CHAPTER 3

Introduction to the Structure and Function of the Central Nervous System

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The human brain has been called the most complicated organization of matter in the known universe. Knowing the most important structures of the brain and their spatial relationships is important for understanding how the brain works. In addition, knowing how different structures are interconnected often provides valuable hints about how the activity of different brain areas is integrated to form a network that supports complex cognitive and emotional functions.

This chapter presents some basic information about the major structures of the nervous system and their interconnections, an area of study called ***neuroanatomy.*** *It also includes a general discussion of the relationship between structure and function, an area of investigation known as* ***functional neuroanatomy.***

GENERAL TERMINOLOGY

To understand neuroanatomy, you will need to know some general terminology. Many of the terms in neuroanatomy are actually Greek or Latin words. It is often useful to look up the literal translations of these words because many very imposing neuroanatomical terms end up having rather straightforward literal meanings. For example, the names of two structures in the brain, the substantia nigra and the locus ceruleus,

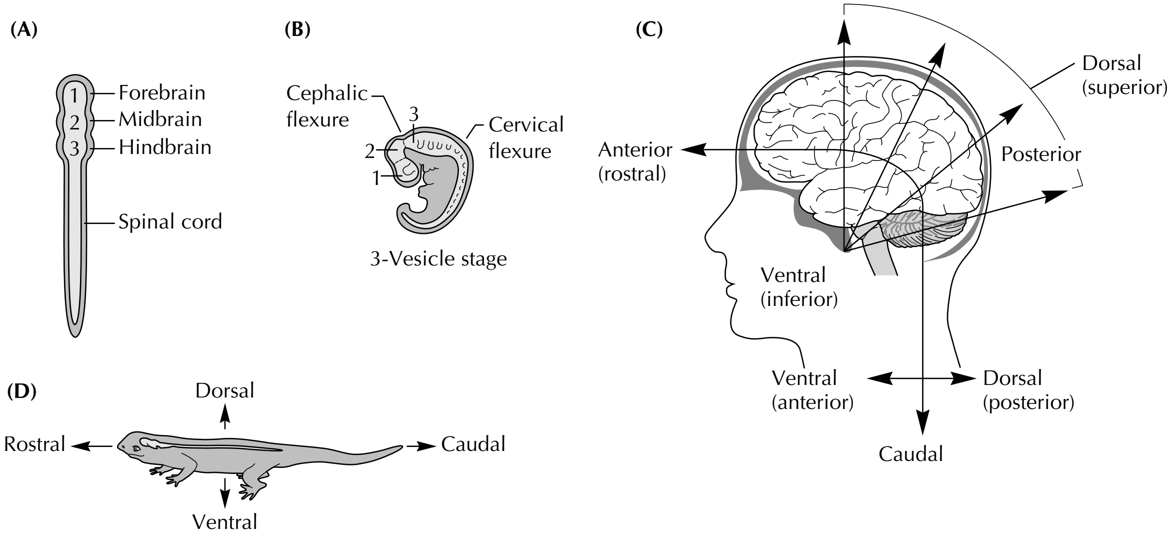


FIGURE 3.1 *(A)* The human brain develops from the embryonic neural tube, its rostral end giving rise to the brain and its caudal end becoming the spinal cord. *(B)* As it develops, the human nervous system flexes at the junction of the midbrain and the diencephalon. *(C)* Because of this flexure, the terms *dorsal* and *ventral* and the terms *anterior* and *posterior* refer to different directions when applied to the brain than to the brain stem and spinal cord. *(D)* In lower vertebrates the nervous system in organized in a straight line, and directional nomenclature is consistent throughout its length. *(From Kandel et al., 1995, p. 78)*

seemingly highly technical terms, translate from the Latin to "black stuff" and "blue place," respectively. Translating neuroanatomical terms makes them less mystifying and sometimes more memorable.

To find our way around the nervous system, we must first know some of the conventional terminology used in anatomy to indicate where a structure is located relative to other structures and relative to the whole brain. The most important terms are **superior** (above), **inferior** (below), **anterior** (front), **posterior** (behind), **lateral** (side), and **medial** (middle). With these six terms we can specify relative position within the three-dimensional framework of the brain and the body (Figure 3.1). Two or more of these terms can be combined to provide even more specific locations.

Although logically these terms are all we need to specify location in three dimensions, some additional terms are also used to denote relative location. Terminology differs to some extent when referring to the brain versus the brain stem and spinal cord. In the brain, the superior/inferior axis is often referred to as the **dorsal/ventral** (literally "back" and "belly," respectively) axis, whereas in the brain stem and spinal cord, *dorsal* (or posterior) refers to the direction toward the back and *ventral* (or anterior) the direction toward the front. In addition, in the brain stem and spinal cord, the direction toward the brain is referred to as **rostral** ("beak"); the direction away from the brain is referred to as **caudal** ("tail") (see Figure 3.1).

These terms originated from the study of the anatomy of four-legged animals, such as dogs. In these animals, the head and brain are aligned with the central axis of the body, so the bottom parts of the brain have the same position relative to the upper parts of the brain as the belly of the animal has to its back. A similar relationship holds for the rostral/caudal areas of the body and the anterior/posterior axis of the brain. If you imagine that you are down on all fours looking straight ahead, the dorsal/ventral and rostral/caudal axes will make sense in a way that they don't when you imagine yourself standing. This is because over the course of evolution (and of individual development) the proliferation of the forebrain has caused the human brain to bend forward 90° relative to the central axis of the body (see Figure 3.1).

Because these terms indicate the location of structures relative to other structures, it is possible for a structure in the anterior portion of the brain to be posterior to a structure that is even further anterior, just as Greenland, north relative to most of the rest of the world, is south of the North Pole. In addition, these terms are used to denote different areas within a single structure. For example, the names of various areas within the thalamus, an egg-shaped structure, are derived from this nomenclature, as illustrated by the dorsomedial nucleus and the ventrolateral nucleus.

The terms **contralateral** (opposite side) and **ipsilateral** (same side), which we encountered in chapter 1, are used to designate the side of the body or brain on which a structure or connection occurs in relation to a reference point. For example, although about 90% of the fibers originating in the motor cortex of one cerebral hemisphere cross over to the contralateral side of the body, about 10% do not cross over and thus form ipsilateral connections. When structures or connections occur on both sides of the body, they are said to be **bilateral. Unilateral** refers to a structure or connection on only one side of the body.

The term **afferent** (from the Latin *ad* + *ferre*, "to carry inward"), encountered in chapter 1, refers to neural input feeding into a structure. Conversely, the term **efferent** (from the Latin *ex* + *ferre*, "to carry outward") denotes neural output leaving a structure. As with the other directional terms we have already discussed, these are relative terms. The same fiber tract will be efferent to one structure and afferent to another. For example, the fornix, an arching fiber tract deep within the base of the forebrain that conveys information from the hippocampus to the hypothalamus, is a hippocampal efferent and a hypothalamic afferent.

Finally, several terms are used to describe the different planes of anatomical section (cut) along which the brain can be dissected or visualized (Figure 3.2). These planes are typically seen in photographs and diagrams of the brain. **Sagittal** sections (from the Latin *sagitta*, "arrow") divide the brain into right and left parts. **Coronal** sections (from the Latin *coronalis*, "crown") divide the brain into anterior and posterior parts. These are also called **frontal** sections. By convention, sections in this plane are viewed from behind, so that the left side of the section is the left side of the brain. **Horizontal** (or **axial**) sections divide the brain into upper (superior) and lower (inferior) parts. Again, by convention, sections in this plane are typically viewed from above.

AN OVERVIEW OF THE CENTRAL NERVOUS SYSTEM

The Central and Peripheral Nervous Systems

The most basic structural subdivisions of the human nervous system are the **central nervous system (CNS)** and the **peripheral nervous system (PNS).** The central nervous system consists of the brain and spinal cord, and the peripheral nervous system consists of the sensory and motor nerves that are distributed throughout the body and that convey information to and from the brain (via 12 pairs of cranial nerves) and the spinal cord (via 31 pairs of spinal nerves). The peripheral nervous system is divided into the somatic nervous system and the autonomic nervous system. The **somatic nervous system** is the part of the PNS that innervates the skin, joints, and skeletal muscles. The **autonomic nervous system (ANS)** is the part of the PNS that innervates internal organs, blood vessels, and glands. Each of these systems has related motor and sensory components. The **somatic motor system** includes skeletal muscles and the parts of the nervous system that control them; the **somatosensory system** involves the senses of touch, temperature, pain, body position, and body movement. The autonomic nervous system also has a motor component, sending motor output to regulate and control the smooth muscles of internal organs, cardiac muscle, and glands (**autonomic motor**). The autonomic nervous system also includes sensory input from these internal structures that is used to monitor their status (**autonomic sensory**). The major sensory modalities other than touch (vision, audition, smell, and taste) are sometimes referred to as **special sensory.**

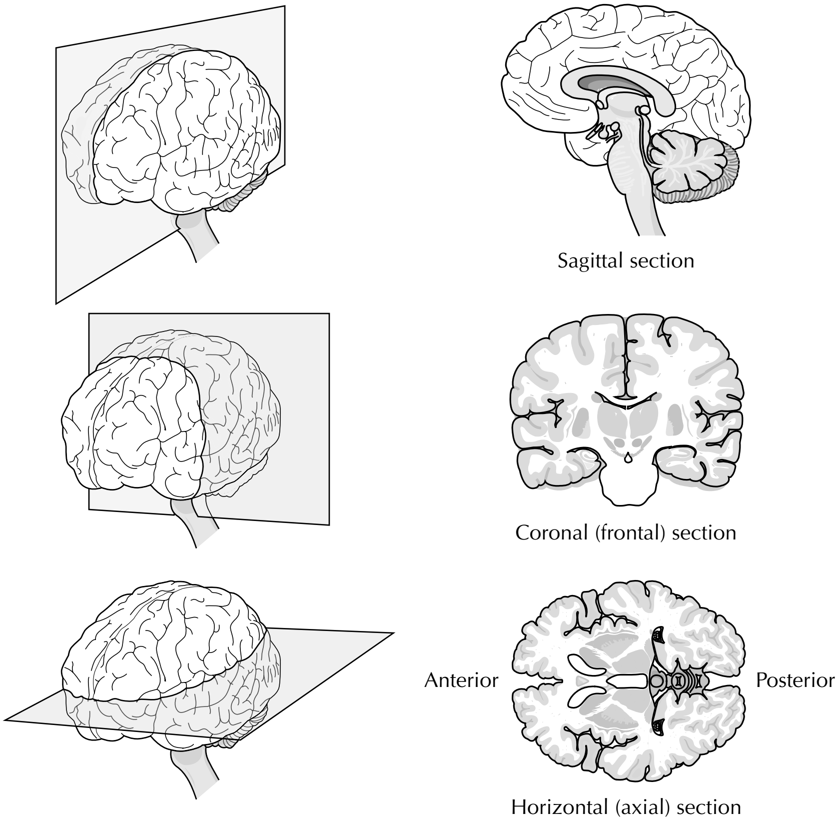


FIGURE 3.2 Terms used to describe the planes of section (cut) through the brain. *(From Rosenzweig & Leiman, 1989, p. 29)*

Major Divisions of the Brain

The brain is divided into three parts: the **forebrain (prosencephalon),** the **midbrain (mesencephalon),** and the **hindbrain (rhombencephalon)** (Table 3.1 and Figure 3.3). The forebrain includes the **cerebral cortex, basal ganglia, limbic system** (together making up the **telencephalon**), and **diencephalon.** The midbrain and hindbrain together constitute the **brain stem,** with the hindbrain being further subdivided into the **pons** and **cerebellum (metencephalon)** and the **medulla oblongata (myelencephalon).** The medulla oblongata is often called simply the medulla.

