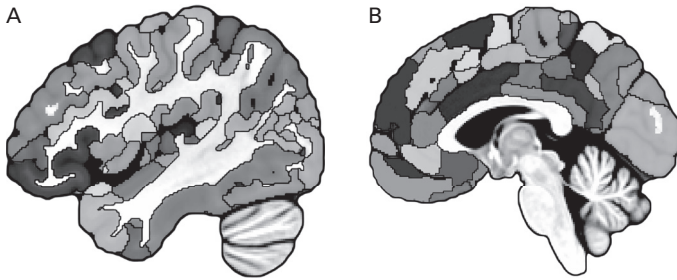


## 1 From One Area at a Time to Networked Systems

We begin our journey into how the brain brings about the mind: our perceptions, actions, thoughts, and feelings. Historically, the study of the brain has proceeded in a divide-and-conquer way, trying to figure out the function of individual areas—chunks of gray matter that contain neurons—one at a time. This book makes the case that because the brain is not a modular system, we need conceptual tools that can help us decipher how highly *entangled*, complex systems function.

In 2016, a group of investigators published a map of the major subdivisions of the human cerebral cortex—the outer part of the brain—in the prestigious journal *Nature* (figure 1.1). The partition delineated 180 areas in each hemisphere (360 in total), each of which represents a unit of “architecture, function, and connectivity” (Glasser et al., 2016, 171).<sup>1</sup> Many researchers celebrated the new result given the long-overdue need to replace the de facto standard called the “Brodmann map.” Published in 1908 by Korbinian Brodmann, the map describes approximately 50 areas in each hemisphere (100 in total) based on local features, such as cell type and density, that Brodmann discovered under the microscope.

Notwithstanding the need to move past a standard created before the First World War, the 2016 cartographic description builds on an idea that was central to earlier efforts: Brain tissue should be understood in terms of a set of well-defined, spatially delimited sectors. Thus the concept of a brain *area* or *region*:<sup>2</sup> a unit that is both anatomically and functionally meaningful. The notion of an area/region is at the core of neuroscience as a discipline, with its central challenge of unraveling how behaviors originate from cellular matter. Put another way, how does function (manifested externally by behaviors) relate to structure (such as different neuron types and their arrangement)? How do groups of neurons—the defining cell type of the brain—lead to sensations and actions?



**Figure 1.1**

Map of brain areas of the cortex published in 2016. Each hemisphere (or half of the brain) contains 180 areas indicated by different shades of gray and outlines. (a) The brain is shown in a side view. (b) The brain is shown through a cut revealing the middle. *Source:* Regions as defined by Glasser et al. (2016).

As a large and heterogeneous collection of neurons and other cell types, the central nervous system—including cortical and subcortical parts—is a formidably complex organ. (The cortex is the outer surface with grooves and bulges; the subcortex comprises other cell masses that sit underneath. We'll go over the basics of brain anatomy in chapter 2.) To unravel how it works, some strategy of *divide and conquer* seems to be necessary. How else can the brain be understood without breaking it down into subcomponents? But this approach also exposes a seemingly insurmountable chicken-and-egg problem: If we don't know how it works, how can we determine the “right” way to subdivide it? Finding the proper unit of function, then, has been at the center of the quest to crack the mind-brain problem.

Historically, two winners in the search for rightful units have been the neuron and the individual brain area. At the cellular level, the neuron reigns supreme. Since the work of Ramon y Cajal,<sup>3</sup> the Spanish scientific giant who helped establish neuroscience as an independent discipline, the main cell type of the brain is considered to be the neuron (and neurons come in many varieties, both in terms of morphology and physiology). These cells communicate with one another through electrochemical signaling. If they are sufficiently excited by other neurons, their equilibrium voltage changes and they generate a “spike”: an electrical signal that propagates along the neuron's thin extensions (called axons), much like a current flowing through a wire. The spike from a neuron can then influence downstream neurons. And so on.

