CHAPTER 3

Organization of the Nervous System

PORTRAIT: Stroke

R.S.'s first job in high school was as an usher in a movie theater. After graduation, he became the manager of the theater and eventually its owner. Not only did he enjoy his business, he also loved movies and had a remarkable knowledge of all aspects of cinema, including movie plots and actors. He enjoyed discussing movies and took pride in being able to answer questions about how they are produced, directed, and marketed.

One day while repairing the roof of his garage, R.S. felt numbness in his left hand and then he collapsed, unable to stand, and fell to the ground. He had suffered a stroke, an interruption of blood to the brain that kills brain cells and causes the sudden appearance of neurological symptoms. His condition resulted from an ischemia, a deficiency of blood flow to the brain due to functional constriction or to the actual obstruction of a blood vessel, such as by a clot.

R.S. was quickly taken to a nearby hospital, where a CT scan showed that the stroke had damaged his right frontal cortex. In the adjoining CT image showing the effects of stroke on the brain, the dark area on the right side is the area that has been damaged by the loss of blood flow. R.S. was given no treatment and was eventually taken to a rehabilitation ward to receive physical therapy.

In the United States, someone suffers a stroke approximately every minute, producing more than a half million new stroke victims every year. Worldwide, stroke is the second leading cause of death. For every 10 people who have a stroke, 2 die, 6 are disabled to varying degrees, and 2 recover to various degrees but still endure a diminished quality of life. With rehabilitation, R.S. recovered the ability to walk, although his left leg was stiff, but his left arm was somewhat rigid and flexed and he made no attempt to use it.

Although to his friends and family R.S. appeared to be able to do most of the things that he had done before his stroke, he was apathetic and appeared to have lost interest in everything. He no longer enjoyed his hobby of gardening, he had no interest in his business, he no longer talked about the movies, and he no longer watched television, as he had done before his stroke. Although formerly talkative, he no longer initiated conversation; when he did speak it was without affect. Ten years after his stroke, despite neuropsychological assessment and a number of attempts at behavioral and physical therapy, R.S. is unchanged.

Unlike the more severe hemorrhagic stroke that results from a burst vessel bleeding into the brain, ischemic stroke can be treated with a drug called tissue plasminogen activator (t-PA) that breaks up clots and allows the return of normal blood flow to the affected region. R.S. was not given the drug within the required 3 hours of suffering his stroke, however, because the attending physician was unsure whether the fall from the garage roof had caused a hemorrhagic stroke as a result of a concussion and burst blood vessel. An anticoagulant drug decreases tissue death in ischemic stroke but aggravates cell death in hemorrhagic stroke.

Scientists are interested in developing new treatments for the postacute stroke period because most patients do not make it to an emergency unit within 3 hours. They are also searching for ways to stimulate the brain to initiate reparative processes for both ischemic and hemorrhagic stroke, because the poststroke survival period for many patients is long. Neuropsychologists also are interested in developing rehabilitative procedures that help patients cope with and overcome not only motor symptoms but also the apathy that so diminished R.S.'s quality of life.
The complexity of the brain and the complexity of behavior present a major challenge to anyone trying to explain how the one produces the other. The human brain is composed of more than 100 billion neurons that engage in information processing. Each neuron receives as many as 15,000 connections from other cells.

The neurons in the brain are organized in layers as well as in groups called nuclei (from the Latin nux, meaning “nut”), groups of cells forming clusters that can be visualized with special stains to identify a functional grouping. Some brain nuclei are folded, and others have distinctive shapes and colors. Within nuclei, cells that are close together make most of their connections with one another.

Thus, the anatomical pattern of the brain is like that of human communities, whose inhabitants share most of their work and engage in social interactions with others who live nearby. Each community of cells also makes connections with more distant neural communities through pathways made by their axons. These connections are analogous to the thoroughfares linking human communities.

The brain can undergo enormous changes during the life span of a person; but after many kinds of damage, its ability to compensate is limited, as R.S.’s case illustrates. What aids neuropsychologists’ efforts to understand brain function is knowledge about the order in the arrangement of neurons and their connections, a topic that we now address in our description of the brain’s anatomy.

**Neuroanatomy: Finding Your Way Around the Brain**

Although the sizes and shapes of the brains of different people vary, just as their facial features do, the component structures—the communities and main roads of the brain—are common to all human beings. In fact, most of these structures seem to be common to all mammals.

About 100 years ago, anatomist Lorente de Nó, making one of the first detailed descriptions of a mouse brain through a microscope, discovered to his surprise that its fine structure is similar to that of the human brain. Because brain cells are similar in all animals and because the structures of animal brains are so similar, a great deal of what we know of the function of parts of the human brain is derived from comparative studies of those same parts in other animals.

**Describing Locations in the Brain**

The locations of the layers, nuclei, and pathways of the brain can be described by their placement with respect to other body parts of the animal, with respect to their relative locations, and with respect to a viewer’s perspective. The most frequently used sets of terms are illustrated in Figure 3.1:

- Figure 3.1A describes brain structures in relation to other body parts. In Latin, *rostrum* is “beak,” *caudum* is “tail,” *dorsum* is “back,” and *ventrum* is “stomach.” Accordingly, *rostral, caudal, dorsal, and ventral* parts of the brain are located toward those body parts. Occasionally, the terms *superior*
and *inferior* are used to refer to structures that are located dorsally or ventrally.

- Figure 3.1B illustrates how brain parts are described in relation to one another from the frame of reference of the face. *Anterior* or *frontal* is in front, *posterior* structures are located behind, *lateral* structures are at the side, and *medial* structures are located at the center or between.

- Figure 3.1C illustrates terms that describe the direction of a cut, or section, through the brain from the perspective of a viewer. A *coronal* section is cut in a vertical plane, from the crown of the head down. A *horizontal* section (because the view or cut is along the horizon) is usually viewed looking down on the brain from above. A *sagittal* section is cut lengthways, front to back, and viewed from the side (imagine the brain oriented as an arrow—in Latin, *sagitta*).

The nervous system, like the body, is symmetrical, with a left side and a right side. Structures that lie on the same side are *ipsilateral*; if they lie on opposite sides, they are *contralateral* to each other. If one of them lies in each hemisphere, the structures are *bilateral*. 
Structures that are close to one another are **proximal**; those far from one another are **distal**. And any movement toward a brain structure is **afferent**, whereas movement away from it is **efferent**. Thus, the body's sensory pathways that carry messages toward the brain and spinal cord are **afferent**, and motor pathways leading to the body from the brain and spinal cord are **efferent**.

You know that humans are distinguished in that they stand upright, and nonhuman animals typically have a quadruped posture. The spatial orientations of human and nonhuman animal brains are similar, but the spatial orientations of their spinal cords are different. Dorsal and ventral in quadrupeds are anterior and posterior in upright humans, but, if humans stand on "all fours," the orientation of the spinal cord is then similar to that of other animals.

### A Wonderland of Nomenclature

To the beginning student, the naming of brain parts might seem chaotic. And it is, because neuroscientists have been at it for a long time, and names accumulate as knowledge of brain parts and their functions grows. Consequently, structures may have several names, often used interchangeably, that describe their appearance, their location, or one or more of their functions.

The **precentral gyrus**, a part of the brain damaged by stroke in R.S. and responsible for his diminished motor ability, has many other names. It is called **gyrus precentralis** in Latin and "the motor strip" in colloquial English. It is also called "Jackson's strip," after Hughlings-Jackson, who noted that, in epileptic attacks, the limbs of the body convulse in an orderly arrangement, suggesting to him that the representation of the body in the brain also is orderly.

Electrophysiologists refer to the precentral gyrus as the **primary motor cortex** or **MI**, to distinguish it from other motor regions of the cortex. Because they can obtain movements of different body parts after stimulating this area, as was first found by Fritsch and Hitzig (see Chapter 1), they have also called it the "somatic motor strip" or "the motor homunculus" (motor human). Additionally, because anatomists such as Gall found that the pyramidal tract that extends from the cortex into the spinal cord comes mainly from this cortical region, they called it "area pyramidalis."

