2 Learning a Bit of Anatomy

Without anatomy, we can't learn much about the brain. Knowing where things are and understanding what is connected to what are starting points to deciphering function, so we must familiarize ourselves with the basics of neuroanatomy. Whereas pure memorization plays an important role, understanding some general principles is also essential.

There's no way around it. Anatomy might be dry, but we need it to be able to navigate around the brain. This chapter provides a very brief overview of neuroanatomy that should be helpful to readers unfamiliar with the basics, whereas others may consider skimming the material. Anatomy and function are never far from each other, and some of the discussion below will deal with conceptual issues of understanding the relationship between structure (brain tissue) and function (behavior); the sections on "biology's axiom," "a brief detour into software," and "thinking about networks, not regions" should be of interest to those more familiar with anatomy, too.

When we think of the human brain, the first thing that comes to mind is the cortex—the outer zone of the cerebrum with bumps and grooves (figure 2.1a). When the brain is sliced and appropriately stained to mark the presence of neurons, we see that the cortex is a thin enclosure of densely packed cells (figure 2.1b). The cortex ("bark" in Latin), like the exterior covering of the trunk and branches of a tree, envelops the brain like a rind. In humans and some other mammals, the cortex is not smooth but highly convoluted; if spread like a dough, it would be the size of a large pizza, so the invaginations help pack a larger brain inside the skull. Microscopically, the cortex has a fine layered structure, like a mille-feuille dessert (containing three layers of puff pastry alternating with two layers of pastry cream), of varying cellular complexity. Although at first glance the cortex looks the

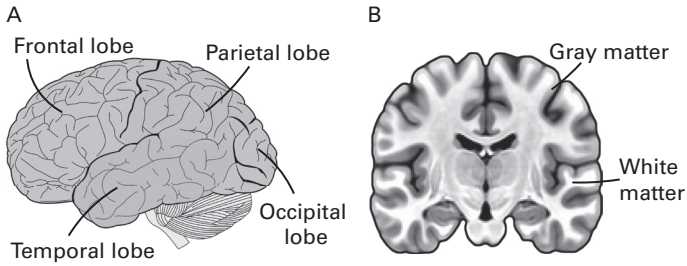

Figure 2.1
Human brain. (a) Side view shows the four major lobes of the brain. The darker traces are invaginations called sulci. (b) The cortex is the outermost part called "gray matter," roughly three millimeters in depth. The white parts, called "white matter," contain nerve fibers that anatomically link parts of the brain.

same everywhere, in some sectors it may have as few as three and in others as many as six discernible cell layers (in some parts sublayers are discernible, too, so even more packing can be identified), and the thickness of the cortex is not the same everywhere but varies between two and three millimeters. But despite important differences in layering and other properties, the cortex is relatively the same whether you are at the front or back, or top or bottom, of the brain.

The brain contains two key types of tissue. *Gray matter* contains neurons, which are thought to be the key processing elements of the nervous system, as well as several other notable cell types that support and protect the cellular environment (and likely contribute to computations in ways as yet poorly understood). *White matter* contains nerve fibers, which are the cell extensions (called axons) of neurons bundled together and that serve as communication highways both within and between brain regions. Many of these nerve fibers are enveloped by myelin, a substance that acts as an electrical insulator and speeds signal conduction along axons—and gives the white matter its color. Further below, we'll discuss neurons and axons, as well as the axons' cousins, the dendrites.

A slice through the brain also reveals concentrations of cells that lie deeper within it and constitute the aptly named subcortex. Whereas the cortex is essentially a thin sheet of neurons (more precisely, multiple sheets stacked together) at the outer edge, the subcortex is wholly different. To the uninitiated, a two-dimensional slice gives little clue as to the underlying