At the supra-cellular level, the chief unit is the *area*. But what constitutes an area? Dissection techniques and the study of neuroanatomy during the European Renaissance were propelled to another level by Thomas Willis's monumental *Cerebri anatome* published in 1664. The book rendered in exquisite detail the morphology of the human brain, including detailed drawings of subcortical structures and the cerebral hemispheres containing the cortex. For example, Willis described a major structure of the subcortex, the striatum, that I will discuss at length in the chapters to follow. With time, as anatomical methods improved with more powerful microscopes and diverse stains (which mark the presence of chemical compounds in the cellular milieu), more and more subcortical areas were discovered. In 1819, the German anatomist Karl Burdach described a mass of gray matter that could be seen in slices through the temporal lobe. He called the structure the "amygdala"<sup>4</sup>—given that it is shaped like an almond ("amygdala" means almond in Latin)—now famous for its contributions to fear processes. And techniques developed in the second half of the twentieth century revealed that it is possible to delineate a least a dozen subregions within its overall territory.

The seemingly benign question—what counts as an area?—is far from straightforward. For instance, is the amygdala one region or 12 regions? This region is far from an esoteric case. All subcortical areas have multiple subdivisions, and some have boundaries that are more like fuzzy zones than clearly defined lines. The challenges of partitioning the cortex, the outer laminated mantle of the cerebrum, are enormous, too. That's where the work of Brodmann and others, and more recently the research that led to the 180-area parcellation (figure 1.1), comes in. These developments introduce a set of criteria to subdivide the cortex into constituent parts. For example, although neurons in the cortex are arranged in a layered fashion, the number of cell layers can vary. Therefore, identifying a transition between two cortical sectors is aided by differences in cell density and layering.

### How Modular Is the Brain? Not Much at All

When subdividing a larger system—one composed of lots of parts—the concept of *modularity* comes into play. Broadly speaking, modularity refers to the degree of interdependence of the many parts that comprise the system of interest. On the one hand, a *decomposable* system is one in which each subsystem operates according to its own intrinsic principles,

independently of the others—we say that this system is highly modular. On the other hand, a *non*-decomposable system is one in which the connectivity and interrelatedness of the parts is such that they are no longer clearly separable. Whereas the two extremes serve as useful anchors to orient our thinking, in practice one finds a continuum of possible organizations, so it's more useful to think of the degree of modularity of a system.

Science as a discipline is inextricably associated with understanding entities in terms of a set of constituent subparts. Neuroscience has struggled with this *modus operandi* since its early days, and debates about “localizationism” versus “connectionism”—how local or how interconnected brain mechanisms are—have always been at the core of the discipline. By and large, a fairly *modular* view has prevailed in neuroscience. Fueled by a reductionistic drive that has served science well, most investigators have formulated the study of the brain as a problem of dissecting the multitude of “sub-organs” that make it up. To be true, brain parts are not viewed as isolated islands and are understood to communicate with one another. But, commonly, the plan of attack assumes that the nervous system is decomposable<sup>5</sup> in a meaningful way in terms of patches of tissue (as in figure 1.1) that perform well-defined computations—if only we can determine what they are.

There have been proposals of non-modular processing, too. The most famous example is that of Karl Lashley who, starting in the 1930s, defended the idea of “cortical equipotentiality”—namely, that most of the cortex functions jointly, as a unit. Thus, the extent of a behavioral deficit caused by a lesion depended on the amount of cortex that was compromised—small lesions cause small deficits, large lesions cause larger ones. Although Lashley's proposal was clearly too extreme and rejected empirically, historically, many ideas of decentralized processing have been entertained by neuroscientists. Let's discuss some of their origins.

### The Entangled Brain

The field of *artificial intelligence* (AI) is said to have been born at a workshop at Dartmouth College in 1956. Early AI focused on the development of computer algorithms that could emulate human-like “intelligence,” including simple forms of problem solving, planning, knowledge representation, and language understanding. A parallel and competing approach—what was to become the field of *artificial neural networks*, or neural networks, for

short—took its inspiration instead from *natural* intelligence and adopted basic principles of the biology of nervous systems. In this non-algorithmic framework, collections of simple processing elements work together to execute a task. An early example was the problem of pattern recognition, such as recognizing sequences of 0s and 1s. A more intuitive, modern application addresses the goal of image classification. Given a set of pictures coded as a collection of pixel intensities, the task is to generate an output that signals a property of interest; say, output “1” if the picture contains a face and “0” otherwise. The underlying idea behind artificial neural networks was that “intelligent” behaviors result from the joint operation of simple processing elements, like artificial neurons that sum their inputs and generate an output if the sum exceeds a certain threshold value. We’ll discuss neural networks again in chapter 8, but here we emphasize their conceptual orientation: thinking of a system in terms of *collective computation*.