For a lot of brain regions, Greek, Latin, French, and English terminology alternate with slang. Additionally, neuroscientists' imaginations have compared brain structures to body anatomy (mammillary bodies, floria (amygdala, or "almond"), fauna (hippocampus, or "sea horse"), and mythology (Ammon's horn). Other terms make use of color—substantia nigra ("black substance"), locus coeruleus ("blue area"), and red nucleus—or of consistency, such as substantia gelatinosa ("gelatinous substance").

Some names are puzzling: substantia innominata ("unnamable substance"), zona incerta ("uncertain area"), nucleus ambiguus ("ambiguous nucleus"); others are based entirely on expediency: cell groups A-1 to A-15 or B1 to B9. The longest name for a brain structure is nucleus reticularis tegmenti pontis Bechterewi, affectionately known as NRTP because, as you will observe, neuroscientists have a special fondness for abbreviations. We attempt to use consistent and simple terms in this book; but, in many cases, because neuroscientists in different fields use different terms in presenting their findings, we must do so as well.
An Overview of Nervous System Structure and Function

From an anatomical viewpoint, the central nervous system (CNS) consists of the brain and the spinal cord, and the peripheral nervous system (PNS) encompasses everything else (see Figure 1.2). In a functional scheme, the focus shifts from anatomy to how the parts of the nervous system work together. Here, both major divisions of the PNS step up to constitute, along with the CNS, the three-part functional scheme illustrated in Figure 3.2:

- The (CNS) consists of the brain and spinal cord.
- The somatic nervous system (SNS) consists of all the spinal and cranial nerves and from the sensory organs and the muscles, joints, and skin. The SNS produces movement and transmits incoming sensory information to the CNS, including vision, hearing, pain, temperature, touch, and the position and movement of body parts.
- The autonomic nervous system (ANS) balances the body's internal organs to "rest and digest" through the parasympathetic (calming) nerves or to "fight and flee" or engage in vigorous activity through the sympathetic (arousing) nerves.

Support and Protection

The brain and spinal cord are supported and protected from injury and infection in four ways:

1. The brain is enclosed in a thick bone, the skull, and the spinal cord is encased in a series of interlocking bony vertebrae. Thus, the CNS lies within bony encasements, whereas the PNS, although connected to the CNS, lies outside them. The PNS, although more vulnerable to injury because it lacks bony protection, can renew itself after injury by growing new axons and dendrites, whereas self-repair is much more limited within the CNS.

2. Within the bony case enclosing the CNS is a triple-layered set of membranes, the meninges, shown in Figure 3.3. The outer dura mater (from the Latin, meaning "hard mother") is a tough double layer of tissue enclosing the brain in a kind of loose sack. The middle arachnoid membrane (from the Greek, meaning "resembling a spider's web") is a very thin sheet of delicate tissue that follows the contours of the brain. The inner pia mater (from the Latin, meaning "soft mother") is a moderately tough tissue that clings to the surface of the brain.

3. The brain and spinal cord are cushioned from shock and sudden changes of pressure by the cerebrospinal fluid that circulates in the four ventricles inside the brain, in the spinal column, and within the subarachnoid space.
Cerebral Security A triple-layered covering, the meninges, encases the brain and spinal cord, and the cerebrospinal fluid (CSF) cushions them.

in the brain's enclosing membranes. Cerebral spinal fluid is continually being made and drained off into the circulatory system. If the outflow is blocked, as occurs in a congenital condition called hydrocephalus (literally, water brain), severe mental retardation and even death can result.

4. The brain and spinal cord are protected from many chemical substances circulating in the rest of the body by the blood-brain barrier. To form this barrier, the cells of the capillaries—the very small blood vessels—form tight junctions with one another, thus preventing many blood-borne substances from crossing from the capillaries into the CNS tissues.

Blood Supply
The brain receives its blood supply from two internal carotid arteries and two vertebral arteries that course up each side of the neck. The four arteries connect at the base of the brain, where they enter the skull. From there, the cerebral arteries branch off into several smaller arteries that irrigate the brainstem and cerebellum and give rise to three arteries that irrigate the forebrain.

The distribution zones of the cerebral arteries in the cortex are shown in Figure 3.4. If you place your hand so that the wrist represents the artery trunk at the base of the brain, the extended digits offer an approximate representation of the area of the cortex that is irrigated in each zone. Thus, the anterior

![Diagram of cerebral arteries]

**Figure 3.4**

**Distribution of the Major Cerebral Arteries** If you align your hand so that your wrist represents the base of an artery, the extended digits will spread over the area of cortex to which blood is distributed by that artery.
cerebral artery (ACA) irrigates the medial and dorsal part of the cortex, the middle cerebral artery (MCA) irrigates the lateral surface of the cortex, and the posterior cerebral artery (PCA) irrigates the ventral and posterior surfaces of the cortex.

For most people, if an artery becomes blocked by the formation of a blood clot, as described for R.S., who suffered an MCA ischemic stroke, stroke symptoms will vary according to the location of the loss of blood supply. Note in Figure 3.4 that a large clot in an initial portion of a blood vessel will deprive a great deal of the cortex of its blood supply, whereas a smaller clot in the more distal branches of the artery will result in more-restricted damage. For some people, there are connections between the different arteries; so, subsequent to a clot, other arteries can supply blood.

The veins of the brain, through which spent blood returns to the heart, are classified as external and internal cerebral and cerebellar veins. The venous flow does not follow the course of the major arteries but instead follows a pattern of its own.

Neurons and Glia

The brain has its origin in a single undifferentiated cell called a neural stem cell (also called a germinal cell). Not only does this stem cell and its progeny produce the various specialized cells that make up the adult brain, they also produce additional stem cells that persist into adulthood.

A stem cell has extensive capacity for self-renewal. To initially form a brain, it divides and produces two stem cells, both of which can divide again (Figure 3.5). In the adult, one stem cell dies after each division; so the mature brain contains a constant number of dividing stem cells. Adult stem cells serve as a source of new neurons for certain parts of the adult brain. Thus, for those regions, they may play a role in brain repair after injuries such as stroke or other trauma.

In the developing embryo, stem cells give rise to progenitor cells that migrate and act as precursor cells, giving rise to nondividing, primitive types of nervous system cells called blasts. Some blasts differentiate into neurons; others differentiate into the glia. These two basic brain-cell types—neurons and glia—take many forms and make up the entire adult brain.

Neuroscientists once thought that the newborn child had all the neurons that it would ever possess. Among the most remarkable discoveries of the past decade is that, in fact, new neurons are produced after birth and, in some regions of the brain, continue to be produced through adulthood.

Neurons differ chiefly in overall size, in the length and branching of their axons, and in the complexity of their dendritic
Figure 3.6

Neuron Types: Neurons are specialized in regard to function. These schematic representations show the relative sizes and configurations, not drawn to scale, of (A) sensory neurons, (B) interneurons in the brain, and (C) motor neurons in the spinal cord.

Table 3.1 Types of glial cells

<table>
<thead>
<tr>
<th>Type</th>
<th>Appearance</th>
<th>Features and Function</th>
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<tbody>
<tr>
<td>Ependymal cell</td>
<td>Small, ovoid; secretes cerebrospinal fluid (CSF)</td>
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<tr>
<td>Astrocyte</td>
<td>Star shaped, symmetrical; nutritive and support function</td>
<td></td>
</tr>
<tr>
<td>Microglial cell</td>
<td>Small, mesodermally derived; defensive function</td>
<td></td>
</tr>
<tr>
<td>Oligodendroglial cell</td>
<td>Asymmetrical; forms insulating myelin around axons in brain and spinal cord</td>
<td></td>
</tr>
<tr>
<td>Schwann cell</td>
<td>Asymmetrical; wraps around peripheral nerves to form insulating myelin</td>
<td></td>
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processes. Figure 3.6 shows examples of the differences in size and shape that characterize neurons from different parts of the nervous system. The simplest sensory neuron, a bipolar neuron shown on the left in Figure 3.6A, consists of a cell body with a dendrite on one side and an axon on the other.

Somatosensory neurons, which project from the body’s sensory receptors into the spinal cord, are modified so that the dendrite and axon are connected, which speeds information conduction because messages do not have to pass through the cell body (Figure 3.6A right). Interneurons within the brain and spinal cord link up sensory- and motor-neuron activity in the CNS. There are many kinds of interneurons and all have many dendrites that branch extensively but, like all neurons, a brain or spinal-cord interneuron has only one axon, although it can branch as well (Figure 3.6B). Motor neurons located in the brainstem project to facial muscles, and motor neurons in the spinal cord project to other muscles of the body (Figure 3.6C). Together, motor neurons are called the final common path because all behavior produced by the brain is produced through them.

