

SOME QUESTIONS WE WILL CONSIDER

- What is cognitive neuroscience, and why is it necessary? (27)
- How is information transmitted from one place to another in the nervous system? (30)
- How are things in the environment, such as faces and trees, represented in the brain? (34)
- What does studying the brain tell us about cognition? (46)

At 7:00 AM, in response to hearing the familiar but irritating sound of his alarm clock, Juan swings his arm in a well-practiced arc, feels the contact of his hand with the snooze button, and in the silence he has created, turns over for 10 more minutes of sleep. How can we explain Juan's behavior in terms of physiology? What is happening inside Juan's brain that makes it possible for him to hear the alarm, take appropriate action to turn it off, and know that he can sleep a little longer and still get to his early morning class on time?

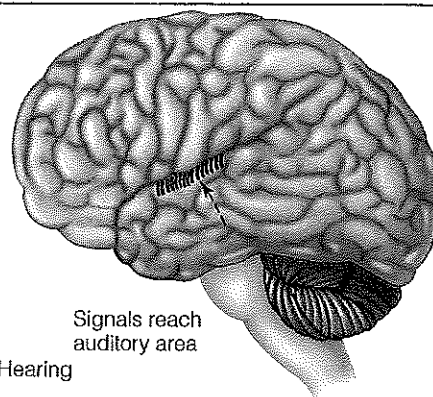
We can give a general answer to this question by considering some of the steps involved in Juan's action of turning off the alarm. The first step in hearing the alarm occurs when sound waves from the alarm enter Juan's ears and stimulate receptors that change the sound energy into electrical signals (Figure 2.1a). These signals then reach the auditory area of Juan's brain, which causes him to hear the ringing of the bell (Figure 2.1b). Then signals are sent from a number of places in the brain to the motor area, which controls movement. The motor area sends signals to the muscles of Juan's hand and arm (Figure 2.1c), which carry out the movement that turns off the alarm.

Figure 2.1 Some of the physiological processes that occur as Juan turns off his alarm. (a) Sound waves are changed to electrical signals in the ear and are sent to the brain. (b) Signals reaching the auditory areas of the brain—located inside the brain, under the hatched area—cause Juan to hear the alarm. (c) After Juan hears the alarm, signals are sent to the motor area. The two dashed arrows symbolize the fact that these signals reach the motor area along a number of different pathways. Signals are then sent from the motor area to muscles in Juan's arm and hand so he can turn off the alarm.

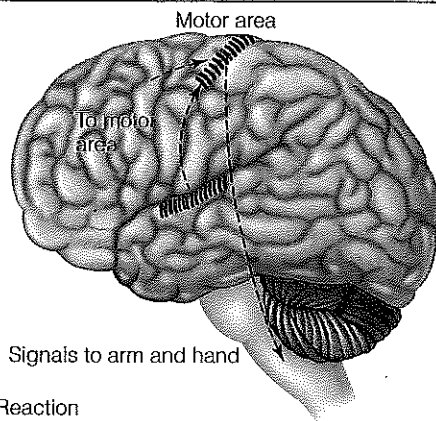
© Cengage Learning



(a) Sound to electricity



(b) Hearing



(c) Reaction

But there is more to the story than this sequence of events. For one thing, Juan's decision to hit the snooze button of his alarm is based on his knowledge that this will silence the alarm temporarily, and that the alarm will sound again in 10 minutes. He also knows that if he stays in bed for 10 more minutes, he will still have time to get to his class. A more complete picture of what's happening in Juan's brain when the alarm rings would therefore have to include processes involved in retrieving knowledge from memory and making decisions based on that knowledge. Thus, a seemingly simple behavior such as turning off an alarm in the morning involves a complex series of physiological events. The purpose of this chapter is to introduce some of the basic physiological principles of cognitive neuroscience—the study of the physiological basis of cognition.

Why Study Cognitive Neuroscience?

Some students taking their first course in cognitive psychology are surprised to find that studying the mind involves both behavioral experiments and physiological experiments. "Why," they ask, "is it necessary to learn about the operation of the brain to understand how people perceive or remember?" But for other students, especially those who have studied the brain in a previous course, it is obvious that taking a physiological approach provides important insights into how the mind works.

The point of view taken in this book is that to understand how the mind works, we need to do both behavioral experiments and physiological experiments. The reasoning behind this conclusion is based on the idea of *levels of analysis*. Levels of analysis refers to the idea that a topic can be studied in a number of different ways, with each approach contributing its own dimension to our understanding. To understand what this means, let's consider a topic outside the realm of cognitive psychology: understanding the automobile.

Our starting point for this problem might be to take a car out for a test drive. We could determine its acceleration, its braking, how well it corners, and its gas mileage. When we have measured these things, which come under the heading of "performance," we will know a lot about the particular car we are testing. But to learn more, we can consider another level of analysis: what is going on under the hood. This would involve looking at the mechanisms responsible for the car's performance: the motor and the braking and steering systems. For example, we can describe the car as being powered by a 4-cylinder 250 HP internal combustion engine and having independent suspension and disc brakes.

But we can look even deeper into the operation of the car by considering another level of analysis designed to help us understand how the car's engine works. One approach would be to look at what happens inside a cylinder. When we do this, we see that when vaporized gas enters the cylinder and is ignited by the spark plug, an explosion occurs that pushes the cylinder down and sends power to the crankshaft and then to the wheels. Clearly, considering the automobile from the different levels of driving the car, describing the motor, and observing what happens inside a cylinder provides more information about cars than simply measuring the car's performance.

Applying this idea of levels of analysis to cognition, we can consider measuring behavior to be analogous to measuring the car's performance, and measuring the physiological processes behind the behavior as analogous to what we learned by looking under the hood. And just as we can study what is happening under a car's hood at different levels, we can study the physiology of cognition at levels ranging from the whole brain, to structures within the brain, to chemicals that create electrical signals within these structures.