The 1940s and 1950s were also a time when, perhaps for the first time, scientists started systematically developing *theories of systems* generally conceived. The intellectual *cybernetics* movement was centrally concerned with how systems regulate themselves so as to remain within stable regimes; for example, normal, awake human temperature remains within a narrow range, varying less than a degree Celsius. *Systems theory*, also called general systems theory or complex systems theory, tried to formalize how certain properties might originate from the interactions of multiple, and possibly simple, constituent parts. How does “wholeness” come about in a way that is not immediately explained by the properties of the parts?

Fast-forward to 1998 and the publication of a paper entitled “Collective Dynamics of ‘Small-World’ Networks” (Watts and Strogatz 1998). The study proposed that the organization of many biological, technological, and social networks gives them enhanced signal-propagation speed, computational power, and synchronization among parts. And these properties are possible even in systems where most elements are connected locally, with only some elements having “arbitrary” connections. (For example, consider a network of interlinked computers, such as the internet. Most computers are only connected to others in a fairly local manner—say, within a given department within a company or university. However, a few computers have connections to other computers that are geographically quite far.)

Duncan Watts and Steven Strogatz applied their techniques to study the organization of a social network containing more than 200,000 actors. As

we'll discuss in chapter 10, to make a "network" out of the information they had available, they considered two actors to be "connected" if they had appeared in a film together. Although a given actor was only connected to a small number of other performers (around 60), they discovered that it was possible to find short "paths" between any two actors. (The path A–B–C links actors A and C, which have not participated in the same film, if both of them have co-acted with actor B.) Remarkably, on average, paths containing only four connections (such as the path A–B–C–D–E linking actors A and E) separated a given pair of actors picked at random from the set of 200,000. The investigators dubbed this property "small world" by analogy with the popularly known idea of "six degrees of separation" and suggested that it is a hallmark of many types of networks—one can travel from A to Z very expediently.

The paper by Watts and Strogatz, and a related paper by Albert-László Barabási and Réka Albert that appeared the following year (1999), set off an avalanche of studies on what has become known as "network science"—the study of interconnected systems comprised of more elementary components, such as a social network of individual persons. This research field has grown enormously since then, and novel techniques are actively being applied to social, biological, and technological problems to refine our view of "collective behaviors." These ideas resonated with research in brain science, too, and it didn't take long before investigators started applying network science techniques to study their data. This was particularly the case in human neuroimaging, which employs magnetic resonance imaging (MRI) scanners to measure activity throughout the brain during varied experimental conditions. Network science provides a spectrum of analysis tools to tackle brain data. First and foremost, the framework encourages researchers to conceptualize the nervous system in terms of network-level properties. That is to say, whereas individual parts—brain areas or other such units—are important, collective or system-wide properties must be targeted.

### Neuroscientific Explanations

Neuroscience seeks to answer the following central question: How does the brain generate behavior?<sup>6</sup> Broadly speaking, there are three types of study: lesion, activity, and manipulation. *Lesion* studies capitalize on naturally occurring injuries, including those caused by tumors and vascular

accidents; in nonhuman animals, precise lesions can be created surgically, thus allowing much better control over the affected territories. What types of behavior are affected by such lesions? Perhaps patients can't pay attention to visual information the way they used to, or maybe they have difficulty moving a limb. *Activity* studies measure brain signals. The classic technique is to insert a microelectrode into the tissue of interest and measure electrical signals in the vicinity of neurons (it is also possible to measure signals inside a neuron itself, but such experiments are more technically challenging). Voltage changes provide an indication of a change in state of the neuron(s) closest to the electrode tip. And determining how such changes are tied to the behaviors performed by an animal provides clues about how they contribute to them. *Manipulation* studies directly alter the state of the brain by either silencing or enhancing signals. Again, the goal is to see how sensations and actions are affected.