Thus, the architecture of neurons differs from region to region in the nervous system. These differences provide the basis for dividing the brain into different anatomical regions. The various types of glial cells have different functions as well. Some are described in Table 3.1.

Gray, White, and Reticular Matter

When a human brain is sectioned to reveal its internal structures, some parts appear gray, some white, and some mottled. In general, these visually contrasting parts are described as gray matter, white matter, and reticular matter (Figure 3.7). Gray matter acquires its characteristic gray-brown color from the capillary blood vessels and neuronal cell bodies that predominate there. White matter consists largely of axons that extend from these cell bodies to form connections with neurons in other brain areas. These axons are covered with an insulating layer of glial cells that are composed of the same fatty substance (lipid) that gives milk its white ap-
Coronal Section Through the Brain

The brain is (A) cut from the top down and (B) frontally viewed at a slight angle. The regions that are relatively white are largely composed of nerve fibers, whereas the relatively gray brown areas are composed of cell bodies. The large bundle of fibers joining the two hemispheres, visible above the ventricles, is the corpus callosum. Each ventricle is a fluid-filled cavity. (Photograph: Glauberman/Photo Researchers.)

Layers, Nuclei, Nerves, and Tracts

As already mentioned, a large, well-defined group of cell bodies can form layers or nuclei. The architecture of these groupings suggests that each nucleus or layer has a particular function, and such is indeed the case. A large collection of axons projecting to or away from a nucleus or layer in the CNS is called a tract (from Old French, meaning “path”) or, sometimes, a fiber pathway.

Tracts carry information from one place to another within the CNS; for example, the corticospinal (pyramidal) tract carries information from the cortex to the spinal cord. The optic tract carries information from the retina of the eye (the retina, strictly speaking, is part of the brain) to other visual centers in the brain. Fibers and fiber pathways that enter and leave the CNS are called nerves, such as the auditory nerve or the vagus nerve; but, after they have entered the central nervous system, they, too, are called tracts.

The Origin and Development of the Central Nervous System

The developing brain is less complex than the adult brain and provides a clearer picture of the vertebrate brain's basic three-part structure (Figure 3.8A). Later in mammals, two of the three regions, the front and back components, expand...
Figure 3.8
Steps in the Development of the Brain (A) A three-chambered brain. (B) A five-chambered brain. (C) Medial view through the center of the human brain.

<table>
<thead>
<tr>
<th>(A) Vertebrate</th>
<th>(B) Mammalian embryo</th>
<th>(C) Fully developed human brain</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prosencephalon (forebrain)</td>
<td>Telencephalon (endbrain)</td>
<td>Telencephalon</td>
</tr>
<tr>
<td>Mesencephalon (midbrain)</td>
<td>Diencephalon (between brain)</td>
<td>Thalamus, hypothalamus, pineal body, third ventricle</td>
</tr>
<tr>
<td>Rhombencephalon (hindbrain)</td>
<td>Mesencephalon</td>
<td>Tactum, tegmentum, cerebral aqueduct</td>
</tr>
<tr>
<td></td>
<td>Metencephalon (across brain)</td>
<td>Cerebellum,pons, fourth ventricle</td>
</tr>
<tr>
<td></td>
<td>Myelencephalon (spinal brain)</td>
<td>Medulla oblongata, fourth ventricle</td>
</tr>
<tr>
<td>Spinal cord</td>
<td>Spinal cord</td>
<td>Spinal cord</td>
</tr>
</tbody>
</table>

greatly and subdivide further, yielding five regions in all (Figure 3.8B). Embryologists use rather cumbersome names for these regions; because some names are also used to describe parts of the adult brain (Figure 3.8C), they are included in the illustration.

The three regions of the primitive, developing brain are recognizable in Figure 3.8A as a series of three enlargements at the end of the embryonic spinal cord. The adult brain of a fish, amphibian, or reptile is roughly equivalent to this three-part brain: the prosencephalon ("front brain") is responsible for olfaction, the mesencephalon ("middle brain") is the seat of vision and hearing, and the rhombencephalon (hindbrain) controls movement and balance. Here, the spinal cord is considered part of the hindbrain.

In mammals (Figure 3.8B), the prosencephalon develops further to form the cerebral hemispheres (the cortex and related structures), which are known collectively as the telencephalon ("endbrain"). The remaining part of the old prosencephalon is referred to as the diencephalon ("between brain") and includes the thalamus. The back part of the brain also develops further. It is subdivided into the metencephalon ("across brain," which includes the enlarged cerebellum) and the myelencephalon ("spinal brain"), the lower region of the brainstem.

The human brain is a more complex mammalian brain, retaining most of the features of other mammalian brains and possessing especially large cerebral hemispheres. As we describe the major structures of the CNS in the sections that follow, we group them according to the three-part scheme of forebrain, brainstem, and spinal cord (Figure 3.8C). These three subdivisions reinforce the concept of levels of function, with newer levels partly replicating the work of older ones. Nevertheless, most behaviors are thus not the product of a single locus in the brain but rather of many brain areas and levels that do not simply replicate function; instead, each region adds a different dimension to the behavior. This hierarchical organization affects virtually every behavior in which humans engage.

The brain begins as a tube, and, even after it folds and matures, its interior remains "hollow." The four prominent pockets created by the folding of this
hollow interior in the brain are called ventricles ("bladders") and are numbered 1 through 4. The "lateral ventricles" (first and second) form C-shaped lakes underlying the cerebral cortex, whereas the third and fourth ventricles extend into the brainstem and spinal cord (Figure 3.9). All are filled with cerebrospinal fluid, which is produced by ependymal glial cells located adjacent to the ventricles (see Table 3.1). Cerebral spinal fluid flows from the lateral ventricles out through the fourth ventricle and eventually drains into the circulatory system.

The Spinal Cord

We begin our description of neuroanatomy with the spinal cord. It is structurally the simplest part of the CNS, and the basic plan of the spinal cord is also seen in the plan of the brainstem. Along with the spinal cord, we also detail the functions of the somatic and the autonomic nervous systems.

Spinal-Cord Structure and the Spinal Nerves

In a simple animal, such as the earthworm, the body is a tube divided into segments. Within the body is a tube of nerve cells that also is divided into segments. Each segment receives nerve fibers from afferent sensory receptors in the part of the body adjacent to it and sends efferent fibers to control the muscles of that part of the body. Each segment functions relatively independently in the earthworm, although fibers interconnect the segments and coordinate their activity. This basic plan also holds for the human body.

Let us take a look at our "tube of nerves." The spinal cord lies inside the bony spinal-column vertebrae, which are categorized into five regions from top to tail. Figure 3.10A details our 30 spinal-cord segments: 8 cervical (C), 12 thoracic (T), 5 lumbar (L), and 5 sacral (S). Figure 3.10B shows the segmental
organization of the human body. The segments, called dermatomes ("skin cuts"), encircle the spinal column as a stack of rings.

Mammalian limbs evolved perpendicularly to the spinal cord, but humans have an upright posture; so the dermatomes in our bodies are distorted into the pattern shown in Figure 3.10B. As many as six segments (C4 through T2) can be represented on the arm. If you imagine the person in the drawing standing on all fours, you can see how this pattern makes sense.

Each spinal segment is connected by SNS spinal nerve fibers to the body dermatome of the same number, including the organs and musculature that lie within the dermatome. In the main, the cervical segments control the forelimbs, the thoracic segments control the trunk, and the lumbar segments control the hind limbs.

Figure 3.11 shows a cross section of the spinal cord. Afferent fibers entering the dorsal part of the spinal cord (posterior in humans) bring information from the sensory receptors of the body. These spinal nerve fibers converge as they enter the spinal cord, forming a strand of fibers referred to as a dorsal root. Different fibers leaving the ventral (anterior in humans) part of the spinal cord, carrying information from the spinal cord to the muscles, form a similar strand of spinal nerves known as a ventral root.