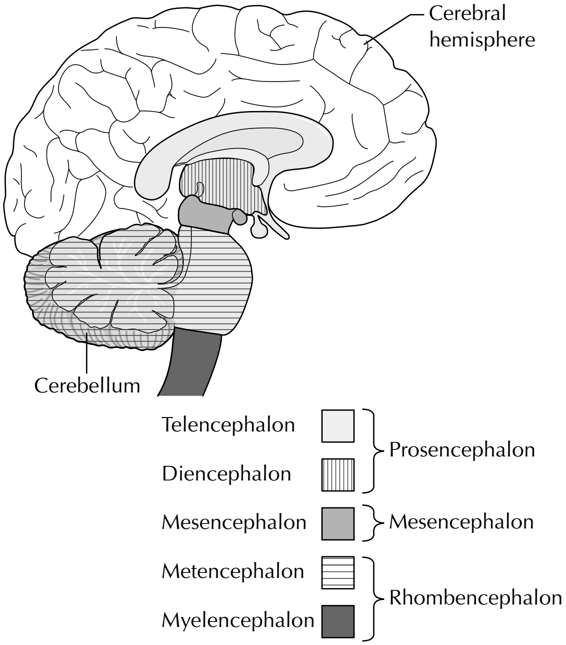
In the course of evolution (and recapitulated in the course of individual human fetal development) these divisions developed from the enlargement of the rostral end of the primordial neural tube. In this process, the most rostral region expanded to become the forebrain, with its two subdivisions, the telencephalon and the diencephalon, while more caudal regions expanded to become the hindbrain, with its two subdivisions, the pons (including the cerebellum) and the medulla. We consider each of these divisions in the remainder of this chapter, working from the most rostral to the most caudal, and end with a discussion of the spinal cord. First, however, we consider some general aspects of the brain.

The Meninges

The brain and the spinal cord are encased in three layers of protective membrane, the dura mater, the arachnoid, and the pia mater (Figure 3.4). These are collectively called the **meninges.** The outermost layer, the **dura mater** (Latin for “hard mother”), is a tough, inelastic membrane following the contour of the skull. Between the dura mater and the pia mater is the **arachnoid membrane** (Greek for “spider,” re-

Table 3.1 Major Divisions of the Brain

Primitive Brain Divisions	Mammalian Brain Divisions	Regions of Human Brain	Alternative Terminology
Forebrain (prosencephalon)	Telencephalon	Neocortex Basal ganglia Lateral ventricles	Forebrain
	Diencephalon	Limbic system Thalamus Epithalamus Hypothalamus Pineal body Third ventricle	Brain stem
Midbrain (mesencephalon)	Mesencephalon	Tectum Tegmentum Aqueduct of Sylvius	
Hindbrain (rhombencephalon)	Metencephalon	Pons Cerebellum Fourth ventricle	
	Myelencephalon	Medulla oblongata Fourth ventricle	



◀ **FIGURE 3.3** The major divisions of the human brain. *(From Kolb & Whishaw, 1996, p. 43)*

ferring to its weblike structure). This consists of two layers of fibrous and elastic tissue and does not follow the sulci and gyri of the cortex. Between the two layers of the arachnoid membrane is the **subarachnoid space,** a spongy structure containing **cerebrospinal fluid (CSF).** The innermost membrane, the **pia mater** (Latin for "pious mother"), adheres to the surface of the cortex, following the contours of its foldings and fissures.

The Cerebral Ventricles

The brain has four cavities filled with cerebrospinal fluid called **cerebral ventricles** (from the Latin for "stomach"). They are portions of the phylogenetically ancient neural canal that enlarged and changed their shape as a result of the massive expansion of

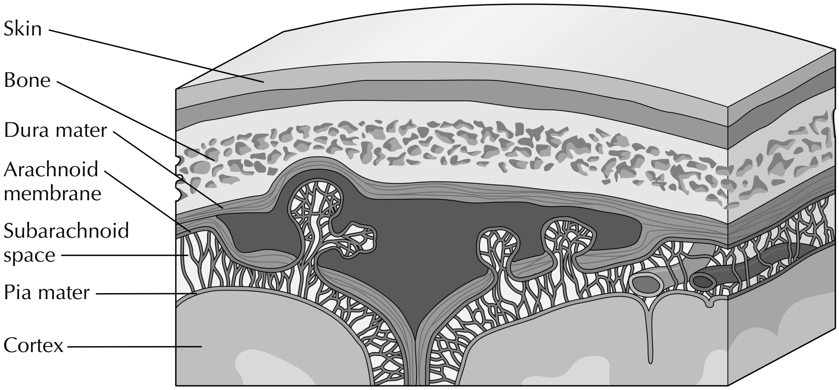


FIGURE 3.4 The membranes surrounding the brain, collectively termed the meninges. *(From Netter, 1974, p. 35)*

the forebrain in the course of evolution. This process has caused the ventricles to have a rather complicated shape (Figure 3.5).

There are two **lateral ventricles** (one in each hemisphere), the **third ventricle** in the diencephalon and the **fourth ventricle** in the hindbrain. Each ventricle contains a tuft of capillary vessels, called a **choroid plexus,** through which CSF enters the ventricles. Narrow channels connect all four ventricles, and CSF circulates through the lateral ventricles to the third and then to the fourth ventricle. From the fourth ventricle CSF leaves the ventricular system and circulates around the surface of the brain and spinal cord in the subarachnoid space. From there CSF is eventually absorbed into the venous circulation.

The brain is thus surrounded by CSF. This provides it with structural support (much as our body is supported by the water we swim in) and also with an added measure of protection from the effects of a blow to the head. If the circulation of CSF through the ventricles is blocked at one of the narrow channels that interconnect them, fluid builds up in front of the blockage. This condition, known as **hydrocephalus** (from the Greek for "water" + "brain"), is serious because as CSF accumulates it displaces and kills neighboring neurons.

Although, as mentioned in chapter 1, in medieval times the ventricles were thought to be directly involved in cognitive function, it is now recognized that there is no evidence that this is the case. They may, however, contain neuroactive molecules that exert some influence over brain function. In our discussions the cerebral ventricles will serve most often as descriptive reference points for location within the brain.

Gray Matter and White Matter

Parts of the central nervous system appear gray or white depending on the parts of the neuron that they contain (Figure 3.6). Where there is a concentration of cell bodies, the tissue appears gray. These areas, known as **gray matter,** have this color because the cell bodies contain the nucleus of the cell, which, in turn, contains darkly colored genetic material called chromatin. Gray matter is where almost all interactions between neurons take place, processes that underlie the complex functioning of the CNS.

Tissue containing axons, the extended part of the nerve cell, appears white because of the fatty myelin sheath surrounding each axon. As we saw in chapter 2, axons convey information from one area of the CNS to another. A large number of axons bundled together and conveying information from one region of gray matter to another is called a **tract** or **fiber tract** (from the Latin *tractus,* "extension" or "track").

The most elaborate concentration of cell bodies in the brain is arranged in a massive sheet, the **cerebral cortex.** In addition to the cortex, there are other concentrations of cell bodies in the central nervous system. Each of these is called a **nucleus** (plural, **nuclei**), not to be confused with the nucleus of an individual cell. The term nucleus is derived from the Latin word for "nut," reflecting the nutlike shape of many of

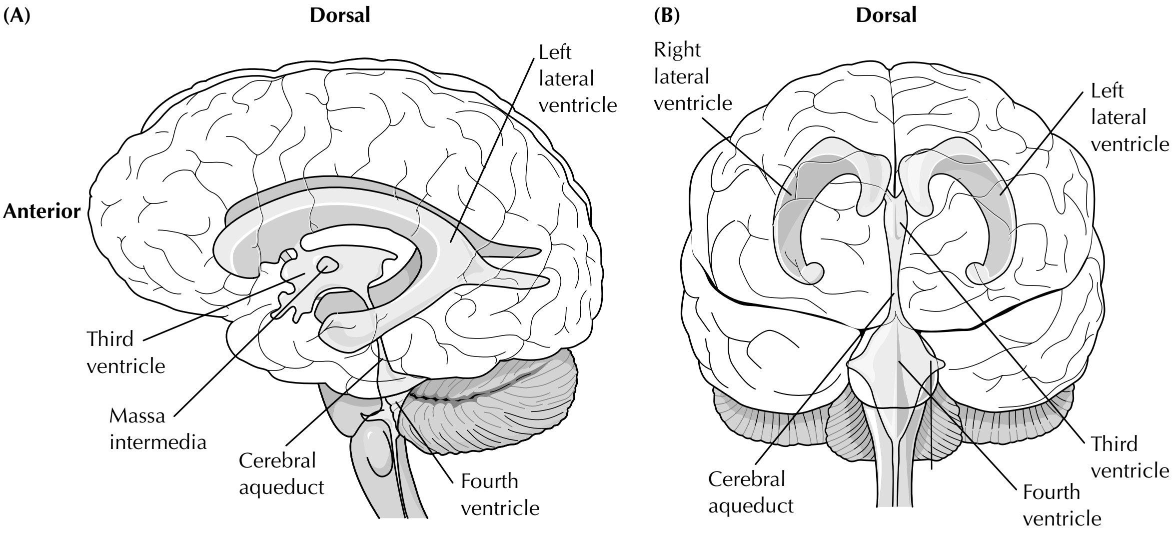


FIGURE 3.5 The cerebral ventricles. *(A)* Lateral view of the left hemisphere. *(B)* Frontal view. *(From Carlson, 1999, p. 63)*

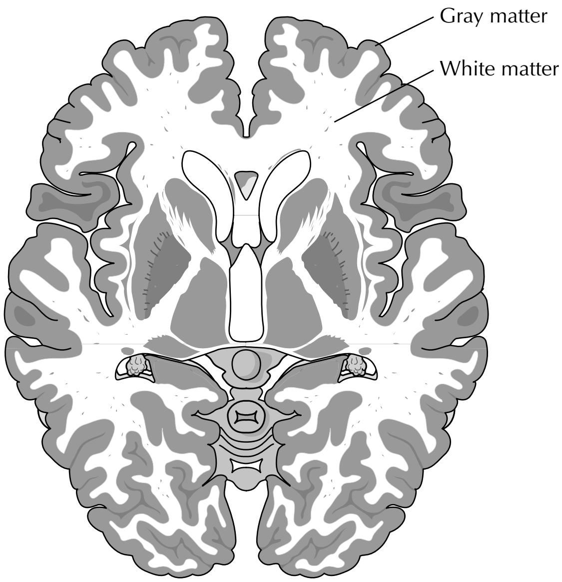


FIGURE 3.6 Horizontal section through the cerebral hemispheres showing gray matter and white matter. In addition to the cerebral cortex, the continuous enfolded sheet of gray matter on the surface of the cerebral hemispheres, this section also shows groups of gray-matter structures located deep within the hemispheres. *(From DeArmond, Fusco, & Dewey, 1974, p. 10)*

these clumps of cell bodies. Nuclei come in various sizes and shapes, ranging from the small and roughly spherical brain-stem nuclei (e.g., the abducens nucleus in the pons) to those that are relatively large and exotically shaped, such as the long, arching caudate nucleus in the forebrain.

Concentrations of cell bodies outside the central nervous system are called **ganglia** rather than nuclei. However, the inconsistent processes of naming and identifying structures have generated several exceptions to this general guideline. Thus, for example, a large and important group of gray-matter structures deep within the forebrain is collectively called the **basal ganglia.**

THE FOREBRAIN

The structures most identified with higher cognitive function are found in the forebrain. Foremost among these is the cerebral cortex.