Although neuroscience studies are incredibly diverse, one way to summarize them is as follows: "Area or circuit X is *involved* in behavior Y" (where a circuit is a group of areas). A lesion study might determine that patients with damage to the so-called cortex of the anterior insula have the ability to quit smoking easily, without relapse, leading to the conclusion that the insula is a critical substrate in the addiction to smoking (Naqvi et al. 2007). Why? Quitting is hard in general, of course. But it turns out to be easy if one's anterior insula is nonfunctional. It is logical, therefore, to surmise that, when intact, this region's operation somehow promotes addiction. An activation study using functional MRI might observe stronger signals in parts of the visual cortex when participants view pictures of faces compared to when they are shown many kinds of pictures that don't contain faces (pictures of multiple types of chairs, shoes, or other objects.). This could suggest that this part of the visual cortex is important for the perception of faces. A manipulation study that enhances activity in the prefrontal cortex in monkeys might observe an improvement in tasks that requires careful attention to visual information.

Many journals require "significance statements" in which authors summarize the importance of their studies to a broader audience. In the instances of the previous paragraph, the authors could say something like this: (1) The insula *contributes* to conscious drug urges and to decision-making processes that precipitate relapse; (2) the fusiform gyrus (the particular area of visual cortex that responds vigorously to faces) is *involved*

in face perception; and (3) the prefrontal cortex *enhances* performance of behaviors that are challenging and require attention.

The examples above weren't gratuitous; all were important studies published in very respected scientific journals. Although these were rigorous experimental studies, they don't quite inform about the underlying mechanisms.<sup>7</sup> In fact, if one combs the peer-reviewed literature, one finds a plethora of *filler terms*<sup>8</sup>—words like “contributes,” “involved,” and “enhances” above (figure 1.2)—that stand in for the processes we presume did the “real” work. This is because, by and large, neuroscience studies don't sufficiently determine, or even strongly constrain, the underlying mechanisms that link brain to behavior.

Scientists strive to discover the mechanisms supporting the phenomena they study. But what precisely is a *mechanism*? Borrowing from the philosopher William Bechtel, it can be defined as “a structure performing a function in virtue of its parts, operations, and/or organization. The functioning of the mechanism is responsible for one or more phenomena” (Bechtel 2008, 13). Rather abstract, of course, but in essence it means *how something happens*. The more clear-cut we can be about it, the better. For example, in physics, precision actually involves mathematical equations. Note that mechanisms and explanations are always at some *level of explanation*. A typical explanation about combustion motors in automobiles will invoke pistons, fuel, or controlled explosions. It will not discuss these phenomena in term of particle physics, for instance; it won't invoke electrons, protons, or neutrons.

### Filler verbs used in neuroscience explanations

Reflects	Encodes	Reveals	Induces
Involves	Enables	Regulates	Ensures
Mediates	Supports	Generates	Promotes
Modulates	Determines	Shapes	Plays a role in
Contributes to	Underlies	Produces	Is associated with

**Figure 1.2**

Because little is known about how brain mechanisms bring about behaviors, neuroscientists use “filler” verbs, most of which add relatively little substantive content to the statements made.

*Source:* List of words from Krakauer et al. (2017).



We currently *lack an understanding* of most brain science phenomena. Therefore, when an experiment finds that changes occur in, say, the amygdala during classical aversive conditioning (learning that a once-innocuous stimulus is now predictive of a shock; see chapter 5), we might find that cell responses there increase in parallel to the observed behavior—as the behavior is acquired, cells responses concomitantly increase. Although this is a very important finding, it remains relatively shallow in clarifying what’s going on. Of course, if through a series of studies we come to discern how amygdala activity increases, decreases, or stays the same when learning changes accordingly, we are closer to legitimately saying that we grasp the underlying mechanisms.

### Pleading Ignorance

How much do we know about the brain today? In the media, there is no shortage of news about novel discoveries explaining why we are all stressed, overeat, or cannot stick to our resolutions for the new year. General-audience books on brain and behavior are extremely popular, even if we don’t count the ever-ubiquitous self-help books, which are themselves loaded with purported insights from brain science. And judging from the size of graduate school textbooks (some of which are even hard to lift), current knowledge is a deep well.

In reality, we know rather little. What we’ve learned barely scratches the surface.

