Signaling in the nervous system occurs along well-defined pathways, and via specific anatomical relays to circumscribed areas of the brain, spinal cord, and peripheral musculature. A review of the nervous system’s anatomical organization clarifies this organization. We begin with a global view; in later chapters we’ll focus on specific anatomical and physiological systems relevant to specific sensory, cognitive, and motor processes.

The nervous system has two major subdivisions: the **central nervous system** (CNS) consisting of the brain and spinal cord, and the **peripheral nervous system** (PNS), consisting of everything outside the CNS. The CNS can be thought of as the command-and-control portion of the nervous system. The PNS represents a courier network that delivers sensory information to the CNS and carries the motor commands of the CNS to the muscles, to control the voluntary muscles of the body (somatic motor system) and the involuntary activity of the smooth muscles, heart, and glands (autonomic motor system). In most of the remainder of this chapter, we focus on describing the CNS, to lay the groundwork for the studies of cognition that follow.

### Cerebral Cortex

The **cerebral cortex** has two symmetrical hemispheres that consist of large sheets of (mostly) layered neurons. It sits over the top of core structures, including parts of the limbic system and basal ganglia, and surrounds the structures of the diencephalon, all of which will be considered later. Together, the cerebral cortex, basal ganglia, and diencephalon form the forebrain. The term cortex means “bark,” as in tree bark, and in higher mammals and humans it contains many infoldings, or convolutions (Figure 3.8). As noted earlier, the infoldings of the cortical sheet are further defined as sulci (the folded regions) and gyri (the crowns of the folded tissue that one observes when viewing the surface). Many mammalian species, such as the rat or even New World monkeys like the owl monkey, have smoother, less folded cortices with few sulci and gyri.

The folds of the human cortex serve a functional purpose: to pack more cortical surface into the skull. If the human cortex were smoothed out to resemble that of the rat, for example, humans would need to have very large heads. Folding of the cortex provides about a one-third savings in space. The total surface area of the human cerebral cortex is about 2,200 to 2,400 cm², but because of the folding, about two thirds of this area is confined within the depths of the sulci. Another advantage of having a highly folded cortex is that neurons are brought into closer three-dimensional relationships to one another, saving axonal distance and hence neuronal conduction time between different areas. This savings occurs because the axons that make long-distance corticocortical connections run under the cortex through the white matter and do not follow the foldings of the cortical surface in their paths to distant cortical areas. In addition, by folding, the cortex brings some nearby regions closer together; for example, the opposing layers of cortex in each gyrus are in closer linear proximity than they would be if the gyri were flattened.

Although the cortex is composed of several cell layers in most regions, its thickness averages only 3 mm and ranges from 1.5 to 4.5 mm in different cortical regions. The cortex itself contains the cell bodies of neurons, their dendrites, and some of their axons. In addition, the cortex includes axons and axon terminals of neurons projecting to the cortex from other brain regions, such as the subcortical thalamus. The cortex also contains blood vessels. Because the cerebral cortex has such a high density of cell bodies, it appears grayish in relation to underlying regions that are composed primarily of axons of neurons and appear slightly paler or even white. As described earlier, for this reason anatomists used the terms gray matter and white matter when referring to areas of cell bodies and axon tracts, respectively. The latter tracts represent the billions of axons that connect the neurons of the cerebral cortex to other locations in the brain (Figure 3.9).

### Anatomical Subdivisions

The cerebral hemispheres have four main divisions, or lobes—and a fifth, if you consider that the limbic system is sometimes referred to as the limbic lobe, as described later. These regions have different functional properties and can usually be distinguished from one another by prominent anatomical landmarks such as pronounced sulci. The names of the brain areas were derived from names originally given to the underlying skull bones; for example, the temporal lobe lies underneath the temporal bone. The temporal bone derived its name from the Latin *temporalis* (meaning “of time”) probably because of the graying of hair overlying the temporal bone—a sign of passing time if there ever was one.
The four lobes are the frontal, parietal, temporal, and occipital lobes (Figure 3.10). The central sulcus divides the frontal lobe from the parietal lobe, and the Sylvian (lateral) fissure separates the temporal lobe from the frontal and parietal lobes. The occipital lobe is demarcated from the parietal and temporal lobes by the parieto-occipital sulcus on the brain’s dorsal surface and the preoccipital notch located on the ventrolateral surface. The left and right cerebral hemispheres are separated by the interhemispheric fissure (also called the longitudinal fissure) that runs from the rostral to the caudal end of the forebrain.