The Cerebral Cortex

The cerebral cortex, forming the outer covering of the cerebral hemispheres (*cortex* comes from the Latin

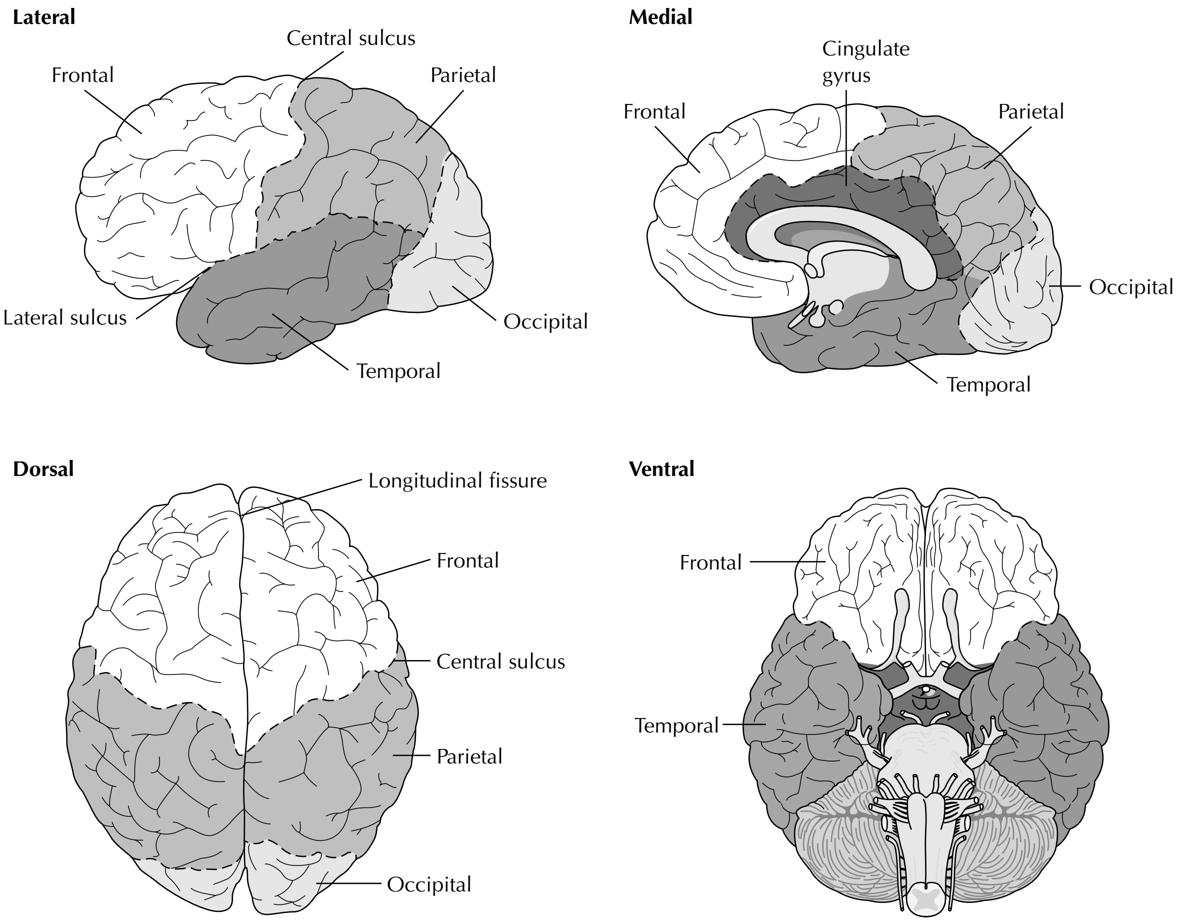


FIGURE 3.7 The four lobes of the cerebral hemispheres, as seen from the lateral, medial, dorsal, and ventral views. The central sulcus is the dividing line between the frontal and parietal lobes. The boundaries between the other three lobes are not precisely defined. Cortex in these border areas is often described in terms of the two adjacent lobes, thus generating such terms as parieto-occipital and parietotemporal. The cingulate gyrus (dark area on the medial surface) is usually identified specifically, rather than being classified as part of any of the four lobes. *(From Kolb & Whishaw, 1996, p. 52)*

word for “bark”) is truly vast, particularly in humans, where it is estimated to contain 70% of all the neurons of the CNS. And if one considers that the medulla oblongata—with a diameter little more than that of a dime and a length of only a few inches—can mediate physiological functioning sufficient to sustain life, the relative enormity of the cerebral cortex, estimated to have an area of about 2,300 square centimeters (cm^2), can be appreciated.

THE FOUR LOBES Each cerebral hemisphere is traditionally divided into four lobes: the **occipital, parietal, temporal,** and **frontal lobes** (Figure 3.7). These areas, taking their names simply from the bones of the skull that overlie them, were defined long before anything significant was known about the functional specialization of the cerebral cortex. Nevertheless, it turns out that these general areas are often useful in describing areas of the cortex that are

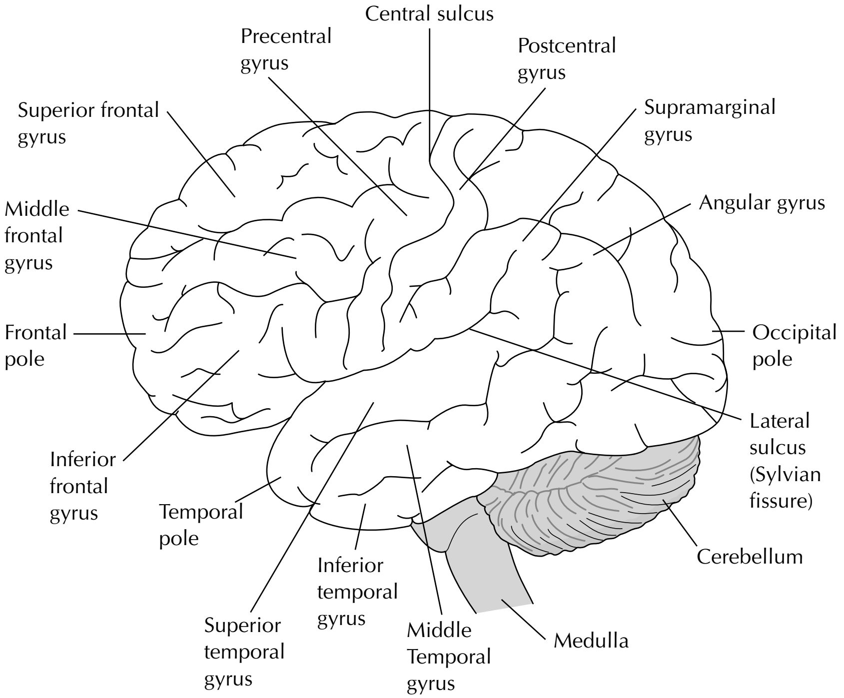


FIGURE 3.8 Lateral view of the left hemisphere, showing some major gyri and sulci. *(From DeArmond et al., 1974, p. 4)*

involved in particular behaviors. Because we will most often be considering functions mediated by the cortex, we will frequently use the names of these lobes to specify cortical location.

MAJOR CORTICAL FEATURES The characteristic folding of the cortex, which allows the enormous cortical surface to fit in the relatively small space enclosed by our skull, creates deep furrows or grooves on its surface. Each of these is called a **sulcus** (plural, **sulci**) and a few of the deeper ones are called **fissures.** Each outfolding is called a **gyrus** (plural, **gyri**). Some of the more important of these features, together with some major brain structures, are shown in Figures 3.8, 3.9, and 3.10.

THE LAYERED ORGANIZATION OF THE CORTEX The vast majority of cerebral cortex in humans has six layers: five layers of neurons and an outermost layer of fibers, termed the **plexiform layer.** This six-layered cortex, which appeared relatively late in evolution, is called **neocortex.** It is also termed **isocortex** (from the Greek *iso*, meaning "same") because all of it is composed of six layers, although, as we will see shortly, the relative thickness of the different layers varies across the cortex. Areas of cortex with fewer than six layers are known as **allocortex** (from the Greek *allos*, meaning "other"). Allocortex has two major components, paleocortex and archicortex. **Paleocortex** includes olfactory cortex and has only two layers. **Archicortex** has only one layer and is found in areas of the hippocampus, including Ammon's horn and the dentate gyrus.

VARIATIONS IN CORTICAL LAYERS: CYTOARCHITECTONICS The relative thickness and cell composition of each of the six cortical layers varies across the neocortex, with different areas of the neocortex having characteristic patterns. The study of these patterns, called **cytoarchitectonics** (literally, "cell architecture"), was begun in the early 20th century. The two most widely accepted cytoarchitectonic

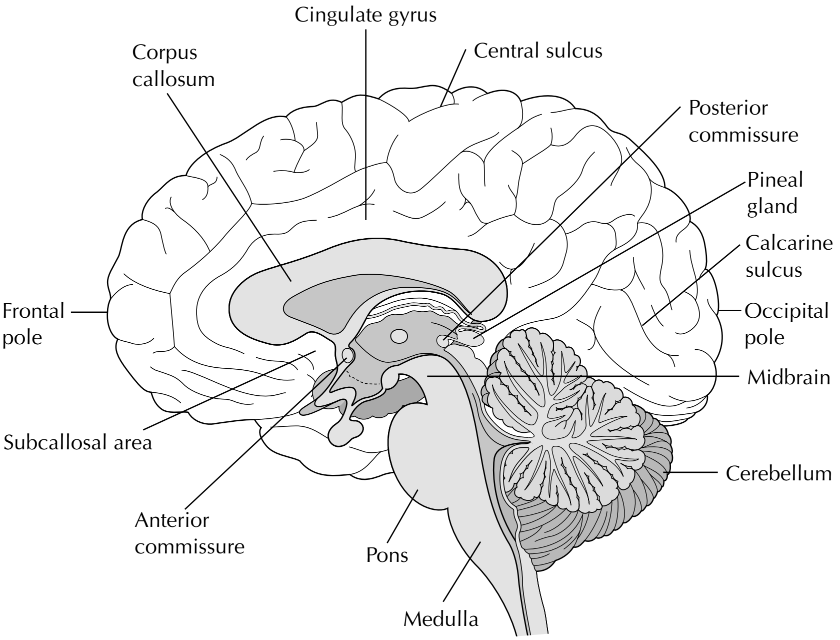


FIGURE 3.9 Medial view of the right hemisphere, showing some important gyri and sulci and the major divisions of the brain stem. *(From DeArmond et al., 1974, p. 8)*

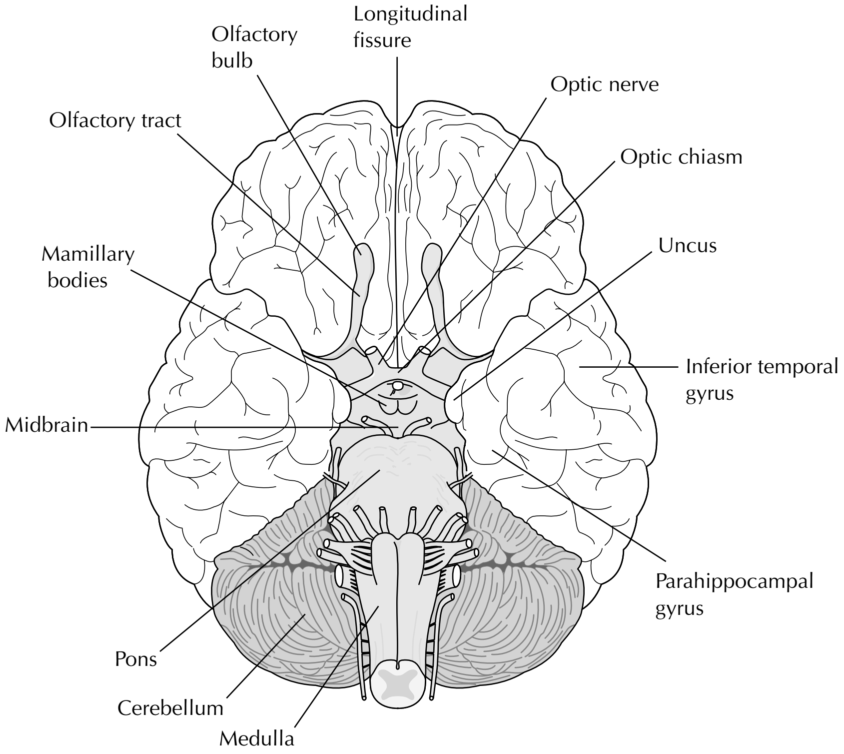


FIGURE 3.10 Ventral view of the brain, showing some important cortical features and brain-stem structures. *(From DeArmond et al., 1974, p. 6)*