Consider, for example, this statement by eminent neuroscientists: “Despite centuries of study of brain–behavior relationships, a clear formalization of the function of many brain regions, accounting for the engagement of the region in different behavioral functions, is lacking” (Genon et al. 2018, 362).<sup>9</sup> A clear-headed description of our state of ignorance was given by Ralph Adolphs and David Anderson, both renowned professors at the California Institute of Technology, in their book *The Neuroscience of Emotion*:

We can predict whether a car is moving or not, and how fast it is moving, by “imaging” its speedometer. That does not mean that we understand how an automobile works. It just means that we’ve found something that we can measure that is strongly correlated with an aspect of its function. Just as with the speedometer, imaging [measuring] activity in the amygdala (or anywhere else in the brain), in the absence of further knowledge, tells us nothing about the causal mechanism and only provides a “marker” that may be correlated with an emotion. (Adolphs and Anderson 2018, 31)

Although these authors were discussing the state of knowledge regarding emotion and the brain, it is fair to say that their summary applies to neuroscience more generally—the science of brain and behavior is still in its (very) early days.

The gap—no, gulf—between scientific knowledge and how it is portrayed by the general media is sizable indeed. We may encounter not only a piece in a popular magazine found in a medical office, but a serious article in, say, the *New York Times* or *The Guardian* newspapers of some heft. The problem even extends to most science communication books, especially those with a more clinical or medical slant.

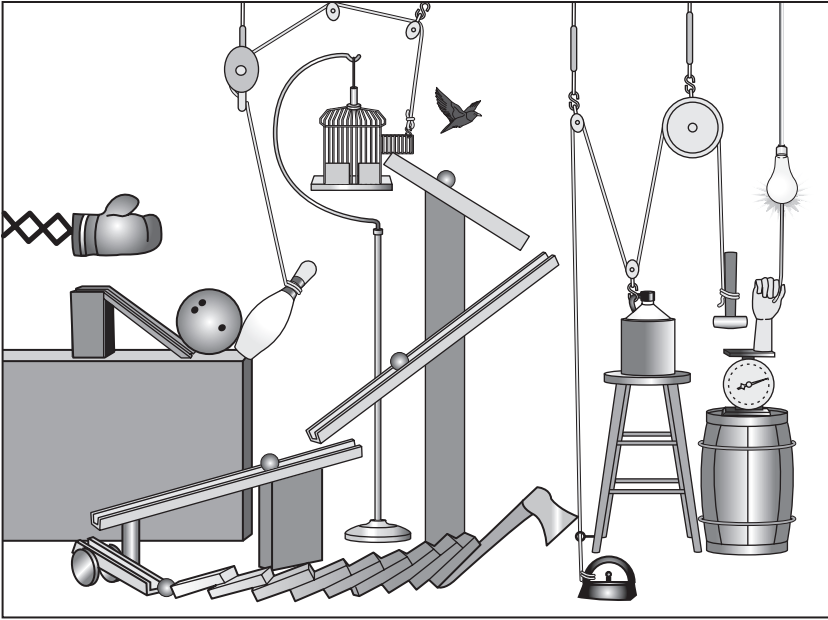
### Mechanisms and Complexity in Biology

How does something work? As discussed above, science approaches this question by trying to work out *mechanisms*. We seek “machine-like” explanations, much like describing how an old, intricate clock functions. Consider a Rube Goldberg apparatus (for an example, see figure 1.3), accompanied by directions on how to use it to light a bulb:<sup>10</sup>

- The boxing glove is triggered.
- The glove punches the bowling ball, which slides down and knocks the pin.
- The bowling pin pulls a string that opens the birdcage door (releasing the bird!) and tilts the wood plank, which makes the billiard ball go down the ramps.
- The billiard ball hits the closest brick, triggering a domino effect that knocks down all bricks.
- . . .
- The hammer hits the hand, which falls and, in so doing, pulls the cord.
- The light bulb lights up!

The “explanation” above works because it provides a *causal* narrative: a series of cause-and-effect steps that slowly but surely lead to the outcome. Although this example is artificial of course (no one would light a bulb like that), it epitomizes a style of explanation that is the gold standard of science.