Connections between the cerebral hemispheres are accomplished by axons from cortical neurons that travel through the corpus callosum, which represents the largest white matter commissure in the nervous system. Commissure is a special term for the white matter tracts that cross from the left to the right side, or vice versa, of
the CNS. The term *corpus callosum* means "hard body," so named because of its tough consistency. Indeed, very early anatomists incorrectly believed that the corpus callosum served a structural function in supporting the cerebral hemispheres because it prevented them from collapsing onto structures below. As we will discuss later in the book, the corpus callosum carries out valuable integrative functions for the two hemispheres.

**CYTOARCHITECTONICS**

The cerebral cortex can be divided more finely than the four or five main lobes, in various ways. For example, it can be divided according to functional subdivisions of the cortex. But there are other, more purely anatomical criteria for subdividing the cortex. One is by the microanatomy of cell types and their organization. This method of subdividing is generally referred to as *cytoarchitectonics*—cyto- means "cell" and architectonics means "architecture"—and has to do with how cells in a region appear morphologically and are arranged with respect to each other. Cytoarchitectonic investigations entail the performance of detailed histological analysis of the tissue from different regions of the cerebral cortex. The goal is to define the extent of regions in which the cellular architecture looks similar and therefore might indicate a homogeneous area of the cortex that represents, perhaps, a functional area. This work began in earnest with Korbinian Brodmann at the beginning of the 20th century.
Brodmann (1909/1960) identified approximately 52 regions of the cerebral cortex. These areas were categorized according to differences in cellular morphology and organization, and numbered (Figure 3.11). Other anatomists further subdivided the cortex into almost 200 cytoarchitectonically defined areas, but many classified transition zones as separate areas when perhaps they should not be considered so. A combination of cytoarchitectonic and functional descriptions of the cortex is probably most effective in dividing the cerebral cortex into meaningful units; this type of work will likely continue into the foreseeable future because we are only beginning to learn the functional organization of the cerebral cortex. In the sections that follow, we use Brodman’s numbering system to describe the cerebral cortex, as well as anatomical names (e.g., superior temporal gyrus).

The Brodman system often seems unsystematic. Indeed, the numbering has more to do with the order in which Brodman sampled a region than with any meaningful relation between areas. Nonetheless, in some regions the numbering system has a rough correspondence with the relations between areas that carry out similar functions, such as vision—Brodman areas 17, 18, and 19. It is worth noting here that the nomenclature of the cortex (and indeed the nervous system) is not uniform. Hence, a region might be referred to by its Brodman name, a cytoarchitectonic name, a gross anatomical name, or a functional name; and functional names change rapidly as new information is gathered. For example, let’s consider the naming of the first area in the cortex to receive visual inputs from the thalamus—the primary sensory cortex for vision. The Brodman name is area 17 (or Brodman area 17; i.e., BA17), another cytoarchitectonic name is striate cortex (owing to its striated appearance under the microscope), the gross anatomical name is calcarine cortex (the cortex surrounding the calcarine fissure in humans), and the functional name is primary visual cortex, which has been labeled area V1 (for “visual area 1”) on the basis of studies of the visual systems of monkeys. The choice here of primary visual cortex as an example is fortuitous because all these different terms refer to the same cortical area. But for much of the cortex this is not the case; that is, different nomenclatures often do not refer to precisely the same area with a one-to-one mapping. BA18 of the visual system, for example, is not synonymous with V2 (for “visual area 2”).

