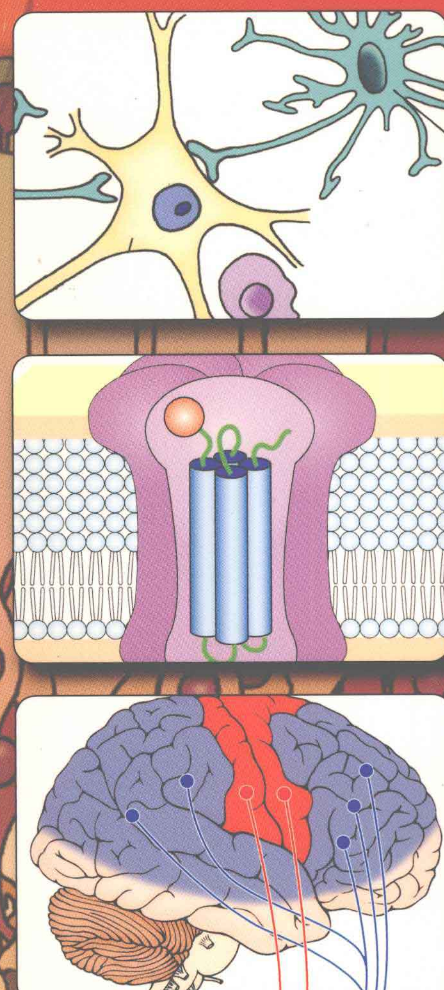
Essential Neuroscience

Second Edition

Allan Siegel
Hreday N. Sapru



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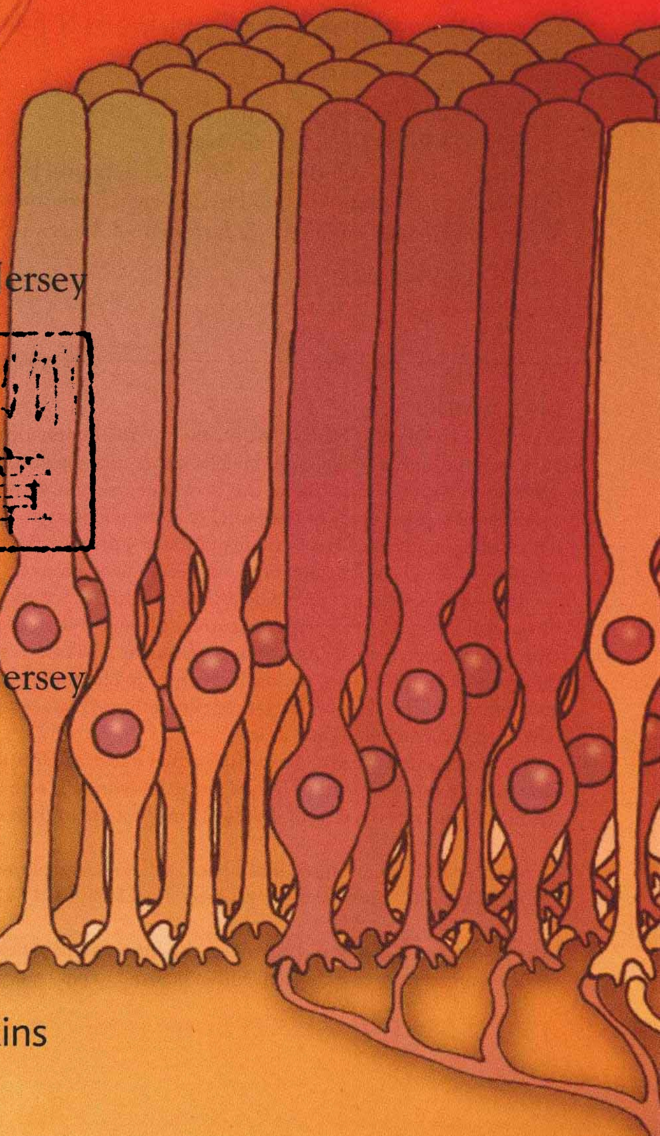

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This book is dedicated to our wives, Carla and Millie.

"We have learned much from our teachers and from our colleagues more than from our teachers, but from our students, more than from them all."

PREFACE

As we noted in the first edition of this text, , there has been a dramatic explosion of information in the field of neuroscience over the last few decades. This explosion of information has presented a great challenge to those of us who teach neuroscience in terms of synthesizing a coherent approach in which the diverse topics encompassed by neuroscience can be taught in a lucid and effective manner. We met this challenge by designing *Essential Neuroscience*, a book that considers all of the basic neuroscience topics to allow the students to focus on the essential concepts and facts intrinsic to any given topic without overwhelming them with distracting or confusing extraneous information. Consistent with this approach, each chapter begins with Learning Objectives followed by a discussion of the subject matter in a succinct yet informative manner. To present the material in an integrated fashion, Clinical Considerations are included as are discussions of the physiological aspects. At the end of each chapter, a Chapter Summary Table is provided that highlights the most important facts and concepts of the chapter and allows for review of the material in a simple, efficient manner. A Clinical Case is also presented, which is followed by a Chapter Test consisting of questions that can also be used effectively for USMLE preparation.

Recent developments in neuroscience have also been incorporated in the text. For example, over the past two decades, there have been significant advances in our understanding of the molecular bases of development. Accordingly, a section has been added in Chapter 2, Development of the Nervous System, which summarizes the key aspects of these developmental mechanisms. In addition, in recent years, great strides have been made in the identification of neurotransmitter malfunction in several diseases. Therefore, a detailed chapter has been included on neurotransmitters and implications of their malfunctions in mental disorders. Similarly, genetic abnormalities involved in certain diseases (e.g., cystic fibrosis, schizophrenia, Huntington's chorea) have been briefly discussed. Malfunctions of the immune system in certain diseases (e.g., Lambert-Eaton syndrome, multiple sclerosis, myasthenia gravis) have also been discussed where applicable.