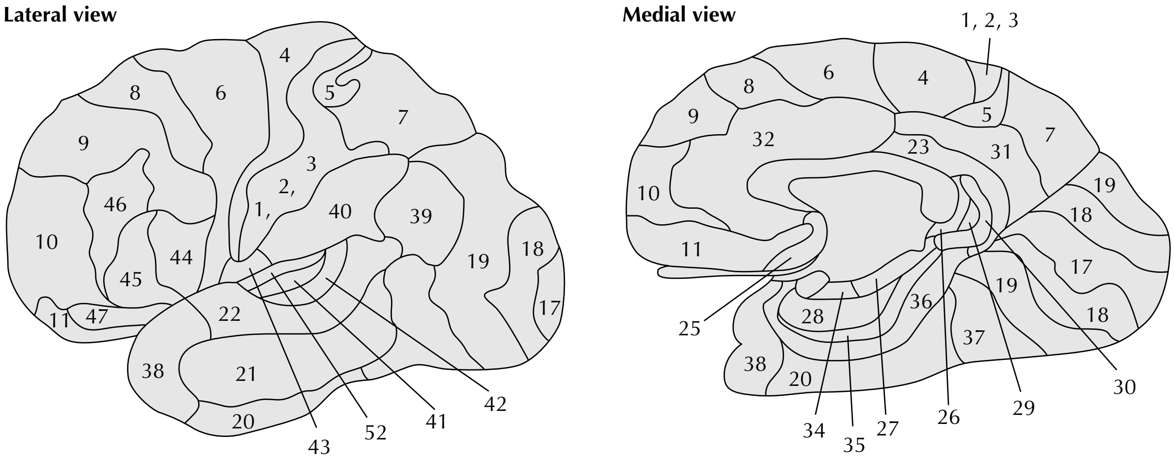


FIGURE 3.11 The most generally accepted cytoarchitectonic map of the cerebral cortex, developed by Korbinian Brodmann in 1909. *(From Nauta & Feirtag, 1986, p. 301)*

maps of the cortex are those developed by Korbinian Broadmann (Figure 3.11) and by von Economo and Koskinas. Broadmann's map is used most widely. The two systems have a fair amount of agreement, and yet they also differ significantly. This disagreement indicates that there is a significant amount of interpretation implicit in cytoarchitectonics, as there is in the development of any system of classification. The Broadmann numbering system is often used simply to identify a particular area of cortex, such as area 17 at the occipital pole of the cerebral hemispheres. It turns out that there is significant correspondence between areas defined by cytoarchitectonic studies and areas identified as having specialized function by other methods. Area 17, for example, turns out to be the primary visual cortex. This and other correspondences suggest that at least some of the areas defined by Broadmann are also areas specialized for particular psychological processes, although this is not always the case.

CORTICOCORTICAL FIBER CONNECTIONS Let's now consider the interconnections between cortical areas, termed **corticocortical connections.** Some of these intracortical connections are short, the fibers taking a U-shaped course that connects adjacent gyri. Others are very long, connecting distant parts of the cortex within the same hemisphere **(ipsilateral corticocortical fibers).** Other long fibers connect **homotopic fields** (corresponding areas) in the right and left hemispheres **(cortical commissural fibers).**

Ipsilateral Corticocortical Fibers Figure 3.12 shows the major ipsilateral corticocortical fibers including the **arcuate fasciculus,** the **uncinate fasciculus,** the **superior longitudinal fasciculus,** the **inferior longitudinal fasciculus,** the **cingulate fasciculus,** and the **superior occipitofrontal fasciculus.**

Commissural Fibers The most prominent example of cortical commissural fibers, the fiber tracts connecting the left and right hemispheres, is the **corpus callosum** (Figure 3.12A; see also Figure 3.9). There are, however, other commissural fibers connecting the two hemispheres. These include the **anterior commissure** and the **posterior commissure** (see Figure 3.9). In chapter 1 we saw how knowledge of corticocortical connections can provide a conceptual framework for understanding patterns of cognitive impairment in terms of the disconnection of brain areas, that is, as disconnection syndromes.

FUNCTIONAL DIVISIONS OF THE CORTEX The major functional divisions of the cerebral cortex are shown schematically in Figure 3.13. In this section we briefly review these divisions.

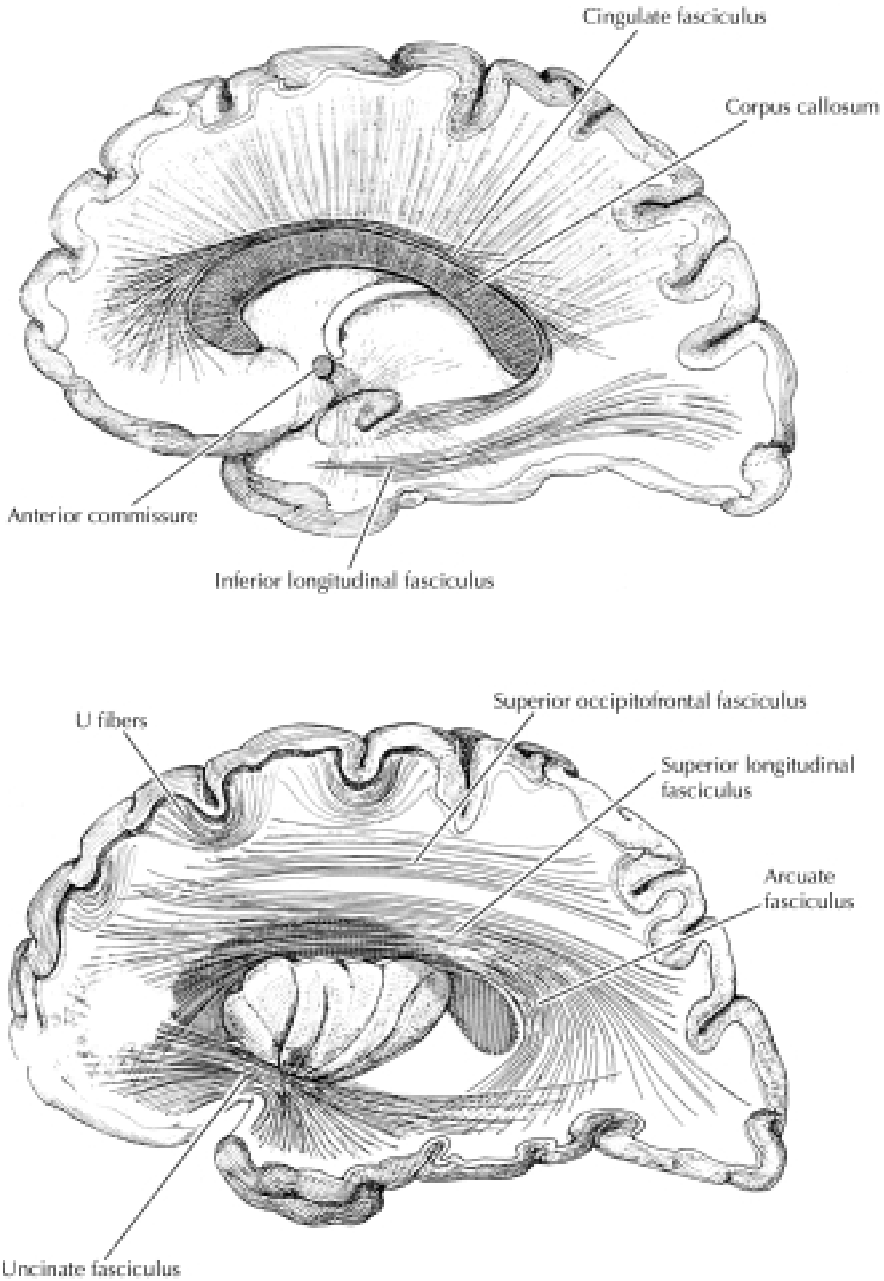


FIGURE 3.12 Some major commissural fibers and ipsilateral corticocortical fibers linking neocortical areas. *(A)* A sagittal cut made near the midline showing the two most important commissural fibers linking the two hemispheres: the corpus callosum and the anterior commissure. *(B)* A more lateral sagittal cut showing the major ipsilateral corticocortical fibers. *(From Nauta & Feirtag, 1986, p. 304)*

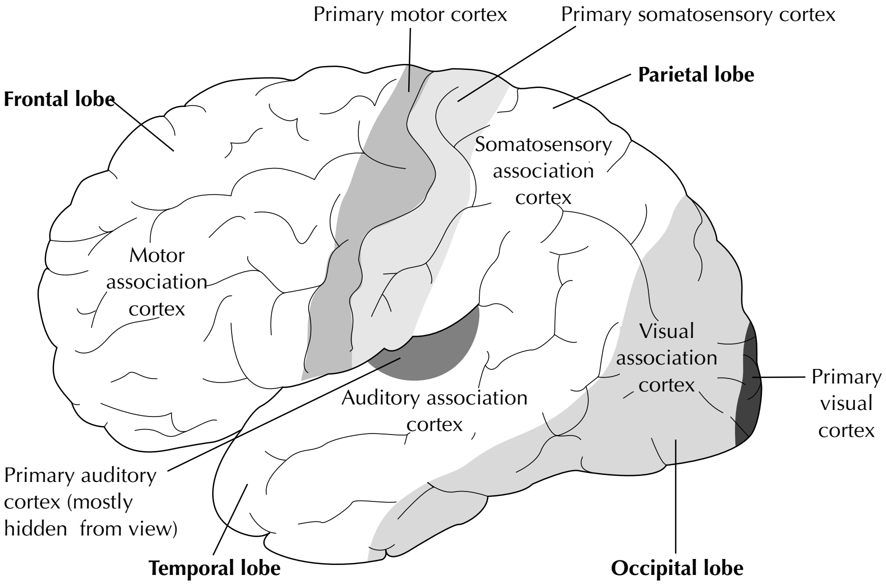


FIGURE 3.13 The main functional divisions of the cortex as seen from a lateral view. Note that most of the primary visual cortex is on the medial surface of each cerebral hemisphere, and so only the small lateral portion is visible in this figure. *(From Carlson, 1998, p. 69)*

Motor Cortex The frontal lobes play a major role in the planning and execution of movement. The **precentral gyrus,** just anterior to the **central sulcus,** is known as the **motor strip, motor cortex,** or **M1** and is involved in the execution of movement. Lesions of the motor cortex result in a loss of voluntary movement on the contralateral side of the body, a condition known as **hemiplegia.** Electrical stimulation of this cortex reveals a complete motor representation of the body on the precentral gyrus, the so-called **motor homunculus** ("little man"; Figure 3.14). Such mapping of a neural structure in terms of associated behaviors is called a **functional map.** There are many functional maps in the cortex and in other brain regions.

Just anterior to the motor cortex are the **premotor area,** on the lateral surface of the hemisphere, and the **supplementary motor area,** on the medial surface. These areas are involved in the coordination of sequences of movement. Frontal areas anterior to the premotor cortex, the **prefrontal cortex,** are involved in the higher-order control of movement, including planning and the modification of behavior in response to feedback about its consquences.

Somatosensory Cortex The **somatosensory cortex,** or **SI,** in the **postcentral gyrus** of each hemisphere receives sensory information from the contralateral side of the body about touch, pain, temperature, vibration, **proprioception** (body position), and **kinesthesis** (body movement). As with the motor cortex, there is an orderly mapping of the body surface represented on the postcentral gyrus, a mapping termed the **sensory homunculus.** Ventral to SI is the **secondary somatosensory cortex,** or **SII,** which receives input mainly from SI. Both SI and SII project to posterior parietal areas where higher-order somatosensory and spatial processing take place.

