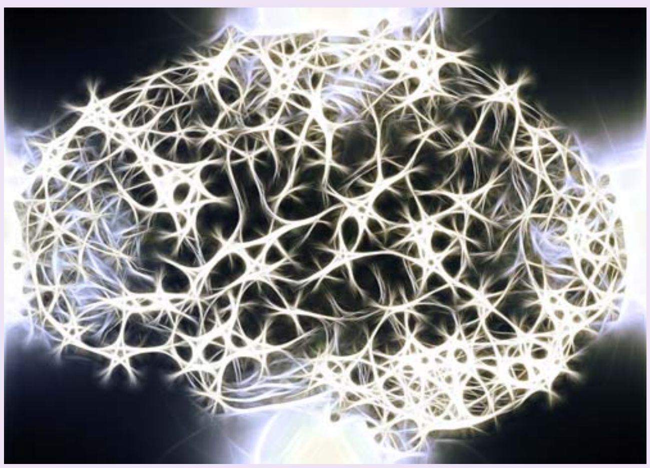
CHAPTER

2

The Brain

THE BRAIN

The human brain has 100 billion neurons, each neuron connected to 10,000 other neurons. Sitting on your shoulders is the most complicated object in the known universe. ***Michio Kaku, American Physicist.***



An abstract view of the brain with neurons. *Source: Public domain.*

1. INTRODUCTION

Ultimately we are each a single person: one human being with one mind and one brain. As we explore the structures and functions of the human brain in this chapter, we will see that the brain is far from a unitary structure, although we do label it as such: *the brain*. Its complexity is staggering. Formed of two major hemispheres, each with four cortical lobes, along with midbrain, brainstem, and cerebellum, the brain does not look like a unitary structure at all. Its many structures and regions combine with its vast connectivity to form a complex universe that drives human thought, actions, desire, and cognition.

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FIGURE 2.1 The planet Earth as seen from space. *Source: Public domain.*

Perhaps it is not surprising that our brain contains so many discrete regions and structures when we consider our mind. It turns out that we humans are not of one mind at all. Scattered throughout human conversations are phrases like "I'm of two minds about this …", "I need to leave but I don't want to leave …", and "I feel I ought to tell him but I don't want to …". We humans are full of conflict. It is represented in classical psychological theory describing the human *id*, *ego*, and *super ego*: levels of human consciousness and behavior that are divided sharply despite representing our personality as a whole (Freud, 1923/1961). So it seems our minds are not so unitary at all, but full of levels of conflicting thought and emotion, and internal dilemmas. Why, then, should our brain be thought of as unitary?

In this chapter, we will explore the many regions of the brain and their relative functions. A central issue in understanding the brain is determining our *level of analysis*. Just as looking at the planet Earth from a distant view from space provides us with a global view of the continents and oceans of the Earth (Fig. 2.1), looking at the human brain as a whole provides information about its major structures and connections (Fig. 2.2). Yet just as a view of the Earth as a whole informs of the entirety of the planet, it provides little information about the depth and breadth of the Florida Everglades, the topography of the Grand Canyon, or the density of the forests of Yosemite National Park. To understand these subregions, we need to "zoom" our analysis in to a more detailed view. So it is with the brain: to understand the totality of brain function, we need to be able to first understand some of its constituent parts such as the cortex, the thalamus, and the brainstem. And then we need to "zoom" in to different subregions to understand them in more depth.

In this chapter, we will describe the key major structures of the brain (Fig. 2.2) and then delve into a bit more detail about the tiny but major working unit of the brain, the neuron. These are the disciplines of *neuroanatomy* and *neurophysiology*. Next, we will see how the many brain areas contribute to our functional selves: ranging from emotional processing to social cognition, to

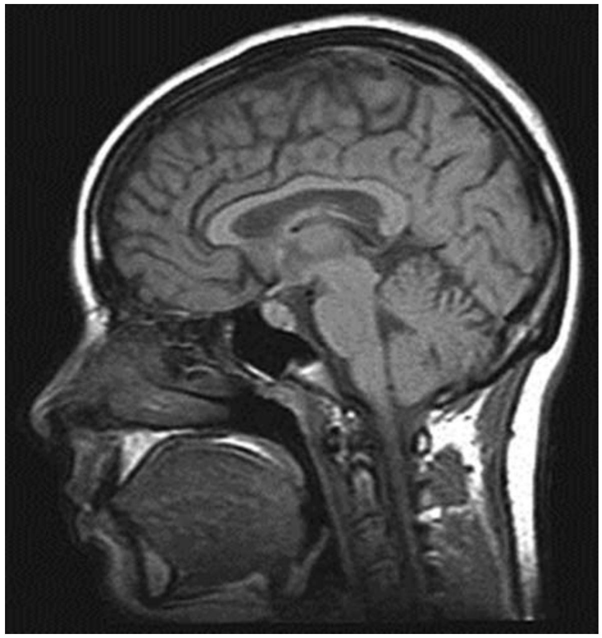

FIGURE 2.2 A side (sagittal) view of the human brain. *Source: Open access. Patrick J. Lynch, medical illustrator; C. Carl Jaffe, MD, cardiologist. http://creativecommons.org/licenses/by/2.5/.*

language and thought, and to attentional processes and future planning. These aspects of the brain are studied in *functional neuroanatomy* investigations. Then we will describe the many connective pathways that form the *street map* of the brain. Investigations into the *neuroconnectivity* of the brain provide important information about how information travels throughout the brain, brainstem, and spinal cord. Finally we will look at the "traffic" on those streets as we explore the brain's *dynamic processes*. *Neurodynamics* is an exciting, relatively new field of study. These aspects of the brain form the separate disciplines of neuroanatomy, neurophysiology, functional neuroanatomy, neuroconnectivity, and neurodynamics, which combine to shed light on the structure and function of the mind/brain.

2. BRAIN STRUCTURE—NEUROANATOMY

The brain sits at the top of the central nervous system (Fig. 2.3), nestled under the protective armor of the skull, and highly interconnected with the body through brainstem regions and the massive spinal cord. The vast peripheral nervous system that extends from the brain to regions throughout the body and back again sends and receives neural signals that provide information spanning from pain, pressure, and touch impulses, movement and balance, to the senses of vision and audition, and the chemical senses of smell and taste.

2.1 The Cortex

The *cortex* or *neocortex* (the terms are used interchangeably) is the seat of most of human cognition, from sensory processing of visual, auditory, somatosensory, smell, and taste inputs, to internal processes such as decision making and planning for the future. The cortex

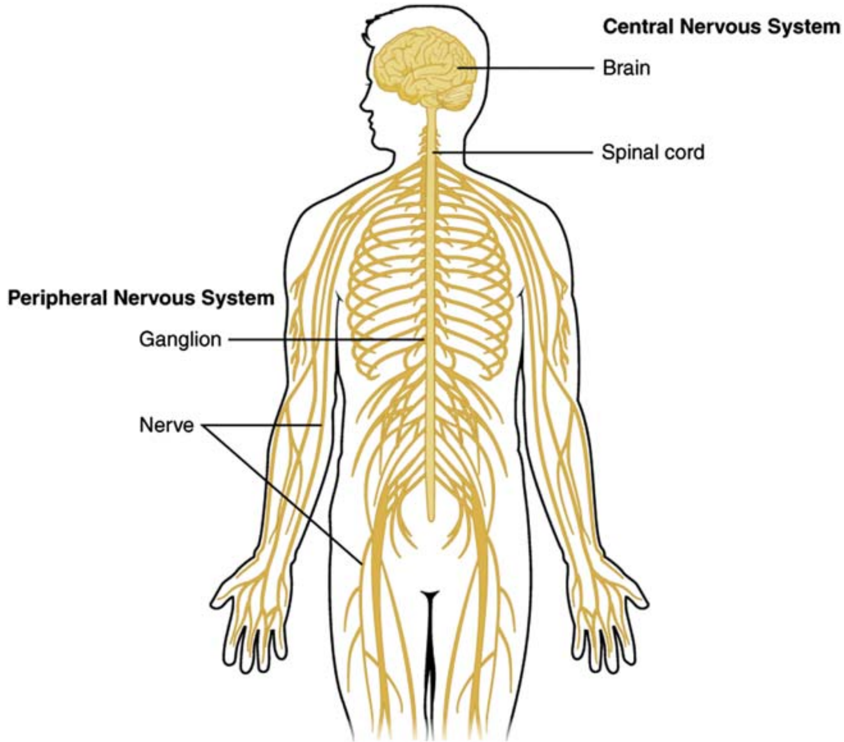

FIGURE 2.3 The central nervous system includes the brain and the spinal cord, while the peripheral nervous system includes the nerves throughout the body. *Source: Public domain. Version 8.25 from the Textbook OpenStax Anatomy and Physiology Published May 18, 2016 https://cnx.org/contents/FPtK1zmh@8.25:fEI3C8Ot@10/Preface.*

is subdivided into regions that are meaningful when we explore the functional roles of the brain later in this chapter and throughout this book. They have signature roles in the many functions that make up brain processing.

2.1.1 Planes of the Brain

Classically, the brain has been "sliced up" using three planes, and these planes are described in similar ways whether the slicing is actual slicing of the brain during, for example, a post mortem examination, or if it is virtual slicing using magnetic resonance images of the brain. The three planes are shown in Fig. 2.4: slicing sideways across the brain—so that you can see the left and right hemispheres—is called an *axial* slice. Sometimes an axial slice is called a *horizontal* slice because it is a horizontal cut through the brain. A second way to slice through the brain is called a *sagittal* slice. This is a slice that cuts down through the brain beginning in one hemisphere, continuing on until the middle of the brain is met: this is called a *mid-sagittal* slice, and continuing still further until the second hemisphere is shown. Think of this slicing as beginning at one ear and continuing through the brain towards the middle of the head and onto the other ear. The third type of brain slice is the *coronal* slice. Think about a slice that begins at the ears but this time the slices will continue forward towards the front of the head or backward towards the back of the head. A coronal slice will show both hemispheres, like the axial slice. These three plane terms—axial, sagittal, and coronal—will be used throughout this book.

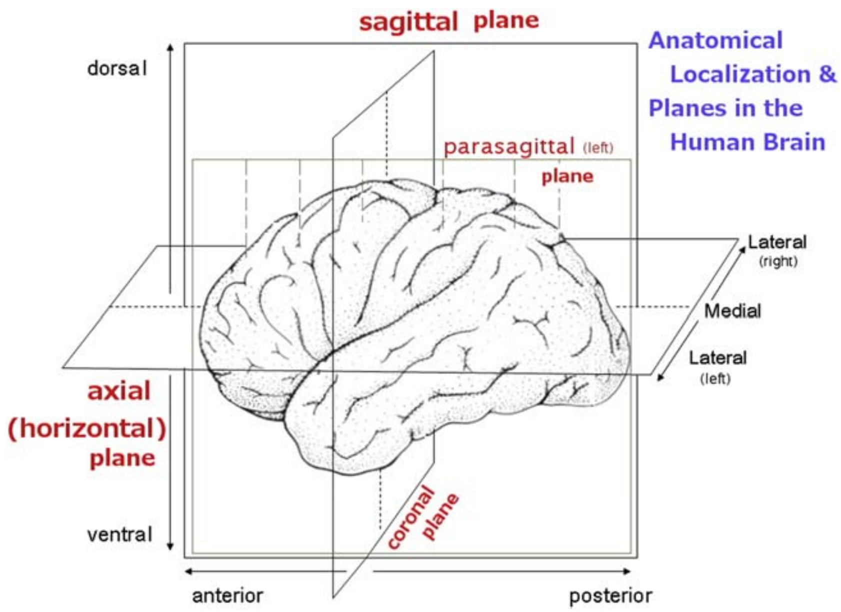

FIGURE 2.4 The planes of the brain. For investigative and clinical purposes, the brain is "sliced" along one of three major planes: *axial*, *sagittal*, and *coronal*. The axial or horizontal plane slices the brain horizontally from the top of the brain to the bottom, the sagittal plane slices the brain vertically from the left side to the right side, and the coronal plane slices the brain vertically from the front of the brain to the back. Other key brain-related terms are *dorsal*, indicating the top of the brain, and *ventral*, indicating the bottom of the brain. The front of the brain is the *anterior* and the back of the brain is the *posterior*. The middle part of the brain is termed the *medial* section and the left and right outside edges are called *lateral*. These terms are frequently used to denote where a region is in the brain, for example the dorsolateral prefrontal cortex or the ventromedial prefrontal cortex. *Source: Open access. Diagram with English annotations for planes and localisations in the human brain. JonRichfield 2014. Creative Commons Attribution-Share Alike 4.0 International license.*

Another set of terms for the brain describes where you are in the brain from the front of the brain, the *anterior* of the brain, to the back of the brain, the *posterior* of the brain (Fig. 2.4). A second set of terms describes where you are in the brain from the top of the brain, the *dorsal* or *superior* part of the brain, to the bottom of the brain, the *ventral* or *inferior* part of the brain. Finally, a third set of terms describes where you are in the brain from the outside edge of the brain, the *lateral* surface, to the middle of the brain, the *medial* surface located between the hemispheres within the longitudinal fissure.

These terms are used to name brain regions, such as the dorsal lateral prefrontal cortex (PFC) or the ventral medial PFC. Once learned, these terms can help you identify where in the brain a specific region is located. They can also help you identify the relative locations of brain areas: for example, the temporal lobe is posterior to the frontal lobe and inferior to the parietal lobe.