Consider, for example, a situation in which Gil is talking with Mary in the park (Figure 2.2a), and then a few days later he passes the park and remembers what she was

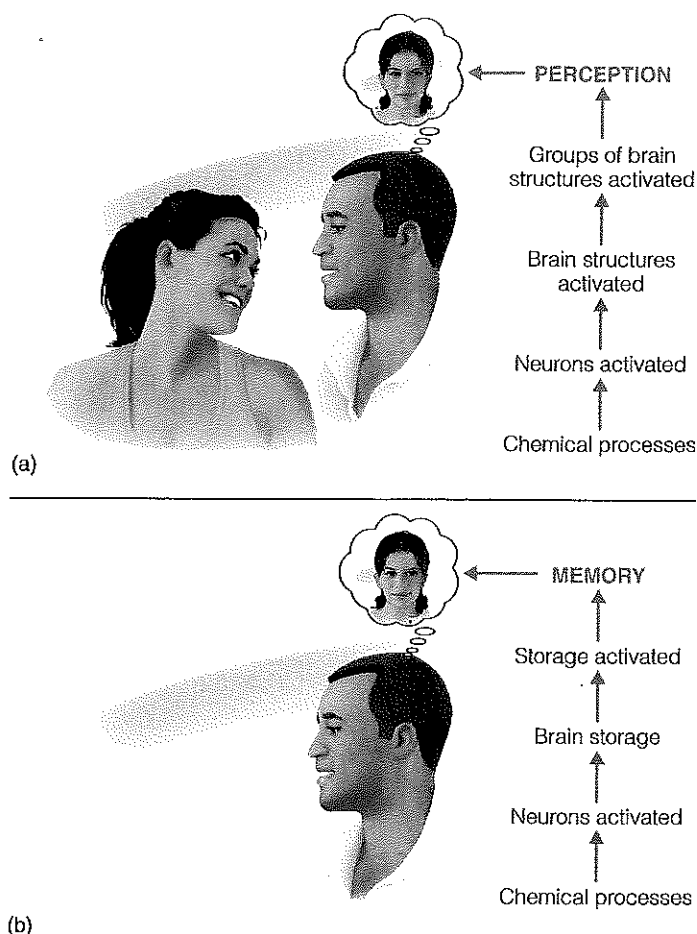


Figure 2.2 Physiological levels of analysis. (a) Gil perceives Mary and their surroundings as he talks with her. The physiological processes involved in Gil's perception can be described at levels ranging from chemical reactions to single neurons, to structures in the brain, to groups of structures in the brain. (b) Later, Gil remembers his meeting with Mary. The physiological processes involved in remembering can also be described at different levels of analysis. © 2015 Cengage Learning

wearing and what they talked about (Figure 2.2b). This is a simple behavioral description of having an experience and later having a memory of that experience.

But what is going on at the physiological level? During the initial experience, in which Gil perceives Mary as he is talking with her, chemical processes occur in Gil's eyes and ears, which create electrical signals in neurons (which we will describe shortly); individual brain structures are activated, then multiple brain structures are activated, all leading to his perception of Mary and what is happening as they talk (Figure 2.2a).

Meanwhile, other things are happening, both during Gil's conversation with Mary and after it is over. The electrical signals generated as Gil was talking with Mary trigger chemical and electrical processes that result in the storage of Gil's experiences in his brain. Then, when Gil passes the park a few days later, another sequence of physiological events is triggered that retrieves the information that was stored earlier, which enables him to remember his conversation with Mary (Figure 2.2b).

We have gone a long way to make a point, but it is an important one. To fully understand any phenomenon, whether it is how a car operates or how people remember past experiences, it needs to be studied at different levels of analysis. In this book, we will therefore be describing research in cognition at both the behavioral and physiological levels.

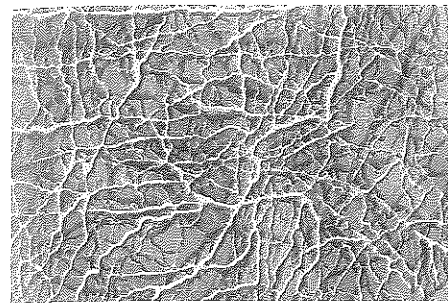
The plan of this chapter is to begin by describing some basic principles of nervous system functioning by first considering the structure and functioning of *neurons*, cells that are the building blocks and transmission lines of the nervous system. We then describe how cognitions are represented by the firing of neurons in the brain, activity in specific areas of the brain, and activity in groups of interconnected areas of the brain. As we do this, we will introduce three methods that have been used to study cognitive neuroscience: recording from single neurons; studying the effects of brain damage in humans; and creating images of the brain.

Neurons: Communication and Representation

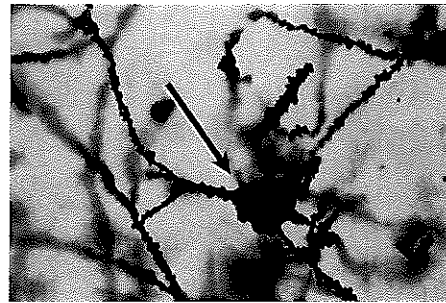
How is it possible that the 3.5-pound structure called the brain could be the seat of the mind? The brain appears to be static tissue. It has no moving parts (like the heart). It doesn't expand or contract (like the lungs), and when observed with the naked eye it looks almost solid. As it turns out, to understand the relation between the brain and the mind, and specifically to understand the physiological basis for everything we perceive, remember, and think, it is necessary to look within the brain and observe the small units called neurons that create and transmit information about what we experience and know.

THE MICROSTRUCTURE OF THE BRAIN: NEURONS

For many years, the nature of the brain's tissue was a mystery. Looking at the interior of the brain with the unaided eye gave no indication that it is made up of billions of smaller units. The nature of electrical signals in the brain and the pathways over which they traveled were just beginning to be discovered in the 19th century.



(a)



(b)

Figure 2.3 (a) Nerve net theory proposed that signals could be transmitted throughout the net in all directions. (b) A portion of the brain that has been treated with Golgi stain shows the shapes of a few neurons. The arrow points to a neuron's cell body. The thin lines are dendrites or axons (see Figure 2.4).

David Spears/Clouds Hill Imaging Ltd./CORBIS

To observe the structure of the brain, 19th-century anatomists applied special stains to brain tissue, which increased the contrast between different types of tissue within the brain. When they viewed this stained tissue under a microscope, they saw a network they called a nerve net (Figure 2.3a). This network was believed to be continuous, like a highway system in which one street connects directly to another, but without stop signs or traffic lights. When visualized in this way, the nerve net provided a complex pathway for conducting signals uninterrupted through the network.

One reason for describing the microstructure of the brain as a continuously interconnected network was that the staining techniques and microscopes used during that period could not resolve small details, and without these details, the nerve net appeared to be continuous. However, in the 1870s, the Italian anatomist Camillo Golgi developed a staining technique in which a thin slice of brain tissue was immersed in a solution of silver nitrate. This technique created pictures like the one in Figure 2.3b, in which fewer than 1 percent of the cells were stained, so they stood out from the rest of the tissue. (If all of the cells had been stained, it would be difficult to distinguish one cell from another because the cells are so tightly packed). Also, the cells that were stained were stained completely, so it was possible to see their structure.