The genesis of this textbook evolved over the past 30 years, as a result of our efforts in teaching neuroscience to medical and graduate students in ways that would make learning the subject matter simple yet meaningful. After testing a variety of approaches, a building-blocks approach in the presentation of the subject matter proved most effective. Consistent with this approach, the book begins with analysis of the single neuron, which then expands to how neurons communicate with each other. Following discussion of the anatomy of the spinal cord and brain, the text continues with a detailed study of the sensory, motor, and integrative systems. This approach was deemed helpful by both students and faculty. Moreover, the building-blocks approach improved student performance on National Board and Neuroscience Shelf examinations.

The book comprises 28 chapters and a glossary. Chapters 1 through 4 ("Overview of the Central Nervous System," "Development of the Nervous System," "Meninges and Cerebrospinal Fluid," and "Blood Supply of the Central Nervous System") provide a background for understanding the structural organization of the brain and spinal cord. These chapters provide a basis for a more in-depth analysis of nervous system functions and clinical disorders.

Having provided the student with a basic understanding of the gross anatomy and general functions of the brain and spinal cord, the book then introduces a series of topics designed to provide an understanding of the basic elements of the nervous system and the role they play in neuronal communication. These topics are discussed in Chapters 5 through 8 ("Histology of the Nervous System," "Electrophysiology of Neurons," "Synaptic Transmission," and "Neurotransmitters"). The basic physiological processes presented in these chapters prepare the student for further understanding of the diverse functions of the nervous system in the subsequent sections. Chapters 9 through 13 ("The Spinal Cord," "Brainstem I: The Medulla," "Brainstem II: Pons and Cerebellum," "Brainstem III: The Midbrain," and "The Forebrain") enable the student to examine the organization of the central nervous system in a systematic way. After learning about the key structures and functions at each level of the neuraxis of the central nervous system, the student will begin to develop an understanding of why damage to a given structure produces a particular constellation of deficits. Because of the importance of Chapter 14, "The Cranial Nerves," and the extent to which this material is tested on USMLE examinations, each cranial nerve is presented separately in terms of its structural and functional properties as well as the deficits associated with its dysfunction.

At this point in the study of the nervous system, the student has developed a basic knowledge of the anatomical organization of the central nervous system and its physiology and neurochemistry. Consequently, the student is now ready to study the sensory, motor, and integrative systems that require the knowledge accumulated thus far. The next section of the book includes Chapters 15 through 18 ("Somatosensory System," "Visual System," "Auditory and Vestibular Systems," and "Olfaction and Taste") and discusses anatomical and physiological properties of sensory systems.

The next section of the text turns to the study of motor systems, and includes Chapters 19 to 21, "The Upper Motor Neurons," The Basal Ganglia," and "The Cerebellum." These chapters examine, in an integrated manner, the anatomical, physiological, and neurochemical bases for normal movement and movement disorders associated with the cerebral cortex, basal ganglia, cerebellum, brainstem, and spinal cord.

The final section of the text (Chapters 22 to 28) concerns a variety of functions of the nervous system characterized by higher levels of complexity. Chapters 22 to 25, "The Autonomic Nervous System," "The Reticular Formation," "The Hypothalamus," and "The Limbic System," include analyses of visceral processes, sleep, and wakefulness (Chapters 22 to 25). In addition, an analysis of the structure, functions, and dysfunctions of the cerebral cortex is provided in Chapter 26, "The Thalamus and Cerebral Cortex." Chapter 27, "Vascular Syndromes," was placed toward the end of the book because by this point the student has gained a deeper understanding and appreciation of brainstem syndromes than if that material had been presented earlier in the text. Vascular syndromes of the brainstem constitute an important review for the student on a topic that is heavily tested on USMLE examinations. The final chapter, "Behavioral and Psychiatric Disorders" (Chapter 28) examines disorders such as schizophrenia, depression, anxiety, and obsessive compulsion. These disorders have a clear relationship to abnormalities in neural and neurochemical functions and, thus, reflect an important component of neuroscience. These topics also receive attention on the USMLE.

Essential Neuroscience proved to be a highly effective tool for students and faculty. The goal of this second edition, therefore, is to perfect the formula with which we had such success. For example, key terms and concepts of neuroscience were highlighted in bold in each chapter and explained in an extensive glossary at the end of the book. In response to readers' appreciation of this helpful feature, we have doubled the glossary size in this edition.

Also in response to reader requests, we have presented Chapter Summary Tables at the end of each chapter in this new edition. These tables will not only help students review chapters as they go, but will be valuable, high-yield tools for study and review at examination time.

The full-color illustrations, which have been universally praised, are even better in the second edition, with additions and enhancements rendering a truly cohesive, instructive art program.

Selected topics have been expanded where appropriate: the functional relationship, memory, and lateralization of the hippocampal formation and limbic cortex; limbic relationships of the basal ganglia (especially in reference to psychiatric issues); the development of the anterior and posterior pituitary; a discussion of prions in relation to Creutzfeldt Jacob disease; and others.

Material has also been integrated in multiple places where it would augment understanding of important concepts. For example, the functional relationships associated with the cerebral cortex are again referred to vis-à-vis sensory and motor systems. Extensive cross referencing among chapters has likewise been incorporated.

Although this text was originally primarily designed for medical students who study neuroscience, it can be used quite effectively by neurology residents and graduate and undergraduate university students specializing in biological sciences. In this latest edition, special topics have been reworked to better accommodate dental students. The trigeminal nucleus, for instance, has been divided into its components for a more detailed study.

Essential Neuroscience, 2nd Edition distinguishes itself from other texts as *the* concise, clinically relevant neuroscience text providing balanced coverage of anatomy, physiology, biology, and biochemistry. With a full array of pedagogical features, it helps students gain conceptual mastery of this challenging discipline and, we hope, foments the urge to continue its exploration.