2.1.2 Cortical Anatomy

The cortex is the outer layer of the brain. *Cortex* comes from the Latin word for bark, and indeed the cortex has a look of the bark of a tree with all of its fine ridges and grooves. The

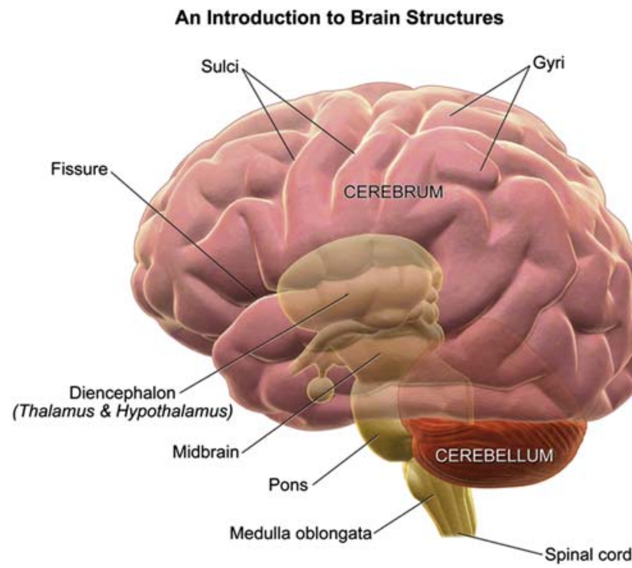

FIGURE 2.5 The many small grooves of the cortex are called sulci: each *sulcus* is a tiny valley that contains more of the *grey matter* that is visible on the surface of the cortex. A large sulcus is called a *fissure*. The many ridges of the cortex are called *gyri*: each *gyrus* is a small bump on the surface of the cortex, also made up of grey matter. *Source: Open access. Blausen.com staff (2014). "Medical gallery of Blausen Medical 2014." Wikiversity Journal of Medicine 1 (2): 10. https://doi.org/10.15347/wjm/2014.010. ISSN 2002-4436.*

cortex is made up of *grey matter*: the cell bodies of the billions of nerve cells—*neurons*—that form the key element of the cortex. The many small grooves of the cortex are called sulci: each *sulcus* is a tiny valley that contains more of the *grey matter* that is visible on the surface of the cortex (Fig. 2.5). The many ridges of the cortex are called *gyri*: each *gyrus* is a small bump on the surface of the cortex, also made up of grey matter.

There are two cerebral hemispheres: a right and a left hemisphere that are completely separate except for the massive connectivity bridge called the *corpus callosum* (Fig. 2.6). The corpus callosum is a major landmark as you observe the brain from various angles and views (Fig. 2.7). Although in Fig. 2.7 the corpus callosum is shaded in red for easy identification, more realistic images of the corpus callosum show that it is very light in color: this is because it is made up of *white matter,* which is formed by the *myelinated* axons that extend from neurons. The *myelin sheath* around the axon is made up of a white fatlike substance that serves to increase the signal transmission along the axon.

Within each hemisphere, there are four cortical lobes: *frontal, parietal, temporal, and occipitaI* (Fig. 2.8). While the four lobes are all part of the cortex, each lobe differs in shape and size, and each has a signature role in human cognition, as we will discuss later in this chapter and throughout this book.

Other key landmarks are three giant sulci: the Sylvian fissure (sometimes referred to as the Lateral Fissure) extending from the frontal lobe back between the parietal and temporal lobes; the central sulcus, which separates the frontal and parietal lobes (Fig. 2.9); and the longitudinal fissure (Fig. 2.6), which runs between the two hemispheres.

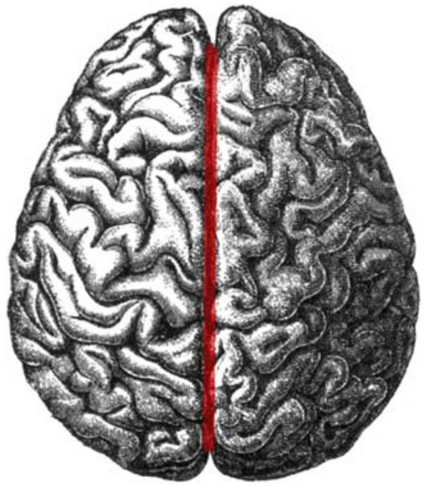

FIGURE 2.6 The brain seen from above showing two cerebral hemispheres separated by the large longitudinal fissure (shown in *red*). The two hemispheres are linked by the corpus callosum. *Source: Public domain. Wikimedia Commons, the free media repository.*

FIGURE 2.7 The massive corpus callosum (shown in *red*) is a white matter tract that links the two cerebral hemispheres. Left: the corpus callosum seen when looking through the cortex in the left hemisphere; right: the corpus callosum seen when looking through the brain from the front. *Source: Open access. Images are from Anatomography maintained by Life Science Databases (LSDB).*

2.2 The Subcortex

Beneath the cortex, the subcortical region contains many bodies or nuclei that perform important functions ranging from control of movement to emotional processing. Chief among these structures is the mighty *thalamus*. Located deep in the center of the brain, the two thalami (one in the left hemisphere, one in the right) are highly interconnected with all parts of the cortex (Fig. 2.10A). Together, they form the *thalamocortical system*. In fact,

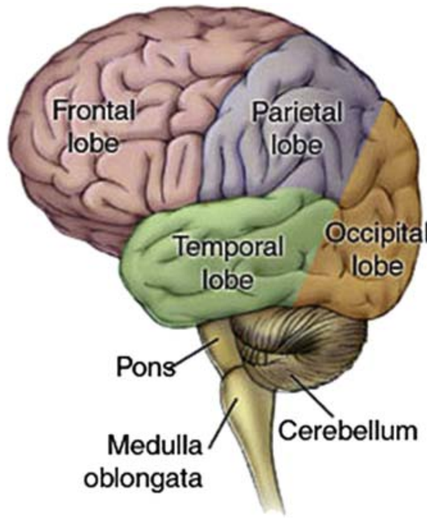

FIGURE 2.8 The four lobes of the cerebrum: frontal (shown in *pink*), parietal (shown in *purple*), temporal (shown in *green*), and occipital (shown in *orange*). *Source: Public domain. https://www.wpclipart.com/medical/anatomy/brain/brain_2/brain_anatomy.png.html.*

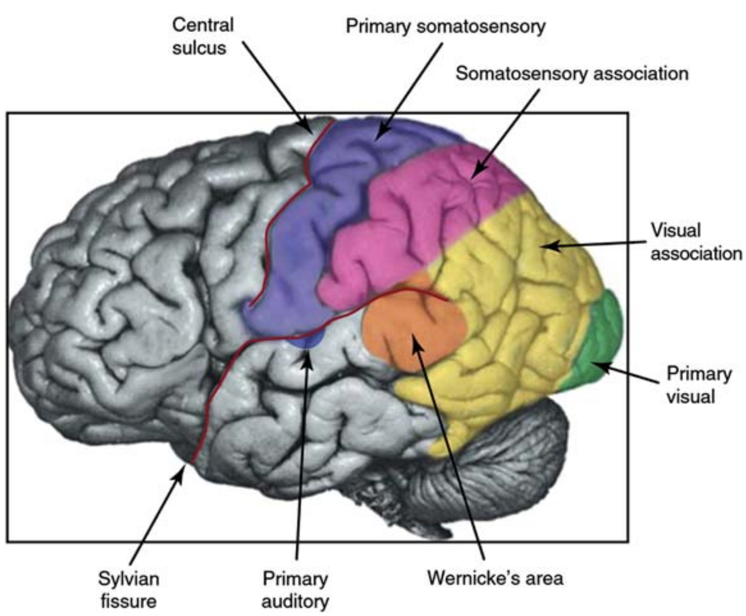

FIGURE 2.9 Brain landmarks: the massive Sylvian fissure runs from the ventral portion of the frontal lobe to the posterior of the brain, separating the parietal and temporal lobes. The central sulcus is a large sulcus separating the frontal lobe from the parietal lobe. *Source: Fig. 22.6, Fundamentals of Sensory Systems, SH Hendry & SS Hsiao, in LR Squire, D Berg, FE Bloom, S du Lac, A Ghosh, & NC Spitzer (Eds),* Fundamental Neuroscience, *4th edition, (pp. 499–511). San Diego: Academic Press.*

the thalamus and cortex are so highly interconnected that they can be thought of as a single massive brain system. The thalamic connections with the four lobes of the cortex are highly structured, with complex connective patterns between the thalamus and each cortical lobe as well as many other subcortical bodies and regions (Fig. 2.10B).

Basal ganglia are a group of subcortical nuclei or bodies that together are primarily engaged in influencing motor (movement) control along with the motor cortex and the spinal cord (Fig. 2.11A). Damage to the basal ganglia leads to motor dysfunction despite an intact motor cortex and spinal cord. The nuclei of the basal ganglia are located posterior to the frontal lobe and include the *putamen*, the *caudate nucleus*, the *globus pallidus*, and the *nucleus accumbens* (Fig. 2.11B). These nuclei play key roles in motor as well as emotional and cognitive functions of the brain.

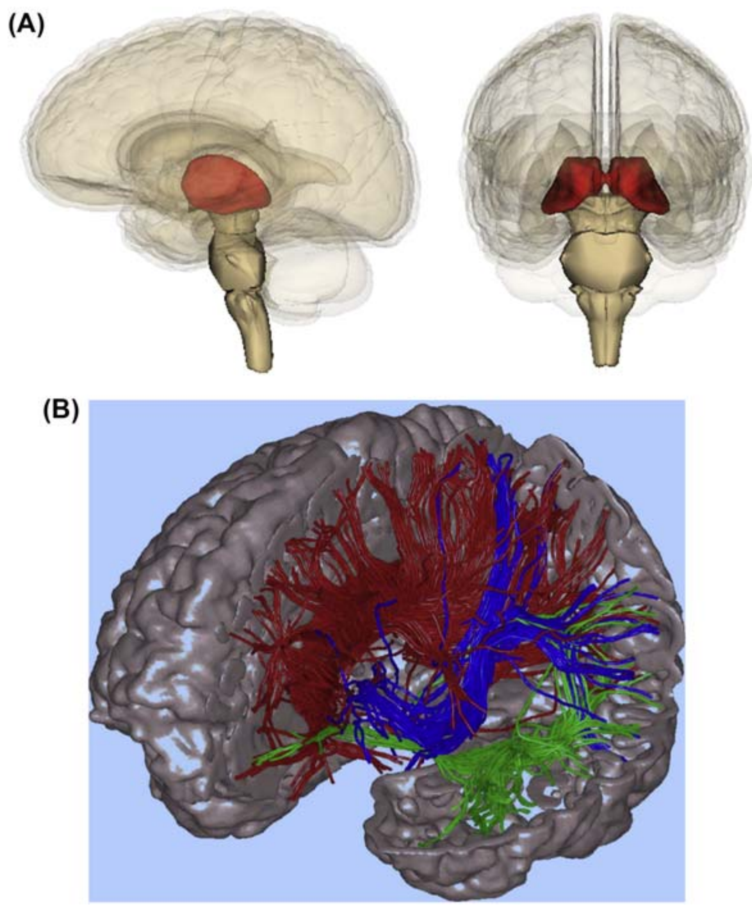

FIGURE 2.10 (A) The thalamus (shown in *red*) is located in the middle of the brain in the subcortical region. (B) The thalamus is highly interconnected with the cortex, with fibers extending to the frontal, parietal, temporal, and occipital lobes (shown in *red*, *blue*, and *green* in this diffusion tensor study). *Source: Left: Images are from Anatomography maintained by Life Science Databases(LSDB). Life Science Databases (LSDB)の Anatomography. Right: Izhikevich, E. M, & Edelman, G. M. 2007.*

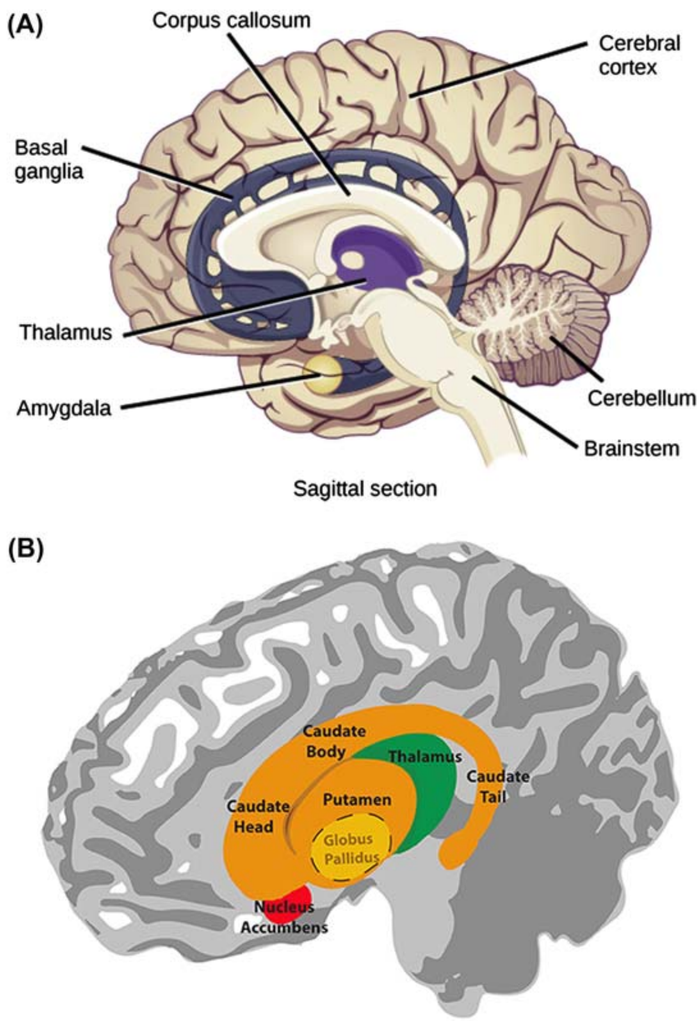

FIGURE 2.11 (A) *Basal ganglia* are a group of subcortical nuclei or bodies that together are primarily engaged in influencing motor (movement) control along with the motor cortex and the spinal cord. *The amygdala* and other regions in the subcortical region primarily function as our emotional processors. The tiny amygdala gets its name from the Latin word for almond: the amygdala is indeed an almond-shaped small body located in the center of the brain below the thalamus. (B) The nuclei of the basal ganglia are located posterior to the frontal lobe and include the *putamen*, the *caudate nucleus*, the *globus pallidus*, and the *nucleus accumbens*. These nuclei play key roles in motor as well as emotional and cognitive functions of the brain. *Source: A. Open Access. Courtesy of https://courses.candelalearning.com/biologymajors/chapter/chapter35-the-nervous-system/. Creative Commons Attribution. B. Open Access. Lim S-J, Fiez JA and Holt LL (2014) How may the basal ganglia contribute to auditory categorization and speech perception? Front. Neurosci. 8:230. https://doi.org/10.3389/fnins.2014.00230. http://journal.frontiersin.org/article/10.3389/fnins.2014.00230/full.*

The amygdala and other regions in the subcortical region primarily function as our emotional processors. The tiny amygdala gets its name from the Latin word for almond: the amygdala is indeed an almond-shaped small body located in the center of the brain below the thalamus (Fig. 2.11A). Highly interconnected with other subcortical regions and the cortex, the amygdala is part of the emotional system in the brain frequently referred to as the *limbic system.* Other brain areas that form part of the limbic system include the olfactory bulb, which provides information regarding the sense of smell; the hippocampus, which is critical for memory processing; and the cingulate gyrus. Together regions in the limbic system provide information to the cortex about emotionally relevant information in our sensory world, such as an angry face or voice. They are also key for the encoding and retrieval of emotional memories.