This brings us to Ramon y Cajal, a Spanish physiologist who was interested in investigating the nature of the nerve net. Cajal cleverly used two techniques to achieve his goal. First, he used the Golgi stain, which stained only some of the cells in a slice of brain tissue. Second, he decided to study tissue from the brains of newborn animals, because the density of cells in the newborn brain is small compared to the density in the adult brain. This property of the newborn brain, combined with the fact that the Golgi stain affects less than 1 percent of the neurons, made it possible for Cajal to clearly see that the nerve net was not continuous, but was instead made up of individual units connected together (Kandel, 2006). Cajal's discovery that individual units called neurons were the basic building blocks of the brain was the centerpiece of neuron doctrine—the idea that individual cells transmit signals in the nervous system, and that these cells are not continuous with other cells as proposed by nerve net theory.

Figure 2.4a shows the basic parts of a neuron. The cell body is the metabolic center of the neuron; it contains mechanisms to keep the cell alive. The function of dendrites that branch out from the cell body is to receive signals from other neurons. Axons (also called nerve fibers) are usually long processes that transmit signals to other neurons. Figure 2.4b shows a neuron with a receptor that receives stimuli from the environment—pressure, in this example. Thus, the neuron has a receiving end and a transmitting end, and its role, as visualized by Cajal, was to transmit signals.

Cajal also came to some other conclusions about neurons: (1) There is a small gap between the end of a neuron's axon and the dendrites or cell body of another neuron. This

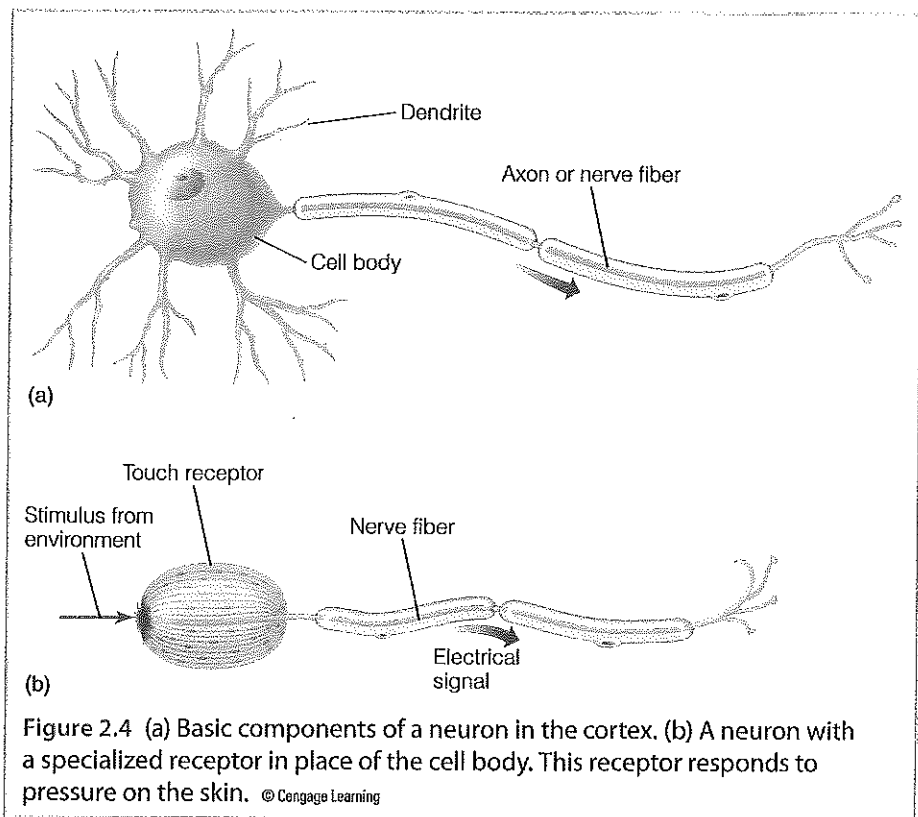


Figure 2.4 (a) Basic components of a neuron in the cortex. (b) A neuron with a specialized receptor in place of the cell body. This receptor responds to pressure on the skin. © Cengage Learning

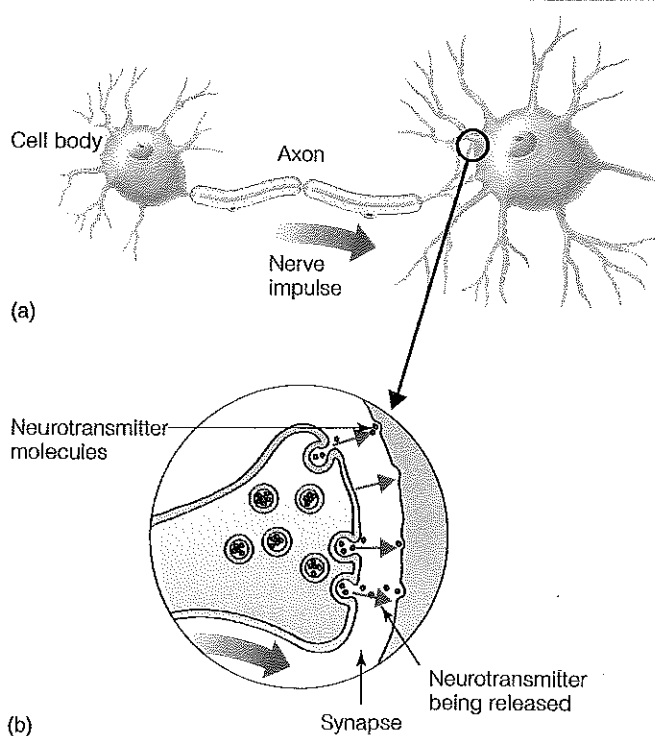


Figure 2.5 (a) Neuron synapsing on cell body of another neuron. (b) Close-up of the synapse showing the space between the end of one neuron and the cell body of the next neuron, and neurotransmitter being released. © Cengage Learning

gap is called a synapse (Figure 2.5). (2) Neurons are not connected indiscriminately to other neurons, but form connections only to specific neurons. This forms groups of interconnected neurons, which together form neural circuits. (3) In addition to neurons in the brain, there are also neurons that are specialized to pick up information from the environment, such as the neurons in the eye, ear, and skin. These neurons, called receptors (Figure 2.4b), are similar to brain neurons in that they have an axon, but they have specialized receptors that pick up information from the environment.

Cajal's idea of individual neurons that communicate with other neurons to form neural circuits was an enormous leap forward in the understanding of how the nervous system operates. The concepts introduced by Cajal—individual neurons, synapses, and neural circuits—are basic principles that today are used to explain how the brain creates cognitions. These discoveries earned Cajal the Nobel Prize in 1906, and today he is recognized as “the person who made this cellular study of mental life possible” (Kandel, 2006, p. 61).