Allan Siegel
Hreday N. Sapru

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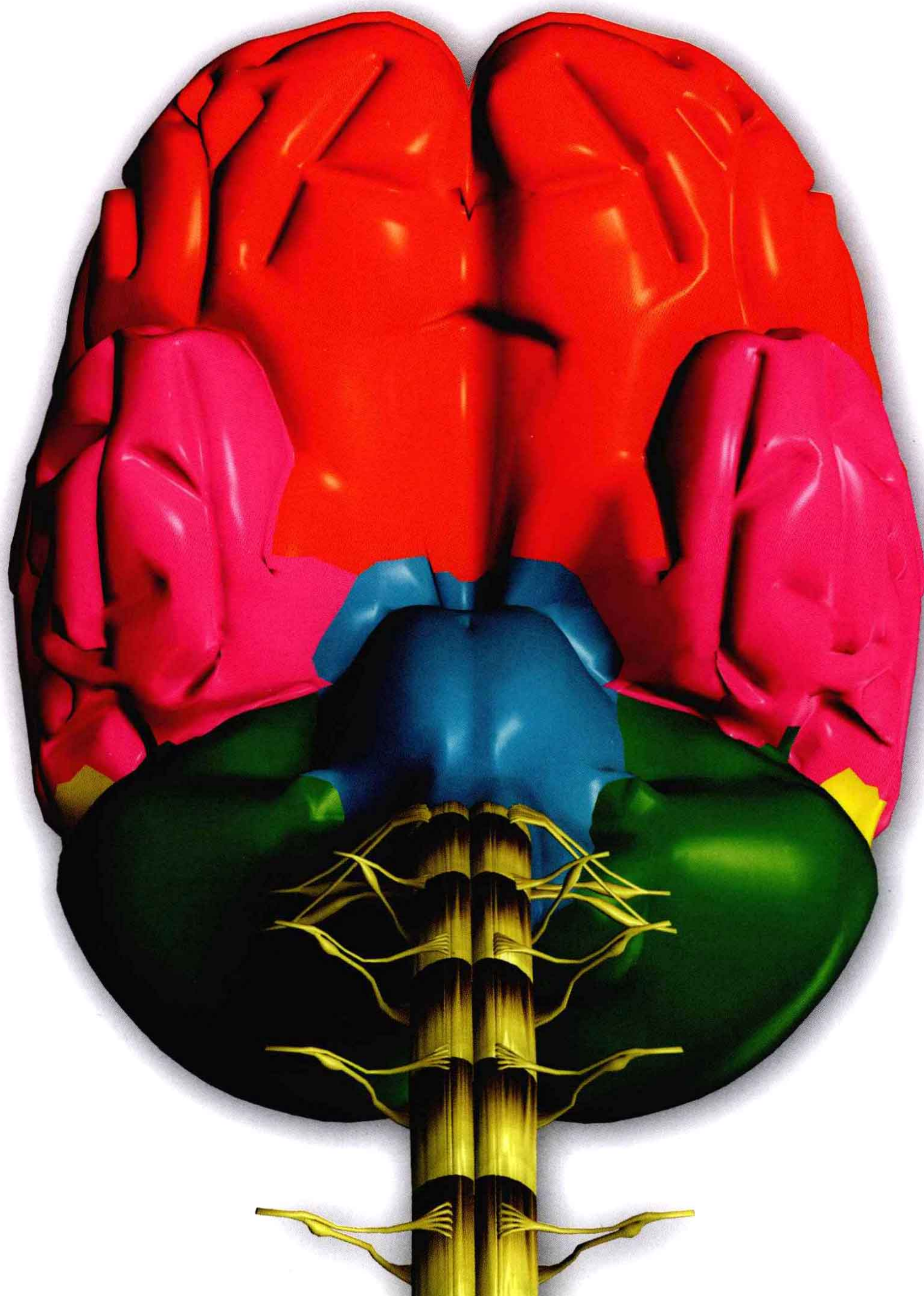
SECTION I

Gross Anatomy of the Brain



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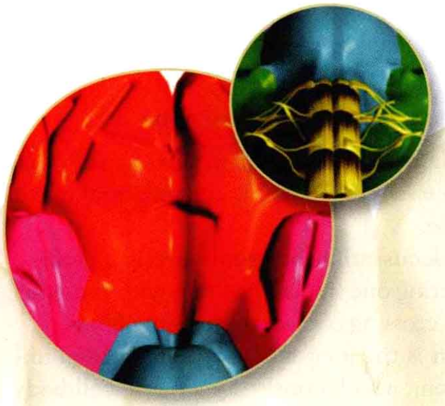

Overview of the Central Nervous System

CHAPTER OUTLINE

OBJECTIVES

In this chapter, the student should:

1. Understand the basic language and terminology commonly used in neuroanatomy.
2. Identify key regions and general functions within the cerebral cortex, including the precentral, prefrontal, postcentral, temporal, and occipital cortices.
3. Identify the major functions of subcortical structures within the forebrain, including the ventricles of the brain, diencephalon, basal ganglia, and the limbic system.
4. Identify surface structures seen from the ventral aspect of the brainstem: the cerebral peduncles, pyramids, and inferior olivary nucleus and from its dorsal surface: colliculi of the midbrain and facial colliculus of the pons.
5. Identify the cerebellum, including the attachments of cerebellum to the brainstem and major lobes of the cerebellar cortex.

GROSS ANATOMY OF THE BRAIN

Neuroscience is a composite of several disciplines including neuroanatomy, neurophysiology, neurology, neuropathology, neuropharmacology, behavioral sciences, and cell biology. An overview of the structural organization of the nervous system is helpful when beginning to study the neurosciences. However, first it would be useful to define some basic terms that will be essential for understanding the anatomy of the nervous system.

