the Sylvian fissure) separates the temporal lobe from the frontal and parietal lobes. The parieto-occipital sulcus forms the boundary between the parietal and occipital lobes. Many additional sulci and gyri are present in the

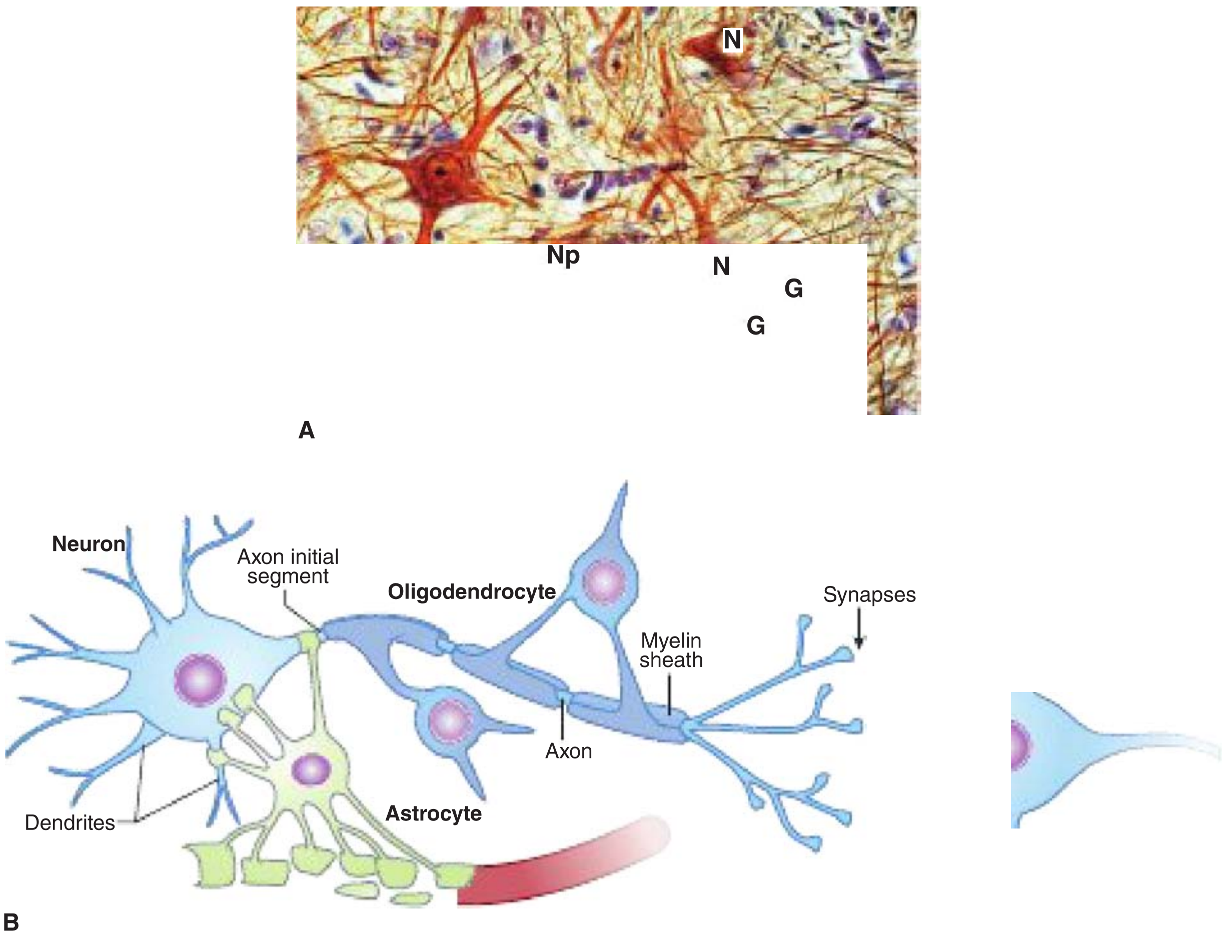

FIGURE 1–3 Cellular components of the nervous system. **A.** Micrograph showing neuronal cell bodies (N) and smaller glial (G) cells that surround them in the CNS. Use of a hematoxylin stain with gold chloride shows the neuropil (Np), which is the dense network of axons and dendrites. **B.** Neurons and glia in the CNS. A typical projection/principal interneuron has a cell body (or soma), multiple dendrites, which receive synaptic responses, and an axon, which sends electrical signals and is insulated by a myelin sheath derived from specialized membrane processes of oligodendrocytes. Astrocytes perform supportive roles in the CNS, and their processes are closely associated with neuronal synapses and capillaries. (Part A, reproduced with permission from Young B, Heath JW: *Wheater's Functional Histology: A Text and Colour Atlas*. Edinburgh: Churchill Livingstone; 2000; part B, reproduced with permission from Katzung BG: *Basic & Clinical Pharmacology,* 14th ed. New York, NY: McGraw Hill; 2018.)