Information from sensory receptors in the body arrives at SI via two major systems, both relaying through the thalamus. The **spinothalamic system** conveys information about pain and temperature via a multisynaptic pathway, whereas the **lemniscal system** conveys more precise information about touch, proprioception, and movement via a more direct pathway. A comparison of the anatomy and function of these two systems exemplifies how different patterns of neuroanatomical interconnection underlie

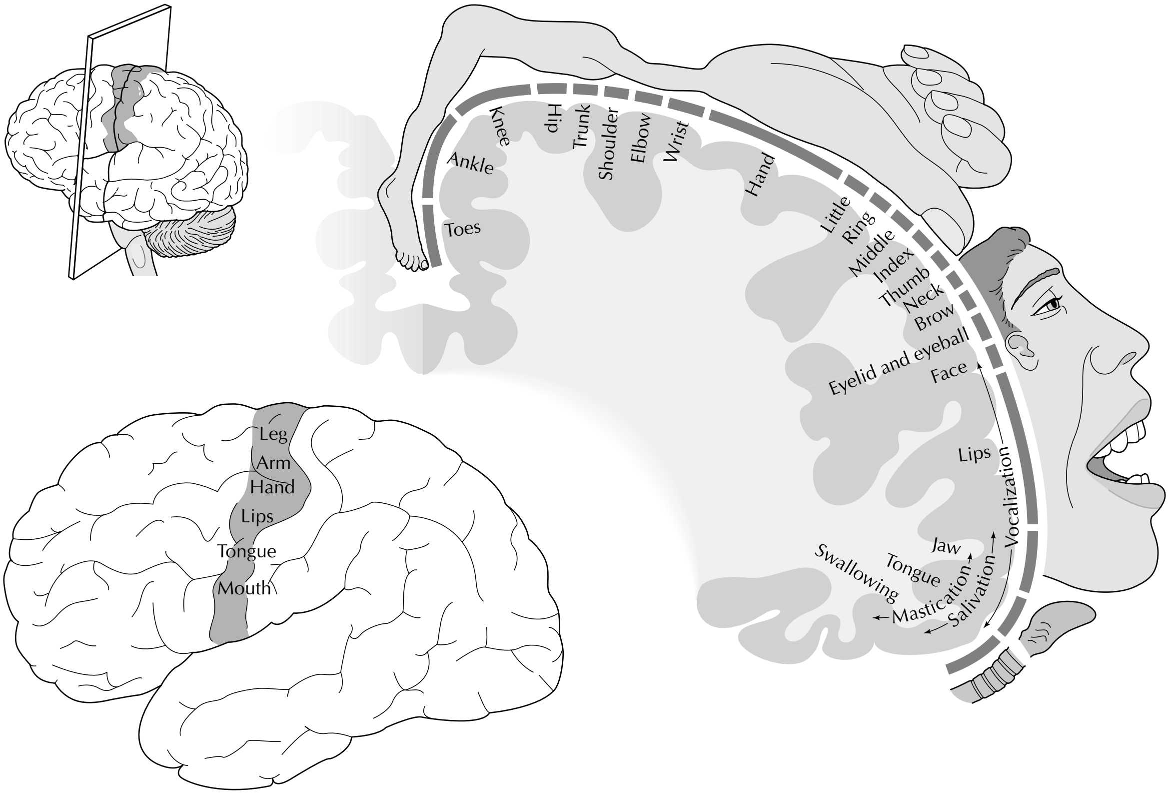


FIGURE 3.14 The motor homunculus on the precentral gyrus. The motor cortex can be seen in the lateral view of the cerebral cortex. *(From Netter, 1974, p. 68)*

specialization of function, a correspondence that we will find throughout the nervous system.

Visual Cortex Visual information is conveyed from the retina to the **lateral geniculate nucleus** of the thalamus before being projected to the banks of the **calcarine sulcus** in the occipital lobes (see Figure 3.9). This route is called the **primary visual pathway,** and its initial cortical destination in the calcarine sulcus is known by several names, including the **primary visual cortex, V1,** and **striate cortex.** The last term is derived from the fact that a thin "thread" (Latin *stria*) of dark tissue is visible in layer IV of this cortical region. As we noted earlier, the primary visual cortex is also known by the area of Brodmann's cytoarchitectonic map corresponding to it: area 17.

The cortical visual system is organized analogously to the somatosensory system in that there is a contralateral relationship between the side (right-left) of the body that is stimulated (or, in the visual system, the side of space in which a stimulus appears) and the hemisphere to which the input is projected. Thus, stimuli from the right side of space (actually stimulating the left side of the retina because of right-left reversal caused by the lens of the eye) are projected to the left hemisphere. Therefore a lesion in the left visual cortex will result in a loss of vision in the right visual field, an impairment known as right **hemianopia** (literally, half-not-seeing).

The cortical visual system supports such critical functions as visual acuity, pattern vision, shape discrimination, and figure-ground discrimination.

Damage to the cortical visual system results in **cortical blindness.** This is experienced as complete blindness, just like that resulting from damage to the two eyes. These patients thus experience no knowledge of their immediate visual world. Nevertheless, unlike in blindness due to damage to the eyes, some residual visual functioning can be demonstrated in cortical blindness. We will discuss this residual function later in this chapter.

Surrounding V1 is cortex known as **extrastriate cortex** ("outside the striate"). It is also sometimes termed **prestriate cortex,** referring to the fact that it is anterior to the striate cortex, or **visual association cortex.** Literally dozens of visual areas have been discovered in extrastriate cortex, each with its own topographically organized map of visual space. These are specialized for the processing of specific aspects of the visual world. Some of these visual areas will be discussed in greater detail in chapter 5.

In addition to the primary visual pathways, there are several secondary visual pathways. The most important of these are the direct retinal projections to the superior colliculus in the midbrain, a structure involved in the mediation of visuomotor coordination. There are also direct retinal projections to the hypothalamus in the diencephalon, which are involved in the process of entrainment of light-dark activity cycles.

Auditory Cortex The **primary auditory cortex (AI)** and the **auditory association cortex (AII)** surrounding it are located in **Heschl's gyrus** in the lower lip of the Sylvian fissure in each temporal lobe (see Figure 3.13). These regions of auditory cortex contain several orderly representations of sound frequency, known as **tonotopic maps,** and are important for the perception of such auditory properties as pitch, location, rhythm, and timbre.

As mentioned in chapter 1, input reaches the auditory cortex in an unusual way. As we have seen, in vision and somesthesis (body sense) there is an orderly contralateral relationship between the side of space from which a stimulus originates and the cerebral hemisphere to which input is projected. This exclusive contralaterality of direct input is not the case in the auditory system. Instead, efferents from the **cochlear nucleus,** the synaptic destination of the **auditory nerve,** cross the midline to form connections with the contralateral cochlear nucleus, as well as continuing ipsilaterally. These fibers course to the **superior olive** and then to the **inferior colliculus.** At each of these levels fibers also cross to the corresponding structure on the contralateral side of the brain stem. From the inferior colliculus these fibers reach the **medial geniculate nucleus** of the thalamus and from there project, via the **auditory radiations,** to the **auditory cortex** in the ipsilateral temporal lobe.

The result of all this crossing over at several levels of the auditory system is that each ear projects to both hemispheres and each hemisphere receives projections from both ears. This pattern of connectivity explains why damage to one auditory cortex does not produce noticeable impairment (as an analogous unilateral lesion in the visual or somatosensory cortex would), although, as we will see in chapter 4, special tests can detect a mild impairment in such cases. It also explains why **cortical deafness** (deafness due to cortical damage) is extremely rare. Such a condition would require damage to both auditory cortices. Because of the widely separated locations of the cortices in the right and left temporal lobes, such a pair of lesions is extremely rare, although cases of cortical deafness have been reported.

Olfactory Cortex The cortical representation for smell is different from that of the three major sensory modalities just discussed. First, rather than being derived from the **transduction** of a specific form of energy into a pattern of neural impulses, as is the case in somesthesis, vision, and audition, olfactory input to cortex is derived from the coding of the presence of particular molecules in the environment of the organism. In addition, although input from each of the three major sensory modalities is relayed to the thalamus before reaching its respective primary cortical area, olfactory information gains access to the olfactory cortex on the ventral surface of the frontal lobes directly, without thalamic mediation. It has been suggested that the directness of this cortical input contributes to the emotional intensity so often associated with olfactory experience.

The Cortical Representation for Taste The cortical representation for taste is the least understood of all cortical sensory areas. Its precise location is unclear, but it is thought to be in the upper lip of the Sylvian fissure. Like the three major sensory modalities, and unlike olfaction, information initially coded in taste buds on the tongue and on neighboring areas reaches its cortical destination after synapsing in the thalamus.

Association Cortex **Association cortex** is traditionally defined as areas of cortex that do not mediate elementary sensory or motor function. This term connotes that elaborate associative or cognitive processes are mediated by these areas, including the higher-order processing of sensory information that underlies perception and the higher-order planning and organization underlying complex behavior. Although in some general sense this is accurate, it is now clear that specific areas within what had been termed association cortex have highly specialized functional roles. As a result, the sketchy notion of association cortex has given way to a more delineated picture of the contribution made by specific cortical areas to higher-order processing. For example, it is now clear that areas outside V1 and extrastriate cortex, in the parietal and temporal lobes, although not involved in the early stages of visual processing, are critical for the perception of specific aspects of the visual world. Similarly, prefrontal cortex, not directly involved in the execution or coordination of specific movements, is critical to the higher-order organization of action, including planning and the regulation of behavior in response to feedback about ongoing behavior. The language areas also exemplify the more specific identification of the functional characteristics of areas not involved in elementary sensory or motor processing.

LURIA'S MODEL OF SEQUENTIAL HIERARCHICAL CORTICAL PROCESSING The Soviet neuropsychologist Aleksandr Luria (1902–1977) has proposed a model for cortical processing. Although in certain respects it is highly oversimplified, retaining, for example, the vague notion of association cortex, it nevertheless serves as a useful framework for thinking about cortical processing. According to Luria's model, each of the major primary sensory projection areas of the cortex (somatosensory, visual, and auditory) projects to a neighboring area of cortex for further processing. These areas are known as the **sensory association area** or **secondary sensory area** for the particular modality in question. For example, the visual association area is a ring of cortex on the lateral and medial surface of the hemisphere adjacent to the primary visual cortex in the occipital lobes. Whereas lesions in a primary sensory projection area are associated with impairments in elementary sensory function, such as visual acuity, lesions to sensory association areas result in impairments in higher-order perceptual processes that are termed **agnosias.** Agnosia can take different forms depending on the sensory modality affected and on other factors. We will consider visual agnosia in greater detail in chapters 5 and 8.

Luria's model goes on to propose that each of the modality-specific sensory association areas then projects to an area in the inferior parietal lobe, the **tertiary sensory area,** where the already highly processed information associated with each modality is integrated to yield a multimodal representation. From here information is projected to the **tertiary motor area** in the dorsolateral frontal cortex. Thus, dorsolateral frontal cortex receives input that is the product of extensive processing throughout the cerebral cortex. In terms of sensory processing, the dorsal region of the frontal lobes is, in the words of the neuroanatomist Walle Nauta, a "neocortical end of the line" (Nauta & Feirtag, 1986).

The frontal lobes then subject this highly processed sensory information to executive control in the form of superordinate motor organization such as planning. The specific behavioral manifestations of this superordinate organization are then implemented by the **secondary motor area,** which coordinates sequences of movements, and the primary motor area, which finally effects movement (Figure 3.15).

The Basal Ganglia

The **basal ganglia** are a group of subcortical gray-matter structures in the forebrain. The three main subdivisions of the basal ganglia are the **putamen,** the **globus pallidus,** and the **caudate nucleus** (Figure 3.16). The caudate and putamen are collectively called

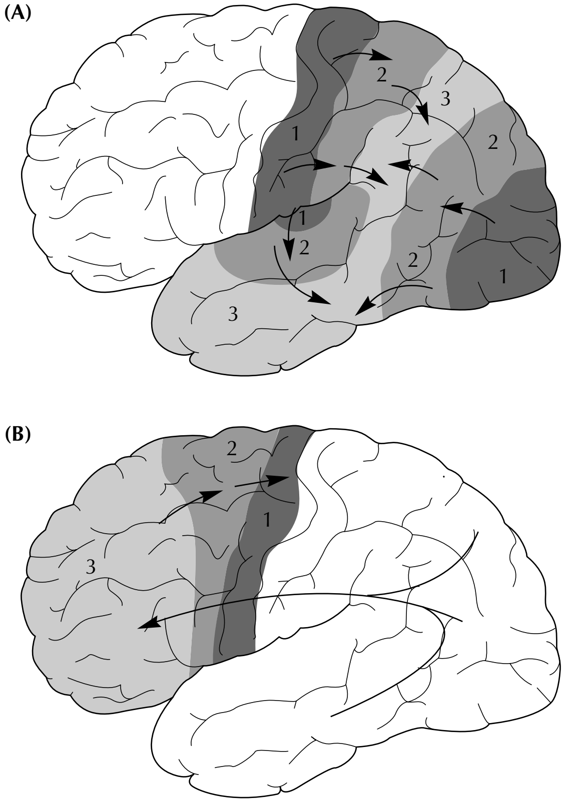


FIGURE 3.15 Luria's model of sequential processing in the cerebral cortex. *(A)* Information arriving at the primary sensory areas (dark shading) is processed and conveyed to secondary (medium shading) and tertiary (light shading) sensory areas for further perceptual and symbolic elaboration. *(B)* From the tertiary sensory area, information is then conveyed to the tertiary motor area (light shading) in the frontal lobes, which mediates higher-order motor processing such as planning and other forms of executive control. Specific motor sequences are then organized by the secondary motor area, (medium shading), which then sends this input on to the primary motor cortex (dark shading) for final implementation. *(From Kolb & Whishaw, 1996, p. 170 [based on information in Luria, 1973])*

the **neostriatum,** a term that reflects the fact that they are phylogenetically most recent and that they are structurally related, being connected by cell bridges. Together, the three structures are referred to as the **corpus striatum.** Because of their functional relationship with the corpus striatum, the **subthalamic nucleus** and the **substantia nigra** are also generally considered to be components of the basal ganglia.