THE SIGNALS THAT TRAVEL IN NEURONS

Cajal succeeded in describing the structure of individual neurons and how they are related to other neurons, and he knew that these neurons transmitted signals. However, determining the exact nature of these signals had to await the development of electronic amplifiers that were powerful enough to make the extremely small electrical signals generated by the neuron visible. In the 1920s, Edgar Adrian was able to record electrical signals from single sensory neurons, an achievement for which he was awarded the Nobel Prize in 1932 (Adrian, 1928, 1932).

METHOD

RECORDING FROM A NEURON

Adrian recorded electrical signals from single neurons using **microelectrodes**—small shafts of hollow glass filled with a conductive salt solution that can pick up electrical signals at the electrode tip and conduct these signals back to a recording device. Modern physiologists use metal microelectrodes.

Figure 2.6 shows a typical setup used for recording from a single neuron. There are two electrodes: a **recording electrode**, shown with its recording tip inside the neuron,¹ and a **reference electrode**, located some distance away so it is not affected by the electrical signals. The difference in charge between the recording and reference electrodes is fed into a computer and displayed on the computer's screen.

When the axon, or nerve fiber, is at rest, the meter records a difference in potential between the tips of the two electrodes of -70 millivolts (a millivolt is $1/1000$ of a volt), as shown on the right in Figure 2.6a. This value, which stays the same as long as there are no signals in the neuron, is called the **resting potential**. In other words, the inside of the

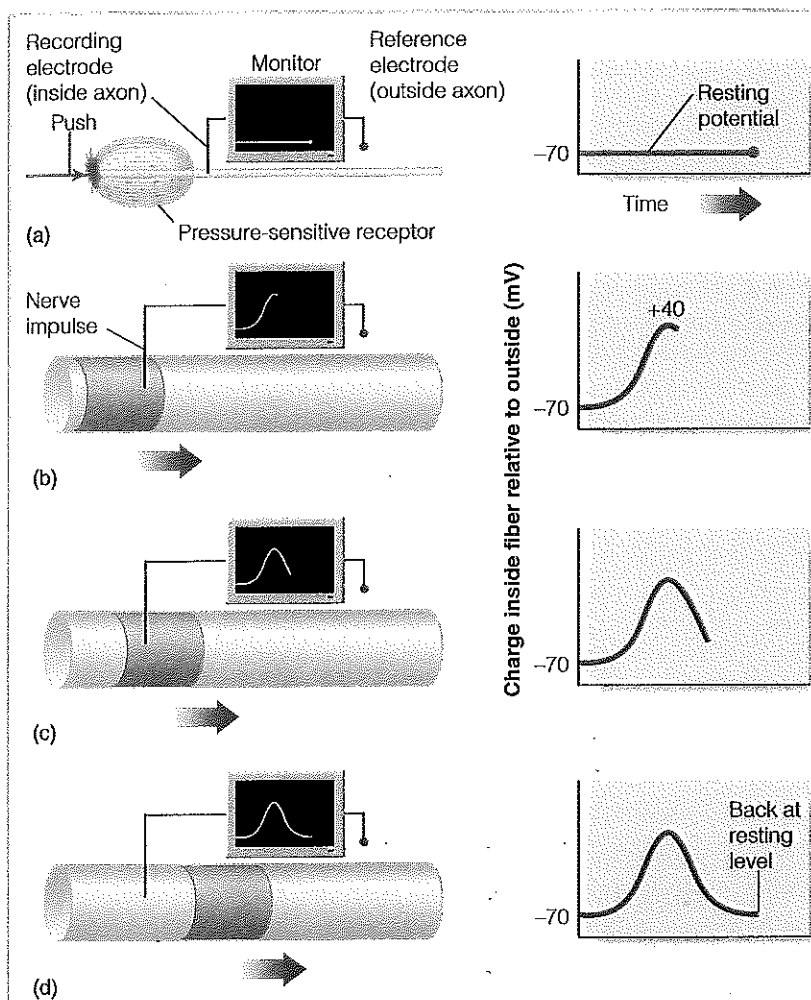


Figure 2.6 Recording an action potential as it travels down an axon. (a) When the nerve is at rest, there is a difference in charge, called the resting potential, of -70 millivolts (mV) between the inside and outside of the axon. The difference in charge between the recording and reference electrodes is fed into a computer and displayed on a computer monitor. This difference in charge is displayed on the right. (b) As the nerve impulse, indicated by the red band, passes the electrode, the inside of the fiber near the electrode becomes more positive. (c) As the nerve impulse moves past the electrode, the charge in the fiber becomes more negative. (d) Eventually the neuron returns to its resting state. © 2015 Cengage Learning

¹In practice, most recordings are achieved with the tip of the electrode positioned just outside the neuron because it is technically difficult to insert electrodes into the neuron, especially if it is small. However, if the electrode tip is close enough to the neuron, the electrode can pick up the signals generated by the neuron.

neuron has a charge that is 70 mV more negative than the outside, and this difference continues as long as the neuron is at rest.

Figure 2.6b shows what happens when the neuron's receptor is stimulated so that a nerve impulse is transmitted down the axon. As the impulse passes the recording electrode, the charge inside the axon rises to +40 millivolts compared to the outside. As the impulse continues past the electrode, the charge inside the fiber reverses course and starts becoming negative again (Figure 2.6c), until it returns to the resting potential (Figure 2.6d). This impulse, which is called the action potential, lasts about 1 millisecond ($1/1000$ second).

Figure 2.7a shows action potentials on a compressed time scale. Each vertical line represents an action potential, and the series of lines indicates that a number of action potentials are traveling past the electrode. Figure 2.7b shows one of the action potentials on an expanded time scale, as in Figure 2.6. There are other electrical signals in the nervous system, but we will focus here on the action potential, because it is the mechanism by which information is transmitted throughout the nervous system.

In addition to recording action potentials from single neurons, Adrian made other discoveries as well. He found that each action potential travels all the way down the axon without changing its height or shape. This property makes action potentials ideal for sending signals over a distance, because it means that once an action potential is started at one end of an axon, the signal will still be the same size when it reaches the other end.

At about the same time Adrian was recording from single neurons, other researchers were showing that when the signals reach the synapse at the end of the axon, a chemical called a neurotransmitter is released. This neurotransmitter makes it possible for the signal to be transmitted across the gap that separates the end of the axon from the dendrite or cell body of another neuron (see Figure 2.5b).