cerebral cortex, with all cortical gyri and sulci containing an outer layer of cortical gray matter and a thin layer of underlying white matter. Each of the 4 main lobes contains distinct anatomic and functional areas.

BASIC SPINAL CORD ANATOMY

The spinal cord emerges caudally from the brainstem, within the spinal canal, and is protected by the vertebral column (also called the spine) and meninges (Figure 1–10). Along their length, the vertebral column and spinal cord inside are separated into 5 regions, called cervical, thoracic, lumbar, sacral, and coccygeal segments. Similar to the brain, the spinal cord is composed of gray and white matter regions but with an opposite organization. Spinal gray matter, composed of neuronal cell bodies, dendrites, and glia, is located medially and is surrounded by spinal white matter, which contains tracts and glia, located in the lateral areas of the spinal cord. The gray matter surrounds the inner central canal, which provides CSF to the spinal cord. Spinal gray matter is separated anatomically and functionally into dorsal (posterior) and ventral (anterior) horns on each side. Sensory information is carried by afferent axons of spinal nerves, which enter the cord via the dorsal roots. These sensory axons branch, and one branch can synapse on interneurons in the dorsal horn, whereas the other branch can ascend to the brain. These axons form the ascending tracts in the spinal cord. Descending tracts in the white matter provide outgoing motor information from the cerebrum or brainstem. The axons in the descending tracts synapse on motor neuron cell bodies in the ventral/anterior horns. The ventral horn motor neurons extend their axons out of the cord via the ventral root, and their axons form the motor components of the spinal nerves. Because the lower motor neurons cell bodies lie in the spinal cord, while their axons form the motor components of the spinal nerves, they are considered part of both the CNS and PNS. The anatomy of the brain and spinal cord is described in greater detail in Chapter 3.