Yet, biological phenomena frequently involve complex, tangled webs of explanatory factors. Consider guppies, small fish native to streams in South America, which show geographical variation in many kinds of traits,

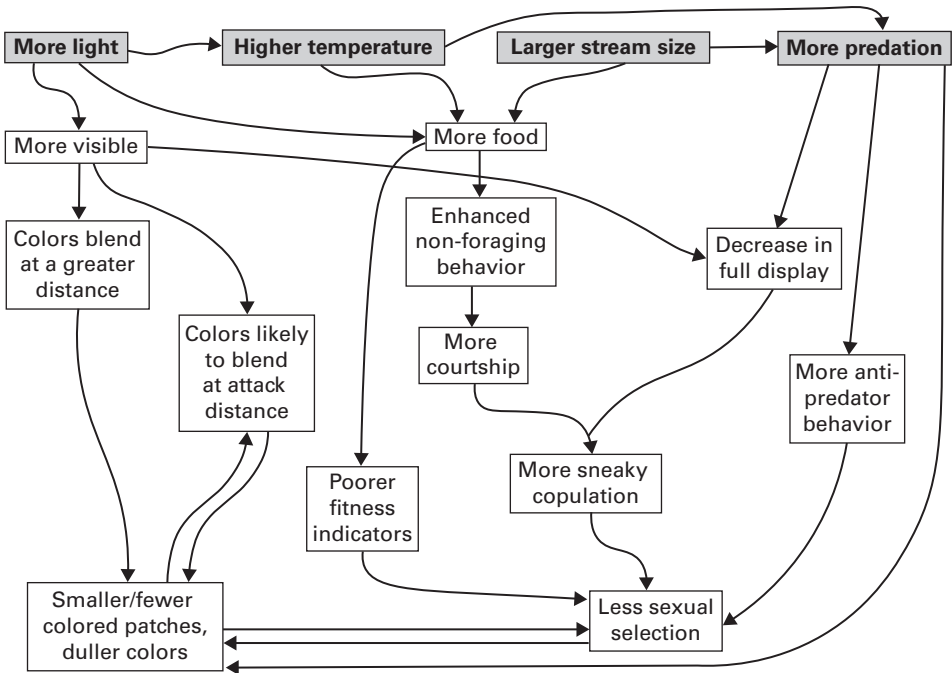


**Figure 1.3**

Rube Goldberg apparatus as an example of mechanical explanation.

including color patterns.<sup>11</sup> To explain the morphological and behavioral variation among guppies, the biologist John Endler suggested that we consider a “network of interactions” (figure 1.4). The key point was not to focus on the details of the interactions, but the fact that they exist. Complex as it may look, Endler’s network is “simple” as far as biological systems go. It doesn’t involve bidirectional influences (double-headed arrows), that is, those in which A affects B and B affects A in turn (see chapter 8). Still, most biological systems are organized like that.

Contrast such state of affairs to the vision encapsulated by Isaac Newton’s statement that “truth is ever to be found in simplicity, and not in the multiplicity and confusion of things” (Mazzocchi 2008, 10).<sup>12</sup> This stance is such an integral part of the canon of science as to constitute a form of First Commandment. Newton himself was building on the shoulders of René Descartes, the French polymath who helped canonize *reductionism* (see chapter 4) as part of Western thinking and philosophy. To him, the world was to be regarded as a clockwork mechanism. That is to say, in order to understand something, it is necessary to investigate the parts and



**Figure 1.4**

Multiple explanatory factors that influence morphological and behavioral variation among South American guppies, illustrating the rich network of relationships. Two of the relationships are bidirectional (see parallel arrows).

*Source:* Figure inspired by Endler (1995).

then reassemble the components to again create the whole—the essence of reductionism. Fast-forward to the second half of the twentieth century. The dream of extending the successes of the Cartesian mindset captivated biologists. As Francis Crick, one of the co-discoverers of the structure of DNA put it, “The ultimate aim of the modern movement in biology is to explain all biology in terms of physics and chemistry” (Mazzocchi 2008, 10). Reductionism indeed.