Although all of these discoveries about the nature of neurons and the signals that travel in them were extremely important (and garnered a number of Nobel Prizes for their discoverers), our main interest is not in how axons transmit signals, but in how these signals contribute to the operation of the mind. So far our description of how signals are transmitted is analogous to describing how the Internet transmits electrical signals, without describing how the signals are transformed into words and pictures that people can understand. Adrian was acutely aware that it was important to go beyond simply describing nerve signals, so he did a series of experiments to relate nerve signals to stimuli in the environment and therefore to people's experience.

Adrian studied the relation between nerve firing and sensory experience by measuring how the firing of a neuron from a receptor in the skin changed as he applied more pressure to the skin. What he found was that the shape and height of the action potential remained the same as he increased the pressure, but the *rate* of nerve firing—that is, the number of action potentials that traveled down the axon per second—increased (Figure 2.8). From this result, Adrian drew a connection between nerve firing and experience. He describes this connection in his book *The Basis of Sensation* (1928) by stating that if nerve impulses “are crowded closely together the sensation is intense, if they are separated by long intervals the sensation is correspondingly feeble” (p. 7).

What Adrian is saying is that electrical signals are *representing* the intensity of the stimulus, so pressure that generates “crowded” electrical signals feels stronger than pressure that generates signals separated by long intervals. Later experiments demonstrated similar results for vision. Presenting high-intensity light generates a high rate of nerve firing and the light appears bright; presenting lower intensity light generates a lower rate of nerve firing and the light appears dimmer. Thus, the rate of neural firing is related to the intensity of stimulation, which, in turn, is related to the magnitude of an experience, such as feeling pressure on the skin or experiencing the brightness of a light.

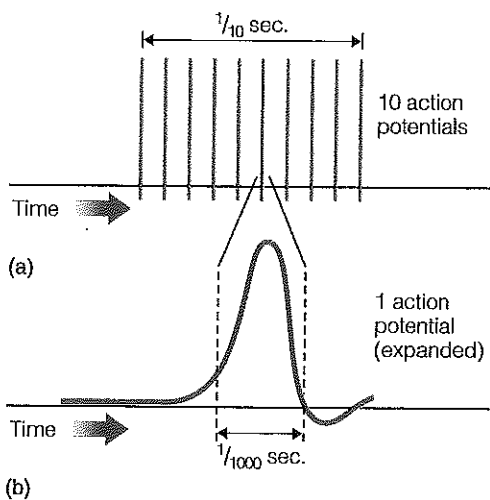


Figure 2.7 (a) A series of action potentials displayed on a time scale that makes each action potential appear as a thin line. (b) Changing the time scale reveals the shape of one of the action potentials. © 2015 Cengage Learning

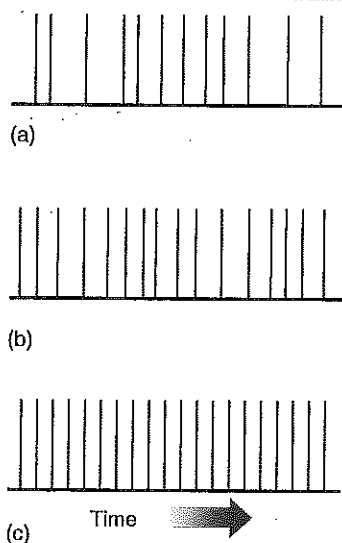


Figure 2.8 Action potentials recorded from an axon in response to three levels of pressure stimulation on the skin: (a) light; (b) medium; (c) strong. Increasing stimulus intensity causes an increase in the rate of nerve firing. © Cengage Learning

We can extend this idea that there is a relationship between nerve firing and perceptual experience by asking how nerve impulses are involved in other aspects of cognition such as memory, language, and thinking. The first step toward doing this is to consider the representational function of nerve impulses.

THE PRINCIPLE OF NEURAL REPRESENTATION

We introduced the idea of representation in Chapter 1, when we defined the mind as *a system that creates representations of the world so that we can act within it to achieve our goals* (page 5). The key word in this definition is *representation*, because what it means is that everything we experience is the result of something that *stands for* that experience. When considering this idea at a neural level, we will study the **principle of neural representation**, which states that everything a person experiences is based not on direct contact with stimuli, but on representations in the person's nervous system.

For example, let's return to Gil's conversation with Mary. Gil sees Mary because light reflected from Mary enters Gil's eyes and Mary's image is focused onto his retina, the layer of neurons that lines the back of the eye (Figure 2.9). The important word here is *image*, because it is the image created by light reflected by Mary that gets into Gil's eye, not Mary herself. The idea of Mary not getting into the eye may seem silly because it is so obvious, but the point is an important one: What enters the eye is a *representation* of Mary—something that stands for her—and one property of this representation is that although it may look like Mary, it is also different from her. It is not only two-dimensional and smaller, but may be distorted or blurred because of the optics of the eye.

The difference between Mary and her representation on the retina becomes more dramatic a few thousandths of a second later when receptors in the retina transform her image into electrical signals, which then travel through the retina, leave the back of the eye in the optic nerve, and eventually reach the **visual cortex**, the area at the back of the brain that receives signals from the eye. Gil's perception of Mary is therefore based not on direct contact with Mary, but on the way she is represented by action potentials in the brain.

Carrying this idea further, we can consider what happens a few days later when Gil passes the park and remembers what Mary looked like and what they talked about. These memories, which are recreations of Gil's experiences from a few days before, are also created by electrical signals in the brain.

This idea of representation is extremely important in cognitive psychology, because one approach to understanding cognition is to consider how our experiences are represented, both in our mind (measured behaviorally) and in the brain (measured physiologically). Since our focus in this chapter is on physiology, we will now consider how our cognitions are represented physiologically. We start with neurons.

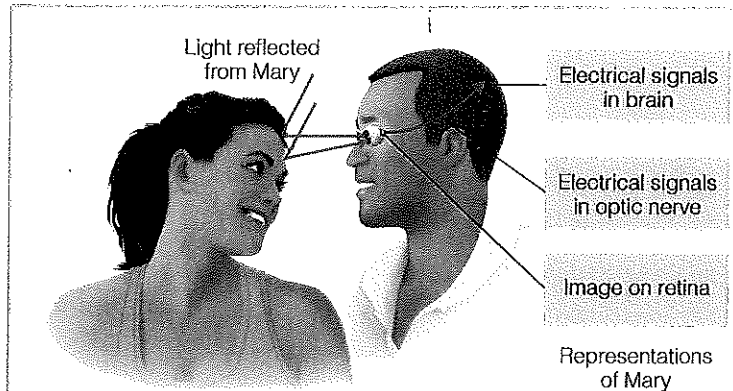


Figure 2.9 A few of the ways that Mary is represented in Gil's visual system. Light reflected from Mary creates an image inside Gil's eye. This image is then transformed into electrical signals that travel out of the eye in the optic nerve and reach the visual area of the brain. © 2015 Cengage Learning

Representation by Neurons

We will use perception as our example to discuss representation by neurons, keeping in mind that the principles that apply to perception also apply to other cognitions such as memory, language, and thinking. Starting with Adrian's idea that the magnitude of experience—our perception of a 100-watt light as brighter than a 40-watt bulb—is related to the rate of nerve firing, we can take the next step and ask, what about the *quality* of experience? For the senses, *quality across the senses* refers to the different experience associated

with each of the senses—perceiving light for vision, sound for hearing, smells for olfaction, and so on. We can also ask about quality *within a particular sense*, such as shape, color, or movement for vision, or recognizing different kinds of objects based on their shapes or different people based on their faces.