NEUROANATOMICAL TERMS

The spatial relationships of the brain and spinal cord usually are described by one or more of five paired terms: medial–lateral, anterior–posterior, rostral–caudal, dorsal–ventral, and superior–inferior (Fig. 1-1).

Medial–lateral: Medial means toward the median plane, and **lateral** means away from the median plane.
Anterior–posterior: Above the midbrain, **anterior** means toward the front of the brain, and **posterior** means toward the back of the brain. At and below the midbrain, **anterior** means toward the ventral surface of the body, and **posterior** means toward the dorsal surface of the body.
Rostral–caudal: Above the midbrain, **rostral** means toward the front of the brain, and **caudal** means toward the back of the brain. At and below the midbrain, **rostral** means toward the cerebral cortex, and **caudal** means toward the sacral end (or bottom) of the spinal cord.
Dorsal–ventral: Rostral to the midbrain, **dorsal** refers to the top of the brain, and **ventral** refers to the bottom of the brain. At the level of and caudal to the midbrain, **dorsal** means toward the posterior surface of the body, and **ventral** refers to the anterior surface of the body.

Superior–inferior: Both at positions above and below the midbrain, **superior** means toward the top of the cerebral cortex, and **inferior** means toward the bottom of the spinal cord.

Other terms commonly used in neuroanatomy are:

Ipsilateral–contralateral: Ipsilateral means on the same side with reference to a specific point; **contralateral** means on the opposite side.
Commissure and decussation: Commissure is a group of nerve fibers connecting one side of the brain with the other. **Decussation** is the crossing over of these nerve fibers.
Neuron: A **neuron** is the anatomical and functional unit of the nervous system, which consists of a **nerve cell body**, **dendrites** (which receive signals from other neurons), and an **axon** (which transmits the signal to another neuron).
Nucleus: Nucleus refers to groups of neurons located in a specific region of the brain or spinal cord that generally have a similar appearance, receive information from similar sources, project their axons to similar targets, and share similar functions.
Tract: Many axons grouped together, which typically pass from a given nucleus to a common target region or to several regions, form a **tract**.
White and gray matter: When examining the brain or spinal cord with the unaided eye, one can distinguish white and gray tissue. The region that appears white is called **white matter**, and the area that appears gray is called **gray matter**. The appearance of the white matter is due to the

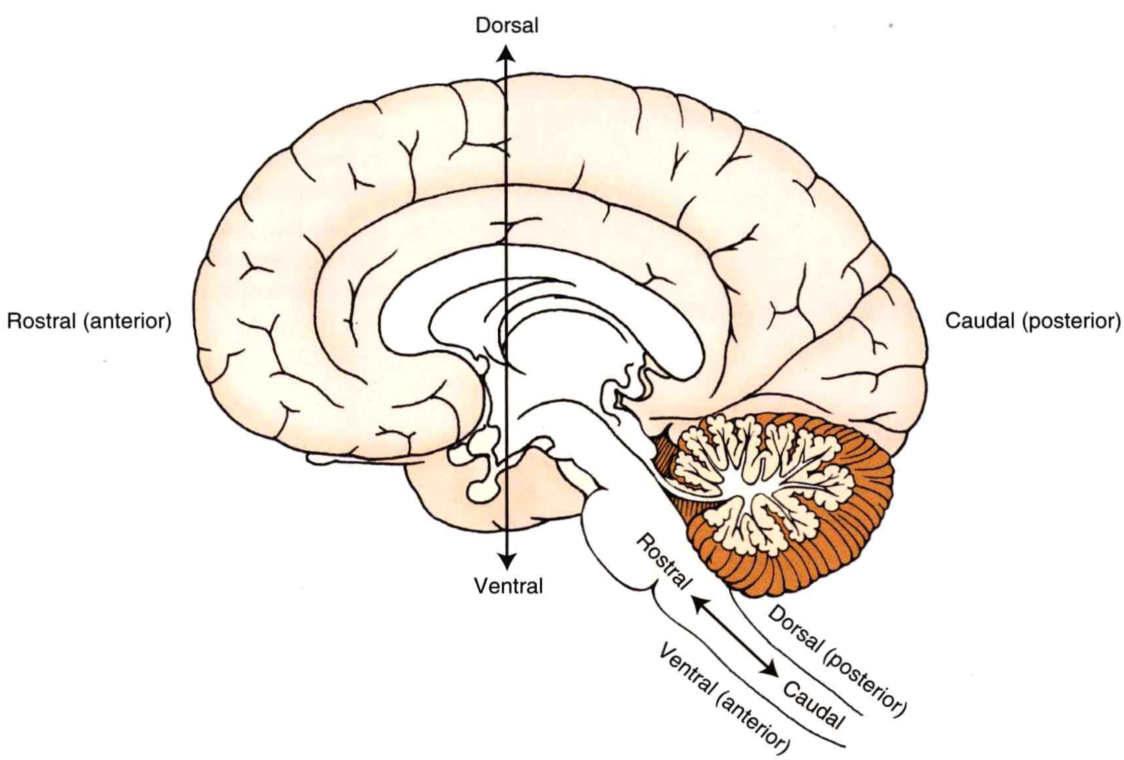

FIGURE 1–1 A variety of terms are used to indicate directionality within the central nervous system (CNS). The fixed axes for anatomical reference planes are superior–inferior and anterior–posterior. The other axes vary according to their location within the CNS.

large number of **myelinated axons** (largely lipid membranes that wrap around the axons) that are present in this region. In contrast, the gray matter consists mainly of neuronal cell bodies (nuclei) and lacks myelinated axons.

Glial cells: These nonneural cells form the interstitial tissue of the nervous system. There are different types of **glial cells**, which include **astrocytes, oligodendrocytes, microglia**, and **ependymal cells**. Details of the functions of each of these components are provided in Chapter 5.