![Figure 3.11](image-url) (a) Brodman’s original cytoarchitectonic map from his work around the start of the 20th century. Different regions of cortex have been demarcated by histological examination of the cellular microanatomy. Brodman divided the cortex into about 52 areas. (b) Lateral view of the left hemisphere showing Brodman’s areas. Over the years, the map has been modified, and the standard version no longer includes some areas. (c) Medial view of the right hemisphere showing Brodman’s areas. Most of Brodman’s areas are symmetrical in the two hemispheres.
It is also possible to subdivide the cerebral cortex according to the general patterns of layering (Figure 3.12). Ninety percent of cortex is composed of neocortex, which typically contains six main cortical layers with a high degree of specialization of neuronal organization (see Figure 3.12c). Layer IV is typically the input layer, receiving information from the thalamus, as well as information from other, more distant cortical areas. Layer VI, on the other hand, is typically considered an output layer that sends information from the cortex back to the thalamus, facilitating feedback. Each layer is anatomically and functionally distinct, though it is important to note that information is shared between the layers via axonal projections.

Neocortex includes areas like primary sensory and motor cortex and association cortex (areas not obviously primary sensory or motor). Mesocortex is a term for the so-called paralimbic region, which includes the cingulate gyrus, parahippocampal gyrus, insular cortex, and the orbitofrontal cortex, all of which will be defined later. Mesocortex is interposed between neocortex and allocortex and has six layers. Allocortex typically has only one to four layers of neurons and includes the hippocampal complex (sometimes referred to as archicortex) and primary olfactory cortex (sometimes referred to as paleocortex). The take-home message here is that the cerebral cortex can be subdivided into major regions that differ according to the degree of complexity of the neuronal layering.

**FUNCTIONAL DIVISIONS**

The lobes of the cerebral cortex have a variety of functional roles in neural processing. Major identifiable systems can be localized within each lobe, but systems of the brain also cross different lobes. That is, these brain systems do not map one to one onto the lobe in which they primarily reside, but in part the gross anatomical structure.

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**Figure 3.12** Cerebral cortex, color-coded to show the regional differences in cortical layering that specify different types of cortex. (a) The lateral surface of the left hemisphere. (b) The medial surface of the right hemisphere. Neocortex is shown in red, mesocortex in blue, and allocortex in green. (c) Idealized cross section of neocortex showing a variety of cell types and the patterns of three different types of staining techniques. On the left, the Golgi preparation is apparent: Only a few neurons are stained, but each is completely visualized. In the middle, we see primarily cell bodies from the Nissl stain. On the right, we see the fiber tracks in a Weigert stain, which selectively stains myelin.
subdivisions of the cerebral cortex can be related to different sensorimotor functions. In their principal organization, cognitive brain systems are often composed of networks whose component parts are located in different lobes of the cortex. Finally, most functions in the brain—whether sensory, motor, or cognitive—rely on both cortical and subcortical components. Because one of the goals of this book is to review what we know about the functional localization of higher cognitive and perceptual processes, what follows in this section is a beginner’s guide to the functional anatomy of the cortex.

**Motor Areas of the Frontal Lobe** The frontal lobe plays a major role in the planning and execution of movements. It has two main subdivisions: the motor cortex and the prefrontal cortex. The motor cortex begins in the depths of the central sulcus and extends in the anterior direction. The primary motor cortex (M1) corresponds to BA4. It includes the anterior bank of the central sulcus and much of the precentral gyrus (the prefix *pre-* in neuroanatomy means “in front of”). Anterior to this area are two more main motor areas of cortex (within BA6): the premotor cortex on the lateral surface of the hemisphere, and the supplementary motor cortex that lies dorsal to the premotor area and extends around to the hemisphere’s medial surface. These motor cortical areas contain motor neurons whose axons extend to the spinal cord and brainstem and synapse on motor neurons in the spinal cord. The output layer of motor cortex contains some of the most amazing neurons in the nervous system: the large pyramidal neurons known as Betz’s cells, named after Vladimir Aleksandrovich Betz, who described them. Betz’s cells are the largest neurons in the cerebral cortex, reaching 60 to 80 mm in diameter at the cell body, with some sending axons several feet long down the spinal cord.

The more anterior regions of the frontal lobe, the **prefrontal cortex**, take part in the more complex aspects of planning and executing behavior—tasks that require the integration of information over time. The prefrontal cortex has three or more main areas that are commonly referred to in descriptions of the gross anatomy of the frontal lobe (although different definitions can be used): the dorsolateral prefrontal cortex, the orbitofrontal cortex (Figure 3.13), and the anterior cingulate and medial frontal regions (not visible in Figure 3.13, but refer to Figure 3.18).