You can see in Figure 3.11A that the outer part of the spinal cord itself consists of white matter, or tracts, arranged so that, with a few exceptions, the dorsally located tracts are sensory and the ventrally located tracts are motor. The spinal tracts carry information to and from the brain. The inner part of the cord consists of gray matter; that is, it is composed largely of neural cell bodies, which, in this case, organize movements and give rise to the ventral roots. In cross section, this gray-matter region has the shape of a butterfly (Figure 3.11B).

**Spinal-Cord Function and the Spinal Nerves**

François Magendie, a French experimental physiologist, reported in a three-page paper in 1822 that he had succeeded in cutting the dorsal roots of one group of puppies and the ventral roots of another group (the youth of the dogs allowed the different surgeries; in adult dogs, the roots are fused). He found
that cutting the dorsal roots caused loss of sensation and cutting the ventral roots caused loss of movement.

Eleven years earlier, in 1811, Charles Bell, a Scot, had suggested the opposite functions for each of the roots, basing his conclusions on anatomical information and the results from somewhat inconclusive experiments on rabbits. When Magendie's paper appeared, Bell hotly disputed priority for the discovery, with some success. Today, the principle that the dorsal part of the spinal cord is sensory and the ventral part is motor is called the Bell-Magendie law.

Magendie's experiment has been called the most important ever conducted on the nervous system. It enabled neurologists for the first time to distinguish sensory from motor impairments, as well as to draw general conclusions about the location of neural damage, on the basis of the symptoms displayed by patients. Because of the segmental structure of the spinal cord and the body, rather good inferences can also be made about the location of spinal-cord damage or disease on the basis of changes in sensation or movement in particular body parts.

Further major advances toward understanding spinal-cord function came from the work of Charles Sherrington and his students, who showed that the spinal cord retains many functions even after it has been separated from the brain. Sherrington published a summary of this research in 1906, and it had an important influence in the treatment of people with spinal-cord injury.

Persons whose spinal cords are cut so that they no longer have control over their legs are paraplegic; if the cut is higher on the cord, making them unable to use their arms either, they are quadriplegic. Once thought untreatable, growing understanding of spinal-cord function has led to such huge improvements in treatment that spinal-cord patients today can lead long and active lives. A Canadian paraplegic, Rick Hansen, the "man in motion," propelled his wheelchair around the world to campaign for the funding of research and treatment of spinal-cord injuries. The late actor Christopher Reeve, famed for his cinematic role as Superman, became quadriplegic after a horse-riding accident yet continued for the rest of his life to make movies and to campaign for medical treatment and research for spinal-cord injuries.

Despite the fact that the spinal cord controls both simple and complex behavior, it does depend on the brain, as evidenced by the severe behavioral impairments that follow spinal-cord injury. Because the main effect of such injury is to sever connections between the cord and the brain, scientists believe that simply reestablishing these connections can restore function to spinal-cord-injured people. Unfortunately, although the fibers in the spinal tracts do regrow in some vertebrates, such as fish, and in the early stages of development in other animals, they do not regrow in adult mammals.

Researchers continue to experiment with various approaches to induce spinal-cord regrowth. These approaches include the idea that new growth is prevented by the presence of certain inhibitory molecules on the tracts of the cord below the cut. If these inhibitory molecules can in turn be inhibited, investigators reason, fibers will begin to grow across the injured zone.

Another line of research is focused on the scarring that accompanies most spinal-cord damage and the possibility that scarring inhibits new growth. Some scientists are conducting experiments in which they attempt to remove the scar, whereas other scientists are attempting to build bridges across the scar over which fibers can grow. All these approaches have been partly successful in nonhuman
animal studies, but they have not approached the level of success to be considered
a cure for spinal-cord injury.

In addition to the local connections that pain and tactile receptors in the
SNS make within the segments of the spinal cord corresponding to their der-
matomes, these receptors communicate with fibers in many other segments of
the spinal cord and can thus produce appropriate adjustments in many body
parts. For example, when one leg is withdrawn in response to a painful stimu-
lus, the other leg must simultaneously extend to support the body’s weight.

The spinal cord is capable of producing actions that are more complex than
just adjustments of a limb. If the body of an animal that has had its spinal cord
sectioned from the brain is held in a sling with its feet touching a conveyor belt,
the animal is capable of walking. Thus, the spinal cord contains all the SNS
connections required for allowing an animal to walk.

Recall from Figure 3.2 that the SNS consists of all the spinal and cranial
nerves that produce movement and transmit incoming sensory information to
the CNS. Sensory information plays a central role in eliciting different kinds

<table>
<thead>
<tr>
<th>Number</th>
<th>Name</th>
<th>Function*</th>
<th>Method of Examination</th>
<th>Typical Symptoms of Dysfunction</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Olfactory</td>
<td>Smell (s)</td>
<td>Various odors applied to each nostril</td>
<td>Loss of sense of smell (anosmia)</td>
</tr>
<tr>
<td>2</td>
<td>Optic</td>
<td>Vision (s)</td>
<td>Visual acuity, map field of vision</td>
<td>Loss of vision (anopia)</td>
</tr>
<tr>
<td>3</td>
<td>Oculomotor</td>
<td>Eye movement (m)</td>
<td>Reaction to light, lateral movements of eyes, eyelid movement (pilocarpus), deviation of eye outward</td>
<td>Double vision, defect of downward gaze</td>
</tr>
<tr>
<td>4</td>
<td>Trochlear</td>
<td>Eye movement (m)</td>
<td>Upward and downward eye movements</td>
<td>Decreased sensitivity or numbness of face, brief attacks of severe pain (trochlear neuralgia); weakness and wasting of facial muscles, asymmetrical chewing</td>
</tr>
<tr>
<td>5</td>
<td>Trigeminal</td>
<td>Masticatory</td>
<td>Light touch by cotton baton; pain by pinprick; thermal by hot and cold tubes, corneal reflex by touching cornea; jaw reflex by tapping chin, jaw movements</td>
<td>Double vision, inward deviation of the eye, facial paralysis, loss of taste over anterior two-thirds of tongue</td>
</tr>
<tr>
<td>6</td>
<td>Abducens</td>
<td>Eye movement (m)</td>
<td>Lateral movements</td>
<td>Deafness, sensation of noise in ear (tinnitus); disequilibrium feeling of disorientation in space</td>
</tr>
<tr>
<td>7</td>
<td>Facial</td>
<td>Facial movement (s, m)</td>
<td>Facial movements, facial expression, testing for taste</td>
<td>Partial dry mouth, loss of taste (ageusia) over posterior third of tongue, anesthesia and paralysis of upper pharynx</td>
</tr>
<tr>
<td>8</td>
<td>Auditory vestibular</td>
<td>Hearing (s)</td>
<td>Audiogram for testing hearing, stimulating by rotating patient or by irrigating the ear with hot or cold water (caloric test)</td>
<td>Hoarseness, lower pharyngeal anesthesia and paralysis, indefinite visceral disturbance</td>
</tr>
<tr>
<td>9</td>
<td>Glossopharyngeal</td>
<td>Tongue and pharynx (s, m)</td>
<td>Tasting for sweet, salt, bitter, and sour tastes on tongue, touching walls of pharynx for pharyngeal or gag reflex</td>
<td>Wasting of neck with weakened rotation, inability to shrug</td>
</tr>
<tr>
<td>10</td>
<td>Vagus</td>
<td>Heart, blood vessels, viscera, movement of larynx and pharynx (s, m)</td>
<td>Observing palate in phonation, touching palate for palatal reflex</td>
<td>Wasting of tongue with deviation to side of lesion on protrusion</td>
</tr>
<tr>
<td>11</td>
<td>Spinal accessory</td>
<td>Neck muscles and viscera (m)</td>
<td>Movement, strength, and bulk of neck and shoulder muscles</td>
<td>Patients are often asymptomatic in the selected patients with spinal accessory nerve -- might consider electrophysiological testing.</td>
</tr>
<tr>
<td>12</td>
<td>Hypoglossal</td>
<td>(m) Tongue muscles</td>
<td>Tongue movements, tremor, wasting or wrinkling of tongue</td>
<td>Patients are often asymptomatic in the selected patients with spinal accessory nerve -- might consider electrophysiological testing.</td>
</tr>
</tbody>
</table>

*The letters "s" and "m" refer to sensory and motor function, respectively, of the nerve.
of movements organized by the spinal cord. Movements dependent only on spinal-cord function are referred to as reflexes, specific movements elicited by specific forms of sensory stimulation. There are many kinds of sensory receptors in the body, including receptors for pain, temperature, touch and pressure, and the sensations of muscle and joint movement. The size of the spinal nerve fiber coming from each kind of receptor is distinctive; generally, pain and temperature fibers are smaller, and those for touch and muscle sense are larger.