Central and peripheral nervous systems: The **central nervous system (CNS)** includes the brain and spinal cord and is surrounded and protected by three connective tissue coverings called **meninges**. Within the CNS are fluid-filled spaces called **ventricles.** The bone of the skull and vertebral column surround the brain and spinal cord, respectively. The **peripheral nervous system (PNS)** consists of spinal and cranial nerves that are present outside the CNS.

Autonomic and somatic nervous systems: These are functional subdivisions of the nervous system (in contrast to the anatomical classifications described earlier). Both of these divisions are present in the CNS and PNS. The **autonomic nervous system** innervates smooth muscle and glands, whereas the **somatic nervous system** innervates mainly musculoskeletal structures and the sense organs of skin.

To understand the function of CNS structures, it is important to be able to identify and locate them in relation to one another. The many structures of the brain and spine may seem confusing in this initial overview, but knowing what they are is essential for developing a broader familiarity with neuroscience. It will not be necessary to memorize every structure and function in this introduction because the chapters that follow present these structures in greater detail.

We will begin with an examination of the major structures of the CNS, taking a topographical approach to the review of anatomical and functional relationships of structures in the cerebral cortex. Key structures will be identified as they appear in different views of the brain.

COMPONENTS OF THE CENTRAL NERVOUS SYSTEM

As we just indicated, the study of the CNS includes both the brain and spinal cord. This chapter provides an initial overview of these regions. A more detailed analysis of the structural and functional properties of the spinal cord is presented in Chapter 9 and is followed by a parallel morphological analysis of the structures contained within the **medulla**, **pons**, **midbrain**, and **forebrain** in subsequent chapters.

The **spinal cord** is a thin, cylinder-like structure with five regions that extend from its attachment to the brain downward. The most rostral region, which is closest to the brain, is the **cervical cord** and contains eight pairs of spinal nerves. Caudal to the cervical cord lies the **thoracic cord**, which contains 12 pairs of spinal nerves. Next is the **lumbar cord**, which contains five pairs of spinal nerves. The most caudal region, called the **sacral cord**, contains five pairs of spinal nerves; the caudal end of the spinal cord is called the **coccygeal region** and contains one pair of spinal nerves. In the cervical and lumbar regions, the spinal cord is enlarged because of the presence of greater numbers of nerve cell bodies and fiber tracts, which innervate the upper and lower limbs, respectively.

The brainstem, cerebellum, and cerebral hemispheres form the brain. The **brainstem** can be divided into three regions: the medulla, rostral to and continuous with the spinal cord; the pons, rostral to the medulla; and the midbrain, rostral to the pons and continuous with the diencephalon. The **cerebellum** is positioned like a tent dorsal to the pons and is attached to the brainstem by three massive fiber groups, or **peduncles**. The **cerebral hemispheres** contain the cerebral cortex, which covers the surface of the brain and is several millimeters thick as well as deeper structures, including the **corpus callosum, diencephalon, basal ganglia, limbic structures**, and the **internal capsule**.

CEREBRAL TOPOGRAPHY

One important aspect of the anatomical and functional organization of the CNS should be remembered throughout the study of neuroscience: For most *sensory* and *motor* functions, the left side of the brain functionally corresponds with the right side of the body. Thus, sensation from the left side of the body is consciously appreciated on the right side of the cerebral cortex. Similarly, motor control over the right arm and leg is controlled by neurons located on the left cerebral cortex.

Lateral Surface of the Brain

Four lobes of the cerebral cortex—the **frontal, parietal,** and **temporal lobes** and a portion of the **occipital lobe**—can be identified on the lateral surface of the brain (Fig. 1-2). The lobes of the cerebral cortex integrate motor, sensory, autonomic, and intellectual processes and are organized along functional lines. For the most part, a fissure, called a **sulcus**, separates these lobes. In addition, pairs of **sulci** form the boundaries of ridges referred to as **gyri**.

The cortex consists of both cells and nerve fibers. The cellular components constitute the gray matter of cortex and lie superficial (i.e., toward the surface of the cortex) to the nerve fibers. As a general rule, the nerve fibers that comprise the white matter of the cortex pass between different regions of cortex, facilitating communication between the lobes of the cerebral cortex. In addition, large components of the white matter consist of fibers passing bidirectionally between the cortex and other regions of the CNS.

Frontal Lobe

The first step in identifying the main structures of the lateral surface of the brain is to locate the **central sulcus**, which serves as the posterior boundary of the frontal lobe (Fig. 1-2). This sulcus extends from near the longitudinal fissure (present along the midline but not visible in the lateral view of the brain shown in Fig. 1-2) ventrally almost