**Somatosensory Areas of the Parietal Lobe** The somatosensory cortex is in the posterior bank of the central sulcus and encompasses the postcentral gyrus and adjacent areas (Brodmann areas 1, 2, and 3). These cortical regions receive inputs from the somatosensory relays of the thalamus and represent information about touch, pain, temperature sense, and limb proprioception (limb position). The primary somatosensory cortex (or S1) is immediately caudal to the central sulcus, and a secondary somatosensory cortex (S2), receiving information via projections primarily from S1,
Cortical Topography

Early insights into human cortical organization were made possible by studies that involved direct stimulation of the cortex of awake humans undergoing brain surgery. Wilder Penfield and Herbert Jasper (1954) at the Montreal Neurological Institute carried out such pioneering work in the 1940s. Taking advantage of the fact that the cortex is exposed during surgery, these surgeons removed damaged brain tissue and systematically explored the effects of small levels of electrical current applied to the cortical surface. Panel (a) of the figure shows the exposed cortex of an epileptic patient and panel (b), a gridwork of electrodes laid over the surface for stimulation and recording; stimulation during surgery can be done with a single electrode rather than a grid. Because there are no pain receptors in the central nervous system, patients experience no discomfort from stimulation. Thus, stimulation can be applied even when they are awake and fully conscious, enabling researchers to gather the patients' subjective experiences—a relative impossibility in animal studies.

In their studies, Penfield and his associates found a topographic correspondence between cortical regions and body surface with respect to somatosensory and motor processes. This correspondence is represented in panel (c) by overlaying drawings of body parts on drawings of coronal sections of the motor and somatosensory cortex. These coronal sections are from the regions indicated by the color codes in the lateral view of the whole brain at the top of panel (c) (only the left hemisphere is shown here, representing the right body surface). The resulting map of the body surface on the cortex is sometimes called a homunculus, referring to the fact that there is an organized representation of the body across a given cortical area. Note that there is an indirect relation between the actual size of body parts and the cortical representation of the body's parts. For example, areas within the motor homunculus that activate muscles in the fingers, mouth, and tongue are much larger than would be expected if the representation were proportional. The large drawings of the fingers and mouth indicate that large areas of cortex are involved in the fine coordination required when we manipulate objects or speak.

Is the representation of the homunculus in the figure correct? Recent evidence from brain-imaging studies using a technique described in Chapter 4—functional magnetic resonance imaging (fMRI)—suggests that it may not be. Ravi Menon and his colleagues (Servos et al., 1999) in Canada stimulated the foreheads and chins of healthy volunteers while their brains were being scanned. In contrast to the results of the electrical-stimulation studies, they found that stimulating the forehead produced activity in a region that was below (inferior to) the region for activity related to chin stimulation—the reverse of the drawing in the figure based on the work of Penfield and his colleagues. If the latter pattern from neuroimaging turns out to be accurate, it will constitute a dramatic example of scientific revisionism.

is located ventrally to S1. Somatosensory inputs projecting to the posterior parietal cortex arise from S1 and S2. Somatosensory information coming into the thalamus and then going to the primary somatosensory cortex traverses two main pathways: the anterolateral system for pain and temperature sense, and the dorsal column—medial lemniscal system for information about touch, proprioception, and movement (Figure 3.14). Receptor cells in the periphery transduce physical stimuli into neuronal impulses conducted to the spinal cord and toward the brain, making synaptic connections at relay sites along the ascending pathway. The two systems for somatosensory information take slightly different paths in the spinal cord, brainstem, and midbrain on their route to the thalamus, and then to the cortex.
**Visual Processing Areas in the Occipital Lobe**  
The primary visual cortex (also known as striate cortex because its surface anatomical organization makes it appear striped to the naked eye, V1 for visual area 1, or BA17) receives visual inputs relayed from the lateral geniculate nucleus of the thalamus (Figure 3.15). In humans, the primary visual cortex is on the medial surface of the cerebral hemispheres, extending only slightly onto the posterior hemispheric pole. Thus, most of the primary visual cortex is effectively hidden from view, between the two hemispheres. The cortex in this area has six layers; it begins the cortical coding of visual features like color, luminance, spatial frequency, orientation, and motion—features that we will take up in detail in Chapters 5 and 6. Visual information from the outside world is processed by multiple layers of cells in the retina and
Figure 3.14 The somatosensory cortex, which is located in the postcentral gyrus. Inputs from peripheral receptors project via the thalamus (shown in cross section) to the primary somatosensory cortex (S1). Secondary somatosensory cortex (S2) is also shown.