The caudate nucleus and the putamen are the major recipients of afferents to the corpus striatum. These afferents originate from areas throughout the cortex, including areas of cortex mediating motor function, and from the substantia nigra. The globus pallidus is the major source of efferents from the basal ganglia, projecting mainly to thalamic nuclei. These, in turn, project to motor cortex, premotor cortex, and prefrontal cortex. Thus, rather than being part of the stream from motor cortex to spinal cord that directly executes motor activity, the basal ganglia and their connections with the thalamus form a cortical-subcortical-cortical loop that appears to monitor and adjust motor activity. The regulatory role of the basal ganglia in motor function is also suggested by the fact that lesions to these structures frequently result in disorders that have unwanted movement as their major symptom. These are discussed in more detail in chapter 9. Some structures of the basal ganglia also have been shown to play a role in certain cognitive processes.

The Limbic System

In the 19th century Paul Broca called the cortical structures at the border between forebrain and brain stem *le grand lobe limbique,* the great limbic lobe (from the Latin *limbus,* meaning "border"). These structures include the **cingulate gyrus** (arching around the superior margin of the corpus callosum), the **subcallosal gyrus,** the **parahippocampal gyrus** (Figure 3.17), and the **hippocampus.**

In 1952 Paul MacLean hypothesized that a number of structures, including this cortical ring, constituted a functional system, which he named the **limbic system.** Although there is some disagreement about the basis for including a particular structure in this system, and even about the very validity of the limbic system concept (see chapter 11), structures traditionally considered to be part of the limbic system include, in addition to the cortical areas just mentioned, the **septum,** the **amygdala,** the **hypothalamus** (including its posterior portion, the **mamillary bodies**), and the **anterior nucleus** of the thalamus (Figure 3.18).

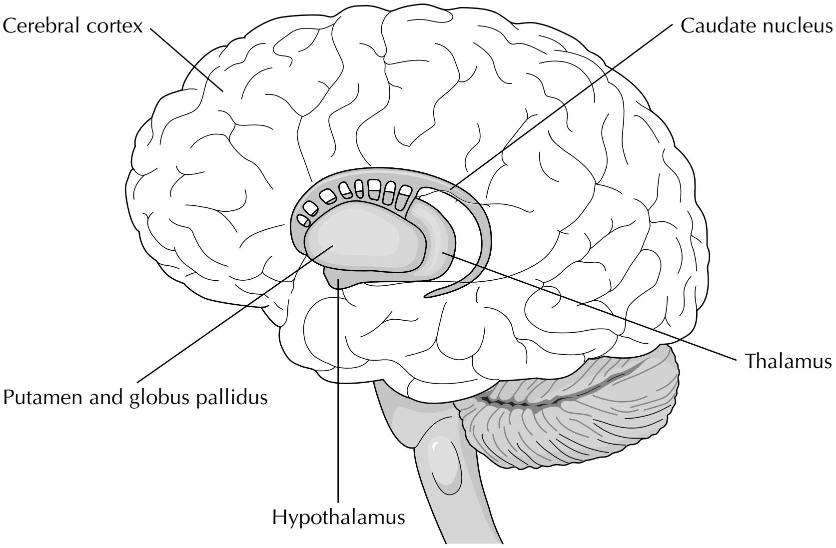


FIGURE 3.16 The three main structures of the basal ganglia: the putamen, the globus pallidus, and the caudate nucleus as viewed through a transparent cerebral hemisphere. The cell bridges connecting the putamen and the caudate nucleus are seen. *(From Gleitman, Fridlung, & Reisberg, 1999, p. 26)*

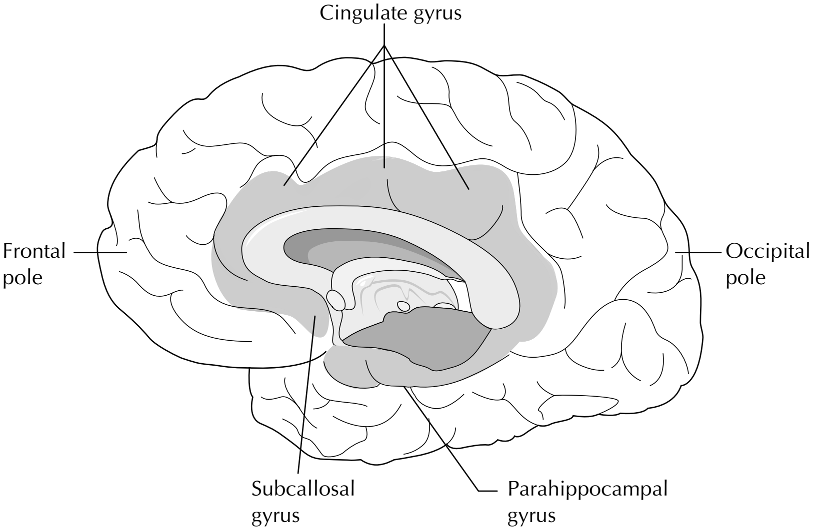


FIGURE 3.17 Medial view of the right hemisphere, with the brain stem and cerebellum removed, showing limbic cortex. The hippocampus is hidden behind the parahippocampal gyrus. *(From Carlson, 1999, p. 69)*

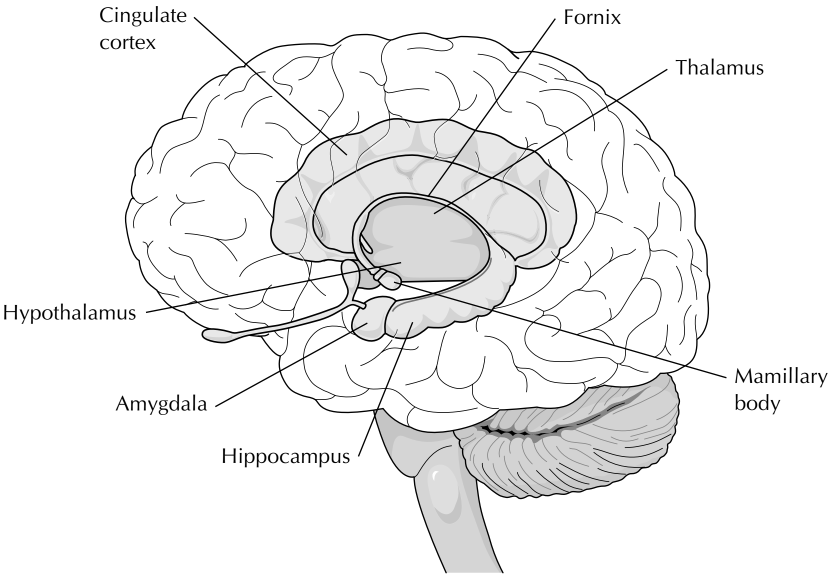


FIGURE 3.18 Some major structures of the limbic system as viewed through transparent cerebral hemispheres. *(From Gleitman et al., 1999, Fig. 2.13, p. 27)*

The limbic system receives three main sources of cortical input: (a) from posterior association cortex via the cingulate gyrus, hippocampus, and **fornix** (the pathway connecting the hippocampus with the mamillary bodies in the posterior hypothalamus); (b) from inferotemporal cortex via entorhinal cortex (the anterior portion of the parahippocampal gyrus) and hippocampus; and (c) from prefrontal cortex (Figure 3.19). Each of these sources of input carry information from association cortices, providing the limbic system with highly processed information about the environment.

There are three major sources of limbic efferents to cortex. The cingulate gyrus receives input from the mamillary bodies via the anterior thalamus. In addition, prefrontal cortex receives limbic input from the hypothalamus and from the amygdala (see Figure 3.19).

Limbic structures have been shown to be important in emotional function and in memory. The hypothalamus, in addition to its role in the regulation of autonomic and endocrine function, plays an important role in the regulation of emotional behavior, including rage behavior. In addition, the septum (and also parts of the hypothalamus) produces intense pleasure when electrically stimulated. The amygdala is involved in emotional processing, particularly conditioned fear. It is also involved in social behavior.

Finally, although there is little evidence that the hippocampus is involved directly in emotion, the hippocampus is critical for normal memory. Bilateral damage to this structure results in a profound inability to remember anything new, a condition known as **anterograde amnesia.** It is not surprising that the same structures or system of structures might mediate both memory and emotion because these two domains of function are closely related.

The Diencephalon

The most important structures in the diencephalon are the thalamus and the hypothalamus (Figure 3.20). The word *thalamus* comes from the Greek for “inner room,” presumably a reference to the fact that the thalamus is situated deep in the brain. Although it is usually referred to in the singular, as if there were only one, there are actually two thalami, one in each hemisphere. Each is an ovoid (roughly egg-shaped) group of nuclei, bordered laterally by the third ventricle, dorsally by the lateral ventricles, and laterally by the internal capsule (fibers from motor cortex to brain-stem nuclei and the spinal cord).

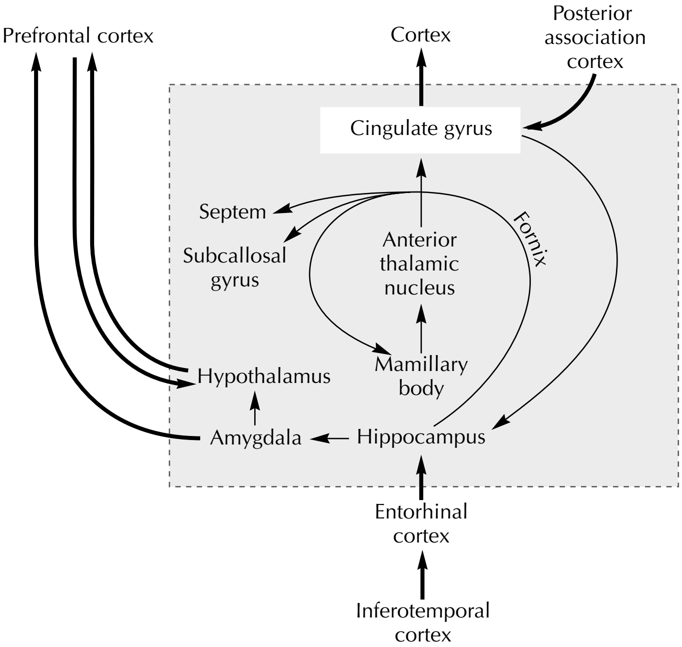


FIGURE 3.19 Major connections within the limbic system and between the limbic system and other regions of the brain. Limbic structures are shown within the rectangle. Bold arrows indicate major sources of input to the limbic system and major targets of output from the limbic system. *(Adapted from Kandel et al., 1995, p. 606)*

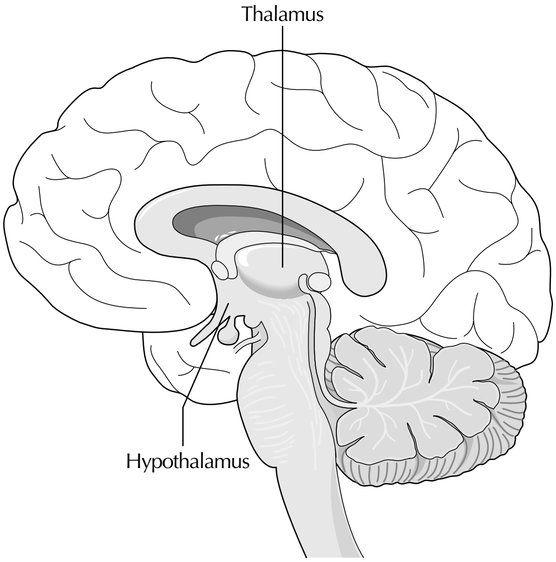


FIGURE 3.20 Medial view of the right hemisphere showing the medial surface of the right thalamus and, just below it, the right half of the hypothalamus. *(From DeArmond et al., 1974, p. 8)*

The thalamus contains many specific nuclei. Some of these are points where neurons carrying incoming sensory information from each sensory modality (except olfaction) synapse on their way to the cortex. Although these are sometimes referred to as relay nuclei, a great deal of processing takes place in these nuclei, so it would be a mistake to think of them as simply passing information on to the next link in the chain. The sensory input from each modality reaches a specific thalamic nucleus. These nuclei include the **lateral geniculate nucleus** (for vision), the **medial geniculate nucleus** (for audition), and specific nuclei for the relay of somatosensory input (Figure 3.21).