2.3 The Cerebellum

Located at the most posterior portion of the brain behind the temporal and occipital lobes, the cerebellum (shown in Figs. 2.5, 2.8, and 2.11A) has a variety of roles in human movement, learning, and cognition. While the cerebellum does not initiate motor commands—these come via the cortical motor pathways—the cerebellum plays a key role in modifying those commands. This results in the cerebellum controlling aspects of movement such as the maintenance of balance and posture and the coordination of complex movements.

The cerebellum also plays a role in motor learning. As you learn to drive a car, surf a wave, or shoot a basketball, the circuitry in the cerebellum is providing adaptive movement information to guide the motor learning process. Although there is less evidence about the cerebellum's role in cognition, converging evidence is providing support for a role for the cerebellum in language processing, which may be related to the complex movements entailed in forming human speech.

2.4 The Brainstem

Connecting the brain to the spinal cord and the rest of the body, the *brainstem* includes three key regions that are critical for human life: the *midbrain*, the *pons*, and the *medulla* (Fig. 2.12). This hub connects the spinal cord, with its many motor and sensory impulses sending key signals to the brain, to the brain itself. Passing through the brainstem region are major nerves that control movement, sensation, breathing control, and other core aspects of the human body. In the midbrain, the *inferior colliculus* transmits auditory signals. The *superior colliculus,* just above, transmits visual signals. The *reticular formation* will be discussed often in this book: this area within the midbrain transmits signals throughout the brain and is implicated in arousal and in human consciousness.

The pons, the middle section of the brainstem, comes from the Latin for *bridge*. Nestled between the midbrain and the medulla, the pons transmits signals from the cortex and subcortex to the medulla and the cerebellum as well as to the thalamus. The pons carries signals that control basic functions such as sleeping, equilibrium, and posture. The medulla, situated below the pons, has similar basic functions but is mostly in control of involuntary functions such as breathing, heart rate, and blood pressure. Damage to the brainstem can cause

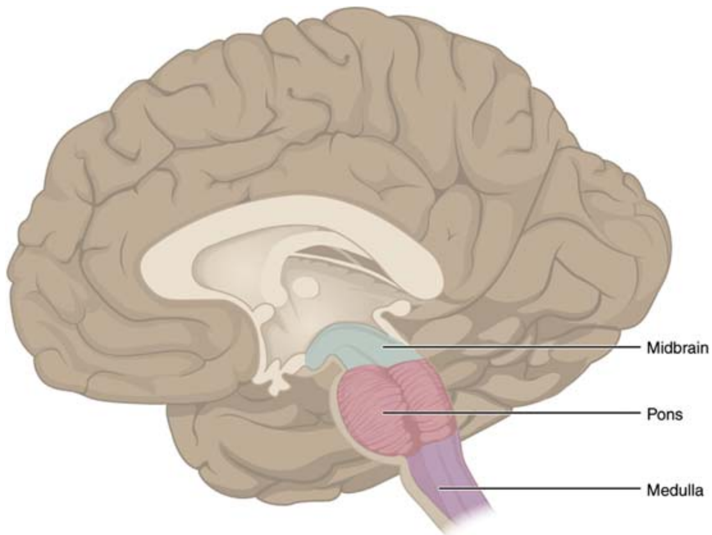

FIGURE 2.12 The brainstem. Connecting the brain to the spinal cord and the rest of the body, the *brainstem* includes three key regions that are critical for human life: the *midbrain* (shown in *green*), the *pons* (shown in *pink*), and the *medulla* (shown in *purple*). This hub connects the spinal cord, with its many motor and sensory impulses sending key signals to the brain, to the brain itself. Passing through the brainstem region are major nerves that control movement, sensation, breathing control, and other core aspects of the human body. *Source: Open Access. Version 8.25 from the Textbook OpenStax Anatomy and Physiology Published May 18, 2016. By OpenStax - https://cnx.org/contents/FPtK1zmh@8.25:fEI3C8Ot@10/Preface, CC BY 4.0.*

widespread impairments ranging from vision and hearing loss, weakness, paralysis, and even death. A key point to remember is that brainstem damage can cause paralysis and loss of movement control; however, if the cortex is unharmed, human awareness, cognition, and thought may be unaffected despite the obvious physical limitations due to brainstem damage. This condition is referred to as the *Locked-in Syndrome* because the patient cannot speak to verbalize their condition (see Chapter 13, Disorders of Consciousness).

Throughout the cortex, the subcortical regions, the cerebellum, and the brainstem, there are billions of *neurons*: the microscopic worker bees of the brain. Although there are hundreds of types of neurons, they share a classic structure, which we will refer to as the "idealized neuron." Let us turn now to a description of how neurons communicate throughout these disparate regions of the brain that, together as an ensemble, form the intricate language of the brain and its connections.

3. BRAIN CELLS—NEUROPHYSIOLOGY

Neurophysiology is the study of the cells in the brain. While there are many types of cells in the brain performing vital functions, we will be discussing the *nerve cell* or the *neuron* in this chapter.

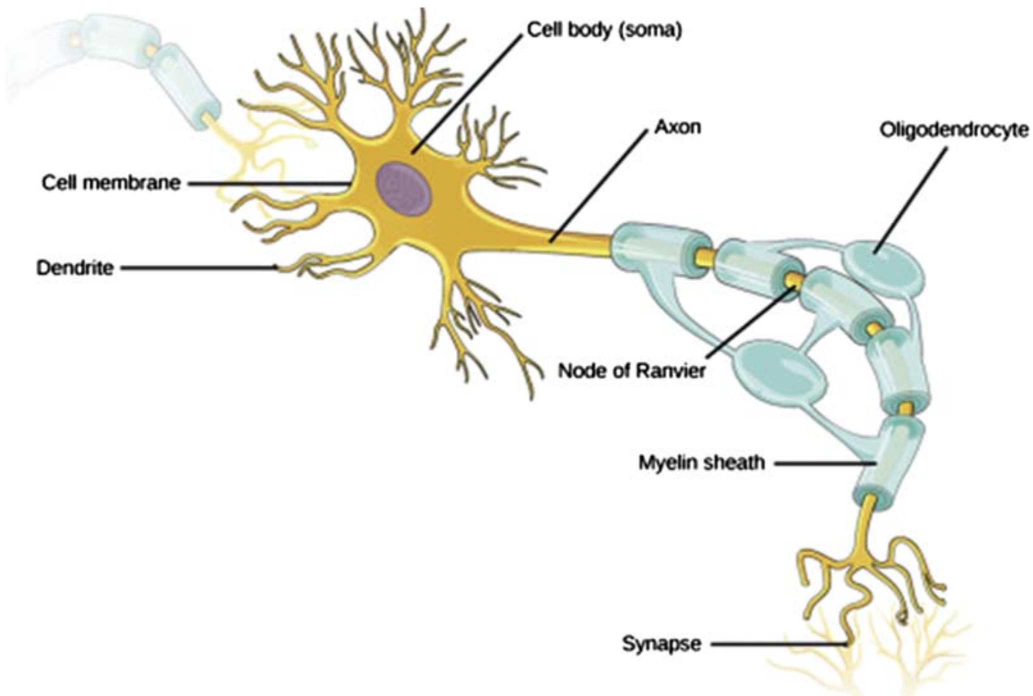

FIGURE 2.13 An idealized neuron. Although there are more than 200 types of neurons in the brain, most share some key features. *Dendrites* (left side of figure) are treelike structures around the *cell body or soma* of the neuron. The many dendrites receive incoming signals from other neurons. This is the *input* to the neuron. Extending from the cell body is the *axon*: axons vary in length and can extend long distances along a hemisphere or across the two hemispheres. Covering many axons is a white fatlike substance: this is the myelin sheath that forms an insulating layer over the axon that increases the electrical conduction rate. When many axons are together in a bundle, the myelinated coverings form a light-colored fiber tract that is referred to as *white matter*. Note the Nodes of Ranvier in the myelin sheath: these are gaps in the myelin sheath that serve an important function. The gaps in the myelin sheath that exposes the axon aid in action potential generation. *Source: Public domain. Courtesy of https://courses.candelalearning.com/biologymajors/chapter/chapter35-the-nervous-system/. Creative Commons Attribution.*

3.1 The Structure of an Idealized Neuron

An "idealized" neuron is shown in Fig. 2.13. While there are hundreds of types of neurons in the brain, they share key features. *Dendrites* are treelike structures around the *cell body or soma* of the neuron. The many dendrites receive incoming signals from other neurons. This is the *input* to the neuron. Extending from the cell body is the *axon*: axons vary in length and can extend long distances along a hemisphere or across the two hemispheres. Covering many axons is a white fatlike substance: this is the myelin sheath, which forms an insulating layer over the axon that increases the electrical conduction rate. When many axons are together in a bundle, the myelinated coverings form a light-colored fiber tract that is referred to as *white matter*. In Fig. 2.13, note the Nodes of Ranvier in the myelin sheath: these are gaps in the myelin sheath that serve an important function. The gaps in the myelin sheath that exposes the axon aid in action potential generation are discussed in the following section.

At the end of the axon, synaptic terminals form the communication method for the *output* of the neuron: *the synapse*. Neurons do not directly connect with one another. Rather, the impulses propagate down to the axon to the *synaptic terminals* where they cross the *synaptic cleft*: a separation between transmitting neuron and the receptors. Although there are many complex ways in which brain cells interact, the *action potential* forms the key communication method for a neuron to communicate with another neuron or group of neurons.

3.2 Action Potentials

Neurons communicate with each other through a combination of electric and chemical processes. The cell membrane of a neuron has a *resting potential*—the voltage of the neuron—that is approximately −70 mV. The chemical aspect of the communication comes via the three basic ions that exist on the inside and outside of the cell membrane: potassium (K^+), calcium (Ca^{2+}), and sodium (Na^+) ions. When the neuron is not firing—i.e., when it is at rest—the *resting potential* of the neuron has potassium ions (K^+) that are more highly concentrated on the inside of the cell while calcium (Ca^{2+}) and sodium (Na^+) ions are more concentrated on the outside (Fig. 2.14).

When incoming input to the neuron increases to a given threshold—the *threshold potential*—the cell membrane will *depolarize*, lowering the voltage within the membrane. Ion channels open, the concentration of K^+, Ca^{2+}, and Na^+ ions within and without the membrane shifts, and an *action potential* occurs. The depolarization spreads down the axon towards the axon terminals where the synapse will occur (Fig. 2.15). The action potential or firing of the neuron is frequently termed a *spike* or an *impulse*. This action potential is propagated to the next neuron(s) via the synapse, thus forming the basic communication method for neurons. Note that the action potential is an *all-or-nothing event*: the neuron either *fires* or it does *not fire*.

3.3 Connectivity Basics

Connectivity patterns within the cortex and throughout the brain are complex and not easily simplified. There are a few basic working assumptions, however, that we will use to describe a general way in which brain connectivity occurs.

First, building upon the description of the action potential, above, neurons work by adding graded voltage inputs until the total membrane voltage on the target neuron goes past a threshold value. If it does, an all-or-nothing spike fires down the output branch, the axon. We will refer to these neurons as *integrate-and-fire* neurons.

Next, connections between neurons are either *excitatory* or *inhibitory*. Thus they can either cause the neuron they are synapsing with to fire (excitatory connection) or not to fire (inhibitory connection).

Third, neurons can form one-way pathways, such as from the optic nerve of the eye to the visual region of the thalamus (the lateral geniculate nucleus). However, one-way pathways are actually quite rare. More likely, neurons run in two directions, forming *two-directional pathways* and networks in which activity at Point A triggers activity at Point B and vice versa. This is often referred to as *reentrant connectivity* (Edelman, 1989).