One way to answer the question of how action potentials determine different qualities is to propose that the action potentials for each quality might look different. However, Adrian ruled out that possibility by determining that all action potentials have basically the same height and shape. If all nerve impulses are basically the same whether they are caused by seeing a red fire engine or remembering what you did last week, how can these impulses stand for different qualities? We begin answering this question by first considering single neurons and then moving on to groups of neurons.

REPRESENTATION BY SINGLE NEURONS

Research on how neural signals represent things followed Adrian's lead and focused on how neurons fire to different sensory stimuli.

FEATURE DETECTORS In the 1960s, David Hubel and Thorsten Wiesel started a series of experiments in which they presented visual stimuli to cats, as shown in Figure 2.10a, and determined which stimuli caused specific neurons to fire. They found that each neuron in the visual area of the cortex responded to a specific type of stimulation presented to a small area of the retina. Figure 2.10b shows some of the stimuli that caused neurons in and near the visual cortex to fire (Hubel, 1982; Hubel & Wiesel, 1959, 1961, 1965). They called these neurons **feature detectors** because they responded to specific stimulus features such as orientation, movement, and length.

This knowledge that neurons in the visual system fire to specific types of stimuli led to the idea that each of the thousands of neurons that fire when we look at a tree fire to different features of the tree. Some neurons fire to the vertically oriented trunk, others to the variously oriented branches, and some to more complex combinations of a number of features.

The idea that the tree is represented by the combined response of many feature detectors is similar to building objects by combining building blocks like Legos. But these feature detectors are in the visual cortex, which is the first place that electrical signals from the eye reach the brain. Further research in areas beyond the visual cortex revealed neurons that respond to stimuli that are more complex than oriented lines.

NEURONS THAT RESPOND TO COMPLEX STIMULI How are complex stimuli represented by the firing of neurons in the brain? One answer to this question began to emerge in the laboratory of Charles Gross. Gross's experiments, in which he recorded from single neurons in the monkey's temporal lobe, on the side of the brain, required a great deal of endurance by the researchers, because the experiments typically lasted 3 or 4 days. In these experiments, the results of which were reported in now classic papers in 1969 and 1972, Gross's research team presented a variety of different stimuli to anesthetized monkeys. On a projection screen like the one in Figure 2.10a, they presented lines, squares, and circles. Some stimuli were light, and some dark.

The discovery that neurons in the temporal lobe respond to complex stimuli came a few days into one of their experiments, when they had found a neuron that refused to respond to any of the standard stimuli like oriented lines or circles or squares. Nothing worked,

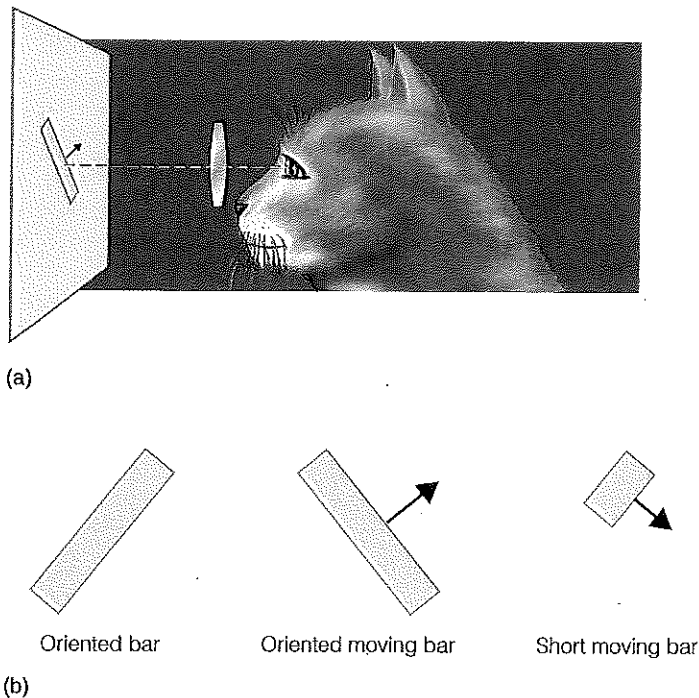


Figure 2.10 (a) An experiment in which electrical signals are recorded from the visual system of an anesthetized cat that is viewing stimuli presented on the screen. The lens in front of the cat's eye ensures that the images on the screen will be focused on the cat's retina. The recording electrode is not shown. (b) A few of the types of stimuli that cause neurons in the cat's visual cortex to fire. © 2015 Cengage Learning

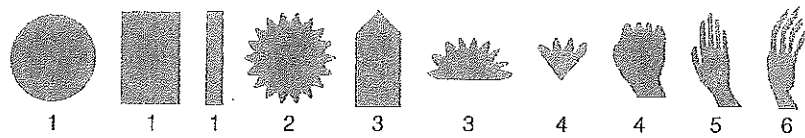


Figure 2.11 Some of the shapes used by Gross et al. (1972) to study the responses of neurons in the temporal lobe of the monkey's cortex. The shapes are arranged in order of their ability to cause the neuron to fire, from none (1) to little (2 and 3) to maximum (6). (Source: Based on C. G. Gross, C. E. Rocha-Miranda, & D. B. Bender, *Visual properties of neurons in inferotemporal cortex of the macaque*. *Journal of Neurophysiology*, 5, 96–111, 1972.)

until one of the experimenters pointed at something in the room, casting a shadow of his hand on the screen. When this hand shadow caused a burst of firing, the experimenters knew they were onto something and began testing the neuron with a variety of stimuli, including cutouts of a monkey's hand. After a great deal of testing, they determined that this neuron responded to a handlike shape with fingers pointing up (Figure 2.11) (Rocha-Miranda, 2011; also see Gross, 2002). After expanding the types of stimuli presented, they also found some neurons that responded best to faces; later researchers extended these results and provided many examples of neurons that respond to faces but don't respond to other types of stimuli (Figure 2.12) (Perrett et al., 1982; Rolls, 1981).