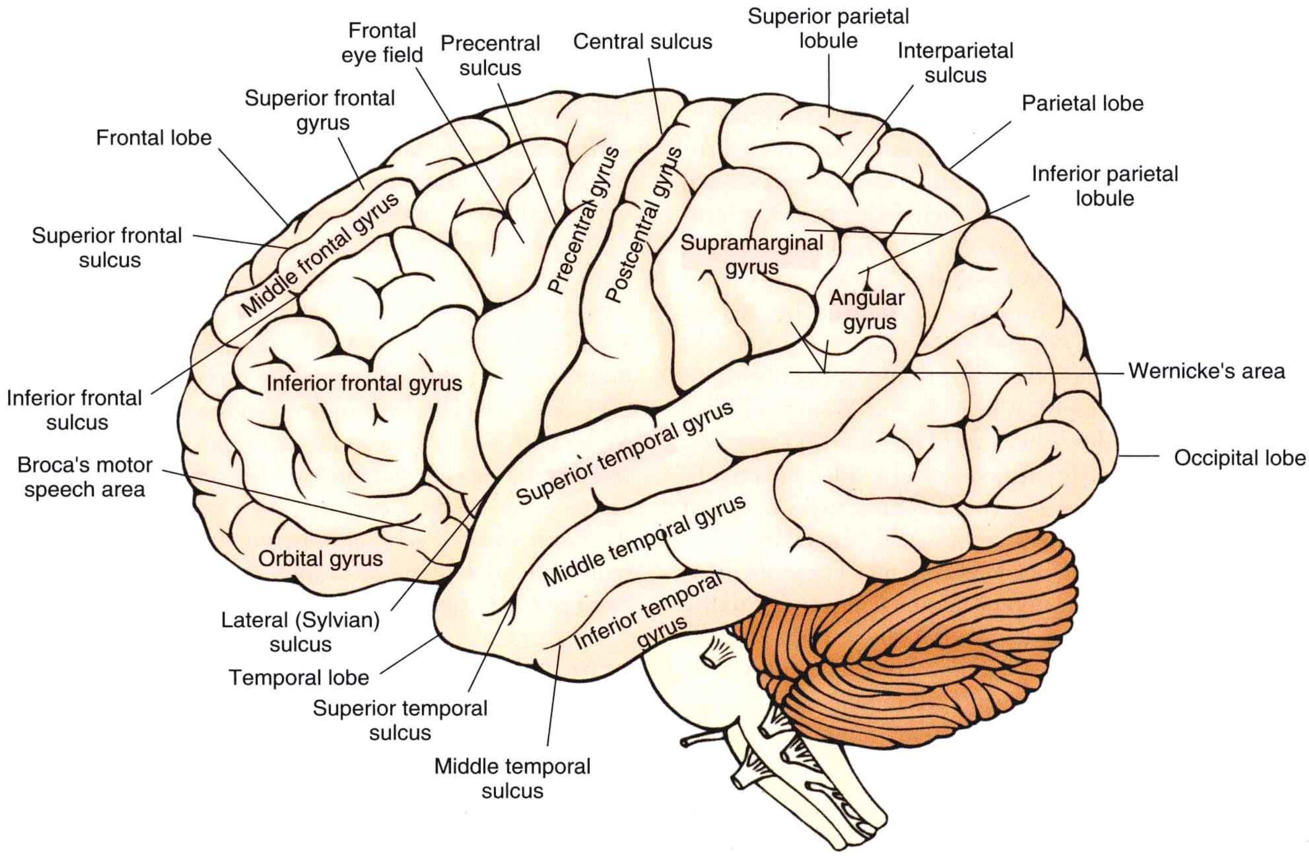

FIGURE 1–2 Lateral view of the cerebral cortex showing the principal gyri and sulci. Major structures include the central sulcus and the precentral (primary motor), premotor, and postcentral (primary somatosensory) gyri. Also note the gyri situated rostral to the premotor cortex, including the orbital gyri, which mediate higher order intellectual functions and contribute to the regulation of emotional behavior. Broca's motor speech area and Wernicke's area (for reception of speech) are important areas associated with speech. Of the three gyri comprising the temporal lobe, the superior temporal gyrus is important for auditory functions, and the inferior and middle temporal gyri mediate complex visual functions. Different aspects of the parietal lobe located just caudal to the primary somatosensory cortex integrate a variety of higher order sensory functions; the occipital lobe contains the primary receiving area for visual impulses.

to the lateral cerebral sulcus (**Sylvian sulcus**). The **frontal lobe**, the largest of the cerebral lobes, extends from the central sulcus to the frontal pole of the brain. It extends inferiorly to the lateral sulcus. The frontal cortex also extends onto the medial surface of the brain, where it borders the **corpus callosum** inferiorly (see Fig. 1-3).

At the posterior aspect of the frontal lobe, the most prominent structure is the **precentral gyrus**, which is bounded posteriorly and anteriorly by the central and precentral sulci, respectively (Fig. 1-2). The function of the precentral gyrus is to integrate motor function signals from different regions of the brain. It serves as the primary motor cortex for control of contralateral voluntary movements. The neurons within the precentral gyrus are somatotopically organized. **Somatotopic** means that different parts of the precentral gyrus are associated with distinct parts of the body, both functionally and anatomically. The outputs from the precentral gyrus to the brainstem and contralateral spinal cord follow a similar functional arrangement. The region closest to the lateral (Sylvian) sulcus (the inferior part of the precentral gyrus) is associated with voluntary control over movements of the face and head. The neurons associated with motor control of the upper and lower limbs are found at progressively more dorsal and medial levels, respectively. The motor neurons associated with control over the lower limbs extend onto the medial surface of the hemisphere. When the parts of the body are drawn in terms of the degree of their cortical representation (i.e., in the form of a somatotopic arrangement), the resulting rather disproportionate figure is commonly called a **homunculus** (see Chapters 19 and 26 for further discussion). The motor homunculus demonstrates how cell groups in the CNS associated with one part of the body relate anatomically to other cell groups associated with other parts of the body. In addition, the illustrative device shows the relative sizes of the populations of neurons associated with specific parts of the body.

Immediately rostral to the precentral gyrus is the **premotor area (premotor cortex)**, which extends from near the lateral fissure on to the medial surface of the brain; this region is referred to as the **supplemental motor area**. This cortex exercises control over movements associated with the contralateral side of the body by playing an important role in the initiation and sequencing of movements. Immediately anterior to the premotor cortex, three parallel gyri—the superior, middle, and inferior **frontal gyri**—are oriented in anterior–posterior positions (Fig. 1-2). In the region of the middle frontal gyrus extending into the inferior frontal gyrus and immediately rostral to the premotor region, lies an area called the **frontal eye fields**. This region coordinates voluntary control of conjugate (i.e., horizontal)