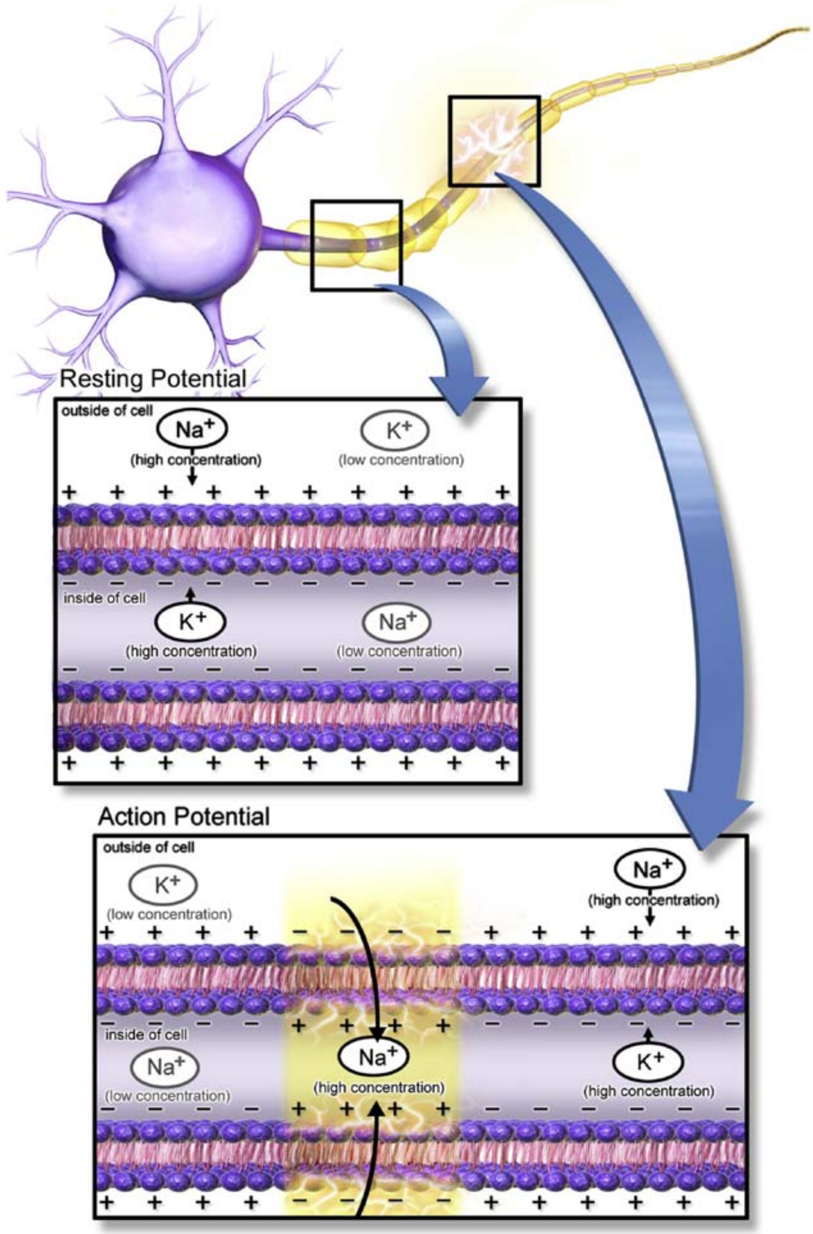

FIGURE 2.14 The resting and action potentials. Neurons communicate with each other through a combination of electric and chemical processes. The cell membrane of a neuron has a *resting potential*—the voltage of the neuron—that is approximately −70 mV. The chemical aspect of the communication comes via the three basic ions that exist on the inside and outside of the cell membrane: potassium ions (K^+), calcium (Ca^{2+}), and sodium (Na^+). When the neuron is not firing—i.e., when it is at rest—the *resting potential* (top insert box) of the neuron has potassium ions (K^+) that are more highly concentrated on the inside of the cell while calcium (Ca^{2+}) and sodium (Na^+) ions are more concentrated on the outside. When incoming input to the neuron increases to a given threshold—the *threshold potential*—the cell membrane will *depolarize*, lowering the voltage within the membrane. Ion channels open, the concentration of K^+, Ca^{2+}, and Na^+ ions within and without the membrane shifts, and an *action potential* occurs (bottom insert box). *Source: Public domain. Courtesy of https://courses.candelalearning.com/biologymajors/chapter/chapter35-the-nervous-system/. Creative Commons Attribution.*

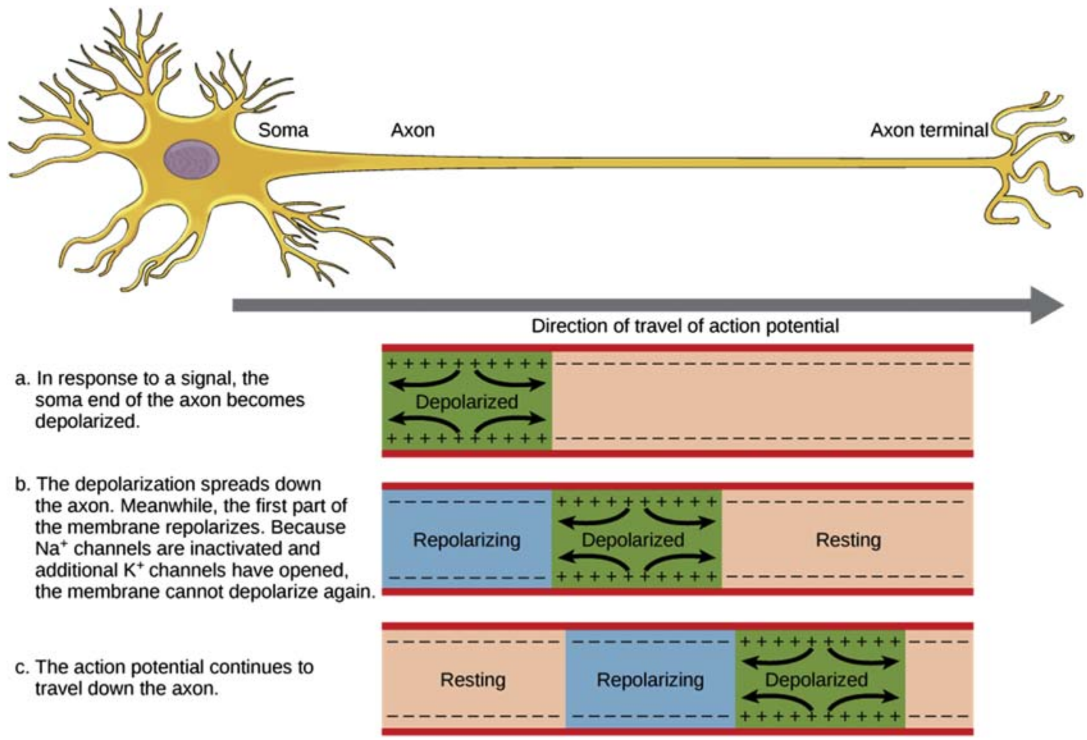

FIGURE 2.15 Action potential propagation. When the action potential occurs, the depolarization spreads down the axon towards the axon terminals where the synapse will occur. This action potential is propagated to the next neuron(s) via the synapse, thus forming the basic communication method for neurons. Note that the action potential is an *all-or-nothing event*: the neuron either fires or it does not. *Source: Public domain. Courtesy of /. Creative Commons Attribution.*

3.4 Brodmann Areas

And finally, the cerebral cortex is a massive six-layer array of neurons, with an estimated 10 billion cells and trillions of synaptic connections. Neurons are organized into arrays, which form maps that can reflect the perceptual world around us, as we will see in Chapter 4, The Art of Seeing. We mentioned at the beginning of this section that there are many, many types of neurons in the brain: more than 200. The study of the arrangement of neurons in the brain—typically under a microscope—provides key information about cortical regions in the brain. This type of study provides information about the cytoarchitecture—the cell architecture—of neurons in the brain. The German anatomist Korbinian Brodmann defined and numbered cortical regions according to their cytoarchitectural structure. These regions, called the Brodmann areas, are still in wide use today in describing discrete cortical subregions (Fig. 2.16, Brodmann regions open source).

While the neuron forms the basic "worker bee" of the brain, the more complete story behind how the brain functions comes from the *dynamical aspects* of their communication across neural arrays and networks. We will discuss these in more depth later in the chapter. First, let us take a look at the basic functions of the brain.

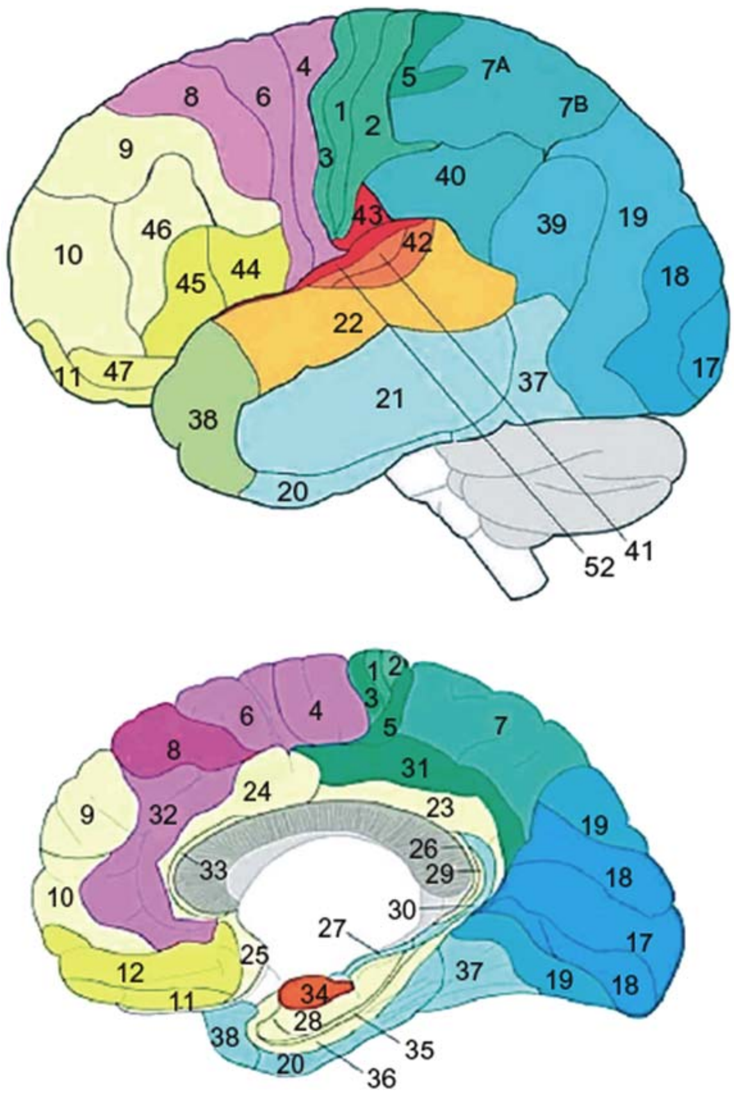

FIGURE 2.16 Brodmann areas. The German anatomist Korbinian Brodmann defined and numbered cortical regions according to their cytoarchitectural structure. These regions, called the Brodmann areas, are still in wide use today in describing discrete cortical subregions. *Source: Baars & Fu, with permission.*

4. BRAIN FUNCTION—FUNCTIONAL NEUROANATOMY

4.1 Right Brain—Left Brain

As we have discussed, there are two cerebral hemispheres linked only by the massive fiber structures that course through the corpus callosum (Fig. 2.7). While the two hemispheres are very similar in structure, they are not identical: there are proportional differences in various regions and especially around the Sylvian Fissure. These anatomical differences have led to investigations of whether the two hemispheres perform differing cognitive functions: are some cognitive functions lateralized to a single hemisphere? Or do both hemispheres participate in all cognitive functions?

Perhaps the most well-understood lateralization of function is human language: for most humans regardless of race or natural language, spoken language function is lateralized to the left hemisphere. We will discuss this in far more depth in Chapter 6, Language and Thought. Briefly, we have learned through cases of brain damage that spoken language can be selectively disrupted if that damage is in the left frontal region of the brain. Other, more subtle lateralization of cognitive functions appears to exist in the two hemispheres, leading to many investigations into "right brain—left brain" cognition. However, as a general rule, both hemispheres participate in cognitive functions and it is likely that the hemispheres play similar but slightly differing roles in these functions rather than performing as specialized for cognitive processes such as attention, memory, and language.

4.2 The "Front-Back" Division

We have mentioned one way to divide the human brain—the left and right cerebral hemispheres form one way to separate regions of the brain. Another basic way to divide the brain's functions is to look at the "front" of the brain and the "back" of the brain. The front-back division in the brain distinguishes the brain regions where most of the incoming sensory information arrives from the periphery (the "back" of the brain) from the brain regions where most of the outgoing motor acts or movements are generated (the "front" of the brain).

Take a look back at Fig. 2.9: the frontal lobe is separated from the remaining three lobes by the Central Sulcus at the top of the brain and the Sylvian fissure in the middle of the brain as seen from the side or lateral view. While the "back" of the brain has many functions it perform, one key set of functions is that it forms the primary "landing place" for sensory inputs that come from the eyes, the ears, and the nerves of the body. These senses, vision, audition, and somatosensory, are the three key cortical senses. Rounding out the five senses are the chemical senses of taste and smell, which have noncortical landing places.