The thalamus also receives input from the basal ganglia, cerebellum, motor cortex, and medial temporal cortex and sends projections back to these areas. It thus serves as a pivotal structure in the formation of many cortical-subcortical-cortical loops that are involved in a broad range of functions. For example, returning connections from primary cortical sensory areas to the thalamus have been implicated in the modulation of thalamocortical input. In the motor domain, a loop involving motor cortex–basal ganglia–thalamus–motor cortex and a loop involving motor cortex–cerebellum–thalamus–motor

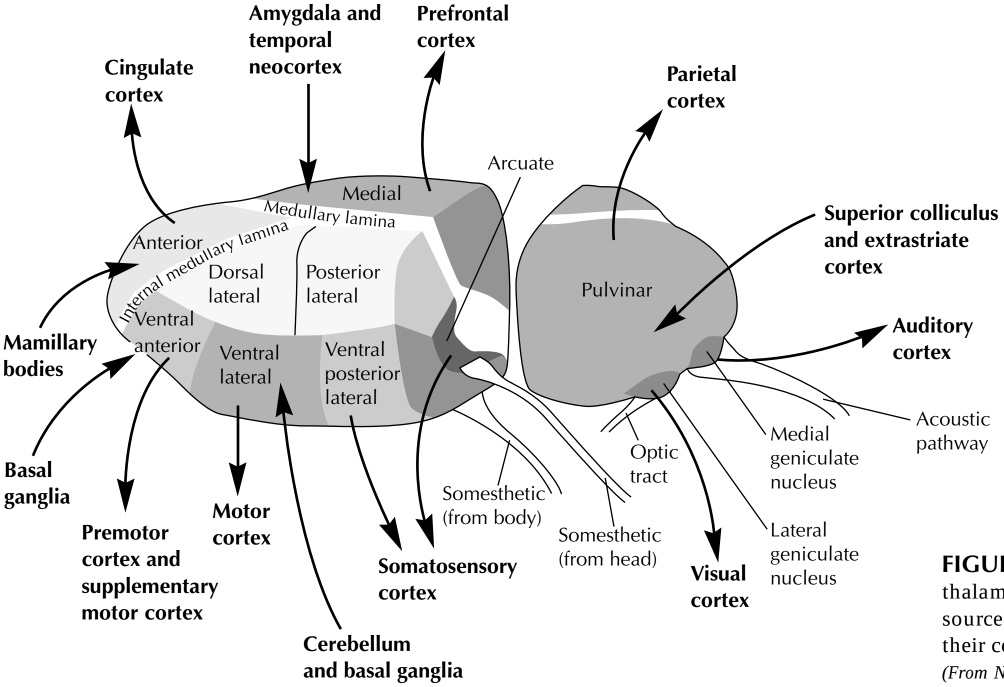


FIGURE 3.21 Major thalamic nuclei, their sources of input, and their cortical projections. *(From Netter, 1974, p. 72)*

cortex have been shown to be important in the control and regulation of movement. The thalamus is also involved in cognitive function, including language and memory.

The **hypothalamus,** true to its name, is located just below the thalamus, comprising the tissue forming lower walls of the third ventricle. This small and compact group of nuclei (Figure 3.22) is involved in an extremely broad range of functions. As we have already noted, the hypothalamus is a central component of the limbic system. In fact, Nauta has suggested that the limbic system should be defined as those structures that are in close synaptic contact with the hypothalamus (Nauta & Feirtag, 1986). It is thus critically involved in limbic-mediated emotional and motivational processes.

Structures sending input to the hypothalamus include limbic cortex, via the hippocampus and fornix, orbital (ventral) prefrontal cortex, the amygdala, and the reticular formation. Thus, the hypothalamus receives both highly processed input from the cortex and information from the internal environment. It also receives direct projections from the retina that are involved in hypothalamic control of circadian rhythms. Major hypothalamic output includes connections to prefrontal cortex, the amygdala, the reticular formation, and the spinal cord. The fact that the hypothalamus receives input from and sends output to both higher cortical centers and lower brain-stem and spinal centers suggests that it serves as an interface between these two neural domains, a notion that is consistent with the influence of the hypothalamus over both behavior and internal physiological state.

The influence of the hypothalamus on inner physiological state is most evident in its central role in the maintenance of **homeostasis,** the internal biological steady state that every living organism must constantly maintain in order to remain alive. It plays its role both by activating specific behaviors (such as drinking and eating) and by directly regulating physiological processes that maintain the integrity of the body's internal environment. Internal regulation is achieved partly through hypothalamic control of the autonomic nervous system, that division of the nervous system that controls smooth muscle, cardiac muscle, and glands. Thus, the hypothalamus may be thought of as the highest regulatory center of the autonomic nervous system. However, its control is far from absolute; it is influenced both by higher cortical centers processing information about the external

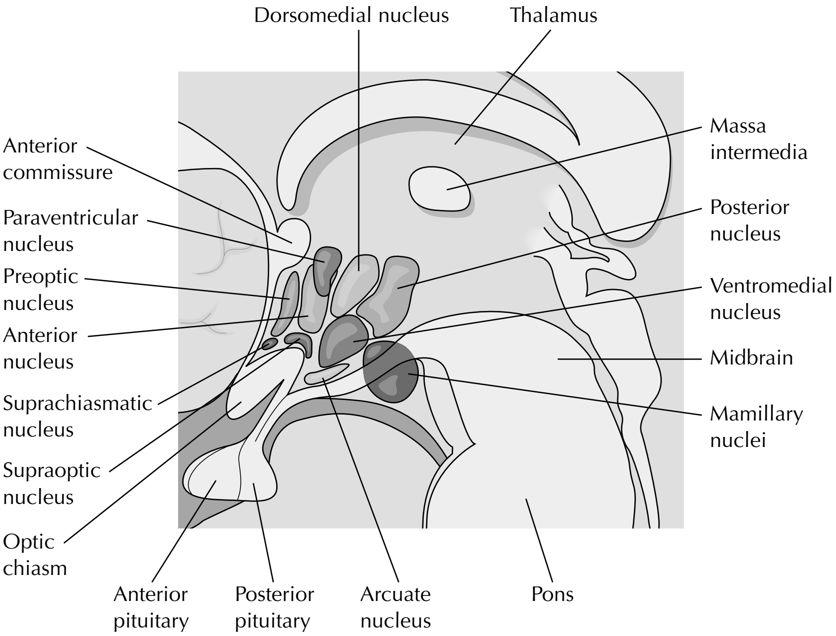


FIGURE 3.22 Midsagittal view of the hypothalamus, showing some major hypothalamic nuclei and some neighboring structures. The optic chiasm is the point at which some fibers from each optic nerve cross over to the other side of the brain. *(From Netter, 1974, p. 76)*

environment and lower brain-stem centers participating in physiological regulation.

The other mechanism by which the hypothalamus exerts control over internal physiology is via regulation of endocrine function. Hormonal regulation of physiological function has certain advantages over neural mechanisms, particularly when slower, more diffuse, and more prolonged influence is required. The hypothalamus regulates endocrine function by controlling the release of hormones from the **anterior pituitary gland,** which protrudes from the base of the hypothalamus (see Figure 3.22). The anterior pituitary has been conceptualized as the "master gland" of the endocrine system in that it triggers the release of hormones by a number of endocrine glands, including the adrenal cortex, the thyroid gland, and the gonads. This anterior-pituitary regulation of endocrine function is, in turn, regulated by the hypothalamus. Interestingly, the hypothalamus achieves this regulation by secreting its own peptide hormones into a vascular portal system that delivers them directly to the anterior pituitary. The hypothalamus also monitors the consequences of this regulatory activity by assessing the levels of circulating hormones present in its blood supply.

Although the anterior pituitary gland is not part of the nervous system, the **posterior pituitary** is composed of axons of neurons whose cell bodies are in specific nuclei in the hypothalamus and whose axon terminals release hormones into the general circulation. These hormones include vasopressin (also called antidiuretic hormone), which regulates water retention, and oxytocin, which is involved in milk production and in uterine contractions. Thus, the hypothalamus is a gland, perhaps a startling conclusion until we realize the kinship between the release of neurotransmitter by neurons throughout the nervous system and the neurosecretory function of hypothalamic cells. As we saw in chapter 2, in a sense all neurons are secretory.

THE BRAIN STEM

The brain stem lies between the diencephalon and the spinal cord (Figure 3.23). It is composed of the midbrain (mesencephalon), the pons (metencephalon), and the medulla oblongata (myelencephalon). Much of the brain stem is primarily concerned with regulating and maintaining life-sustaining processes such as respiration, cardiac function, and homeosta-

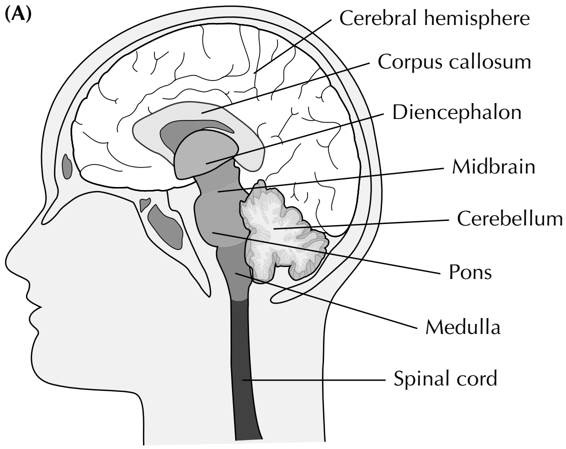


FIGURE 3.23 *(A)* Midsagittal section of the brain, brain stem, and spinal cord. *(B)* An MRI of the same structures in the living brain. *(From Kandel et al., 1995, p. 9)*

sis. It is also involved in the control of sleep and wakefulness, emotion, attention, and consciousness.

The brain stem contains groups of motor and sensory nuclei, as well as nuclei that exert a modulatory (regulatory) effect on higher brain centers by releasing specific neurotransmitters. An example of such a nucleus is the substantia nigra, a major site of dopamine synthesis. Axons projecting from this nucleus release dopamine at synapses in widespread areas of the anterior forebrain, including the basal ganglia and prefrontal cortex. In addition to its many nuclei, the brain stem has major ascending (sensory) and descending (motor) white-matter tracts running through it.

It may be tempting, in the context of considering higher-order brain function, to consider the brain stem as a simple conduit through which information flows back and forth between the forebrain and the spinal cord. This would be an error, however. As we have indicated, the brain stem plays a central role in the neural control of some extremely complex functions that are essential for survival and also participates in the regulation of a number of higher-order functions (Damasio, 1999).

The Midbrain

The midbrain lies between the diencephalon and the pons. The part of the midbrain dorsal to the cerebral aqueduct is called the **tectum** (Latin, "roof") and consists of two paired structures, the superior and inferior colliculi. The **tegmentum** (Latin, "covering") lies ventral to the aqueduct. The most ventral region of the midbrain contains larger fiber tracts carrying information from the forebrain to the spinal cord (the **corticospinal tract**) and from the forebrain to the brain stem (**corticobulbar tract**). Connections between the forebrain and the cerebellum, running in both directions, also pass through the midbrain.