Let's stop for a moment and consider the results we have presented so far. We saw that neurons in the visual cortex respond to simple stimuli like oriented bars, neurons in the temporal lobe respond to complex geometrical stimuli, and neurons in another area of the temporal lobe respond to faces. What is happening is that neurons in the visual cortex that respond to relatively simple stimuli send their axons to higher levels of the visual system, where signals from many neurons combine and interact; neurons at this higher level, which respond to more complex stimuli such as geometrical objects, then send signals to higher areas, combining and interacting further and creating neurons that respond to even more complex stimuli such as faces. This progression from lower to higher areas of the brain is called **hierarchical processing**. Does hierarchical processing solve the problem of neural representation? Could it be that higher areas of the visual system contain neurons that are specialized to respond only to a specific object, so that object would be represented by the firing of that one type of specialized neuron? As we will see, the problem of neural representation most likely involves a number of neurons working together.

SENSORY CODING

The problem of neural representation for the senses has been called the *problem of sensory coding*, where the **sensory code** refers to how neurons represent various characteristics of the environment. The idea that an object could be represented by the firing of a specialized neuron that responds only to that object is called **specificity coding**. This is illustrated in Figure 2.13, which shows how a number of neurons respond to three different faces. Only neuron #4 responds to Bill's face, only #9 responds to Mary's face, and only #6 responds to Raphael's face. Also note that the neuron specialized to respond only to Bill, which we can call a "Bill neuron," does not respond to Mary or Raphael. In addition, other faces or types of objects would not affect this neuron. It fires only to Bill's face.

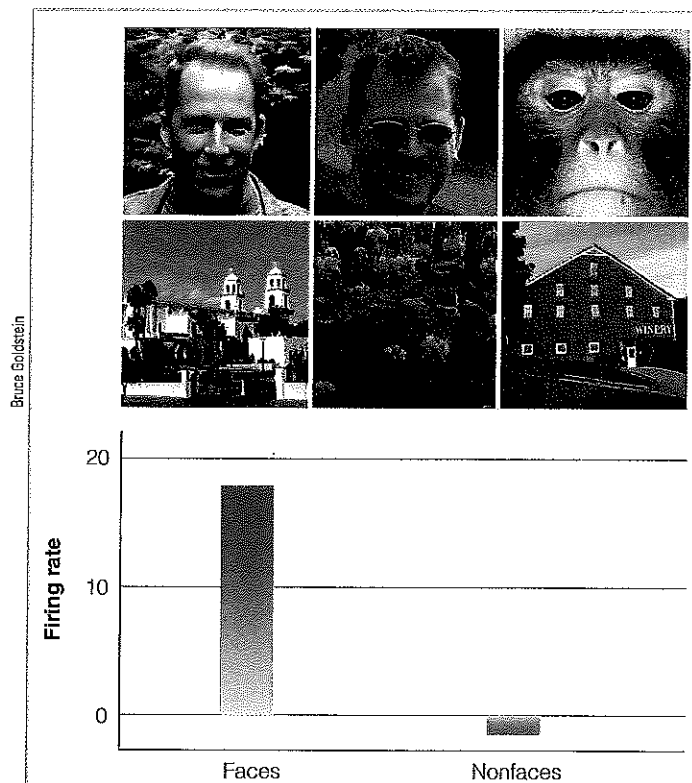
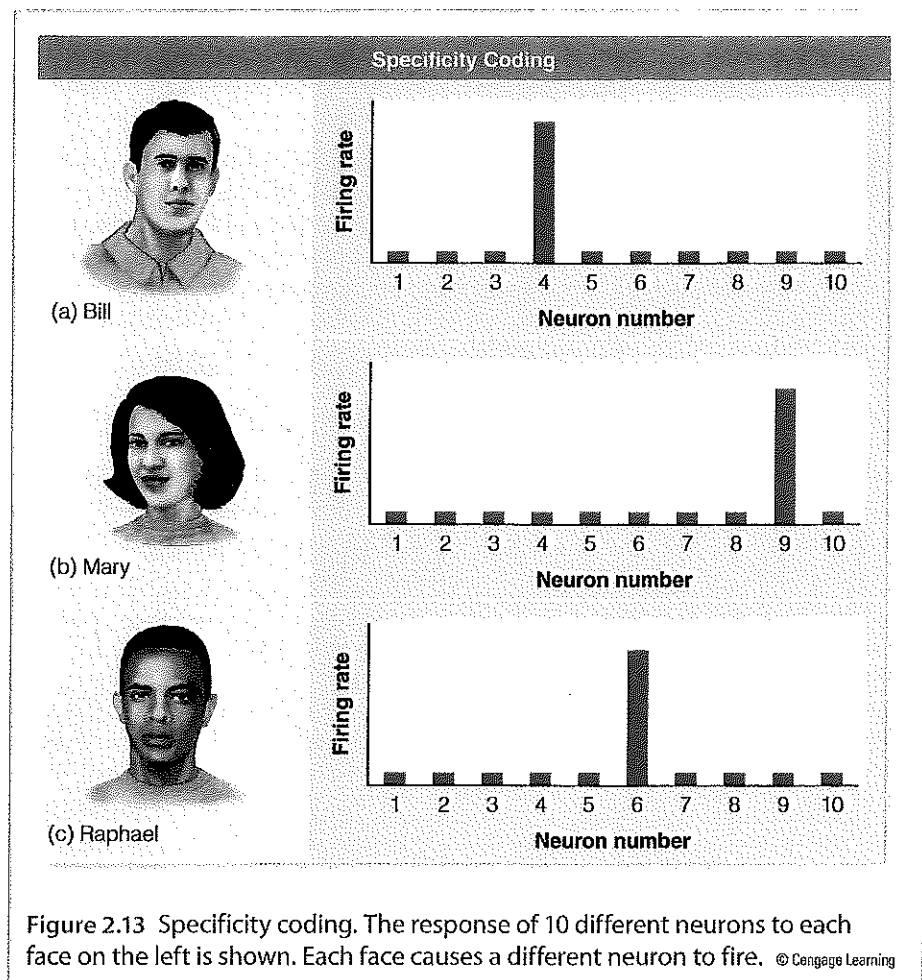