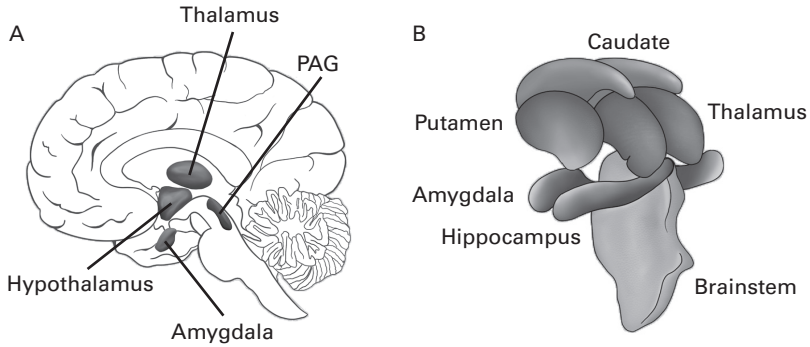

Figure 2.2
Subcortical brain regions. (a) Cut through the middle of the brain illustrates the position of some subcortical regions (PAG is the periaqueductal gray). (b) Rendering of some important structures. The striatum, which is discussed at length throughout the book, has two parts: the caudate and the putamen.

shape of subcortical regions, as this realm is full of oddly shaped masses of tissue (figure 2.2). Here is where neuroanatomist's imaginations have run wild with the challenge of naming structures (possibly creating a modern-day nightmare for medical students prior to exams). Knowledge of Greek and Latin comes in handy because we find structures with names like hippocampus (for its seahorse shape), amygdala (for its almond shape), caudate (for looking like a tail), and even substantia nigra—when creativity fails, name it (the thing/substance) for its color when chemically stained.

Despite the complexity revealed by slicing brain tissue, the brain's organization can be better appreciated if we consider how is forms embryologically. The entirety of the organ originates from a structure called the neural tube, which is literally shaped like a cylinder. At some point during embryonic development, this tube, which is fairly regular at first, creases at three places and bulges so that four compartments can be discerned (figure 2.3). These are the forebrain (front brain), midbrain (middle brain), hindbrain (back brain), and spinal cord. The last three contain no cortex; the first contains both the cortex and several subcortical structures, which we'll learn about later. If it seems confusing to have both cortex and subcortex in the forebrain, remember that this is not arbitrary. Embryologically, they both originate from the segment of the neural tube that differentiates into the forebrain. As the embryo changes in shape, names are needed to keep track

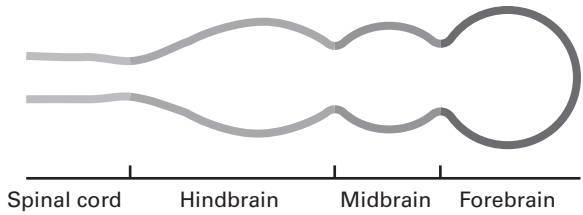

Figure 2.3
Embryonic brain sectors marked to indicate the portions that give rise to segments of the adult brain. For example, the rightmost sector gives rise to all forebrain regions, including the entire cortex, and all subcortical structures above the midbrain.

of its multiple parts. And as these shapes evolve into a mature state, the forebrain gives rise to both the cortex externally and multiple subcortical, inner structures.

The Outer Blanket of the Cerebrum: Cortex

Although the cortex has a fairly regular structure throughout, it is large enough that we need to subdivide it to be able to orient ourselves (see figure 2.1). Its main parts are named after skull bones to which they are adjacent: *occipital*, in the back of the skull; *temporal*, near the temples and on the side of the skull; *parietal*, at the side and top toward the back of the skull; and *frontal*, around the front part of the skull. Two other parts of the cortex are not visible from the outside and need to be seen from the inside to reveal themselves: the *cingulate* (see figure 6.1), which lies along the middle part of each hemisphere (the brain is made up of two halves, or hemispheres), and the *insula* (see figure 6.6), which is hidden by the "lid" of the frontal and parietal cortices (the name insula comes from "island," and indeed this part of the cortex is somewhat like an island off the parietal, temporal, and frontal cortices). Finally, the hippocampus is a cortical structure with simple lamination located close to the medial wall of the hemispheres (where they come closest to touching).