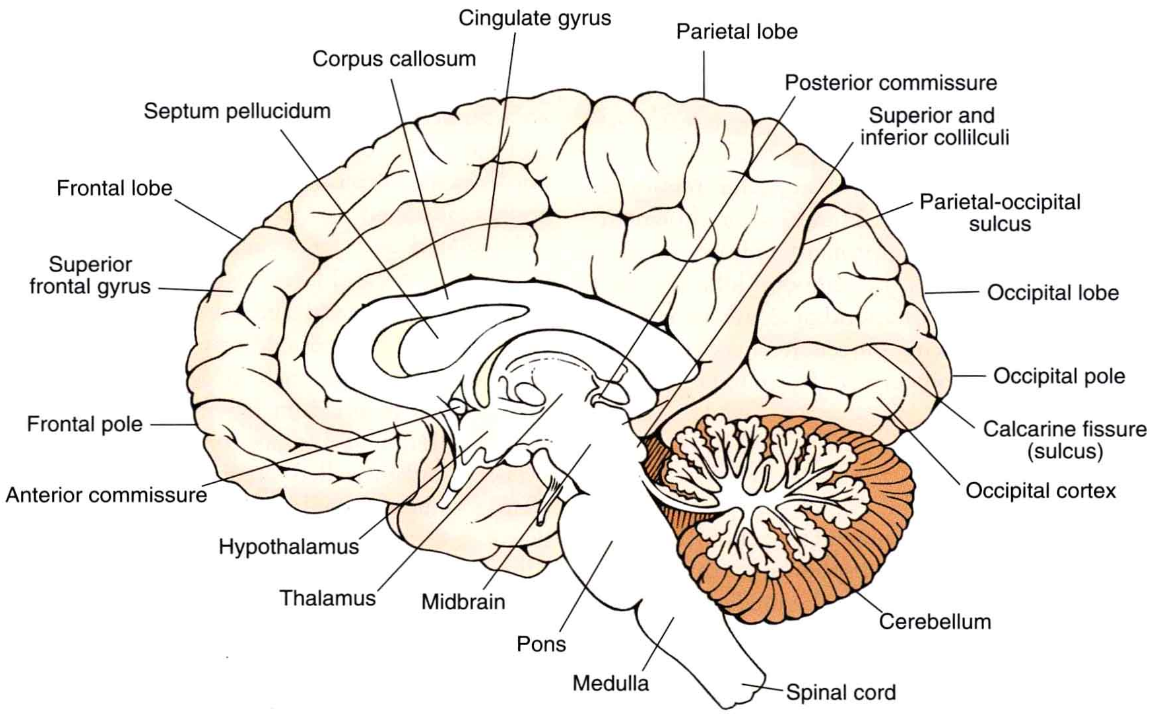

FIGURE 1–3 Midsagittal view of the brain. Visible are the structures situated on the medial aspect of the cortex as well as subcortical areas, which include the corpus callosum, septum pellucidum, fornix, diencephalon, and brainstem structures.

movement of the eyes. Portions of these gyri are also involved in the integration of motor processes. For example, one part of the inferior frontal gyrus of the dominant (left) hemisphere is **Broca's motor speech area** and is important for the formulation of the motor components of speech. When damaged, the result is Broca's **aphasia** (or motor aphasia), a form of language impairment in which the patient has difficulty in naming objects and repeating words, while comprehension remains intact. Far rostral to this region, an area that includes inferior (orbital gyri), medial, and lateral aspects of the frontal lobe, called the **prefrontal cortex,** also plays important roles in the processing of intellectual and emotional events. Within the depths of the lateral (Sylvian) sulcus is a region of cortex called the **insula,** which can be seen only when the temporal lobe is pulled away from the rest of the cortex. It reflects a convergence of the temporal, parietal, and frontal cortices and has, at different times, been associated with the reception and integration of taste sensation, reception of viscerosensations, processing of pain sensations, and vestibular functions.

Parietal Lobe

The **parietal lobe** houses the functions that perceive and process **somatosensory** events. It extends posteriorly from the central sulcus to its border with the occipital lobe (Fig. 1-2). The parietal lobe contains the **postcentral gyri,** which has the central sulcus as its anterior border and the postcentral sulcus as its posterior border. The postcentral gyrus is the primary receiving area for **somesthetic** (i.e., kinesthetic and tactile) information from the periphery (trunk and extremities). Here, one side of the cerebral cortex receives information from the opposite side of the body. Like the motor cortex, the postcentral gyrus is somatotopically organized and can be depicted as having a sensory homunculus, which parallels that of the motor cortex.

The remainder of the parietal lobe can be divided roughly into two regions, a superior and an inferior parietal lobule, separated by an **interparietal sulcus.** The inferior parietal lobule consists of two gyri: the supramarginal and angular gyri. The **supramarginal gyrus** is just superior to the posterior extent of the lateral sulcus, and the **angular gyrus** is immediately posterior to the supramarginal gyrus and is often associated with the posterior extent of the superior temporal sulcus (Fig. 1-2). These regions receive input from auditory and visual cortices and are believed to perform complex perceptual discriminations and integrations. At the ventral aspect of these gyri and extending onto the adjoining part of the superior temporal gyrus is **Wernicke's area.** This region is essential for comprehension of spoken language. Lesions of this region produce another form of aphasia, Wernicke's aphasia (or sensory aphasia), which is characterized by impairment of comprehension and repetition, although speech remains fluent. The superior parietal lobule integrates sensory and motor functions and aids in programming complex motor functions associated with the premotor cortex. Damage to this region produces CNS disturbances, such as apraxia of movement and sensory neglect (see Chapters 19 and 26).

Occipital Lobe

Although a part of the **occipital lobe** lies on the lateral surface of the cortex, the larger component occupies a more prominent position on the medial surface of the hemisphere.

Temporal Lobe

One of the most important functions of the **temporal lobe** is the perception of auditory signals. Situated inferior to the lateral sulcus, the temporal lobe consists of superior, middle, and inferior temporal gyri. On the inner aspect of the superior surface of the **superior temporal gyrus** lie the transverse **gyri of Heschl** (not shown in Fig. 1-2), which constitute the primary auditory receiving area. The other regions of the temporal lobe, including the **middle** and **inferior temporal gyri**, are associated with the perception of moving objects in the visual field and recognition of faces, respectively (see Chapter 26 for details).