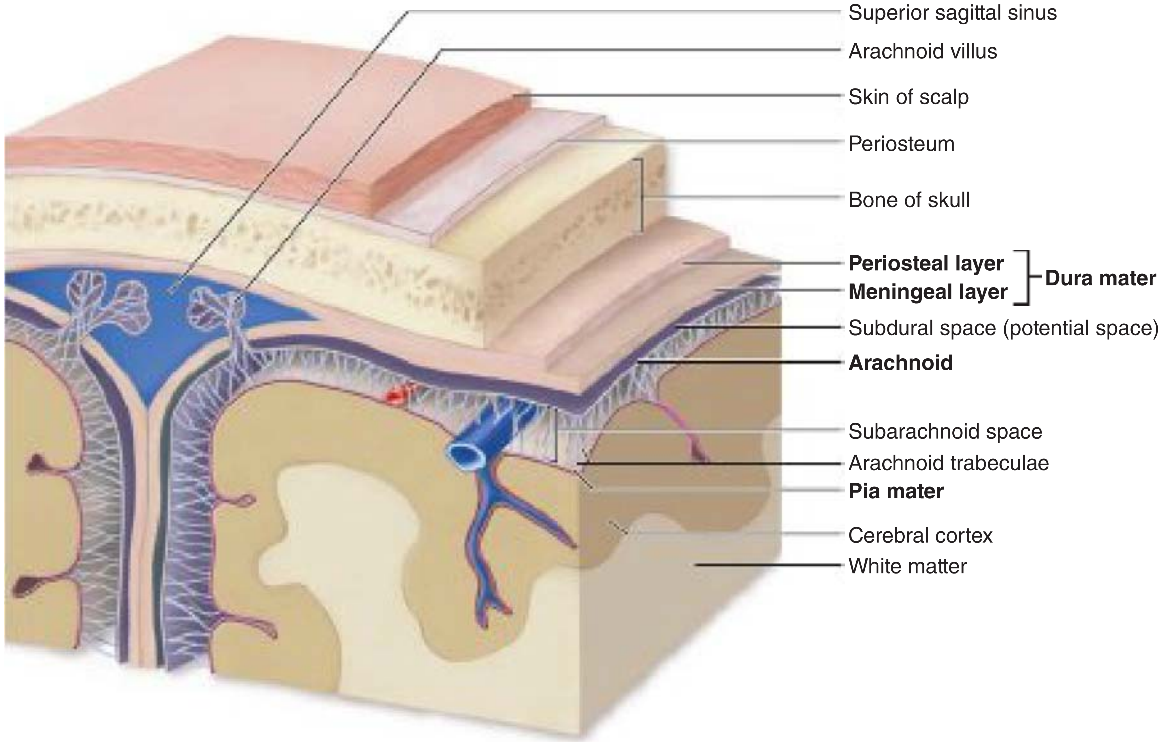

FIGURE 1–4 Meninges around the brain. Composed of the dura mater, arachnoid mater, and pia mater, the meninges form a membrane system that surrounds the brain and the spinal cord. The diagram also show the subarachnoid space filled with cerebrospinal fluid (CSF), and arachnoid villi, which function to resorb CSF and transfer it into the blood. (Reproduced with permission from McKinley MP, O'Loughlin VD, Bidle TS. *Anatomy and Physiology: An Integrative Approach.* New York, NY: McGraw Hill; 2013.)

PNS: FUNCTIONAL DIVISIONS

The PNS has 3 functional divisions: the somatic, autonomic (also called visceral), and enteric nervous systems. The somatic nervous system mediates conscious/voluntary movement via regulation of skeletal muscle contraction and provides sensory information from the skin, muscles, and joints. The autonomic nervous system involves unconscious/involuntary control of cardiac muscle, smooth muscle, and glands. Its sensory

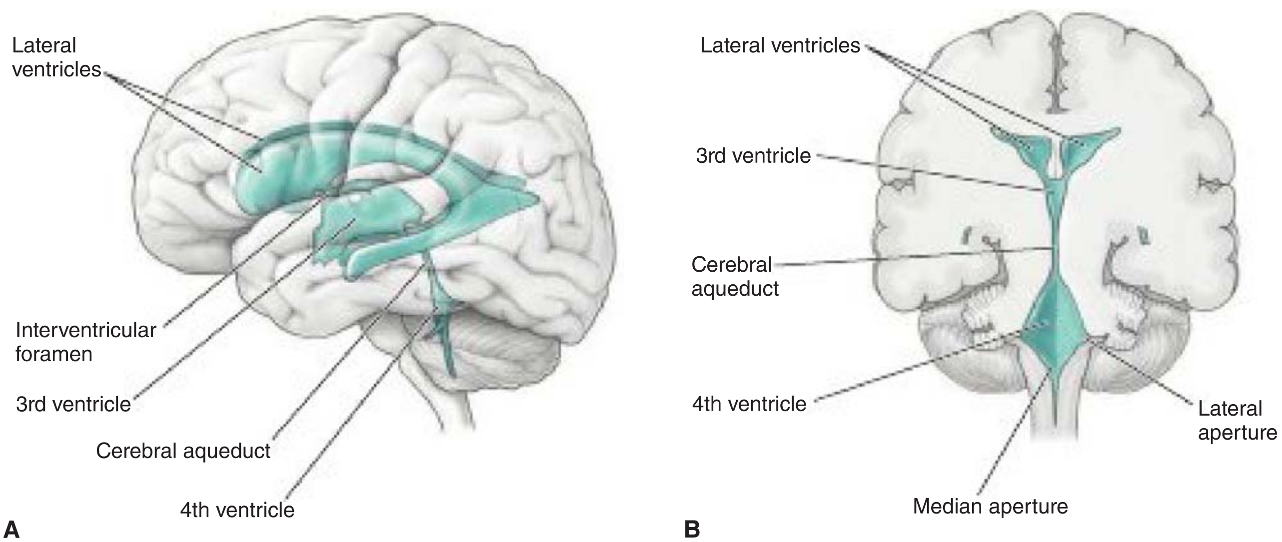

FIGURE 1–5 The ventricular system. **A.** Three-dimensional lateral view of the ventricles of the brain. **B.** Coronal section of the brain showing the ventricles. The ventricles are lined with ependymal cells, and contain the choroid plexus, which synthesize cerebrospinal fluid (CSF). The two lateral ventricles lie within the left and right cerebrum, the third ventricle (between the halves of the diencephalon), the cerebral aqueduct, and the fourth ventricle within the brainstem. (Reproduced with permission from Morton DA, Foreman KB, Albertine KH. *The Big Picture: Gross Anatomy,* 2nd ed. New York, NY: McGraw Hill; 2019.)