The stimulation of pain and temperature receptors in a limb usually produces flexion movements that bring the limb inward, toward the body and away from injury. If the stimulus is mild, only the distal part of the limb flexes in response to it but, with successively stronger stimuli, the size of the movement increases until the whole limb is drawn back.

The stimulation of fine touch and muscle receptors in a limb usually produces extension movements, which extend the limb outward, away from the body. The extensor reflex causes the touched part of the limb to maintain contact with the stimulus; for example, the foot or hand touching a surface will maintain contact with the surface through this reflex. Because each of the senses has its own receptors, fibers, connections, and reflex movements, each sense can be thought of as an independent sensory system.

Connections Between Central and Somatic Nervous Systems

The somatic nervous system is monitored and controlled by the CNS. The spinal cord oversees the spinal nerves, and the brain oversees the 12 pairs of cranial nerves. The linkages provided by the cranial nerves between the brain and various parts of the head and neck as well as various internal organs are tabulated in Table 3.2 and illustrated in Figure 3.12. Cranial nerves can have afferent functions, such as for sensory inputs to the brain from the eyes, ears, mouth, and nose, or they can have efferent functions, such as for motor control of the facial muscles, tongue, and eyes.

Some cranial nerves have both sensory and motor functions, such as the modulation of both sensation and movement in the face, and the vagus nerve makes connections with many body organs, including the heart. Knowledge of the organization and function of the cranial nerves is important for making neurological diagnoses.

Autonomic Nervous System Connections

The internal autonomic nervous system (see Figure 3.2) is a hidden partner in controlling behavior. Even without our conscious awareness, it stays on the job to keep the heart beating, the liver releasing glucose, the pupils of the eyes adjusting to light, and so forth. Without the ANS, which regulates the internal organs and glands by connections through the SNS to the CNS, life would quickly cease.

Although the exertion of some conscious control over some of these vegetative activities can be learned, such conscious interference is unnecessary. One important reason is that the ANS must keep working during sleep when...
conscious awareness is off-duty. Recall that the functions retained by Terri Schiavo were vegetative (see Chapter 1).

The two divisions of the ANS—sympathetic and parasympathetic—work in opposition. The sympathetic system arouses the body for action, for example, by stimulating the heart to beat faster and inhibiting digestion when we exert ourselves during exercise or times of stress, referred to as the "fight or flight" response. The parasympathetic system calms the body down, for example, by slowing the heartbeat and stimulating digestion to allow us to "rest and digest" after exertion and during quiet times.

Like the SNS, the ANS interacts with the rest of the nervous system. Activation of the sympathetic system starts in the thoracic and lumbar spinal-cord regions, as illustrated on the left in Figure 3.13. But note that the spinal nerves...
do not directly control the target organs. Rather, the spinal cord is connected to a chain of autonomic control centers, collections of neural cells called sympathetic ganglia. These ganglia, collections of nerve cells that function somewhat like a primitive brain, control the internal organs.

A part of the parasympathetic system also is connected to the spinal cord—specifically, to the sacral region as diagrammed in the middle and on the right in Figure 3.13. As the illustration reveals, however, the greater part of the parasympathetic system derives from three cranial nerves: the vagus nerve, which calms most of the internal organs; the facial nerve, which controls salivation; and the oculomotor nerve, which controls pupil dilation and eye movements. In contrast with the arousing sympathetic system, which forms a chain running parallel to the spinal cord, the calming parasympathetic system connects with parasympathetic ganglia near the target organs, as shown in the middle and on the right in Figure 3.13.

The internal organs, although arranged segmentally in relation to the spinal cord, appear not to have their own sensory representation within it. Pain in these organs is perceived as coming from the outer parts of the dermatome and so is called referred pain. For example, pain in the heart is felt in the shoulder and arm, and kidney pain is felt in the back. Physicians use what is known about the location of referred pains to diagnose problems within the body.

The Brainstem

The brainstem begins where the spinal cord enters the skull and extends upward to the lower areas of the forebrain. Figure 3.14 shows its three main regions: the diencephalon, the midbrain, and the hindbrain. In general, the brainstem produces more-complex movements than does the spinal cord, but its overall plan is similar, with the region dorsal to the fourth ventricle responsible for sensory functions and that ventral to the ventricle (posterior and anterior for the upright human brain) responsible for motor functions.

A distinctive part of the brainstem comprises the many cranial-nerve nuclei that converge there and send their axons to the muscles of the head. The core of the brainstem consists of those cranial-nerve nuclei as well as many bundles of fibers from the spinal cord that pass through the brainstem on their way to the forebrain. Conversely, fibers from the forebrain connect with the brainstem or pass through it on their way to the spinal cord. The brainstem also regulates many complex functions, with the diencephalon, midbrain, and hindbrain regulating somewhat different functions as described next.

The Hindbrain

The most distinctive part of the hindbrain is the cerebellum. It protrudes above the core of the brainstem, and its surface is gathered into narrow folds, or folia, like the gyri and sulci of the cortex but smaller (Figure 3.15). At
the base of the cerebellum are several nuclei that send connections to other parts of the brain.

The cerebellum plays a role in coordinating and learning skilled movements. Thus, damage to the cerebellum results in equilibrium problems, postural defects, and impairments of skilled motor activity. The parts that receive most of their impulses from the vestibular system (sensory receptors for balance and movement located in the middle ear) help to maintain the body's equilibrium. Cerebellar parts receiving impulses mainly from the receptors in the body's trunk and limbs control postural reflexes and coordinate functionally related groups of muscles.

Within the core of the hindbrain's mixture of nuclei and fibers lies a network referred to as the reticular formation, diagrammed in Figure 3.16. In 1949, Giuseppe Moruzzi and Horace Magoun stimulated this area electrically in anesthetized cats and found that the stimulation produced a waking pattern of electrical activity in the cats' cortices. They concluded that the function of the reticular formation is to control sleeping and waking—that is, to maintain "general arousal" or "consciousness." As a result, the reticular formation came to be known as the reticular activating system.

Neuroscientists now recognize that the various nuclei within the upper part of the brainstem (the pons) and the lower part (the medulla) serve many functions; some take part in waking and sleeping and others take part in locomotion.

### The Midbrain

The midbrain, diagrammed in Figure 3.17, has two main subdivisions: located dorsally is the tectum, or "roof," which is the roof of the third ventricle, and located ventrally is the tegmentum, or "floor" of the third ventricle. The tectum receives a massive amount of sensory information from the eyes and ears. Located on the brainstem's posterior, the tectum consists primarily of two sets of bilaterally symmetrical nuclei. The superior colliculi ("upper hills") receive projections from the retina of the eye, and they mediate many visually related behaviors. The inferior colliculi ("lower hills") receive projections from the ear, and they mediate many auditory-related behaviors. Another class of behaviors mediated by the colliculi is the orientation of movements related to sensory input, such as turning your head to look at the source of a sound.

Lying ventral to the tectum, as shown in Figure 3.17, the tegmentum is composed of nuclei related to motor functions, diagrammed at the upper right in the illustration. The red nucleus controls limb movements, and the substantia nigra (black substance) is
connected to the forebrain, a connection important for reward and for initiating movements. The periaqueductal gray matter, made up of cell bodies that surround the aqueduct joining the third and fourth ventricles, contains circuits for controlling species-typical behaviors (for example, sexual behavior) and for modulating responses to pain.

The Diencephalon

The diencephalon borders the older and newer parts of the brain (see Figure 3.14). Its "between brain" status is reinforced in a neuroanatomical inconsistency; some anatomists place it in the brainstem, as we do; others place it in the forebrain (see Figure 3.8). The diencephalon consists mainly of the three thalamic structures: hypothalamus ("lower room"); epithalamus ("upper room"); and thalamus ("inner room" or "chamber").