4.2.1 Sensory and Motor Functions

Sensory information comes to the cortex from pathways from the eyes, ears, and body to regions of cortex specialized for processing that sensory information (Fig. 2.17). The brain areas that correspond to these specialized regions are called *primary sensory areas* because they are typically the first or main "landing spot" for those pathways. Thus there is a *Primary Visual Cortex*, *Primary Auditory Cortex*, and *Primary Somatosensory Cortex* located in each

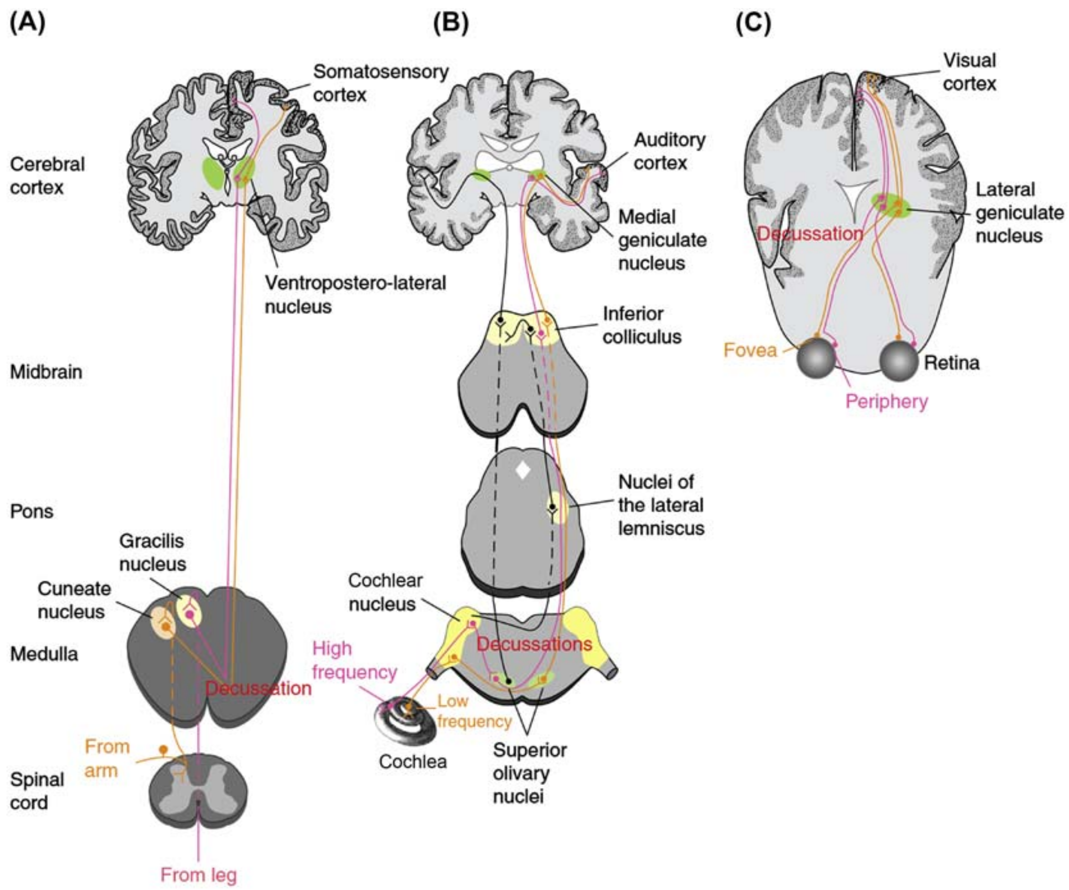

FIGURE 2.17 Sensory information comes to the cortex from pathways from the body, ears, and eyes to regions of cortex specialized for processing that sensory information. The somatosensory pathways from the body to the somatosensory cortex in the parietal lobe are shown in (A). These pathways carry pain, pressure, and touch signals. The auditory pathways from the ears to the auditory cortex in the temporal lobe are shown in (B). These pathways carry sound signals. The visual pathways from the eyes to the visual cortex are shown in (C). These pathways carry visual signals. The brain areas that correspond to these specialized regions are called *primary sensory areas* because they are typically the first or main "landing spot" for those pathways. Thus there is a *Primary Somatosensory Cortex*, a *Primary Auditory Cortex*, and a *Primary Visual Cortex* located in each hemisphere: therefore there are actually two Primacy Somatosensory Cortices, two Primary Auditory Cortices, and two Primary Visual Cortices. *Source: Fig. 22.5, Fundamentals of Sensory Systems, SH Hendry & SS Hsiao, in LR Squire, D Berg, FE Bloom, S du Lac, A Ghosh, & NC Spitzer (Eds),* Fundamental Neuroscience, *4th edition, (pp. 499−511). San Diego: Academic Press.*

hemisphere: therefore there are actually two Primacy Visual Cortices, two Primary Auditory Cortices, and two Primary Somatosensory Cortices.

Motor information goes from the motor cortex to the body via the brainstem and spinal cord. As in the case of the sensory systems, there is a *Primary Motor Cortex*. In this case, the Primary Motor Cortex is generally the *last* cortical region before the signals are sent on

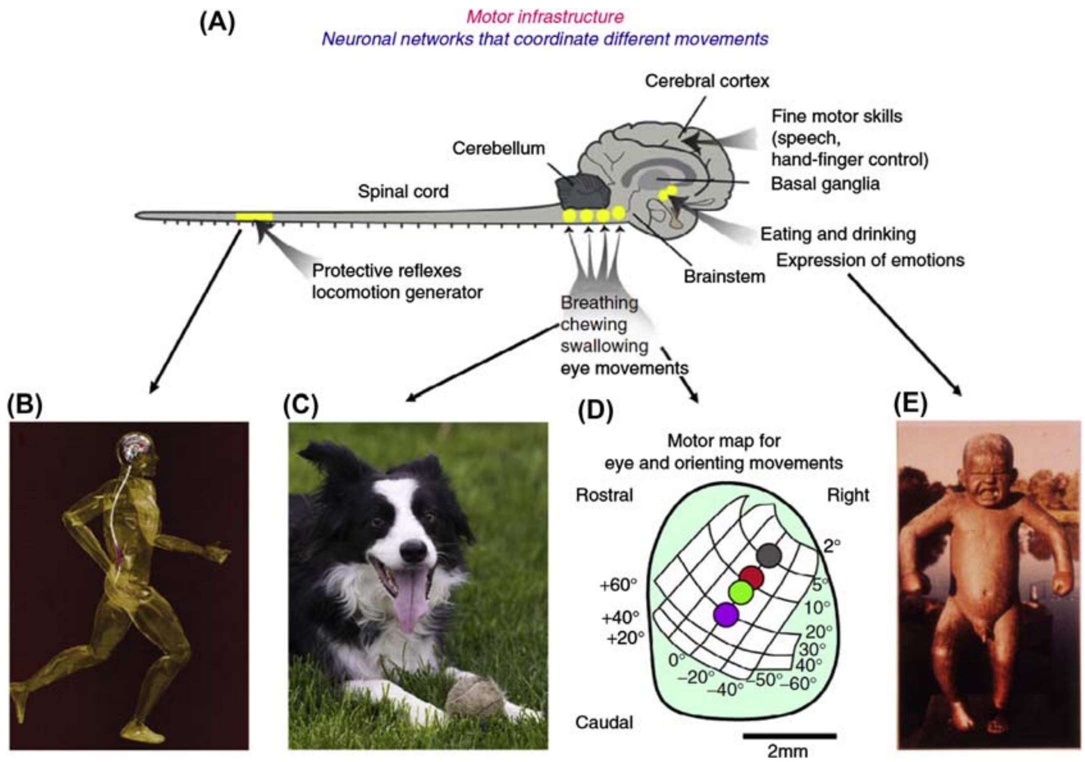

FIGURE 2.18 The motor system is complex, with many layers of circuitry that control fine motor skills, such as speech, and more automatic functions, such as breathing and swallowing, and even more basic motor functions, such as reflexes. The neural circuitry of the motor system reflects these disparate functions. (A) The neural circuitry of the motor system reflects these disparate functions, with functions ranging from the spinal cord (left of figure), to the cerebellum (center of figure), brainstem (to the right of the cerebellum), and to the cerebral cortex (top right of figure). (B) The spinal cord contains the network for moving or locomotion. (C) The brainstem contains networks that control basic and largely automatic movements such as breathing, swallowing, and eye movements. (D) A motor "map" in the brainstem for controlling eye movements. (E) More complex movements such as those underlying the expression of emotion (as shown in this sculpture of an angry child by Vigeland), are controlled largely in the cerebral cortex. *Source: Fig. 27.5, Fundamentals of Motor Systems, S Grillner, in LR Squire, D Berg, FE Bloom, S du Lac, A Ghosh, & NC Spitzer (Eds),* Fundamental Neuroscience, *fourth edition, (pp. 599−611). San Diego: Academic Press.*

to the body. The motor system is complex, however, with many layers of circuitry that control fine-motor skills, such as speech, and more automatic functions, such as breathing and swallowing, and even more basic motor functions, such as reflexes. The neural circuitry of the motor system reflects these disparate functions (Fig. 2.18).

4.3 The Cerebral Lobes

While the two hemispheres and the front-back division of the brain provide a basic sense of how the brain's functions are organized, the four cerebral lobes are perhaps the clearest way to understand the way sensory and cognitive processes are organized in the cortex. Underlying the functional roles that are organized across the four lobes are the vast white matter networks that connect them and the key subcortical regions that form the massive hub of the thalamocortical network.

4.3.1 The Frontal Lobe

As we discussed in the "front-back division" section, the frontal lobe is the site for motor planning and motor output. The motor areas are located just anterior to the Central Sulcus (Fig. 2.9). The motor cortex is structured with a "map" of the body: this is referred to as the *homunculus* ("little man") as it contains all parts of the body. The representation of differing body parts in the motor cortex is not proportional to those body parts; however, some areas of the body—such as the face, mouth, and hands—have a proportionately larger representation in motor cortex than other body areas such as the back and trunk of the body (Fig. 2.19). The fine dexterity of the mouth and speech−generating apparatus and the hands and fingers reflects the high proportion of neurons governing their movements from the motor cortex. The relatively low dexterity and fineness of motion control in the back and trunk of the body also reflects the lower proportion of neurons governing their movements.

Note that the motor cortex is closely situated to the somatosensory areas that are located just posterior to the Central Sulcus. In fact, there is a homunculus in this region as well, with a similar disproportionate representation of the face, hands, and fingers for the sensations of touch, pressure, and pain. This makes some logical sense as you consider that the senses of pain, pressure, and touch are tightly coupled with motor movements and reactions.

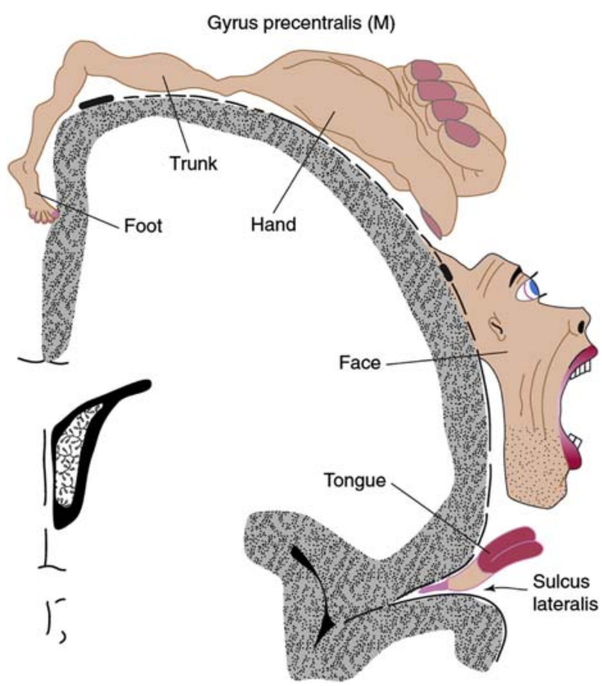

FIGURE 2.19 The motor homunculus. The motor cortex is structured with a "map" of the body: this is referred to as the *homunculus* ("little man") as it contains all parts of the body. The representation of differing body parts in the motor cortex is not proportional to those body parts; however, some areas of the body—such as the face, mouth, and hands—have a proportionately larger representation in motor cortex than other body areas such as the back and trunk of the body. *Source: Fig. 27.6, Fundamentals of Motor Systems, S Grillner, in LR Squire, D Berg, FE Bloom, S du Lac, A Ghosh, & NC Spitzer (Eds),* Fundamental Neuroscience, *4th edition, (pp. 599−611). San Diego: Academic Press.*

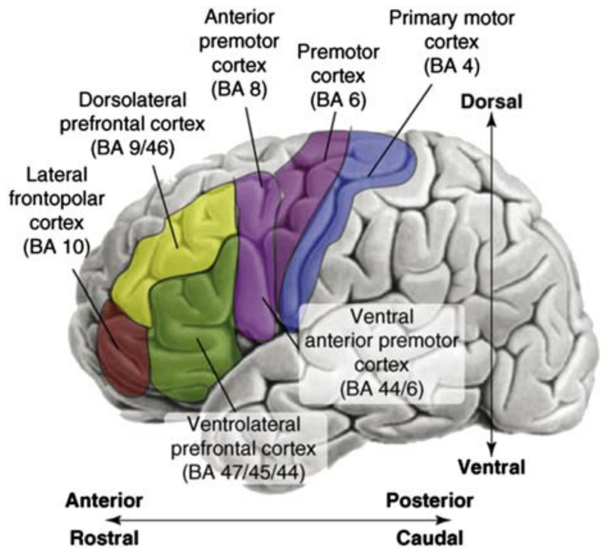

FIGURE 2.20 The functional organization of the frontal lobe. The frontal lobe is home to Motor Cortex, which controls movement. However, much of the frontal lobe is devoted to many key areas of human cognition. The *prefrontal cortex (PFC)*—that is, the area in front region of the frontal lobe—is the nonmotor area of the frontal lobe. In some ways, the PFC is the most cognitive region of the brain. The PFC is highly interconnected with the thalamus, other subcortical regions, as well as with the other three lobes of the cerebral cortex. Note: BA refers to approximate Brodmann area locations. *Source: Fig. 1, Badre, D. 2008 Cognitive control, hierarchy, and the rostro-caudal organization of the frontal lobes. TICS 12(5), 193–200, with permission.*

Returning to the functional organization of the frontal lobe, many other key cognitive functions are located in the massive frontal lobes. The Prefrontal Cortex—PFC—that is, the area in the front region of the frontal lobe—is the nonmotor area of the frontal lobe. In some ways, the PFC is the most cognitive region of the brain. It is here that our "*executive*"functions are located: those processes that allow us to plan for the future, make decisions, and focus our attention on one thing and not another. Like an executive in a large firm, the PFC does not do all of the cognitive "work" of the brain but rather controls it and synthesizes it. The PFC is highly interconnected with the thalamus, other subcortical regions, as well as with the other three lobes of the cerebral cortex (Fig. 2.20).