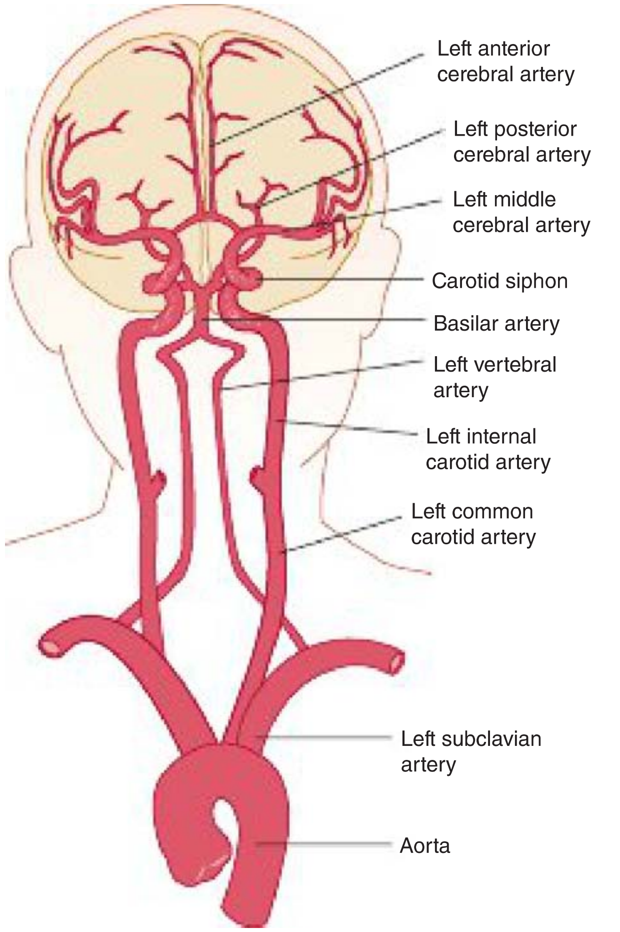

FIGURE 1–6 Blood supply to the brain and the major cerebral arteries. Arterial blood for the brain enters the cranial cavity by way of two pairs of large vessels. The pair of internal carotid arteries supplies arterial blood to most of the forebrain while the pair of vertebral arteries supplies the brainstem, cerebellum, occipital lobe, and parts of the thalamus. (Reproduced with permission from Waxman SG. *Clinical Neuroanatomy,* 28th ed. New York, NY: McGraw Hill; 2017.)

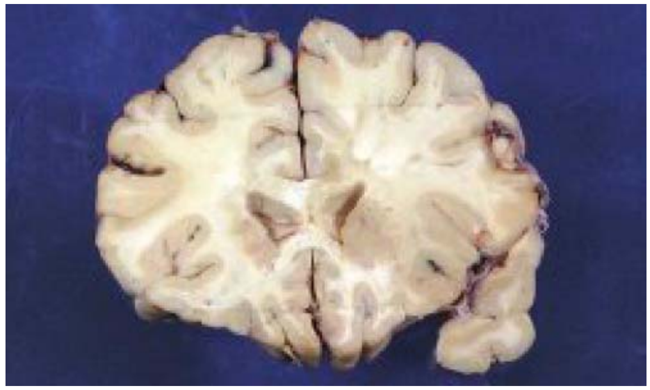

FIGURE 1–8 Brain gray and white matter areas. Coronal section from postmortem human brain. (Reproduced with permission from Kemp WL, Burns DK, Travis Brown TG. *Pathology: The Big Picture.* New York, NY: McGraw Hill; 2008.)

component, often called the visceral sensory system, provides information from the viscera, the internal organs, and vasculature. The autonomic motor system is divided into the sympathetic and parasympathetic nervous systems. The sympathetic nervous system, referred to as the “fight or flight” system, is activated under conditions requiring mobilization of energy. The parasympathetic nervous system, referred to as the “rest and digest” or “feed and breed” system, is activated when organisms are in a relaxed state. The enteric nervous system, which is also under involuntary control, governs the GI system. Although it receives considerable input from the autonomic nervous system, the enteric nervous system can function independently and is considered a separate system in the PNS.