Although we often associate the cortex with the human brain, this type of tissue is present in all mammals. (Curiously, it is observed in parts of the forebrain of some reptiles, although it is fairly small. And as discussed in chapter 9, fishes, amphibians, and birds have brain parts that are related to those containing the cortex in mammals.) In a basic sense, what makes

the cortex "cortex" is that it contains a laminated pattern. The six-layer cortex found only in mammals appears to be related to the three-layer cortex found in some reptiles. Indeed, it has been suggested that common elements in three- and six-layer cortex are much like the common set of bones of the basic vertebrate skeleton: "Just as the hand has been adapted from forelimb digits by evolutionary pressures, so have the circuit elements of the basic cortical microcircuit become adapted during cortical evolution" (Shepherd 2011, 44). Such commonalities in traits are called *homologies*, which is to say that they stem from a common evolutionary ancestor. Note, however, that reptiles and mammals diverged more than 300 million years ago! But let's not get ahead of ourselves. We will discuss the evolution of the vertebrate brain in more detail in chapter 9.

Despite the heterogeneity of layering across the human cortex, this tissue type is relatively uniform. If scientists are often classified as "lumpers" or "splitters," it is probably safe to say that most neuroanatomists would fall squarely in the latter camp. In fact, it is not surprising that neuroanatomists have been trying to break up the cortex into smaller parts from the very beginning of neuroscience as a modern discipline (as discussed in chapter 1).

Biology's Axiom

In 1899, upon arriving in Berlin, Cécile and Oskar Vogt established the Neurobiological Laboratory, at first a private institution for the anatomical study of the human brain. Cécile Vogt was one of only two women in the entire Kaiser Wilhelm Institute for Brain Research (which included the Neurobiological Laboratory). In Prussia (with Berlin as its capital since 1701), until around the end of World War I, women were not granted access to regular university education, let alone the possibility to have a scientific career (Cécile obtained her doctoral degree while she was still in France and studied myelination in the cerebral hemispheres). The Vogts collaborated scientifically from 1899 to 1959, an effort that at first depended solely on the earnings from their private medical practice and on the support from the Krupp family, a 400-year-old German dynasty.[1] Two years after the Neurobiological Laboratory was founded, Korbinian Brodmann (chapter 1) joined the group and was encouraged to undertake a systematic study of the cells of the cerebral cortex using sections stained with a new cell-marking method.[2]

Cécile and Oskar Vogt, and Brodmann working separately in their lab, were part of a first wave of anatomists trying to establish a *map* of the cerebral cortex. Neurons are diverse, and several cell classes can be determined based on both shape and size. Researchers used these properties, as well as spatial differences in distribution and density, to define the boundaries between potential sectors. In this manner, Brodmann subdivided the cortex into approximately 50 regions per hemisphere.[3] The Vogts, in contrast, thought that there might be over 200 of them, each with its own distinguishing cytoarchitectonic pattern (that is, cell-related organization). Brodmann's map is the one that caught on and stuck, and today students and researchers alike still refer to cortical parts by invoking his map. Although relatively little was known about the functions of cortical regions at the time, Brodmann believed that his partition identified "organs of the mind"—he was convinced that each cortical area subserved a particular function. Indeed, when he joined the Vogts' laboratory, they had encouraged him to try to understand the organization of the cortex in light of their main thesis: different cytoarchitectonically defined areas are responsible for specific physiological responses and functions.

There is a deep logic to what the Vogts and Brodmann were following. In fact, it is an idea that comes close to being an axiom in biology: Function is tied to structure such that, in the case at hand, parts of the cortex that are structurally different (contain different cell types, cell arrangements, cell density, and so on) carry out different functions. In this manner, they believed they could inform the understanding of how function is implemented from a detailed characterization of the underlying microanatomy. In effect, they were in search of the *functional units* of the cortex. Unlike other organs of the body which have more clear-cut boundaries, the cortex's potential subdivisions are not readily apparent at a macroscopic level. One of the central goals of many neuroanatomists in the first half of the twentieth century was to unravel such "organs" (an objective that persists to this day!). A corollary of this research program was that individual brain regions—say, Brodmann's area 17 in the back of the brain—implemented specialized mechanisms (in this case related to processing visual sensory stimuli). Therefore, it was vital to understand the operation of individual parts as the area was the rightful mechanistic *unit* to understand how the brain works.