The PFC is critical for many key human processes such as

- initiating activities
- planning
- holding critical information ready for use (an aspect of working memory)
- changing mental set from one line of thinking to another, mental flexibility
- monitoring the effectiveness of one's actions
- detecting and resolving conflicting plans for action
- inhibiting plans and actions that are ineffective or self-defeating

This brief list—and the many other cognitive processes that the PFC regulates—demonstrates how critical this part of the brain is to human cognition. Other key functions of the mighty frontal lobe include emotional and personality processing that is important for social cognition. Human expressive speech systems are also located in the frontal lobe in a region called Broca's area, named after Paul Pierre Broca (see Chapter 6, for more on this region).

4.3.2 The Parietal Lobe

Just posterior to the frontal lobe is the parietal lobe. The anterior region of the parietal lobe, just posterior to the Central Sulcus, is home to the somatosensory cortex (Fig. 2.9). As mentioned previously, the somatosensory cortex has a body "map"—homunculus—similar to the one in the motor cortex (Fig. 2.19) that has a disproportionate representation of the body, similar to the motor homunculus. In the case of the somatosensory cortex, the expanded neural representation corresponds to finer senses of touch, pressure, and pain in regions such as the hands, mouth, and face.

The location of the somatosensory cortex in the parietal lobe is just the beginning of this lobe's complex role on human brain function. The parietal lobe is a key region of the visual "where" pathway (see Chapter 4, for more on this). This pathway is instrumental in object location, among many other visual processes. Another important function of the parietal lobe is the integration of multiple maps of body space. These maps reflect several key regions for mapping motor activity with the visual system, for example. Think about approaching a coffee cup on a nearby table. Your visual system is mapping where the cup is, while your body maps are preparing the neural code for the action of reaching your hand out to grasp the cup. Let us imagine that you were a distance away from that coffee cup: other body maps would integrate information from the visual system with your body's motor system so that you could guide your movements to walk to the table, reach for the cup, grasp the cup, and so on. These body maps provide us with the idea of where we are in space: multiple maps can guide our hands vis a vis our mouth, for example, while we are eating, while others can guide us in other complex body mapping situations such as learning to skate board or surf. While these body maps seem to be tightly related to the visual system in helping to guide our movements, other sensory inputs are also actively involved.

The inferior portion of the parietal lobe—the inferior parietal lobe or IPL—is thought to be a multisensory region where information from the somatosensory, visual, and auditory systems is combined or integrated. The specific nature of the IPL and the parietal lobe's role in cognition is still being elaborated.

4.3.3 The Temporal Lobe

The temporal lobe is nestled posterior to the frontal lobe and inferior to the parietal lobe. The temporal lobe is home to the auditory system for sound processing: Primary Auditory Cortex is tucked into the upper bank of the temporal lobe within the Sylvian fissure (Fig. 2.9), thus is it not visible from a lateral view of the cortex. Just posterior to the auditory cortex is a region known as Wernicke's area, named after Carl Wernicke who studied speech perception pathways in the brain (see Chapter 6, for more on this). The middle sections of the lateral aspect of the temporal lobe are key regions for conceptual knowledge, with many theories of conceptual representation in the brain identifying these areas as important for conceptual knowledge storage. The temporal lobe is a key region of the visual "what" pathway (see Chapter 4, for more on this). This pathway is instrumental in object and face recognition, among many other visual processes.

4.3.4 The Medial Temporal Lobe

The medial section of the temporal lobe plays such a key role in human cognition that it is singled out with its own functional description. Located in the heart of the brain in the medial region of the temporal lobe (Fig. 2.21), the function and the anatomy of the

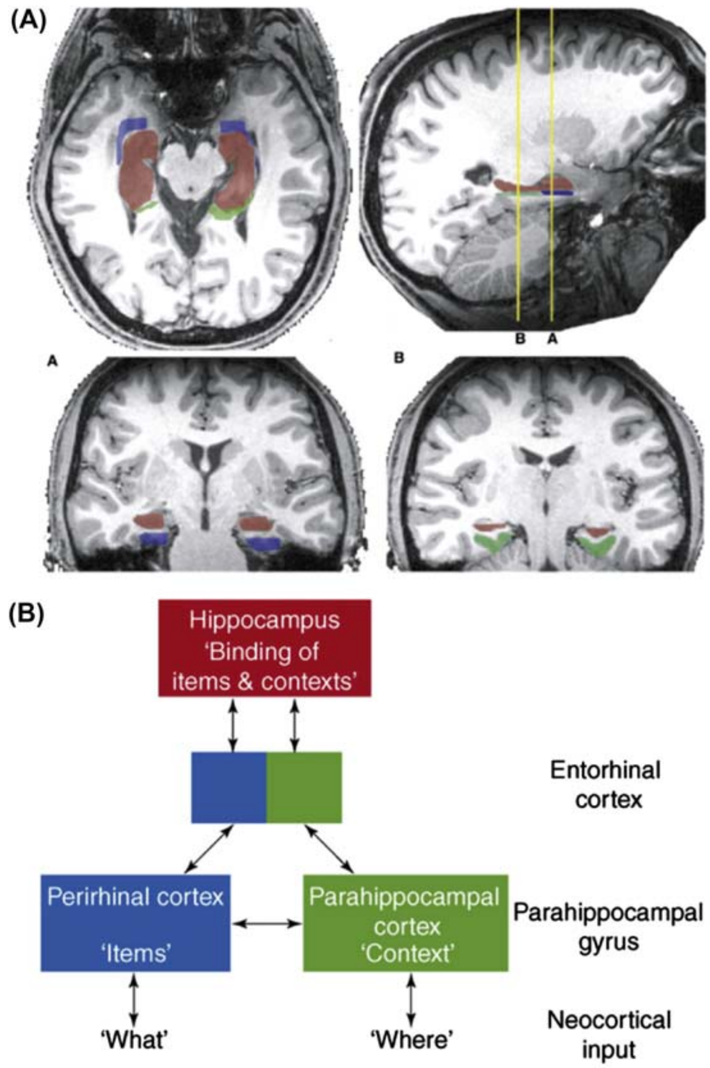

FIGURE 2.21 The medial temporal lobe. (A) The anatomy of the medial temporal lobe (MTL) is shown on axial (left top), sagittal (top right), and coronal (bottom central) slices of the brain. The approximate locations of the hippocampus are shown in *red*, the perirhinal cortex is shown in *blue*, and the parahippocampal cortex is shown in *green*. Note that these brain structures tucked into the MTL are overlapping due to their close proximity (B). The hypothesized connectivity and functional roles of the regions within the MTL in memory processing according to the authors' '"binding of item and context"' (BIC) model: the *arrows* between the hippocampus (*red rectangle*) extending through the entorhinal cortex to the perirhinal cortex (in *blue*) and parahippocampal gyrus (in *green*) reflect bidirectional connections for encoding "'item-related aspects'" such as what is an item (*blue rectangle*) and "'context-related aspects"' such as where that item is located (*green rectangle*). *Source: Diana, Yonelinas, and Ranganath (2007). Medial Temporal Lobe Trends in Cognitive Sciences 11(9), 379–386. Fig. 3, with permission.*

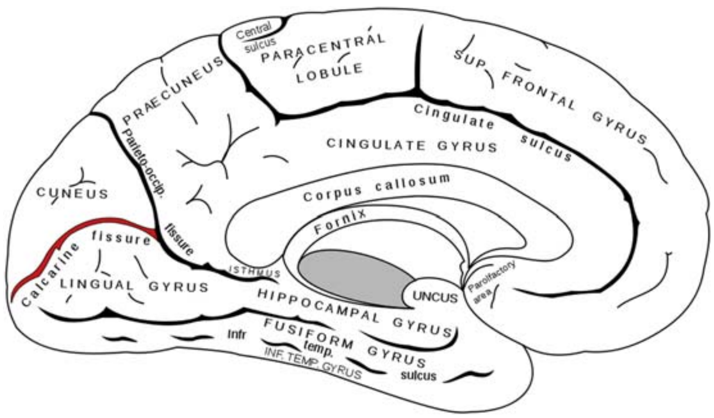

FIGURE 2.22 The Calcarine fissure. Much of visual cortex is tucked into the *Calcarine sulcus* (or fissure) that is located on the inside of the occipital lobe between the hemispheres (shown in *red* in the posterior region of the brain). *Source: Public domain. https://en.wikipedia.org/wiki/Calcarine_sulcus#/.*

medial temporal lobe (MTL) differs strikingly from the rest of the temporal lobe and is further justification to provide a separate description of its role in the brain. The MTL is home to the hippocampus and related regions that are associated with memory functions, including the perirhinal, parahippocampal, and entorhinal cortical regions (Fig. 2.21). As we will see in more detail in Chapter 7, Learning and Remembering, the MTL is key to memory formation and memory storage.

4.3.5 The Occipital Lobe

The occipital lobe, posterior to both the parietal and temporal lobes, is home to Primary and Association Visual Cortex (Fig. 2.9). Much of visual cortex is tucked into the *Calcarine sulcus* (or fissure) that is located on the inside of the occipital lobe between the hemispheres (Fig. 2.22). Thus, the occipital lobe contains the complex, multifaceted neural ensembles that form the basis for human vision and visual perception. As we will see in Chapter 4, there are many subregions within visual cortex in the occipital lobe that play central roles in our sense of the sights in the world around us.

5. BRAIN PATHWAYS: NEUROCONNECTIVITY

The brain has massive interconnectivity, the heart of which is the *thalamocortical hub* connecting virtually every region of cortex with the thalamus and other cortical and subcortical regions (Fig. 2.10) (Box 2.1).

Several major fiber pathways—white matter tracts—course through the brain. Three major ones are the *arcuate fasciculus*, the *corpus callosum*, and the *internal capsule/corona radiata*; however there are many more.

BOX 2.1

THE CONNECTOGRAM

Is there an easy way to "see" the brain's massive, multidimensional interconnectivity? This has been a challenge for the field of neuroscience but recent progress has revolutionized the way we visual the brain and its connections. Enter the *Connectogram* (Fig. 2.23).

Visualizing Brain Interconnectivity

Brain regions are hugely interconnected: for example, the thalamocortical circuitry connects almost every region of the cortex to the mighty thalamus and back. A central goal in understanding brain connectivity is to provide ways to visualize these highly interconnected pathways that course throughout the brain. Many methods for displaying them use three-dimensional graphical programs and a user interface. These methods do not lend themselves to an easy-to-use two-dimensional website, figure, or printout of the brain's connectivity.

The Connectogram was developed as a graphical representation of brain connectivity data studied using *connectomics*, the discipline for mapping and interpreting fiber connections in the brain. An early version was devised by Andrei Irimia and Jack Van Horn and colleagues (Irimia, Chambers, Torgerson, & Van Horn, 2012). Today there are many versions of connectograms, all building around a similar theme.

Interpreting A Connectogram

Although not an easy graph to understand at first sight, the connectogram provides many levels of analysis in a single graph. Let us step through those levels of analysis.

Take a look at Fig. 2.23: the circle reflects the entire brain (but dominated by the cortex). The left side of the circle reflects the left hemisphere, and the right side reflects the right hemisphere. On the outside edge of the circle, the lobes and brain regions are listed beginning with the left and right frontal lobes on the left and right upper sides of the circle. Moving down the outside of the circle, you will see Insula cortex, Limbic lobe, and down through the brain regions until you arrive at the brainstem at the center bottom of the connectogram. Subregions within each lobe and brain region are detailed along the outside edge of the connectogram. Each subregion has been given a color coding. Their abbreviations and fully detailed region names can be found on Wikipedia (https://en.wikipedia.org/wiki/Connectogram).