PNS: ANATOMIC COMPONENTS

Anatomically, the PNS is composed of ganglia and nerves. Ganglia are clusters of functionally related neuronal cell bodies and their accompanying glial cells in the PNS.

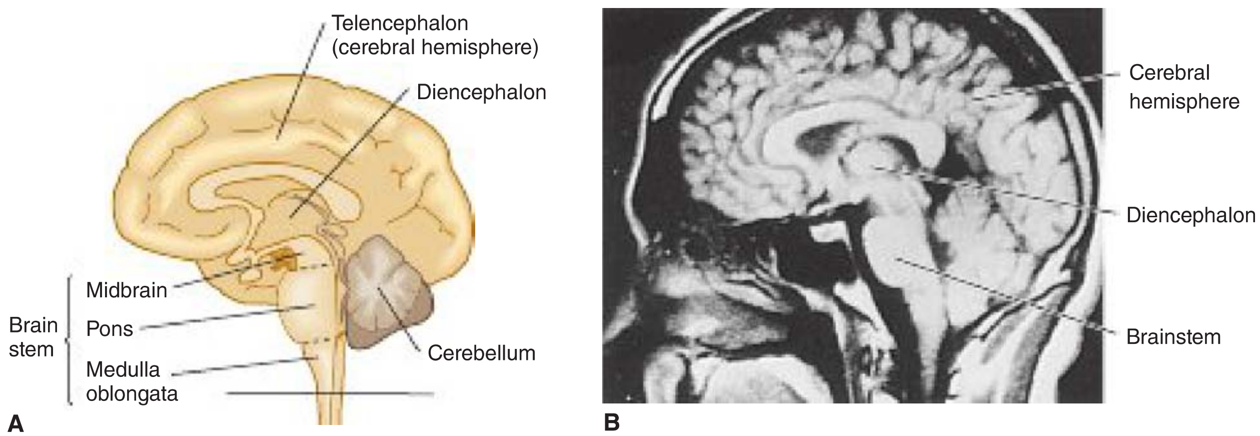

FIGURE 1–7 Major anatomic divisions of the brain. **A.** Illustration of the midsagittal plane. **B.** Magnetic resonance image of a midsagittal section through the head. (Reproduced with permission from Waxman SG. *Clinical Neuroanatomy,* 28th ed. New York, NY: McGraw Hill; 2017.)