Although the brain map produced by the Vogts, with close to 200 areas, was not widely adopted by the scientific community, their approach was

clearly superior to that of most of their contemporaries (Brodmann included) because they explicitly compared cellular and functional data. They performed electrophysiological studies in patients and monkeys (they also studied cats) and compared the independently achieved architectonic and functional results in both species to clarify the operation of structurally defined areas (Vogt and Vogt 1926; Amunts and Zilles 2015). Of course, electrophysiological methods of the time were rather crude and amounted to using low-intensity electrical stimulation to observe what behaviors were produced (see chapter 5). Whereas the techniques available severely limited what could be learned (though they produced many pioneering observations), theirs was an extremely advanced conceptual framework that continues to inspire neuroscience today.

A Brief Detour into Software

Let's reconsider "biology's axiom"—different structure implies different function—in the context of concepts outside biology. The development of the computer in the 1940 and 1950s led to important new insights, including those of "software" and "hardware." Software stands for a set of basic instructions or commands that, together, determine how some algorithm is computed (say, factorizing a non-prime number like 2010, which can be written as $2 \times 3 \times 5 \times 67$). In a stunning paper published in 1936, Alan Turing devised an imaginary machine that was capable of calculating *anything* that can be algorithmically computed! This was, of course, before any hardware computer was ever constructed. The first computers were built in the 1940s (although most of us would not recognize them as such in a museum), including the Colossus, which was created to help British code breakers (Turing included) read encrypted German messages during World War II.

The ideas by Turing, as well as those by the mathematicians Alonzo Church, Kurt Gödel (among the all-time most significant logicians), and John von Neumann (famous for designing the basic logic architecture of modern computers), among many others, had a profound effect on philosophers and scientists trying to understand the notion of "computation" in both natural systems (including the nervous system) and artificial ones. An influential framework to emerge in the new field called "philosophy of mind" was that of *functionalism*, which asserts that mental states are identified by their functional role—not by how they are physically implemented.

Thus, a "mind" can be instantiated by various physical systems, possibly even computers, as long as they carry out appropriate computations. According to functionalism, the human brain is one of possibly many physical devices capable of implementing mental functions. In theory, at least.

If some of this feels like armchair philosophy to you, well, it is. Until it isn't. To this day, neuroscience faces these very questions. To what extent do different structural properties (say, neurons of different shapes) affect the functions carried out? Under what circumstances do different organizations of structure lead to similar computations? And so on. As an example, the avian brain is organized in some ways that are rather different from that of mammals. Although a cortex is not found in birds, the dorsal forebrain of the two groups of vertebrates appears to follow similar computational principles that are implemented differently (Dugas-Ford and Ragsdale 2015).

Before proceeding, let's define a few terms of orientation that allow us to navigate up, down, front, and back in the brain. Convenient terms for up and down are "superior" and "inferior" but "dorsal" and "ventral" are used correspondingly, too. The back of the brain is arbitrarily defined as "posterior," so the front is "anterior." Sometimes these terms need to be used carefully because, whereas the human brain is vertically oriented with respect to the main body axis, in other species the body axis is horizontal (think of a fish). But we won't worry about that too much in the book.

The Great Cell Masses: Subcortex

Describing subcortical structures would fill an entire book—and that's a massive understatement. That's not only because there are already quite a few books written about them, but because each structure is pretty complex and heterogeneous. For example, the amygdala, a region that is popular enough that most readers will have encountered it a few times in the popular media, extends no more than 10 millimeters (mm) along its longest axis and 6 mm in the orthogonal one (it is shaped more or less like an almond). Yet, as mentioned in chapter 1, it has more than a dozen subparts (they are called "subnuclei") that are structurally different (given varied neuronal types and patterns of input-output connections) and possibly even more, depending on how it is partitioned.