The hypothalamus, comprising about 22 small nuclei and the fiber systems that pass through it, interacts with the pituitary gland. Although only about 0.3% of the brain's weight, the hypothalamus takes part in nearly all aspects of motivated behavior, including feeding, sexual behavior, sleeping, temperature regulation, emotional behavior, movement, and, through its interactions with the pituitary gland, endocrine function.

The thalamus, the largest structure in the diencephalon, is composed of 20-odd large nuclei, each of which projects to a specific area of the cerebral cortex, as shown in Figure 3.18. These nuclei route information from three sources to the cortex:

1. One group of thalamic nuclei relays information from sensory systems to their appropriate targets. For example, the lateral geniculate body (LGB) receives visual projections; the medial geniculate body (MGB) receives auditory projections; and the ventrolateral posterior nuclei (VLP) receive touch, pressure, pain, and temperature projections from the body. In turn, these areas project to the visual, auditory, and somatosensory regions of the cortex.

2. Some thalamic nuclei relay information between cortical areas. For example, a large area of the posterior cortex sends projections to the pulvinar nucleus (P) at the tip of the thalamus and receives projections back from that nucleus.

3. Some thalamic nuclei relay information from other forebrain and brainstem regions.

![Figure 3.18](image)

**Thalamus** (A) The arrows indicate the sources of input and output from major nuclei of the thalamus:
- anterior nucleus, A;
- dorsomedial nucleus, DM;
- ventral anterior nucleus, VA;
- ventrolateral nucleus, VL;
- lateral posterior nucleus, LP;
- pulvinar, P;
- lateral geniculate body, LGB;
- medial geniculate body, MGB.  
**Cortex** (B) The relations between major thalamic nuclei and the various areas of the cortex to which they project.
In short, almost all the information received by the cortex is first relayed through the thalamus.

The **epithalamus** is a collection of nuclei at the posterior of the diencephalon. Its overall function is poorly understood, but one of its structures, the pineal gland, secretes the hormone melatonin, which influences daily and seasonal body rhythms. Another structure, the habenula, regulates hunger and thirst.

### The Forebrain

Of the three main forebrain structures, two are subcortical: the basal ganglia and the limbic system. Enveloping all is the cerebral cortex. These regions share many connections, forming functional circuits. Nevertheless, each is sufficiently anatomically and functionally distinct to describe separately.

#### The Basal Ganglia

The **basal ganglia** ("lower knots," referring to "knots below the cortex") are a collection of nuclei lying mainly beneath the anterior regions of the cortex (Figure 3.19). They include the **putamen** ("shell"), the **globus pallidus** ("pale globe"), and the **caudate nucleus** ("tailed nucleus"). The basal ganglia form a circuit with the cerebral cortex.

The caudate nucleus receives projections from all areas of the cortex and sends its own projections through the putamen and globus pallidus to the thalamus and, from there, to the frontal cortical areas. The basal ganglia also have reciprocal connections with the midbrain, especially with the substantia nigra in the midbrain tegmentum (see Figure 3.17). The ganglia have functions related to movement and to simple forms of learning.

#### The Basal Ganglia and Movement

Damage to different parts of the basal ganglia can produce changes in posture, increases or decreases in muscle tone, and abnormal movements such as twitches, jerks, and tremors. So the ganglia are thought to take part in such motor functions as the sequencing of movements into a smoothly executed response. Three diseases of the basal ganglia illustrate its motor functions:

1. **In Huntington’s chorea**, a genetic disorder, cells of the basal ganglia die progressively, and, associated with this cell death, many involuntary movements of the body occur almost continuously. These abnormal movements have a “dancelike” quality, which is what *chorea* means in Latin.

2. **In Parkinson’s disease**, the projections from the substantia nigra to the basal ganglia die. Associated with this cell death, the patient becomes rigid.
and has difficulty moving and maintaining balance. The patient may also display rhythmical tremors of the hands and legs.

3. In **Tourette's syndrome**, another disorder of the basal ganglia, the most frequent symptoms are involuntary motor tics, especially of the face and head, and complex movements, such as hitting, lunging, or jumping. Tourette's is also characterized by involuntary vocalizations, including curse words and animal sounds.

These disorders of the basal ganglia are not disorders of producing movements, as in paralysis. Rather they are disorders of controlling movements. The basal ganglia, therefore, must play a role in the control and coordination of movement patterns, not in activating the muscles.

**The Basal Ganglia and Learning**

The second function of the basal ganglia is to support stimulus-response, or habit, learning. For example, a bird learns, after a number of experiences, that brightly colored butterflies have a bitter taste. Its basal ganglia are critical in learning the association between taste and color and in refraining from eating the insects. Similarly, many of our actions are responses to sensory cues—for example, flicking a light switch to turn on a light or turning the handle on a door to open it. People with basal ganglia disorders can have difficulty performing such stimulus-response actions.

**The Limbic System**

In the course of evolution in amphibians and reptiles, a number of three-layered cortical structures that sheath the periphery of the brainstem developed. With the subsequent growth of the *neocortex* ("new bark"), these older cortical structures became sandwiched at the border between the new brain and the old. Because of their evolutionary origin, some anatomists have referred to them as the *reptilian brain*, but the term **limbic lobe** (from the Latin *limbus*, meaning "border" or "hem"), coined by Broca in 1878, is more widely recognized among neuroscientists.

The limbic lobe is also referred to as the **limbic system**, which has proved to be a misnomer. The first theory of limbic function stemmed from the observation that connections exist between the olfactory system and the limbic lobe. On this evidence, anatomists hypothesized that the limbic structures processed olfactory information, and so collectively the structures became known as the *rhinencephalon*, or "smell-brain." A number of subsequent experiments have been unable to precisely demonstrate what olfactory function the limbic lobe has, but it is not required for simply identifying odors.

The limbic lobe consists of a number of interrelated structures, including the **amygdala** ("almond"), **hippocampus** ("sea horse"), and the **septum** ("partition"). The cingulate ("girdle") gyrus, or **cingulate cortex**, is a strip of limbic cortex that lies just above the corpus callosum along the medial walls of the cerebral hemispheres as shown in **Figure 3.20A**. The nuclei that form the amygdala and the septum play roles in emotional and species-typical behaviors. The hippocampus is proposed to mediate memory and spatial navigation and is particularly vulnerable to the effects of stress. The history of how the limbic
"lobe" became the limbic "system" is one of the most interesting chapters in neuroscience.

In 1937, James Papez, in what at the time amounted to a scientific tour de force, asked, "Is emotion a magic product, or is it a physiologic process which depends on an anatomic mechanism?" He suggested that emotion, which had no known anatomic substrate, is a product of the limbic lobe, which had no recognized function at the time. Papez proposed that the emotional brain consists of a circuit in which information flows from the mammillary bodies in the hypothalamus to the anterior thalamic nucleus to the cingulate cortex to the hippocampus and back to the mammillary bodies (Figure 3.20B).

Input could enter this circuit from other structures to be elaborated as emotion. For example, an idea ("It is dangerous to walk in the dark") from the neocortex could enter the circuit to be elaborated as a fear ("I feel frightened in the dark") and ultimately influence the hypothalamus to release a hormone to prompt the appropriate physical response to the idea and its emotional corollary. The hippocampus contains many receptors for the stress hormone corticosterone, which is seen as support for Papez's idea.

In Chapter 1, we described Scoville and Milner's now-famous patient H.M., whose medial temporal lobe, including his hippocampus, was removed bilaterally as a treatment for epilepsy. His primary deficits were not emotional; rather, he displayed little ability to learn new information. Thereafter, the limbic system was proposed to be the memory system of the brain. In the years since H.M. was first described, many other regions of the brain also have become recognized as playing a part in memory, diminishing the apparent role of the limbic system in that function.

Today, neuroscientists have concluded that the limbic lobe is not a unitary "system" at all. Although some limbic structures play roles in emotional and sexual behaviors, limbic structures also serve other functions in memory, motivation and reward, and navigation.

The Neocortex

Anatomists use the term cortex to refer to any outer layer of cells. In neuroscience, the terms cortex and neocortex (new cortex) are often used interchangeably to refer to the outer part of the forebrain, and so, by convention, "cortex" refers to "neocortex" unless otherwise indicated, for example, as the older limbic cortex (see Figure 3.20A). The neocortex is the part of the brain that has
expanded the most in the course of evolution: it comprises 80% by volume of the human brain and is unique to mammals. Its primary function is to create and respond to perceptions of the world.