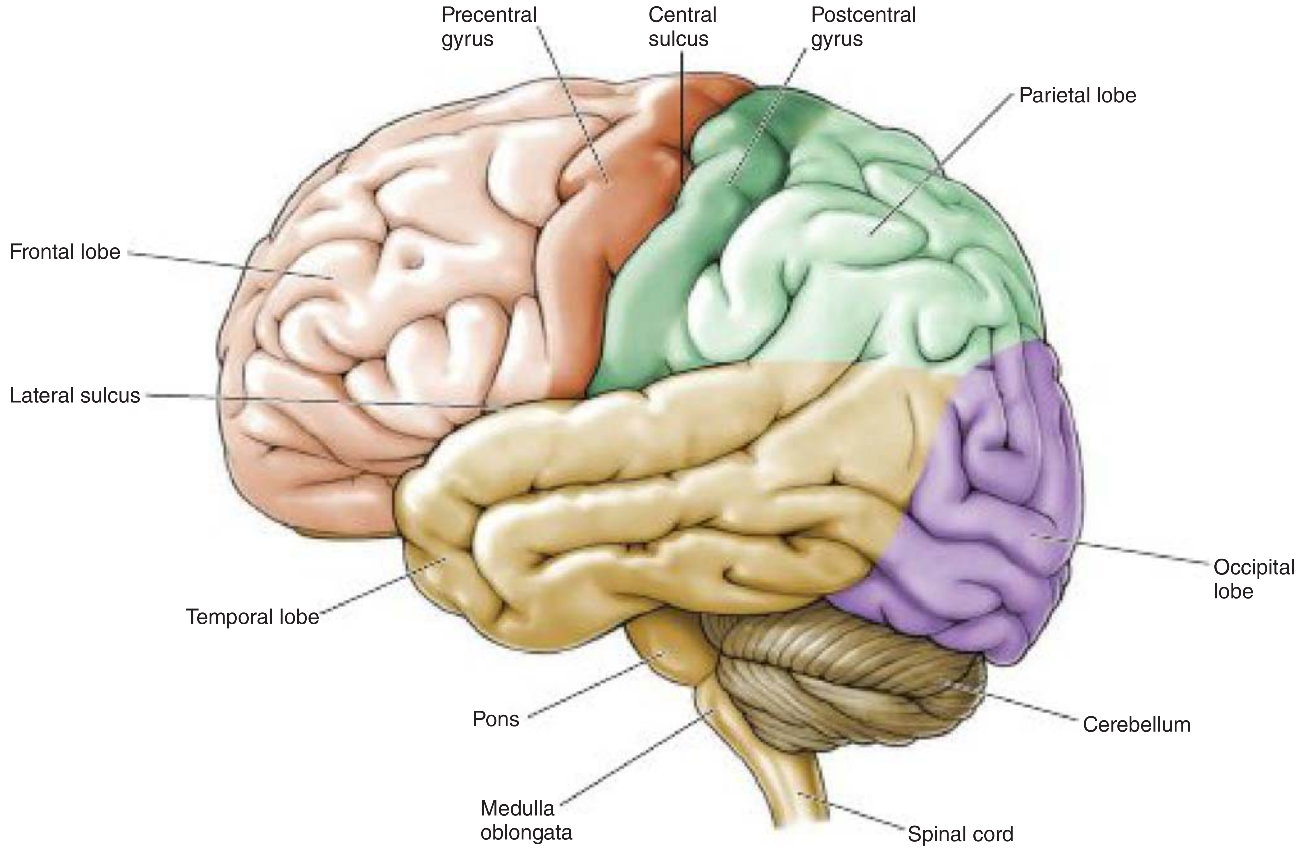

FIGURE 1–9 Lateral view of the brain. This view illustrates the left cerebral hemisphere with its major sulci and gyri, cortical areas, and several subcortical structures. (Reproduced with permission from Morton DA, Foreman KB, Albertine KH. *The Big Picture: Gross Anatomy,* 2nd ed. New York, NY: McGraw Hill; 2019.)

Cell bodies of somatic sensory neurons form the dorsal root ganglia, whereas cell bodies of autonomic neurons form the sympathetic and parasympathetic ganglia. The sympathetic ganglia lie outside of but close to the spinal cord and communicate to form the sympathetic chain. The parasympathetic ganglia in the body lie close to the organ they innervate. The cranial ganglia contain parasympathetic or sensory cell bodies.

Nerves are bundles of axons ensheathed in connective tissue that innervate all parts of the body, sending messages to and receiving messages from the CNS (**Figure 1–11**). The neuronal cell bodies that give rise to nerves do not lie within the nerves themselves. Rather, their cell bodies reside within the brain, spinal cord, or ganglia. Nerves can contain both efferent and afferent axons. Efferent axons transmit motor signals from the CNS to the PNS and can be somatic or autonomic. Afferent axons transmit sensory signals from the PNS to the CNS; afferents can be somatic or visceral. Afferent and efferent axons are protected by several layers of connective tissue, which together with glia and blood vessels form nerves.

Spinal and cranial nerves supply input to and output from the CNS. There are 31 pairs of spinal nerves, which emerge from and travel to the spinal cord and which are named for the spinal cord segment to which they connect (Figure 1–11). Spinal nerves are mixed nerves, containing both motor efferents and sensory afferents and containing both somatic and autonomic components. As they leave or enter the spinal cord, the afferents from the dorsal root and efferents from the ventral root bundle together, but then branch to form the rami (singular: ramus). The gray and white rami contain autonomic components, whereas the dorsal/posterior and ventral/anterior rami contain both somatic and autonomic components. Some rami form a nerve plexus, a network of interconnecting nerves. In the somatic motor system, axons emerge from lower motor neurons in the spinal cord, travel in the spinal nerves, and directly innervate skeletal muscles. In the autonomic nervous system, motor neurons in the spinal cord (called preganglionic neurons) send their axons to synapse onto a postganglionic neuron (whose cell bodies lie in the autonomic ganglia), which then send axons to innervate the target organ. Some nerve components form large distinctive bundles or branches and are referred to by their specific names, such as the splanchnic nerves or sciatic nerve.

Sensory and motor information for the head and neck (and several other parts of the body) is supplied by the 12 pairs of cranial nerves. The majority (10 of 12) of the cranial nerves are part of the PNS, with their cranial nerve nuclei located in the brainstem and nerves traveling outside the CNS.