As we know, the forebrain contains both cortex and subcortex. The subcortical part is located at the base, toward the middle (see figures 2.1b and 2.2).

Many prominent subcortical structures are found there, including the thalamus, hypothalamus, amygdala, and striatum (for the latter, see figure 5.10). At times, the hippocampus is listed as a subcortical structure, but technically it isn't part of the subcortex (even neuroscientists slip here because of its close association with other subcortical areas and simple laminar structure.)

Among the most important subcortical regions of the forebrain is the thalamus (figure 2.2), which lies at the "inner chamber" of the brain (from the Greek *thalamos*, or "chamber"). The term was used by the Greek physician Galen in *De Usu Partium* by way of comparing the human brain with the ground plan of a Greek house, with the bridal chamber at its heart (whereas the name "thalamus" is still used, Galen was probably referring to what's called the third ventricle today[4]). For vision, audition, somatosensation, and taste, individual pathways carrying signals from the sensory periphery pass through the thalamus before reaching the respective cortical areas. For instance, fibers (that is, bundles of axons) leaving the retina of the eye are directed to a part of the thalamus that is connected with the visual cortex in the back of the brain (in the occipital cortex); the part receiving thalamic projections is called primary visual cortex or area V1, for "visual area one." Likewise, fibers leaving the inner ear, after some stops along the way, reach a part of the thalamus that is connected with the auditory cortex (in the temporal cortex); analogously, this part of the brain is called primary auditory cortex or area A1, for "auditory area one." But the thalamus is much more than a simple "relay station" for sensory information reaching the cortex. Anatomists subdivide it into more than 10 subregions with complex connectivity patterns with both the cortex and a very rich array of subcortical regions. Indeed, in later chapters, we will discuss how the thalamus is critically involved in cortical-subcortical loops that play essential computational roles.

Adjacent to the thalamus, we find the striatum, so named given its striped or furrowed appearance. Macroscopically, it contains a few subdivisions, including the caudate and putamen (figures 2.2 and 2.4). A remarkable property of the striatum is that, with the exception of the primary visual cortex, *all* of the cortex projects to it, from sensory regions with simple responses to frontal areas that participate in abstract processes. The striatum projects to subcortical regions, among others, that have a direct impact on motor actions. Indeed, historically, the striatum and adjacent structures forming what is called the basal ganglia (plural for ganglion or cell mass) have been

understood as a "motor system." As stated in chapter 1, as early as 1664, Thomas Willis described the striatum, noting degeneration of this structure in patients who suffered from severe paralysis, an observation that led him to link it with body movements (he believed the striatum contained channels for the flow of spirits controlling the muscles).[5] Throughout the book, we will discuss how the striatum, in particular, and the basal ganglia, more generally, are involved in much more than motor functions.

In humans, below the forebrain, the central nervous system extends downward into the midbrain, hindbrain, and spinal cord. The brainstem frequently refers to the large collection of structures in the midbrain and hindbrain (figure 2.2), although the usage is not always consistent across authors. As the name suggests, the overall arrangement resembles a stem on top of which the rest of the brain stands. Given that the brainstem is relatively large, it is typically subdivided into three sectors: the midbrain itself, in addition to the pons and medulla in the hindbrain. These three sectors are quite complex and far from homogenous, and they contain dozens of small zones or areas, each of which participates in multiple functions. The brainstem is the home of many circuits essential for basic processes, such as breathing and controlling heart rate—in short, the regulation of life. In fact, damage to the upper brainstem can cause coma and the so-called persistent vegetative state of partial arousal but not true awareness, in which patients can open their eyelids occasionally and exhibit sleep-wake cycles but completely lack cognitive function. Stroke affecting the brainstem can also cause "locked-in syndrome," in which the patient is completely paralyzed but remains conscious, a devastating condition hauntingly described from the first-person perspective in the book *The Diving Bell and the Butterfly* (popularized as a movie, too).