Figure 3.15 The visual cortex, which is located in the occipital lobe. Brodmann area 17, also called the primary visual cortex (V1), is located at the occipital pole and extends onto the medial surface of the hemisphere, where it is largely buried within the calcarine fissure.
transmitted via the optic nerve to the lateral geniculate nucleus of the thalamus, and from there to V1—a pathway often referred to as the \textit{retinogeniculostriate, or primary visual, pathway}. Note that visual projections from the retina also reach other subcortical brain regions by way of secondary projection systems. The superior colliculus of the midbrain is the main target of the secondary pathway and participates in visuomotor functions such as eye movements. In Chapter 12 we will review the role of the cortical and subcortical projection pathways in visual attention.

Surrounding the striate cortex is a large visual cortical region called the \textit{extrastriate} ("outside the striate") visual cortex (sometimes referred to as the \textit{prestriate} cortex in monkeys, to signify that it is anatomically anterior to the striate cortex). The extrastriate cortex includes BA18 and BA19.

\textbf{Auditory Processing Areas in the Temporal Lobe} The auditory cortex lies in the superior part of the temporal lobe and is buried within the Sylvian fissure (Figure 3.16). The projection from the cochlea (the auditory sensory organ in the inner ear) proceeds through the subcortical relays to the medial geniculate of the thalamus, and then to the supratemporal cortex in a region known as Heschl's gyri. This region represents A1, the primary auditory cortex, and A2, the auditory association area surrounding it and posterior to the primary auditory cortex (BA41 and BA42). BA22, which surrounds the auditory cortex, aids in the perception of auditory inputs; when this area is stimulated, sensations of sound are produced in humans. One can represent the sensory inputs to the auditory cortex using a tonotopic map: the orderly representation of sound frequency within the auditory cortex can be determined with several tonotopic maps.

\textbf{Association Cortex} The portion of neocortex that is not sensory or motor has traditionally termed the \textbf{association cortex}. These regions receive inputs from many cortical areas, contain cells that may be activated by more than one sensory modality, and have specific functional roles that are not exclusively sensory or motor. For example, take the visual association cortex. Though the primary visual cortex is necessary for normal vision, neither it nor the extrastriate cortex is the sole locus of visual perception. Regions of visual association cortex in the parietal and temporal lobes are important for correct perception of the visual world (see Chapters 5 and 6). Moreover, visual association cortex can be activated during mental imagery when we call up a visual memory even in the absence of visual stimulation. As another example, the association areas of the parietal—temporal—occipital junction of the left hemisphere have a prominent role in language processing, whereas this region in the right hemisphere is implicated in attentional orienting (see Chapter 12). Thus, higher mental processes are the domain of the association cortical areas, in interaction with sensory and motor areas of cortex (Figure 3.17).

\textbf{Limbic System, Basal Ganglia, Hippocampus, and Diencephalon}

In the preceding sections we focused on the neocortex. Here we will consider the mesocortical and allocortical
regions of the cerebrum. Then we will look at the subcortical structures of the basal ganglia and the diencephalon.

**Limbic Lobe**

Let's look at the portions of the forebrain that are collectively known as the limbic lobe or **limbic system** (Figure 3.18). These include several structures that form a border (in Latin, *limbus*) around the brainstem, named the *grand lobe limbique* by Paul Broca (see Chapter 1). A band of cortex known as the cingulate gyrus extends above the corpus callosum in the anterior–posterior direction. Together, the cingulate gyrus, hypothalamus, anterior thalamic nuclei, and hippocampus constitute the "classical" limbic lobe (Figure 3.19). In the 1930s James Papez (pronounced "payps") first suggested the idea that these structures were organized into a system for emotional behavior, which led to use of the term Papez circuit.