So, where is neuroscience today? The mechanistic tradition set off by Newton’s *Principia Mathematica*—arguably the most influential scientific achievement ever—is a major conceptual driving force behind how brain scientists think. Although many biologists view their subject matter as different from physics, for example, scientific practice is very much dominated by a mechanistic approach. The present book embraces a different way of

thinking, one that revolves around ideas of “collective phenomena,” ideas of networks, and ideas about complexity. The book is as much about what we know about the brain as it is a text to stimulate how we can think about the brain as a highly complex network—indeed entangled—system.

Before we can start our journey, we need to define a few terms and learn a little about anatomy.

### Road Ahead

If the central nervous system is indeed highly networked, then after learning some anatomy, you might expect that a natural subsequent chapter would be one on *complex systems*, including some introduction to *network science*. This was *not* the approach I took, however. Instead, my aim was to *build up the need* to consider the brain as a complex, entangled system. Thus, chapters 2 to 7 consider brain regions in a fair amount of isolation. In part, this is done so the reader can, in fact, gradually appreciate the limitations of this way of thinking. The approach is also pragmatic because the field of neuroscience has tended to study parts of the brain separately. So, we will use the knowledge accrued as a starting point, without forgetting the need to move beyond this type of description.

Before we get to chapter 8, which discusses complex systems, we have a few stops along the way. We start with some neuroanatomy (chapter 2), as we must learn how to orient ourselves around the target territory and learn its overall organization. In chapter 3, I describe the idea of a hypothetical “minimal brain” that allows an animal to defend itself and seek rewards, essential components of survival. How do sensations lead to actions via simple sensorimotor circuits? We’ll see that action flexibility necessitates uncoupling sensory and motor components. The objectives of chapter 3 are twofold. First, it is meant to introduce you to some brain regions/sectors and some of the functions they contribute to. (The linguistic construction of the previous sentence—“functions they contribute to”—may seem a poor one, but it is a consequence of the following central notion: Regions *contribute to* functions; by and large, they don’t have isolated functions.) Second, the intent is to show that the business of a brain region, according to the view espoused here, needs to be situated in the context of multi-region circuits: What does a brain region do *in combination* with other areas? In a sense, when one discusses regions  $R_1, \dots, R_4$  as part of some function

(such as avoiding threats in chapter 3), the decision to *not* discuss other areas is fairly arbitrary. We could have discussed the roles of regions  $R_5$ ,  $R_6$ , and so on. One of the main reasons we don't is due to the limitations of the tools available to neuroscientists, which are ill-suited to investigating large-scale, distributed systems (although techniques are advancing fast; see chapter 12). In the end, we still don't know much about collective computations involving larger numbers of gray matter components.

Because the concept of *function* is so central to our discussion, chapter 4 is entirely devoted to unpacking the idea. This is important because of the knee-jerk tendency to think in terms of “one area, one function”—for example, the function of the amygdala has to do with emotion or fear. In contrast, chapter 4 describes how a given brain area is always involved in multiple functions, in effect exhibiting a *functional repertoire*. But if so, how should we think of brain areas?

In chapters 5 to 7, I discuss several much-researched regions in relative isolation, providing historical context. This exposition provides some of the basics that will then allow us to delve into their large-scale networks. Chapters 8 to 11 are intended to work as a unit to advance how we need to embrace networks, fully, to understand the brain and behavior at a deeper level. So, as you read chapters 5 to 7, bear in mind the present considerations when a given brain region (say, the striatum) and some of “its functions” are discussed. In chapter 11, we reach the point where we can put things together and see that neural processes and mechanisms are not bound by territorial boundaries. There is no circumscribed place in the brain where, say, “reward” resides—instead, processes and mechanisms related to reward span multiple sectors of the brain. Finally, chapter 12 concludes our journey by revisiting some of the central themes covered in the preceding chapters.

A comment on the word “entangled” in the book title, which conjures multiple interrelated ideas. What I roughly want to convey by using it is *not* something like threads that are mixed together but can be separated if only one has enough time and patience. The meaning I want to convey is closer to “integrated,” but single words do not do justice to the general theme permeating the book—for example, cars are highly integrated systems, but are designed with parts with well-defined functions. Instead, the sense of *entangled* that I want to express is one in which brain parts dynamically assemble into coalitions that support complex cognitive-emotional behaviors, coalitions comprised of parts that jointly do their job.

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# The Entangled Brain

## How Perception, Cognition, and Emotion Are Woven Together

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