The Specialized Cells of the Nervous System: Neurons

The human body has over 200 cell types that make up our tissues. An adult male human brain has approximately 86 billion neurons (16 billion of which are in the cerebral cortex), the cell type that is believed to be responsible for most of its unique functions.[6] (The current estimate is a downward revision from the popular 100 billion figure that appears to have been a guesstimate; the number 86 billion may be revised, too, given that it is based on a very small sample of brains, all male at that.) Neurons themselves are a diverse

group of cells, including cells specialized to capture sensory information (such as light sensing cells in the eyes) and motor neurons that innervate particular appendages (such as feet) and lead to muscle movements. A typical neuron has two main distinguishable parts: a region that contains the cell nucleus and a set of thin, tube-like radiations that extend outwardly. The central part is called the cell body, or soma. The radiating tubes are of two types: axons and dendrites (figure 2.4).

The cell body usually gives rise to a single axon, which can extend over great distances. Some of the longest ones can exceed a meter, such as the ones from the lower back to the big toe (the part of the nervous system outside the cranium is called the "peripheral nervous system"). Because neurons extend long distances, it was suspected early on that they acted as "wires" that carry output signals. Dendrites, on the other hand, are quite short and rarely longer than two millimeters. Because dendrites come in contact with many axons, they were suggested to act as neuronal "antennae" and contribute to collecting incoming signals.

One of the main ways that neurons communicate with one another is through *action potentials*, also called spikes or nerve impulses. An action potential is only triggered if the electrical voltage crosses a threshold value, at which point it is generated in an all-or-none fashion. Thus, the electrical

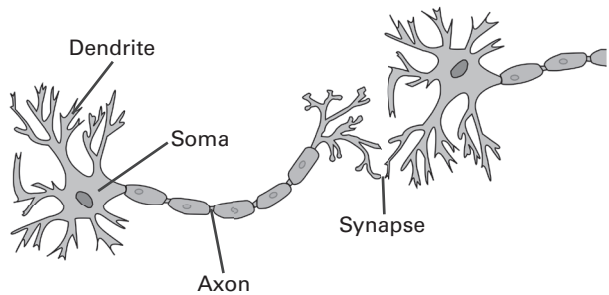

Figure 2.4
Schematic diagram of a neuron. Radiating away from the cell body (also called soma), we see an axon, the component that typically conveys signals to other neurons (this axon is enveloped by a myelin sheath that speeds up impulse transmission). The other extensions are dendrites, which are parts that typically receive inputs from other neurons. The synapse refers to the end of the axon, the narrow space between neurons, and the dendritic contact on the postsynaptic cell. The synapse is where chemical communication between cells takes place.

signal generated at the base of the axon travels along its entire extent at a constant intensity as it propagates. In this manner, the nerve impulse functions as a binary on/off signal, but the frequency and pattern of action potentials provide key information that is communicated between neurons.

(Action potentials are measured by inserting microelectrodes into the extracellular space and measuring electrical voltage. Functional MRI, a technique we'll also discuss in the book, does not measure electrical signals but instead oxygen consumption at a small patch of tissue. But because neuronal activity is costly metabolically, and thus consumes oxygen, functional MRI measures a proxy for neuronal electrical activity. Whereas the technique is very useful in studying brain function, it is important to remember that it provides an indirect measure of the electrical signals that neuroscientists are most interested in.)

How does information pass between neurons? A chief mode of transmission is through *chemical synapses*. Synapses are sites of quasi-contact between neurons, often between a cell's axon and another cell's dendrite. When nerve impulses reach the end of an axon, they cause the release of specific chemicals at the synaptic cleft (the narrow space between cells, 20 to 50 nanometers wide) called *neurotransmitters*. A neurotransmitter released from the presynaptic cell acts on the postsynaptic cell by altering the latter's cell membrane permeability properties, producing excitation or inhibition of the postsynaptic cell (due to the inflow or outflow of ions). When the postsynaptic cell is sufficiently excited, it will generate an action potential, thereby propagating an electrical signal that influences other neurons downstream. This cascade of firing, reverberating across the brain, is at the core of all mental activity! But remember that communication is not only electrical, like a set of electrical cables passing their signals along. It is electrochemical—and arranged in a way that multiple signals can converge and be integrated to lead to further action potentials.