Since that initial formulation, much has been learned about the structures participating in the limbic system, and today the **amygdala**, a group of neurons anterior to the hippocampus, is usually considered a key component, along with the orbitofrontal cortex and parts of the basal ganglia (described in the next section, but not shown in Figure 3.19); in some descriptions, the medial dorsal nucleus of the thalamus is also included. The organization and role of the limbic system are described in more detail in Chapter 9. The limbic system participates in emotional processing, learning, and memory. With each passing year we discover new functions of this system.

**Basal Ganglia**

The **basal ganglia** are a collection of subcortical neuronal groups in the forebrain located beneath the anterior portion of the lateral ventricles (see "How the Brain Works: The Chambers of the Mind," on p. 72). The basal ganglia have a significant role in the control of movement. The three main subdivisions are the globus pallidus, caudate nucleus, and putamen (Figure
The caudate and putamen are referred to together as the neostriatum.

Some anatomists have considered the amygdala and associated nuclei (amygdaloid complex) to be part of the basal ganglia, but this is not the convention agreed on by most neuroscientists today. The subthalamic nucleus and the substantia nigra are considered part of the basal ganglia because of their strong interconnectivity with the principal cell groups forming the basal ganglia. Yet these nuclei are quite distant from the rest of the basal ganglia. The substantia nigra is located in the midbrain—actually at the juncture of the midbrain and diencephalon—and the neostriatum and globus pallidus are in the forebrain. This gross anatomical distinction between the substantia nigra and the nuclear groups of the basal ganglia may not be
Figure 3.20  (a) Cross sections through the brain at two anterior–posterior levels (as indicated), showing the basal ganglia. (b) Corresponding high-resolution, structural MRI (4-tesla scanner) taken at approximately the same level as the more posterior drawing in (a). This image also shows the brainstem, as well as the skull and scalp, which are not shown in (a).
as important as the microanatomical (cellular) and functional relationships, however. We will return to this idea with respect to the basal ganglia in detail in Chapter 7.

The basal ganglia, subthalamic nucleus, and substantia nigra participate in circuits with the cortex and thalamus to mediate aspects of motor control (both somatic motor and oculomotor systems), as well as some cognitive functions.

The primary circuits projecting to the basal ganglia include a corticostriatal projection that contains direct projections from all major cortical regions onto neurons in the caudate and putamen, which are the input structures of the basal ganglia. In addition, motor areas of cortex can project to the basal ganglia via the cell groups in the thalamus and the subthalamic nucleus. The major outputs of the basal ganglia project from the globus pallidus to thalamic nuclei and then to cortex—primarily motor and premotor cortex, as well as prefrontal cortex (Figure 3.21). Thus, the basal ganglia are not in a projection pathway from motor cortical areas to the spinal cord, to control muscular activity directly, but instead are part of a cortical-subcortical motor loop that is thought to monitor aspects of how motor activity, as well as nonmotoric functions are progressing.

**Figure 3.21** Major inputs and outputs of the basal ganglia. The basal ganglia form a cortical–subcortical motor loop that monitors motor behavior.

**Hippocampal Formation and Medial Temporal Lobe**

The region of the forebrain along the ventral medial surface of the temporal lobe contains the hippocampus and the associated areas of the dentate gyrus, parahippocampal gyrus, and entorhinal cortex—the latter being the anterior portion of the parahippocampal gyrus (BA28) (Figure 3.22). The hippocampus and dentate gyrus are composed of three- or four-layer cortex (archicortex), whereas entorhinal cortex and the parahippocampal gyrus in humans are composed of six-layer cortex (although it is mesocortex, not neocortex).

The hippocampus has been subdivided into zones referred to as the CA fields (cornu ammonis is Latin for "horn of Ammon"), which are divided into CA1, CA2, CA3, and CA4 based on differences in cellular morphology, connectivity, and development (Figure 3.23). As we will see in Chapter 8, the hippocampus plays a central role in memory or, to be more precise, learning.