The midbrain contains several structures involved with vision. These include the superior colliculus, which is involved in the mediation of visuomotor function. Earlier in this chapter we mentioned that patients with cortical blindness nevertheless have some preserved visual function. For example, they are able to accurately point to the location of a spot of light even though they have no conscious experience of seeing the stimulus. This paradoxical ability, which has been termed **blindsight** (Weiskrantz, 1986), may be mediated by the superior colliculus.

The midbrain is also the site of two of the three cranial nerve nuclei that control eye movement, the **occulomotor nucleus** and the **trochlear nucleus.** The **pupillary reflex** (constriction of the pupil of the eye in response to intense light) is mediated by a nucleus incorporated in the occulomotor nucleus. The pupillary reflex is tested to assess the integrity of midbrain structures in patients who are unconscious.

The inferior colliculus, an auditory relay, is located in the midbrain, just below the superior colliculus. The mesencephalic tegmentum contains a number of nuclei involved in motor function, including the red nucleus and the substantia nigra. Finally, the mesencephalic reticular formation, part of the diffuse set of nuclei extending from the lower medulla to the thalamus, takes up much of the midbrain. The reticular formation is involved in a number of functions, including arousal, autonomic regulation, and the regulation of pain.

The Hindbrain

The hindbrain (rhombencephalon) is made up of the pons (metencephalon) and the medulla (myelencephalon). The cerebellum is also considered to be part of the metencephalon, but it will be considered in a separate section.

PONS The pons is composed of the pontine tegmental region, forming the floor of the fourth ventricle, and, more ventrally, a number of fiber tracts interspersed with pontine nuclei. In addition to the continuation of cortical projections to the brain stem and spinal cord, pontine fibers include massive connections between cortex and cerebellum, the **cerebellar peduncles** (Latin for “little feet”). Nuclei in the pons include those having auditory and **vestibular** (sense of head position and motion) function, as well as sensory and motor nuclei for the face and mouth. One of the three nuclei controlling the extraocular muscles of the eyes is also found in the pons. The pons also contains a large portion of the reticular formation.

MEDULLA The medulla lies just caudal to the pons and rostral to the spinal cord. As the medulla extends caudally, the fourth ventricle narrows and shifts ventrally until it becomes a narrow, centrally located tube as the medulla merges with the spinal cord. The medulla contains a number of important nuclei, fiber tracts, and the most caudal portion of the reticular formation.

At the dorsal edge of its rostral end, the medulla contains two pairs of large nuclei, the gracile nuclei and the cuneate nuclei, relay nuclei for the ascending lemniscal pathways, the somatosensory pathways carrying information about touch, body position sense, and kinesthesis from the spinal cord to the thalamus and then on to the cortical somatosensory area. In the ventral portion of its rostral part is the olivary complex, including the inferior and medial accessory olivary nuclei. This highly enfolded nucleus receives input from the cortex and the red nucleus and projects to the cerebellum. The medulla also contains several sensory nuclei, including those processing vestibular input and sensory input from the face, mouth, throat, and abdomen. The medulla also contains motor nuclei innervating the neck, tongue, and throat. Finally, motor nuclei in the medulla innervate organs of the body that are crucial for the maintenance of life, including the viscera, the heart, and muscles involved in respiration.

In the ventral medulla are found the continuations of the corticospinal motor projections. About halfway down the length of the medulla, 90% of the corticospinal fibers on each side cross over to the contralateral side. This point of crossover (**decussation**) is called the **pyramidal decussation.**

THE CEREBELLUM

Bulging out of the dorsal surface of the pons, the cerebellum is part of the hindbrain. However, its function is different from that of the brain-stem structures we have just discussed. Although the term *cerebellum* comes from the Latin for “little brain,” it is actually a massive structure. The cerebellum overlies the dorsal surface of the brain at the level of the pons, forming the roof of the fourth ventricle and sitting on the massive cerebellar peduncles. The cerebellum has a cortex, the surface of which, because of its intricate infoldings, has an area equal to that of the cerebral cortex. In the depths of the cerebellum are

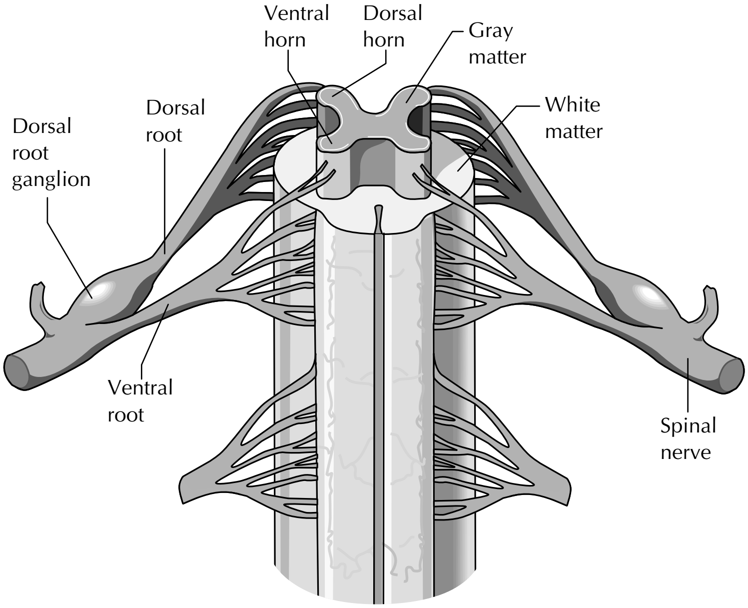


FIGURE 3.24 Ventral view of a section of the spinal cord. *(From Netter, 1974, p. 52)*

four pairs of deep nuclei. Between the cortex and the deep nuclei is internal white matter.

Most input to the cerebellum reaches the cerebellar cortex via relays in the deep nuclei, although some arrives at the cortex directly. Cerebellar afferents bring information about the state of the body from sensory areas processing somatosensory, visual, auditory, and vestibular information. In addition, the cerebellum also receives afferents from structures involved in motor function, including the motor and premotor cortices.

Cerebellar output, almost entirely from the deep nuclei, projects, via the thalamus, to motor and premotor cortex. Cerebellar efferents also project to brain-stem nuclei that send descending projections to the spinal cord, and to the rhombencephalic reticular formation.

The multisensory and motor input to the cerebellum, together with its output to motor-related cortex and to spinal centers mediating posture and gait, suggest that the cerebellum plays a central role in the modulation, adjustment, and coordination of body movement on the basis of information about current body state and current and intended movement. This notion is supported by the fact that, despite the extensive sensory and motor input the cerebellum receives, lesions to the cerebellum do not cause sensory deficits or paralysis. Instead, cerebellar lesions cause disruptions in the maintenance of posture and in the sequential coordination of movement on the side of the body ipsilateral to the lesion. (The ipsilateral effect is due to the fact that cerebellar efferents cross over to the other side of the brain stem, affecting brain-stem fibers that then themselves cross over again at the pyramidal decussation.) These disruptions are generally termed **cerebellar ataxia** (literally, “lack of order”) and are exemplified by the disruption of the attempt to carry out a command, such as “extend your arm in front of you and then bring your finger to your nose.” A patient with cerebellar ataxia who attempted this would evidence a marked instability of movement, with the hand increasingly lurching from side to side as the finger approached the nose.

THE SPINAL CORD

The **spinal cord** extends from the medulla, rostrally, to the **cauda equina** (“horse tail”) caudally. Thirty-one pairs of **spinal nerves** leave the spinal cord, passing through small openings in the spinal column. The cauda equina is composed of the lowest spinal nerves as they continue to course caudally beyond the end of the spinal cord before leaving the spinal column.

In cross section the spinal cord has a butterfly-shaped center of gray matter, surrounded by white matter (Figure 3.24). The white matter consists of ascending somatosensory tracts, descending motor tracts, and intraspinal projection fibers connecting different regions within the spinal cord. On each side the gray matter is divided into a **ventral horn** and a **dorsal horn.** The ventral horn is the site of cell bodies of α motor neurons, the final link in the neuronal chain that activates muscle contraction. Axons of α motor neurons leave the spinal cord in the **ventral root.** The dorsal horn contains cell bodies of interneurons that convey input from primary somatosensory neurons to the brain and to motor neurons at the same and at other levels of the spinal cord. These latter pathways connecting somatosensory input with motor output are the basis for spinal reflexes. Axons of primary somatosensory neurons enter the spinal cord in the **dorsal root.** However, the cell bodies of these neurons are not in the dorsal horn, but remain outside the central nervous system in the **dorsal root ganglia.**

SUMMARY

There are several general terms that help us orient ourselves within the nervous system. *Anterior* (rostral) refers to the front, and *posterior* (caudal) refers to the back. *Superior* (dorsal) denotes the top or upper portion of a structure, and *inferior* (ventral) the bottom or underside. *Medial* refers to the middle, and *lateral* to the side. These terms are used to indicate the position of a structure relative to the whole brain and also relative to other structures.

The central nervous system consists of the brain and the spinal cord. The peripheral nervous system includes all of the sensory and motor nerves coursing through the body and conveying signals to and from the central nervous system.

The brain is traditionally divided into three parts: the forebrain (prosencephalon), the midbrain (mesencephalon), and the hindbrain (rhombencephalon). The forebrain includes the cerebral cortex, the basal ganglia, the lateral ventricles, and the limbic system. The cerebral cortex, the most highly evolved region of the human brain, is traditionally divided into four lobes: the occipital, parietal, temporal, and frontal. The surface of the cortex has many sulci and gyri that increase the area of cortex that can be contained in the limited volume of the skull. They also conveniently serve as landmarks for identifying cortical regions. Most cortex has six layers of cells, although a few regions have only one or two layers. Different cortical regions vary with respect to the thickness and cellular composition of these layers, and the study of this variation, called cytoarchitectonics, has yielded cortical maps that have turned out to be useful in identifying functional areas of the cortex.

Fibers tracts of varying length connect areas within each hemisphere and between the two hemispheres. Many patterns of cognitive impairment can be understood in terms of interruption of specific fiber tracts and the resulting disconnection of specific cortical regions.

Different cortical regions have been shown to be specialized for specific functions. These include the primary motor cortex and cortical areas that are specialized for the processing of elementary sensory information from each sensory modality. The term *association cortex* was long used to indicate cortex mediating higher-order processing. This concept has given way to a more delineated understanding of the specialized functions mediated by specific cortical regions outside the primary sensory and motor areas.

The basal ganglia are gray-matter structures located deep in the base of the forebrain. They are important for the regulation and control of movement. Structures within the basal ganglia have also been shown to play a role in some areas of cognition.

The limbic system includes a number of cortical and subcortical structures at the border between the forebrain and the brain stem. The limbic system serves as a useful term to describe structures involved in emotion, motivation, and the maintenance of homeostasis, although the validity of this concept has been questioned. Some structures within this system, including the hippocampus and the mamillary bodies, have been shown to be important for memory.

The diencephalon includes the thalamus and the hypothalamus. The thalamus receives information from each sensory modality (except olfaction) and conveys this information on to the respective primary cortical sensory area. The thalamus also receives input from the basal ganglia, cerebellum, and motor cortex and sends projections back to these areas. It thus serves as a central component in many cortical-subcortical-cortical loops. The hypothalamus is involved in an extremely broad range of functions, many of which have the goal of maintaining homeostasis, both through the regulation of behavior and the regulation of the body's internal state. The hypothalamus mediates control of the organism's internal state through the regulation of the autonomic nervous system and through the control of endocrine function.

The brain stem includes the midbrain, the pons, and the medulla. These structures contain groups of motor and sensory nuclei and neurons that exert a modulatory effect on higher brain centers. They also contain ascending and descending fiber tracts that mediate somatosensory and motor function. Many of the nuclei in the medulla mediate processes that are essential for life, such as cardiac function and blood pressure. For this reason, major lesions of the medulla often result in death.

The cerebellum plays a central role in the modulation and coordination of body movement on the basis of information about current body state and current and intended movement.

The spinal cord conveys motor commands from the brain to the muscles of the body via α motor neurons that leave the spinal cord in the ventral root. Axons of primary somatosensory neurons, conveying information about the body to the brain, enter the spinal cord in the dorsal root. The spinal cord also mediates many reflexes that allow for rapid and automatic responses to a variety of stimuli.

Now that we have surveyed the major structures of the central nervous system, we turn to a discussion of experimental methods in neuropsychology.