What prevents the brain from going into uncontrolled firing, in effect creating an uncontrollable electrical storm? Indeed, if unchecked, excitation can lead to seizures, from relatively mild to extreme ones. So-called tonic-clonic seizures (formerly known as "grand mal" seizures) can be the most frightening to observe. Typically, the person suffering from such a seizure initially stiffens and loses consciousness, thus falling to the ground. During the second phase, the muscles may begin to spasm and jerk. This terrifying experience mercifully lasts only a few minutes, although it can certainly

seem like forever if one is helplessly watching it. It's perhaps not entirely surprising, though utterly tragic, that in Europe of the Middle Ages, epilepsy was confused with witchcraft, especially when accompanied by tremors, convulsions, or loss of consciousness. But what prevents undampened excitation? Neurons influence each other not only in an excitatory fashion but also through inhibition. In the latter case, when a neuron fires, it makes the neurons connected to it *less* likely to generate an action potential.

Neurotransmitters are very diverse (around 100 different molecules have been cataloged), but approximately 10 of them do most of the heavy lifting. They go by names such as dopamine, serotonin, acetylcholine, histamine, and so on, some of which are even household names. For example, antidepressants like Prozac and other variants (fluoxetine, paroxetine, etc.) act on serotonin neurotransmission. These medications are in fact called "selective serotonin reuptake inhibitors" (SSRIs) and lead to an *increased* effect of serotonin on the postsynaptic cell. More generally, alcohol and drugs, including "recreational drugs" like cannabis and hashish, all affect neurotransmission, thereby leading to altered states of consciousness that modify perceptions and feelings. If you thought chemistry was boring, think again.

It is quite humbling that we don't really know how SSRIs work; the mechanisms of action are not well understood. Like many medical treatments, they were discovered by accident, and physicians prescribe them for depression and anxiety based on clinical experience. Ralph Adolphs and David Anderson go as far as suggesting that "trying to cure these [depressed] patients without understanding how the brain generates an emotion state would be like trying to cure the bubonic plague in the fifteenth century without understanding that bacteria and viruses cause infectious disease" (Adolphs and Anderson 2018, 32). As discussed in chapter 1, neuroscience is "observation rich" but not "mechanism rich." We know rather little.

The Massive Highways System

Gray matter is so important that the other part, white matter, receives short shrift. Gray matter is where all the cellular action takes place, white matter is "just a bunch of cables," or so it goes. Much of the communication in the brain occurs locally—for example, within specific areas in the cortex or between two adjacent areas (say, the amygdala and the hippocampus). In such cases, axons are relatively short. However, another type of

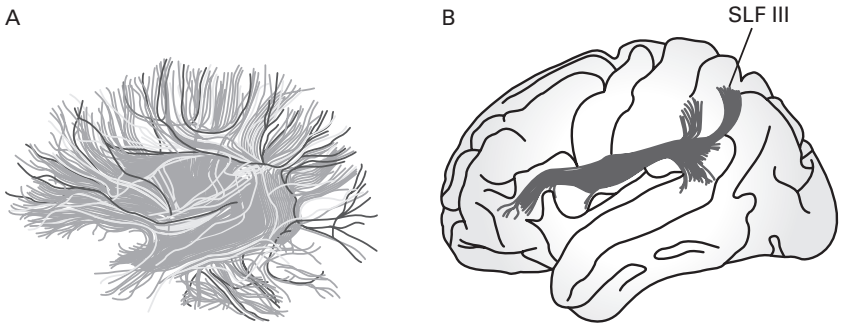

Figure 2.5
White matter. (a) The extensive white matter fibers of the brain interlink brain regions. (b) The fibers are organized in terms of fasciculi (a fasciculus is a bundle of axons), such as the superior longitudinal fasciculus (SLF) III.

connectivity relies on *white matter tracts*—namely, bundles of axons packed together that form a major road system that is essential for signal transmission across the brain (figure 2.5).