Medial Surface of the Brain

The principal structures on the medial aspect of the brain can be seen clearly after the hemispheres are divided in the **midsagittal plane** (Fig. 1-3). On the medial aspect of the cerebral cortex, the **occipital lobe** can be seen most clearly. It contains the primary visual receiving area, the visual cortex. The primary visual cortex is located inferior and superior to the **calcarine sulcus (calcarine fissure)**, a prominent sulcus formed on the medial surface that runs perpendicular into the **parieto-occipital sulcus**, which divides the occipital lobe from the parietal lobe (Fig. 1-3).

Located more rostrally from the occipital lobe and situated immediately inferior to the precentral, postcentral, and premotor cortices is the **cingulate gyrus**. Its ventral border is the corpus callosum. The cingulate gyrus is generally considered part of the brain's limbic system, which is associated with emotional behavior, regulation of visceral processes, and learning (see Chapter 25).

Another prominent medial structure is the **corpus callosum**, a massive fiber pathway that permits communication between equivalent regions of the two hemispheres. The **septum pellucidum** lies immediately ventral to the corpus callosum and is most prominent anteriorly. It consists of two thin-walled membranes separated by a narrow cleft, forming a small cavity (cavum of septum pellucidum). It forms the medial walls of the lateral ventricles. The septum pellucidum is attached at its ventral border to the fornix.

The **fornix** is the major fiber system arising from the **hippocampal formation**, which lies deep within the medial aspect of the temporal lobe. It emerges from the hippocampal formation posteriorly and passes dorsomedially around the thalamus to occupy a medial position inferior to the corpus callosum but immediately superior

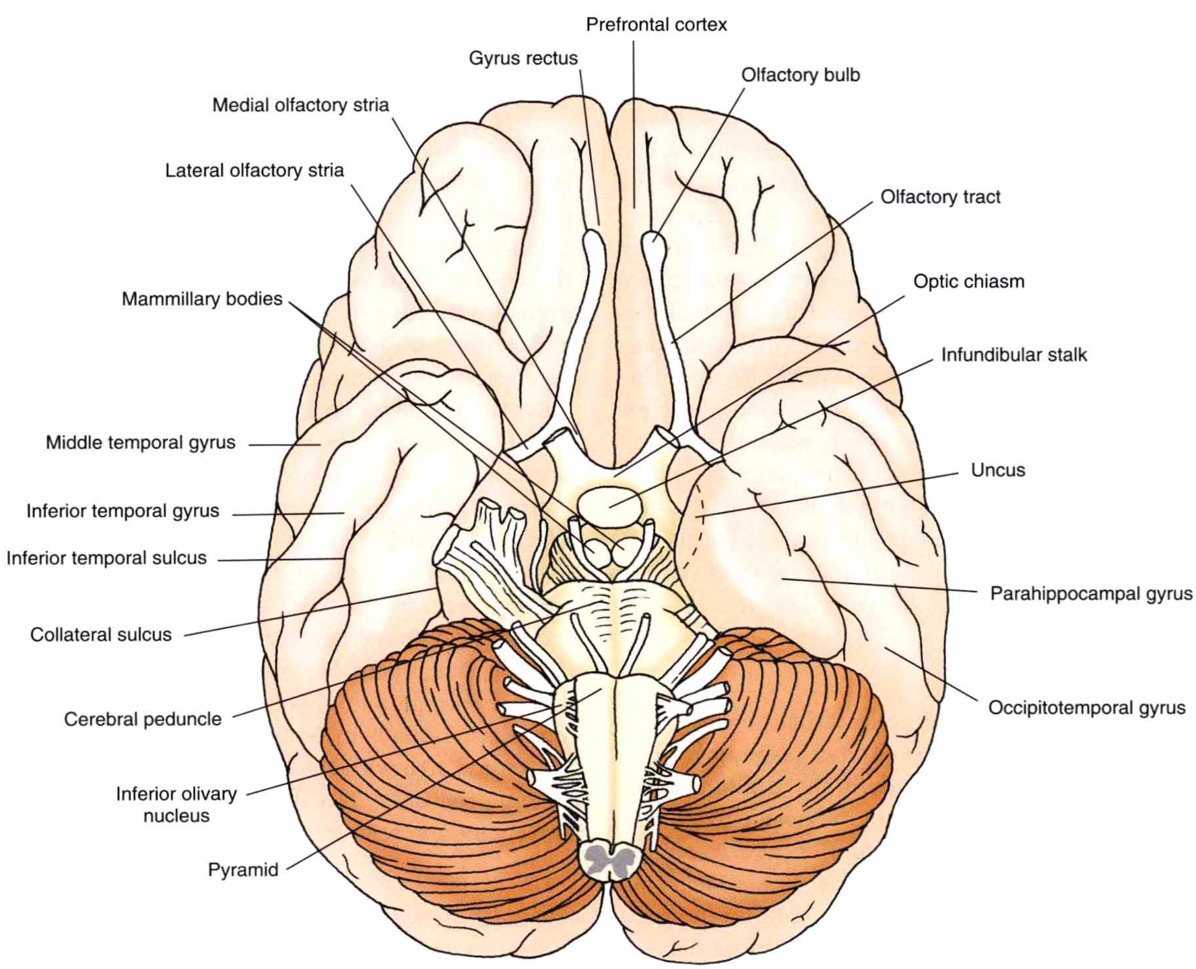

FIGURE 1–4 Inferior surface of the brain showing the principal gyri and sulci of the cerebral cortex. On the inferior surface, the midbrain, pons, parts of the cerebellum, and the medulla can be clearly identified.