**Diencephalon**

The remaining portions of the forebrain to consider are the thalamus and hypothalamus, which together constitute the diencephalon. These subcortical nuclei are composed of groups of specialized cells with interconnections to widespread brain areas.

**Thalamus** Although its name is Greek for “inner chamber,” the thalamus is not actually hollow. It lies at

**Figure 3.22** Anatomy of the hippocampal formation. The hippocampus is located on the inferior and medial aspect of the temporal lobe.
the most rostral end of the brainstem (Figure 3.24), in the dorsal part of the diencephalon in each hemisphere, and is bordered medially by the third ventricle, dorsally by the fornix and corpus callosum, and laterally by the internal capsule—the projection fibers from the motor cortex to the brainstem and spinal cord. In some people, the thalamus in the left hemisphere and the thalamus in the right hemisphere are connected by a bridge of gray matter called the massa intermedia.

The thalamus has been referred to as the "gateway to the cortex" because, with the exception of some olfactory inputs, all sensory modalities make synaptic relays in the thalamus before continuing to the primary cortical sensory receiving areas. The thalamus is divided into several nuclei that act as specific relays for incoming sensory information. The lateral geniculate nucleus receives information from the ganglion cells of the retina and sends axons to the primary visual cortex, BA17 (Figure 3.25). Similarly, the medial geniculate nucleus receives information from the inner ear, via other brainstem nuclei in the ascending auditory pathway, and sends axons to the primary auditory cortex (A1). Somatosensory information projects via the ventral posterior (medial and lateral) nuclei of the thalamus and then to primary somatosensory cortex in BA1, BA2, and BA3. Sensory relay nuclei of the thalamus not only project axons to the cortex but also receive heavy descending projections back from the same cortical area that they contact.

Not only is the thalamus involved in relaying primary sensory information, but also it receives inputs from the basal ganglia, cerebellum, neocortex, and medial temporal lobe and sends projections back to these structures to create circuits involved in many different functions. One important structure within the thalamus is the pulvinar nucleus, located at the posterior pole of the thalamus, which is involved in integrative functions involving multiple cortical areas.

**Hypothalamus** Below the thalamus is the hypothalamus, a small collection of nuclei and fiber tracts that lie on the floor of the third ventricle (Figure 3.26). The hypothalamus is important for the autonomic nervous system and the endocrine system, and it controls functions necessary for the maintenance of homeostasis (i.e., maintaining the normal state of the body). The hypothalamus is also involved in emotional processes and in control of the pituitary gland, which is attached to the base of the hypothalamus.
Figure 3.25  The left thalamus, showing inputs and outputs and major subdivisions. The various subdivisions of the thalamus serve different sensory systems and participate in various cortical–subcortical circuits. The posterior portion of the thalamus (lower right) is cut away in cross section to separate from the rest of the thalamus to reveal the internal organization of the thalamic nuclei (upper left).

The hormones produced by the hypothalamus control much of the endocrine system. For example, hypothalamic neurons in the region that surrounds the third ventricle send axonal projections to an area at the border of the hypothalamus and pituitary gland—the median eminence—where releasing factors (e.g., peptides) are released into the system that provides circulation to the anterior pituitary gland. In the anterior pituitary, these hypothalamic peptides trigger or inhibit the release of a variety of hormones into the bloodstream: growth hormone, thyroid-stimulating hormone, adrenocorticotropic hormone, and the gonadotropic hormones are examples of those released by the cells of the anterior pituitary under hypothalamic control. Hypothalamic neurons in the anteromedial region, including the suprachiasmatic nucleus and paraventricular nuclei, send axonal projections into the posterior pituitary, where they stimulate the posterior pituitary to release the hormones vasopressin and oxytocin into the blood to regulate water retention in the kidneys, and milk production and uterine contractility, respectively.

The hypothalamus receives inputs not only from the limbic cortex but also from other brain areas, including the mesencephalic reticular formation, amygdala, and the retina, to control circadian rhythms (light–dark cycles). Projections from the hypothalamus include a major projection to the prefrontal cortex, amygdala, and spinal cord. One of the most prominent projections is the one to the pituitary.