If we consider a brain slice (such as in figure 2.1) and mentally remove the outer layer of cortex and other internal clumps that are stained for cell bodies (that is, subcortical areas), it is surprising at first to consider how much remains. All of that is white matter! Anatomists have identified around 20 large tracts that interlink different lobes. Particular tracts differ a little from person to person (slightly thinner/thicker or angled a little differently), but they are found in all typical brains.

Thinking about Networks, Not Regions

White matter is of obvious interest to anatomists and neurologists. When this tissue is compromised, perhaps because of a tumor removal, behavioral deficits are observed. But consideration of white matter has implications that are conceptual in nature and inform one of the central questions occupying neuroscientists: How are functions implemented in the brain?

The dominant theoretical stance in neuroscience has tended to view functions as the product of a particular brain areas—somewhat like a dedicated computer chip that performs specialized computations.[7] As we saw, this idea was very much in line with Brodmann's anatomical research program, and indeed it was part of scientific zeitgeist at the turn of the twentieth century. The existence of fiber tracts was known since the sixteenth

century. In *De Humani Corporis Fabrica* (published in 1543), Andreas Vesalius provided a comprehensive account of the corpus callosum and recognized that it links the two halves of the brain. Yet, anatomists like Brodmann who sought to produce "brain maps" paid little attention to the white matter of the brain. But Brodmann's wasn't the only view.

During the last decades of the nineteenth century, at the same time that many researchers were busy studying the impact of lesions to specific parts of the brain, a different school of thought was emerging. The *associationists* argued that, if one observed behavioral change caused by a lesion in a brain area, the deficit could be due to impairment in regions distant from the damaged site. Although magical and spiritual influences were very much in vogue during this period (social gatherings to summon spirits, called séances, were popular at the time), nothing of the sort was being proposed here. Instead, two not mutually exclusive mechanisms were entertained for such "action-at-a-distance" effects: *diaschisis* and *disconnection*. Diaschisis (from the Greek and meaning roughly "shocked throughout") meant that a given region was affected because it was connected with a damaged area, which thereby produced a disruption of the function of the former. The disturbances could be relatively mild but could also be consequential. On the other hand, "disconnection" refers to a situation in which two intact areas are partially or completely disconnected because of an insult to the major tract linking them. Although the two areas remain unperturbed (in contrast to the case of diaschisis), they still may exhibit disturbances of function leading to considerable behavioral alterations. Why? Because their functions depend on their talking to each other. A prime example is the disconnection of the so-called Wernicke's area in parietal cortex and Broca's area in frontal cortex (because of the damage to the tract that interlinks them), regions that play important roles in speech production and language comprehension. What the associationists were hinting at can be viewed as an early incarnation of "network theories." In a nutshell, brain functions are not carried out by single, isolated regions but by coalitions of regions that may be involved in *neural circuits* that are not local—for instance, involving parts of parietal and frontal cortex in the case of speech and language.

Coda

Learning about neuroanatomy can be rather dull. That is in part why it is common to teach students about cortical and subcortical organization by

pairing regions with their "main" function, or a small set of functions; say, the hippocampus is important for memory, the prefrontal cortex is important for attention and reasoning, and so on. We will avoid this approach here not because of a possibly better didactic approach but because of the central thesis of the book: Brain areas don't compute specific functions—they are *not* segregated "organs of the mind," as Brodmann put it. The brain is not a modular system that can be understood a region at a time. Instead, we need to unravel how collections of cortical, subcortical, and brainstem regions work together to support complex behaviors. And, as discussed in chapter 9, this is not just the case for the human brain but across all vertebrates—even "simple" ones.

The Entangled Brain

How Perception, Cognition, and Emotion Are Woven Together

By: Luiz Pessoa

Citation:

The Entangled Brain: How Perception, Cognition, and Emotion Are Woven Together
By: Luiz Pessoa
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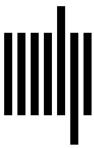

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