Concentric Rings Provide More Structural Information

Next, there are five rings that form concentric circles inside the connectogram. The legend for these rings is shown in Fig. 2.23B, and briefly refers to structural attributes of each region such as gray matter volume and surface area. The innermost ring is labeled as "degree of connectivity," with the darker colors reflecting more fibers (connections) initiating or terminating in that brain region. Take a look at the upper left section of the connectogram in Fig. 2.23 and search for a

BOX 2.1 *(cont'd)*

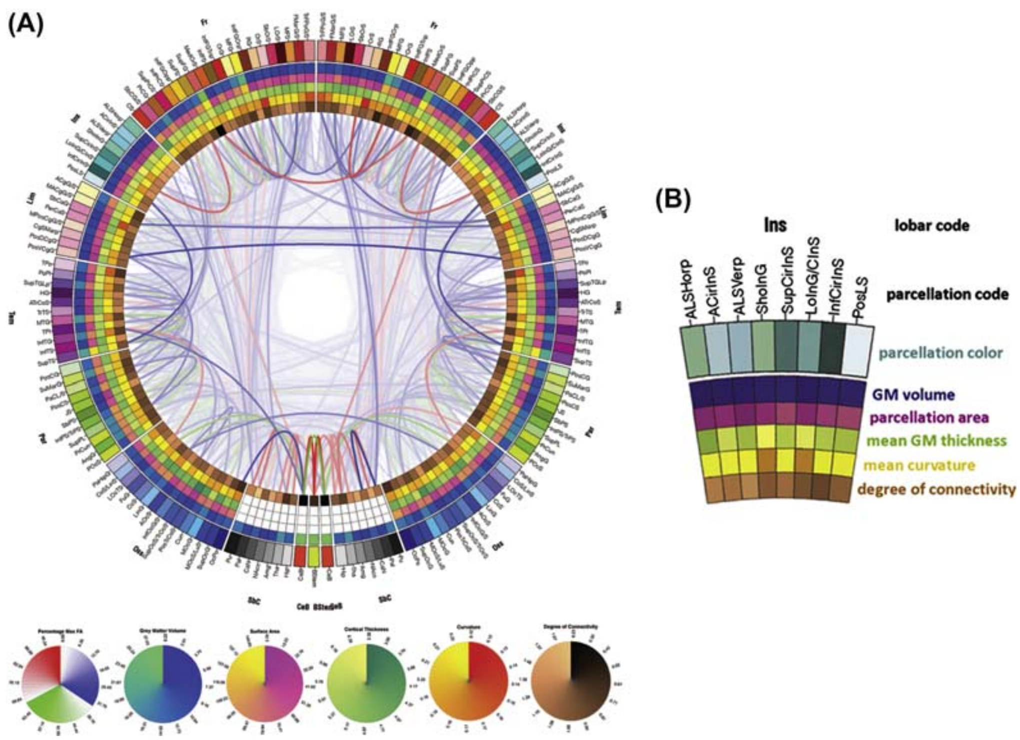

FIGURE 2.23 The Connectogram. (A) The circular Connectogram is a graphic way to show brain connectivity. The left half of the circle depicts the left hemisphere and the right half depicts the right hemisphere. The lobes and subregions of each hemisphere are shown and labeled, beginning at the top of the circle, as frontal lobe (fr), insular cortex (Ins), limbic lobe (Lim), temporal lobe (Tem), parietal lobe (Par), occipital lobe (Occ), subcortical structures (SbC), and cerebellum. The brainstem (BStem) is shown at the bottom of the circle, between the two hemispheres. Within the lobes, each cortical area is labeled with an abbreviation and an assigned color. Note the five rings that are inside the Conneectogram, just next to the color-coded cortical regions. The legend for these rings is shown in B. In the center of the Connectogram, lines connect regions that are structurally connected. The relative density (number of fibers) of these connections is reflected in the opacity of the lines, with the more opaque lines reflecting less densely connected regions and the less opaque lines reflecting more densely connected regions. The color of the line is color coded to reflect the density of fibers within that connection. (B) The legend describing the rings of the Connectogram, which show different attributes of the corresponding cortical regions. From outermost to innermost, the rings represent the grey matter volume, surface area, cortical thickness, curvature, and degree of connectivity. *Source: Open access. John Darrell Van Horn - PLoS One, http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0037454. A connectogram showing the average connections and cortical measures of 110 normal, right-handed males, aged 25–36.*

Continued

BOX 2.1 *(cont'd)*

very dark brown, almost black, inner ring. You will find one labeled as SupFG: this is the Superior Frontal Gyrus in the frontal lobe that has many fibers beginning and ending in its region as compared to the rest of the brain. At the bottom of the connectogram, you will see similar dark boxes in the innermost ring at the BStem, the brainstem.

Connectivity Shown With Lines in the Center of the Connectogram

Now take a look at the center of the connectogram. This is a key region for beginning to visualize brain connectivity. You will see many lines that extend from one brain region to another that vary sharply in their opacity. The *opacity* of the line reflects the *density of the fibers* in that connection, with darker or less opaque lines referring to dense connections between those brain regions. The color of the lines reflects the *fractional anisotropy* of the connection, with blue associated with lower values, green with mid values, and red with higher values. Fractional anisotropy is a measure of the directional dependence of the connection, which is based on the diffusion tensor imaging technique, which provides the data for the color-coding of these lines (see Chapter 3, Observing the Brain).

Comparing Group Data to Individuals With Brain Damage

One interesting use of the connectogram is to visualize individual brain data as compared to group data of healthy individuals. The connectogram shown in Fig. 2.23 reflects data from a group of healthy young men between the ages of 25–35 years. How is the connectogram changed when evaluating someone with brain damage?

The Famous Case of Phineas Gage

You may have read about the case of Phineas Gage, a 25-year old railroad construction supervisor. In 1848, an accident caused a tamping iron to shoot through his skull and brain in the left frontal area (Fig. 2.24A). His cognitive and personality changes following the accident were well documented and led to our understanding of the role of the left ventral PFC in human cognition. What happened to the massively interconnected frontal lobe when this terrible brain injury occurred? Irimia, Van Horn, and colleagues were curious about this question and using the CT scan of Gage's brain, developed a connectogram just for him (Fig. 2.24B, Van Horn et al., 2012). In this connectogram, the color of the lines in the center of the figure that reflect the connectivity of the brain regions is coded so that gray-scale lines reflect completely severed connections between those brain regions while tan-scale lines reflect partially severed connections.

The Future of the Connectogram

The connectogram showed in Fig. 2.23 was developed from data from a sample of men aged 25–35 years and thus represents brain connectivity in healthy young men. This raises many interesting questions for future research. Does a connectogram differ for healthy young women? For children?

BOX 2.1 (cont'd)

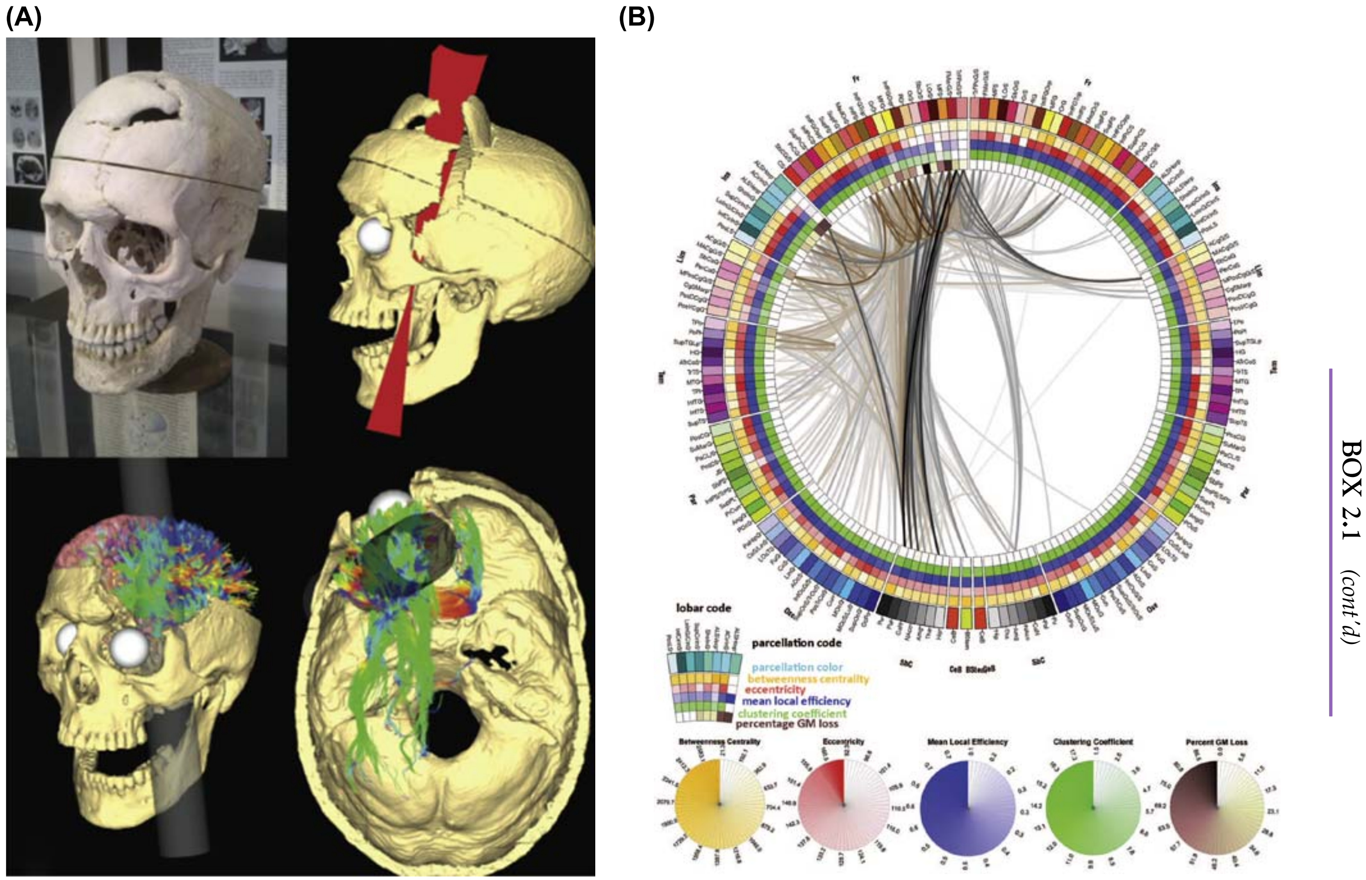

FIGURE 2.24 The case of Phineas Gage. (A) A computed tomography scan of Phineas Gage's brain damage due to the tamping iron accident where the iron entered his skull and brain through his left cheek and eye. (B) The connectogram of Gage's brain. In this connectogram, the color of the lines in the center of the figure that reflect the connectivity of the brain regions is coded so that gray-scale lines reflect completely severed connections between those brain regions while tan-scale lines reflect partially severed connections. *Source: Open access. Mapping Connectivity Damage in the Case of Phineas Gage (2012). John Darrell Van Horn, Andrei Irimia, Carinna M. Torgerson, Micah C. Chambers, Ron Kikinis, Arthur W. Toga. PLOS One Open Access Journal PLoS ONE 7(5): e37454. Figs. 1 and 3,* https://doi.org/10.1371/journal.pone.0037454.

Continued

BOX 2.1 *(cont'd)*

And how does it change in normal aging and in disorders and diseases such as autism, Alzheimer disease, and schizophrenia? Because the connectogram can be developed for a single individual, as well as in a group study, there are likely many clinical applications that will be very useful for individuals with traumatic brain injury or stroke. Perhaps the connectogram will provide information for recovery from these disorders and diseases—or at least provide information about which pathways have been affected so that clinical treatment and therapy can be individually adapted for each person.

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(1) Irimia, A., Chambers, M. C., Torgerson, C. M., & Van Horn, J. D. (2012). Circular representation of human cortical networks for subject and population-level connectomic visualization. *NeuroImage*, *60*(2), 1340—1351. http://doi.org/10.1016/j.neuroimage.2012.01.107

(2) Van Horn, J. D., Irimia, A., Torgerson, C. M., Chambers, M. C., Kikinis, R., Toga, A. W. (2012). Mapping connectivity damage in the case of Phineas Gage. *PLoS One*, *7*(5), 1—23.

5.1 The Arcuate Fasciculus

The arcuate fasciculus is a major anterior/posterior tract (Fig. 2.25). The arcuate fasciculus is a white matter bundle that contains both long and short fibers that connect the frontal, parietal, and temporal lobes (Catani & Thiebaut de Schotten, 2008). The arcuate plays a key role in the left hemisphere in language processing (Fig. 2.26) and in the right hemisphere in visuospatial processing and some aspects of language processing (Fig. 2.27), such as prosody and semantics (Catani & Thiebaut de Schotten, 2008).

5.2 The Corpus Callosum

The corpus callosum contains millions of axon fibers sending neural transmissions across the two hemispheres. Take a look at Fig. 2.28, and you will get a sense of the mighty mass of connectivity that forms the linkage between the two hemispheres of the brain. Most of the callosal connections across the hemispheres are connecting similar regions in the opposite hemisphere: right hemisphere visual cortex callosal fibers travel across to left hemisphere visual cortex, and vice versa. Similarly, PFC fibers connect similar regions in the left and right frontal lobe.