The human neocortex has an area as large as 2500 square centimeters but a thickness of only 1.5 to 3.0 millimeters. It consists of six layers of cells (gray matter) and is heavily wrinkled. This wrinkling is nature's solution to the problem of confining the huge neocortical surface area within a skull that is still small enough to pass through the birth canal. Just as crumpling a sheet of paper enables it to fit into a smaller box than it could when flat, the folding of the neocortex permits the human brain to fit comfortably within the relatively fixed volume of the skull.

To review some of the main features of the cortex introduced in Chapter 1, Figure 3.21 shows the two nearly symmetrical cerebral hemispheres, the left and the right, separated by the longitudinal fissure and subdivided into four lobes: frontal, parietal, temporal, and occipital. The frontal lobes have fixed boundaries: they are bounded posteriorly by the central sulcus, inferiorly by the lateral fissure, and medially by the cingulate sulcus.

The anterior boundary of the parietal lobes is the central sulcus, and their inferior boundary is the lateral fissure. The temporal lobes are bounded dorsally by the lateral fissure. On the lateral surface of the brain, there are no definite boundaries between the occipital lobes and the parietal and temporal lobes.

**Fissures, Sulci, and Gyri**

The most conspicuous surface feature of the neocortex is its crinkled tissue, consisting of clefts and ridges. Recall from Chapter 1 that a cleft is called a sulcus if it extends deeply enough into the brain to indent the ventricles; it is called a sulcus (plural, sulci) if it is shallower. A ridge is called a gyrus (plural, gyri).

![Figure 3.21](https://example.com/figure321.png)

*Views of the Human Brain*

Locations of the lobes of the cerebral hemispheres are shown in these top, bottom, side, and midline views, as are the cerebellum, the central sulcus, and the longitudinal and lateral fissures. (Photographs courtesy of Yakovlev Collection/AFIP)
Figure 3.22 shows the location of the more important fissures, sulci, and gyri of the brain. The location and shape of these features vary somewhat on the two sides of a person's brain, and the location, size, and shape of the gyri and sulci vary substantially in the brains of different persons. Adjacent gyri differ in the way that cells are organized within them, and the shift from one kind of arrangement to another is usually at the sulcus. There is evidence that gyri can be associated with specific functions.

The major gyri on the outer surface of the neocortex are shown in Figure 3.22A, and those on the inner surface of the neocortex are shown in Figure 3.22B. Note that the cingulate gyrus, located just above the corpus callosum, spans the inner surface of the four neocortical lobes. Figure 3.22C illustrates the main sulci and fissures on the lateral surface of the cortex, and Figure 3.22D locates some of the main sulci and fissures on the medial surface of the cortex.

Organization of the Cortex in Relation to Its Inputs and Outputs

The locations of the various inputs and outputs to the cortex can be represented by a projection map, which is constructed by tracing axons from the sensory systems into the brain and by tracing axons from the neocortex to the motor systems of the brainstem and spinal cord (Figure 3.23). Different regions of the neocortex have different functions. Some regions receive information from sensory systems, others command movements, and still others are the sites of connections between the sensory and the motor areas, enabling them to work in concert.

Recall that inputs to the cortex are relayed through the thalamic nuclei (see Figure 3.18). Overall, the neocortex can be conceptualized as consisting of a
number of fields: visual, auditory, body senses, and motor (see Figure 2.11A). Because vision, audition, and body senses are functions of the posterior cortex, this region of the brain (parietal, temporal, and occipital lobes) is considered largely sensory; because the motor function is located in the frontal neocortex, that lobe is considered largely motor. Finally, because each lobe contains one of the primary projection areas, it can be associated roughly with a general function:

Frontal lobes: motor functions
Parietal lobes: body senses
Temporal lobes: auditory functions
Occipital lobes: visual functions

**Primary Areas**

As Figure 3.23 shows, sensory projections from the eye can be traced to the occipital lobe, projections from the ear to the temporal lobe, and projections from the somatosensory system to the parietal lobe. The olfactory system sends projections to the ventral frontal lobe (see Figure 3.21 ventral view). The major motor projection to the spinal cord originates in the frontal lobe.

The areas that receive projections from structures outside the neocortex or send projections to it are called **primary areas**. Note that the lateral view of the brain presented in Figure 3.23 does not represent the entire extent of these primary projection areas, because they also extend down into the cortical gyri and fissures. Much of the auditory zone, for example, is located within the lateral fissure. Nevertheless, the primary projection areas of the neocortex are small relative to its total size.

**Secondary Areas**

The primary sensory areas send projections into the areas adjacent to them, and the motor areas receive fibers from areas adjacent to them. These adjacent **secondary areas** are less directly connected with the sensory receptors and motor neurons. The secondary areas are thought to be more engaged in interpreting sensory input or organizing movements than are the primary areas.

**Tertiary Areas**

The cortical areas between the various secondary areas may receive projections from them or send projections to them. These patches of cortex are referred to as **tertiary areas** and often as **association cortex** because early views of neocortical function proposed that tertiary areas serve to connect and coordinate the functions of the secondary areas. Tertiary areas encompass all cortex that is not specialized for sensory or motor function but rather mediates complex activities such as language, planning, memory, and attention. The accompanying Snapshot describes a newly found connection between such neural activity and heretofore unexplained physical symptoms.
Understanding brain function requires knowledge not only of neuroanatomy but also of what specific brain regions do. New insights into an old disorder illustrate the understanding obtained by combining anatomical and functional views of the brain.

Conversion reaction was once called hysteria (the Greek term for "uterus"). Coined by the Egyptian physician Hippocrates, hysteria has been assigned to the present day to a variety of disorders, mainly in women, including paralysis, changes in sensory ability such as loss of vision, and a variety of other illnesses that seemingly could not be explained as physical ailments. According to Hippocrates, if the uterus wandered in the body and became lodged in a particular body part, the functional blockade of the part resulted in a patient's symptoms.

Hysteria was popularized by Sigmund Freud's account of his patient Anna O. and his theory that unconscious conflict manifests as physical symptoms. The term conversion reaction has now replaced hysteria in the Diagnostic and Statistical Manual of Mental Disorders (DSM).

In contrast with the general finding of an absence of a physical cause for conversion reactions, brain imaging of patients with its symptoms reveals changes in the function of certain brain regions (Black et al., 2004). The brain-imaging studies do not explain the cause of conversion reaction, but they do, for the first time, reveal a physical basis for the condition. For example, Sean Spence (2000) used positron emission tomography to reveal the extent of brain blood flow, hence revealing brain regions that are hypoactive or hyperactive, to examine brain function in three patients who suffered from forelimb paralysis. To obtain a comparison group, control subjects were asked to feign comparable paralysis.

As participants attempted limb movements, regional cerebral blood flow was decreased in the paralyzed patients' left dorsolateral prefrontal cortices (red areas) but in the right anterior prefrontal cortices of the feigners (green areas). Because the dorsolateral prefrontal cortex is associated with movement planning, the investigators suggested that the patients' paralysis is associated with the brain's executive control of movement.


### Cellular Organization of the Cortex

The neurons of the neocortex are arranged in six layers, as shown in Figure 3.24. There are regional differences in the shape, size, and connections of the cells among the six layers:

- **Layers V and VI** send axons to other brain areas. Both the layers and the cells of which they are composed are particularly large and distinctive in the motor cortex, which sends projections to the spinal cord. (Large size is typical of cells that send information long distances.)

- **Layer IV** receives axons from sensory systems and other cortical areas. This layer features large numbers of small, densely packed cells in the primary areas of vision, somatosensation, audition, and taste--olfaction, which receive large projections from their respective sensory organs.

- **Layers I, II, and III**, receive input mainly from layer IV and are quite well developed in the secondary and tertiary areas of the cortex.
A map based on the organization, structure, and distribution of cortical cells is called a cytoarchitectonic map. One in wide use, known as Brodmann’s map, is shown in lateral and medial views in Figure 3.25A. In Brodmann’s map, the different areas are numbered, but the numbers themselves have no special meaning.

To perform his analysis, Brodmann divided the brain at the central sulcus and then examined the front and back halves separately, numbering new conformations of cells as he found them but without following a methodical path over the surface or through the layers. Thus, he named areas 1 and 2 in the posterior section, then switched to the anterior section and named areas 3 and 4, then switched back again, and then looked somewhere else.

The regions of Brodmann’s map correspond quite closely with regions discovered with the use of noncytoarchitectonic techniques, including electrical stimulation, tract tracing, and analysis of brain injury. Figure 3.25B summarizes some of the relations between areas on Brodmann’s map and areas that have been identified according to their known functions. For example, area 17 corresponds to the primary visual projection area, whereas areas 18 and 19 correspond to the secondary visual projection areas. Area 4 is the primary motor cortex. Broca’s area, related to the articulation of words, is area 44. Similar relations exist for other areas and functions.

One problem with Brodmann’s map is that new, more powerful analytical techniques have shown that many Brodmann areas can be further subdivided. For this reason, the map has been updated and now consists of a mixture of numbers, letters, and names.

(A) Lateral view
(B) Function Map code Brodmann area
Vision primary 17 18, 19, 20, 21, 37
primary secondary
Auditory primary 41 18, 19, 20, 21, 37
primary secondary
Body senses primary 1, 2, 3
primary secondary 5, 7
Sensory, tertiary 7, 22, 37, 39, 40
Motor primary 4 9, 10, 11, 45, 46, 47
primary secondary eye movement speech
Motor, tertiary 6

Figure 3.24
Layering in the Neocortex As this comparison of cortical layers in the sensory and motor cortices shows, layer IV is relatively thick in the sensory cortex and relatively thin in the motor cortex, whereas layers V and VI are relatively thick in the motor cortex and thin in the sensory cortex.

Figure 3.25
Mapping the Cortex
(A) Brodmann’s areas of the cortex. A few numbers are missing from the original sources of this drawing, including 12 through 15 and 48 through 51. (B) This table coordinates known functional areas and Brodmann cytoarchitectonic areas. (Part A after Elliott, 1969.)
Connections Between Various Regions of the Cortex

Connections Between Cortical Areas

The various connections between regions of the cortex are of functional interest because, as you know, damage to a pathway can have consequences as severe as damage to the functional areas connected by the pathway. A glance at Figure 3.26 shows that it is difficult indeed to damage any area of the cortex without damaging one or more of its interconnecting pathways. The various neocortical regions are interconnected by four types of axon projections:

1. Long connections between one lobe and another (Figure 3.26A)
2. Relatively short connections between one part of a lobe and another (Figure 3.26B)
3. Interhemispheric connections (commissures) between one hemisphere and the other (Figure 3.26C)
4. Connections through the thalamus

Most interhemispheric connections link homotopic points in the two hemispheres—that is, contralateral points that correspond to each other in the brain’s mirror-image structure. Thus, the commissures act as a zipper to link together the two sides of the brain’s representation of the world and of the body in it. The two main interhemispheric commissures are the corpus callosum and the anterior commissure (see Figure 3.26C).

The Crossed Brain

One of the most peculiar features of the brain’s organization is that each of its symmetrical halves responds mainly to sensory stimulation from the contralateral side of the body or sensory world and controls the musculature on the contralateral side of the body. The visual system, diagrammed in Figure 3.27, is illustrative.

For animals, such as the rat, with eyes located on the side of the head, about 95% of the optic fibers from one eye project to the opposite hemisphere. For primates, such as humans, having their eyes on the front of the head, about 50% of the optic fibers from each eye project to the opposite hemisphere. Thus, for both kinds of animals, visual pathways are arranged to ensure that each hemisphere gets visual information from the opposite visual field.
Figure 3.27

Crossed Neural Circuits (Left) The projection of visual and somatosensory input to contralateral areas of the cortex and the projection of the motor cortex to the contralateral side of a rat’s body. The rat’s eyes are laterally positioned, and so most of the input from each eye travels to the opposite hemisphere. (Right) In the human head, the two eyes are frontally placed. As a result, visual input is split in two, and input from the right side of the world as seen by both eyes goes to the left hemisphere, whereas input from the left side of the world as seen by both eyes goes to the right hemisphere. Somatosensory input of both rats and humans is completely crossed: information coming from the right paw or hand goes to the left hemisphere.

In a similar arrangement, about 90% of the fibers of the motor and the somatosensory systems cross over in the spinal cord. Projections from the auditory system go to both hemispheres, but there is substantial evidence that auditory excitation from each ear sends a stronger signal to the contralateral hemisphere.

As a result of this arrangement, numerous crossings, or decussations, of the sensory and motor fibers are found along the center of the nervous system. Functionally, the existence of these crossings means that damage to a hemisphere produces symptoms related to perception and movement related to the opposite side of the body. Recall that, for R.S., who suffered a stroke to the right cerebral hemisphere, impairments in movement were in his left leg and arm. Later chapters contain detailed descriptions of some of the decussations, when they are relevant to the discussion of how a given system works.

Summary

Neuroanatomy: Finding Your Way Around the Brain
The brain’s anatomy is organized but complex, and the names of its many structures provide a wonderland of nomenclature related to the rich history behind its description and determination of the functions of its parts.

Overview of Nervous System Structure and Function
The brain is protected by the skull and by the meninges that cushion it. It is also protected by a blood–brain barrier that excludes many substances from entry into neural tissue. The brain receives its blood supply from the internal carotid arteries and
the vertebral arteries and distributes blood through a number of arteries to specific brain regions.

The brain is composed of neurons and glial cells, each present in many forms. The brain is organized into layers, nuclei, and tracts, with the layers and nuclei appearing gray and the tracts appearing white on visual inspection. The visualization of brain anatomy in greater detail requires that tissue be stained to highlight differences in the biochemical structures of different groups of nuclei and tracts.

**Origin and Development of the Central Nervous System**

The developing central nervous system first consists of three divisions surrounding a canal filled with cerebrospinal fluid. In adult mammals, increases in the size and complexity of the first and third divisions produce a brain consisting of five separate divisions.

**The Spinal Cord**

The spinal cord communicates with the body through dorsal roots, which are sensory, and ventral roots, which are motor. The spinal cord is also divided into segments, each representing a dermatome, or segment, of the body. This segmentation and the dorsal-is-sensory and ventral-is-motor organization continue into the brainstem.

The cranial and spinal nerves of the somatic nervous system carry afferent sensory input to the central nervous system and transmit efferent motor output from the brain to the body. The autonomic nervous system acts either to activate (sympathetic nerves) or to inhibit (parasympathetic nerves) the body's internal organs.

**The Brainstem**

Hindbrain structures include the cerebellum, and its core contains the nuclei giving rise to the cranial nerves. The midbrain contains the superior and inferior colliculi (for vision and hearing) in its tectum (roof) and a number of nuclei for motor function in its tegmentum (floor). The diencephalon consists of the three thalamic structures: the epithalamus (including the pineal gland for biorhythms); the thalamus (for relaying sensory information); and the hypothalamus (which contains many nuclei for regulatory functions such as temperature, eating and drinking, and sexual activity).

**The Forebrain**

The forebrain consists of three functional regions: the basal ganglia, associated with motor coordination; the limbic system, associated with emotion and memory; and the neocortex, associated with sensory, motor, and cognitive functions.

The neocortex, or cortex, comprising about 80% of the adult human brain, consists of a large sheet of neurons organized into six layers. In the adult brain, the sheet is crinkled to form gyri and sulci. The cortex can be divided into functional regions and continues the spinal-cord organization, with motor functions in the front and sensory functions in the rear.

Individual lobes also can be associated with general functions: vision in the occipital lobe, audition in the temporal lobe, somatosensation in the parietal lobe, and movement in the frontal lobe. The lobes can be further subdivided into primary, secondary, and tertiary regions, each of which deals with more-complex and associative functions.

The cortex does not function in isolation from its subcortical structures but receives sensory information through the thalamus and works through the basal ganglia to produce movement and through the limbic system to organize emotion and memory.

**The Crossed Brain**

In the main, each hemisphere of the cortex responds to sensory stimulation on the side opposite that hemisphere and produces movements of the opposite side of the body.

**References**