5.3 The Internal Capsule/Corona Radiate

A third major white matter tract is the internal capsule/corona radiata (Fig. 2.29). These pathways contain fibers that ascend from the thalamus up to the cortex. They also contain descending fibers from the frontal and parietal lobes down to subcortical bodies such as

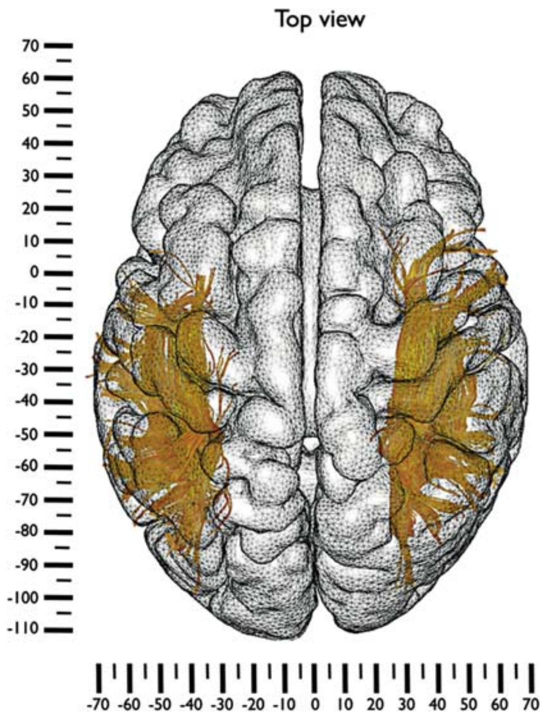

FIGURE 2.25 Arcuate fasciculus. The large fiber tract arcuate fasciculus, which connects the frontal, parietal, and temporal lobes, viewed from the top of the brain. The left hemisphere is shown on the left side of the figure, the right hemisphere is shown on the right. *Source: Catani & Thiebaut de Schotten 2008 Cortex 44, 1105–1132. Fig. 1, with permission.*

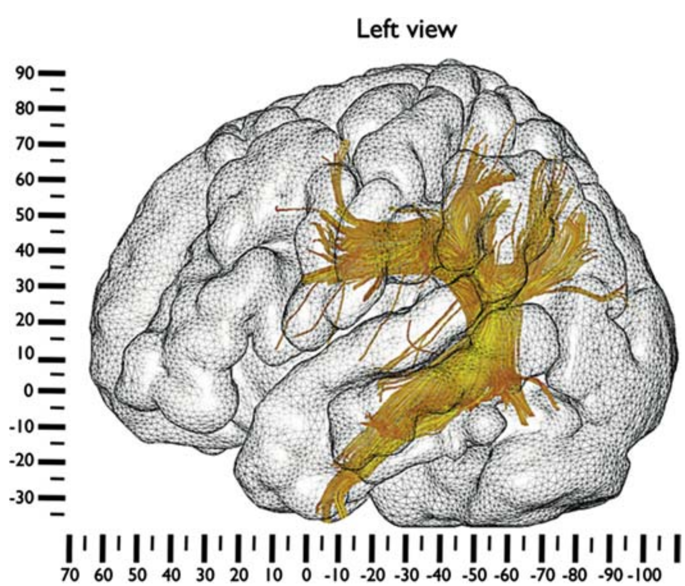

FIGURE 2.26 Arcuate fasciculus in the left hemisphere. The arcuate plays a key role in the left hemisphere in language processing. *Source: Catani & Thiebaut de Schotten 2008 Cortex 44, 1105–1132. Fig. 1, with permission.*

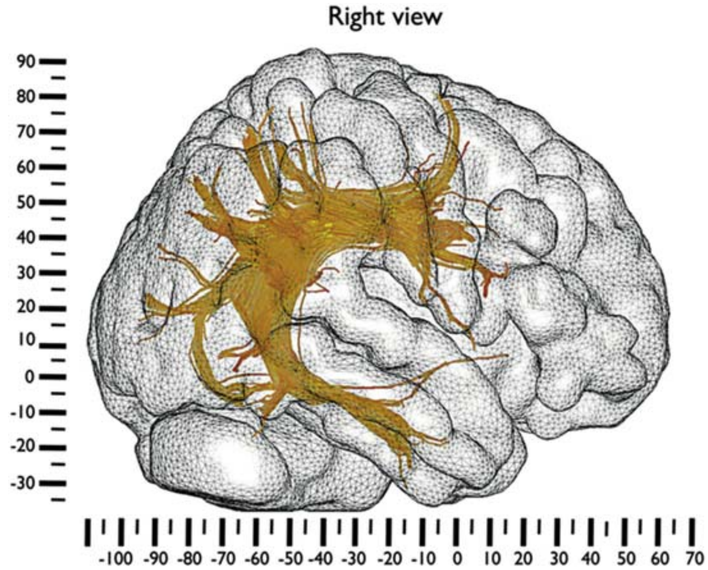

FIGURE 2.27 Arcuate fasciculus in the right hemisphere. The arcuate plays a key role in the right hemisphere in visuospatial processing and some aspects of language processing. *Source: Catani & Thiebaut de Schotten 2008 Cortex 44, 1105–1132. Fig. 1, with permission.*

the basal ganglia, and also to the brainstem and spinal cord. The internal capsule/corona radiate is the anatomic linkage that supports cognitive and perceptual and motor systems in the cortex.

In addition to these three massive white matter tracts, there are other white matter bundles, large and small, connecting cortical areas and subcortical bodies. Together these pathways form a multidirectional connectivity system that links the brain's lobes and hemispheres to each and to the body via the spinal cord.

Despite this massive array of pathways, it is important to note that not every region in the brain is connected to every other region. Think of a large state highway system: there are large superhighways that course long distances between major cities, smaller highways connecting smaller cities to larger ones, and still smaller routes and streets connecting areas of cities to other areas and suburban regions. Typically, although there is usually a major superhighway connecting the large metropolitan regions in a state, there are also other options for travel that may be less rapid but provide more options for stopping off at various subroutes along the way. Pathways in the brain are laid out in a similar manner: there are major white matter tracts that course throughout the brain and across the hemispheres combined with smaller white matter bundles that provide more localized connectivity.

6. BRAIN DYNAMICS—BRAIN RHYTHMS AND OSCILLATIONS

We mentioned earlier in the chapter that most neural pathways are bidirectional. We have described some of the major anterior-posterior and left-right pathways above, as well as the

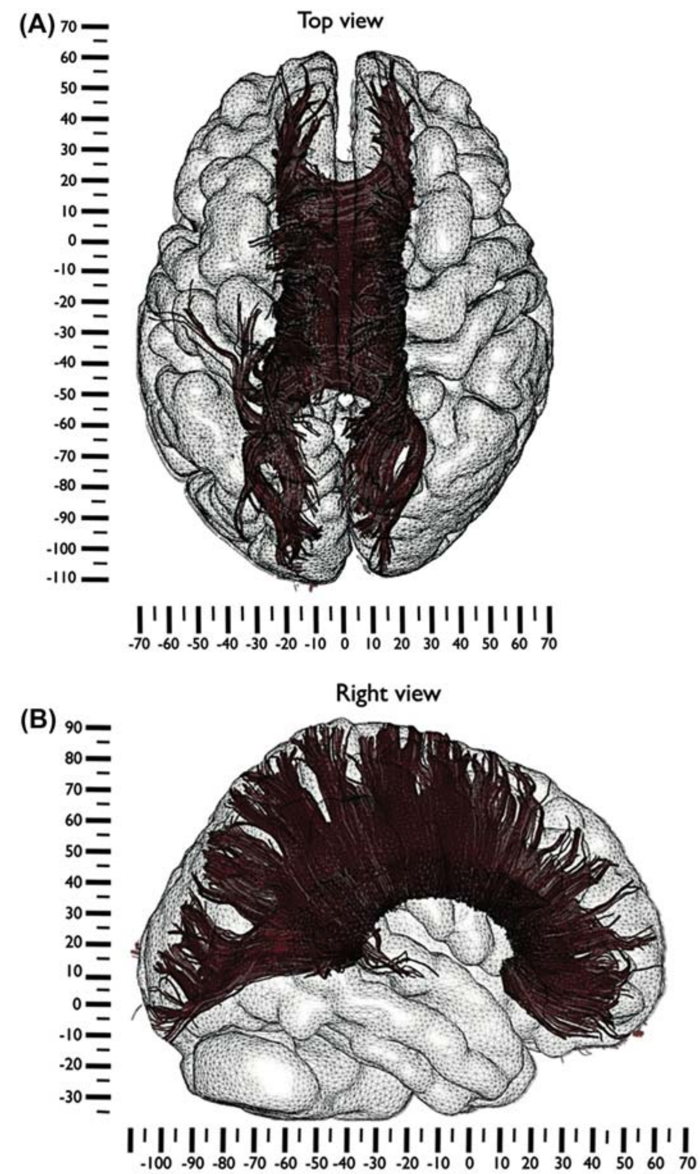

FIGURE 2.28 Corpus callosum. The fiber tracts of the massive corpus callosum are shown from the top of the brain (A), right side of the brain (B), and left side of the brain (C). *Source: Catani & Thiebaut de Schotten 2008 Cortex 44, 1105–1132. Fig. 6, with permission.*

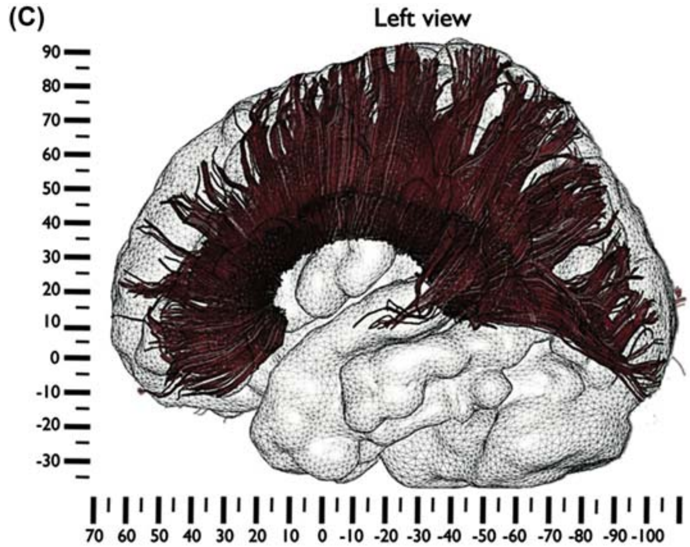

FIGURE 2.28 cont'd

massive thalamocortical hub formed by the thalamus and the cerebral cortex. A key aspect of brain function is elucidating how these many bidirectional pathways form our mind/brain, with an integrated sense of awareness of our world around us, our inner thoughts, and our very consciousness.

Wolf Singer and his colleagues have shed new light on these processes in their investigations into neural synchrony in cortical networks (for example, see Uhlhaas et al., 2009 for a review). Singer and his colleagues describe the cortex as a system comprised of many distinct, distributed networks that process information in parallel through these bidirectional pathways that are called "re-entrant." Since these many networks do not converge on a single hub or higher order region in the brain, a central question is how this distributed system gives rise to our conscious experience. One hypothesis for how this happens in the brain is the *synchrony of the oscillations* produced by these many networks across brain regions. The *temporal dynamics* of the oscillations across the brain are thought to provide the neural bases of neural synchrony in the brain that leads to our perceptions, thoughts, and coherent experience with the world around us, as well as with our internal thoughts and consciousness. More specifically, the action potentials of groups of neurons phase-lock with the wider scale oscillations to form a method to bind or link neural activity across wide ranging cortical regions.

7. PUTTING IT ALL TOGETHER

We have discussed five central aspects of brain study: *neuroanatomy* for studying the structure of the brain; *neurophysiology* for studying the cellular aspects of the brain; *functional*

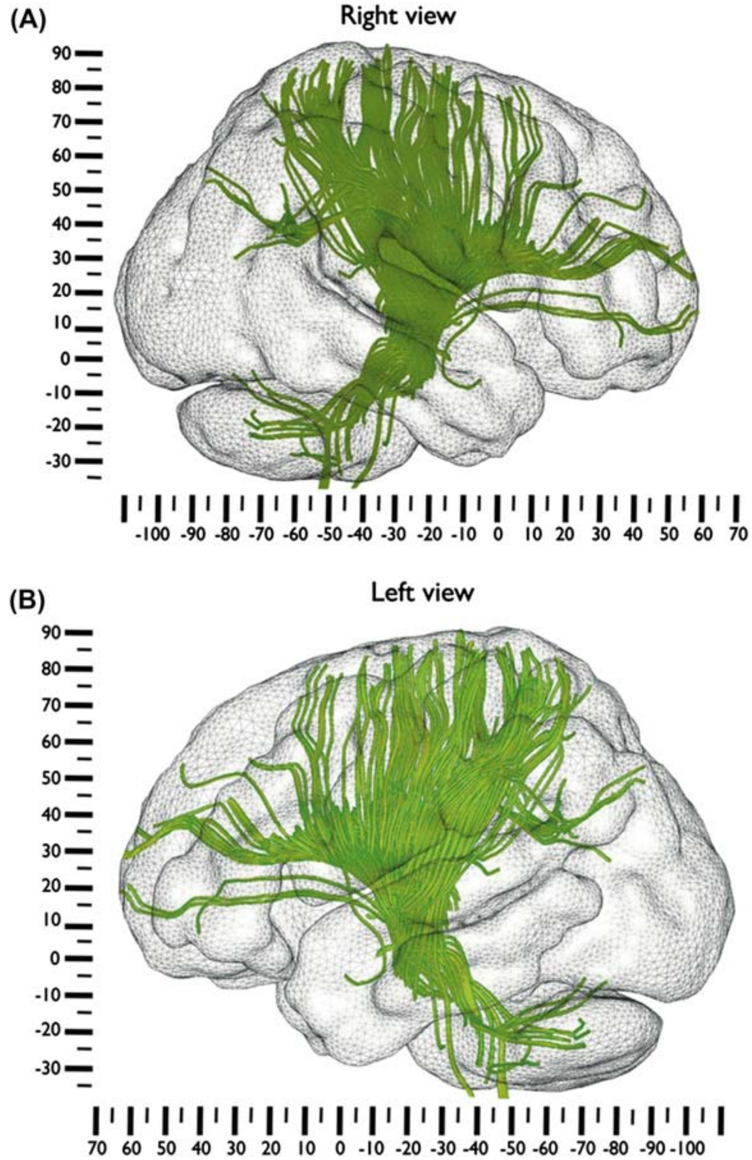

FIGURE 2.29 The internal capsule/corona radiata. The fiber tracts of the internal capsule/corona radiata are shown from the right side (A) and left side of the brain (B). *Source: Catani & Thiebaut de Schotten 2008 Cortex 44, 1105–1132. Fig. 9, with permission.*

neuroanatomy for studying the perceptual, motor, and cognitive processes of the brain; *neuroconnectivity* for studying brain pathways; and neurodynamics to study the rhythms and oscillations of the brain. Together these disciplines enable us to understand both small-scale and wide ranging aspects of the human brain. In the following chapter, we will investigate how brain visualization systems and methods allow us to further the study of these five key aspects of the brain and how they correspond to human behavior.

8. STUDY QUESTIONS

1. What does "level of analysis" refer to when investigating the human brain?
2. What is the difference between *neuroanatomy* and *functional neuroanatomy*?
3. Name the three planes of the brain and describe how they "slice" the brain.
4. What are some major landmarks of the brain?
5. What is an action potential? How (when) does it occur?
6. What role does the PFC play in human cognition?
7. What is a *homunculus*?
8. Describe three major white matter (fiber) tracts in the brain.
9. What is a connectogram and what information does it provide about the brain?