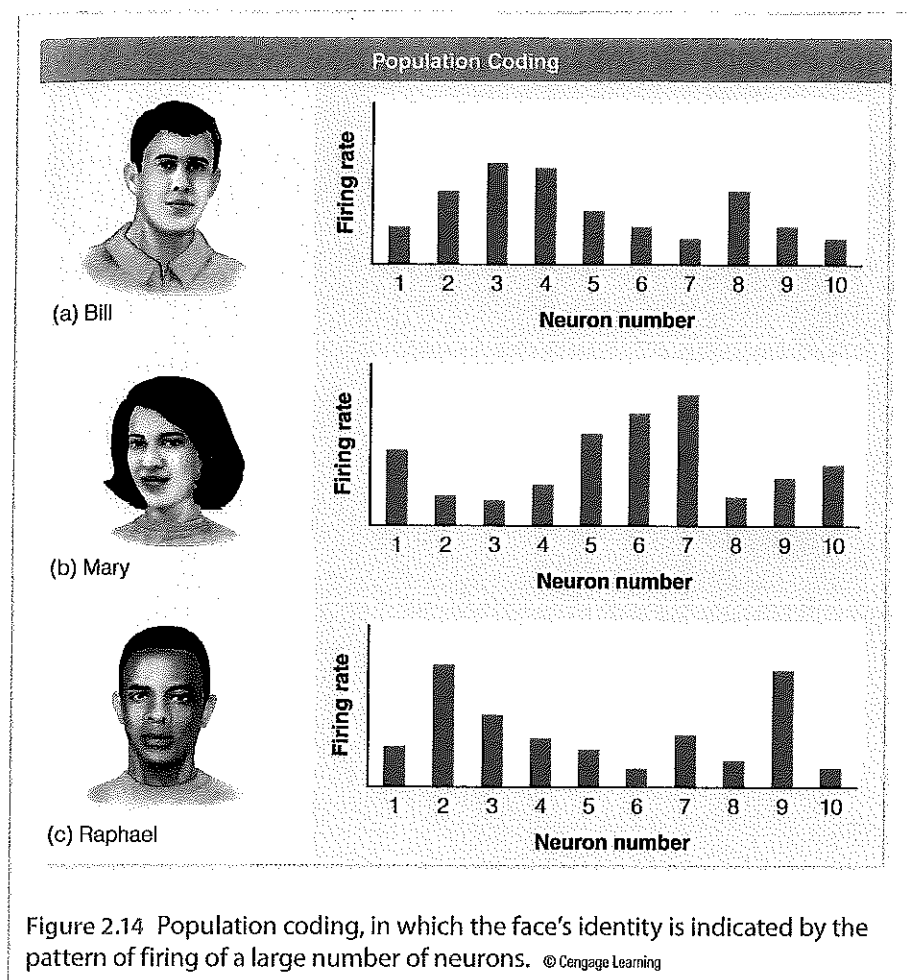
Figure 2.12 Firing rate, in nerve impulses per second, of a neuron in the monkey's temporal lobe that responds to face stimuli, but not to nonface stimuli. (Source: Based on E. T. Rolls & M. J. Tovee, *Sparseness of the neuronal representation of stimuli in the primate temporal visual cortex*, *Journal of Neurophysiology*, 73, 713–726, 1995.)



Although the idea of specificity coding is straightforward, it is unlikely to be correct. Even though there are neurons that respond to faces, these neurons usually respond to a number of different faces (not just Bill's). There are just too many different faces and other objects (and colors, tastes, smells, and sounds) in the world to have a separate neuron dedicated to each object. An alternative to the idea of specificity coding is that a number of neurons are involved in representing an object.

Population coding is the representation of a particular object by the pattern of firing of a large number of neurons. According to this idea, Bill's face might be represented by the pattern of firing shown in Figure 2.14a, Mary's face by a different pattern (Figure 2.14b), and Raphael's face by another pattern (Figure 2.14c). An advantage of population coding is that a large number of stimuli can be represented, because large groups of neurons can create a huge number of different patterns. There is good evidence for population coding in the senses and for other cognitive functions as well. But for some functions, a large number of neurons aren't necessary. *Sparse coding* occurs when small groups of neurons are involved.

Sparse coding occurs when a particular object is represented by a pattern of firing of only a small group of neurons, with the majority of neurons remaining silent. As shown in Figure 2.15a, sparse coding would represent Bill's face by the pattern of firing of a few neurons (neurons 2, 3, 4, and 7). Mary's face would be signaled by the pattern of firing of a few different neurons (neurons 4, 6, and 7; Figure 2.15b), but possibly with some overlap with the neurons representing Bill, and Raphael's face would have yet another pattern (neurons 1, 2, and 4; Figure 2.15c). Notice that a particular neuron can respond to more



than one stimulus. For example, neuron #4 responds to all three faces, although most strongly to Mary's.

Recently, neurons were discovered when recording from the temporal lobe of patients undergoing brain surgery for epilepsy. (We should point out that stimulating and recording from neurons is a common procedure before and during brain surgery, because it makes it possible to determine the exact layout of a particular person's brain.) These neurons responded to very specific stimuli. Figure 2.16 shows the records for a neuron that responded to pictures of the actor Steve Carell and not to other people's faces (Quiroga et al., 2007). However, the researchers who discovered this neuron (as well as other neurons that responded to other people) point out that they had only 30 minutes to record from these neurons and that if more time were available, it is likely that they would have found other faces that would cause this neuron to fire. Given the likelihood that even these special neurons are likely to fire to more than one stimulus, Quiroga and coworkers (2008) suggested that their neurons are probably an example of sparse coding.

There is also other evidence that the code for representing objects in the visual system, tones in the auditory system, and odors in the olfactory system may involve the pattern of activity across a relatively small number of neurons, as sparse coding suggests (Olshausen & Field, 2004).

Memories are also represented by the firing of neurons, but there is a difference between representation of perceptions and representation of memories. The neural firing associated with experiencing a perception is associated with what is happening as perception is occurring, as in our example in Figure 2.9 when Gil is looking at Mary. Firing

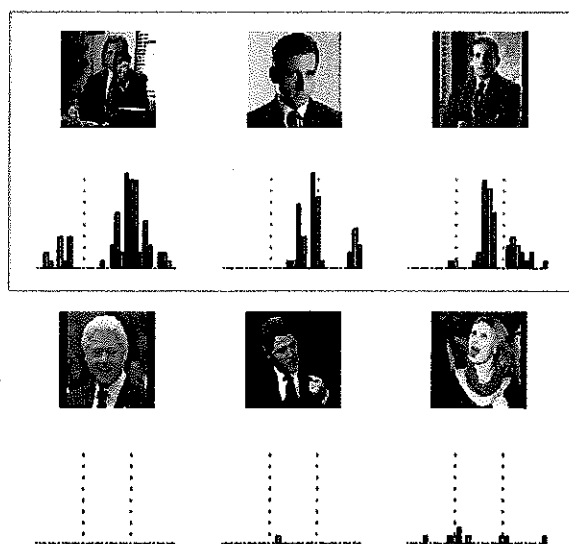
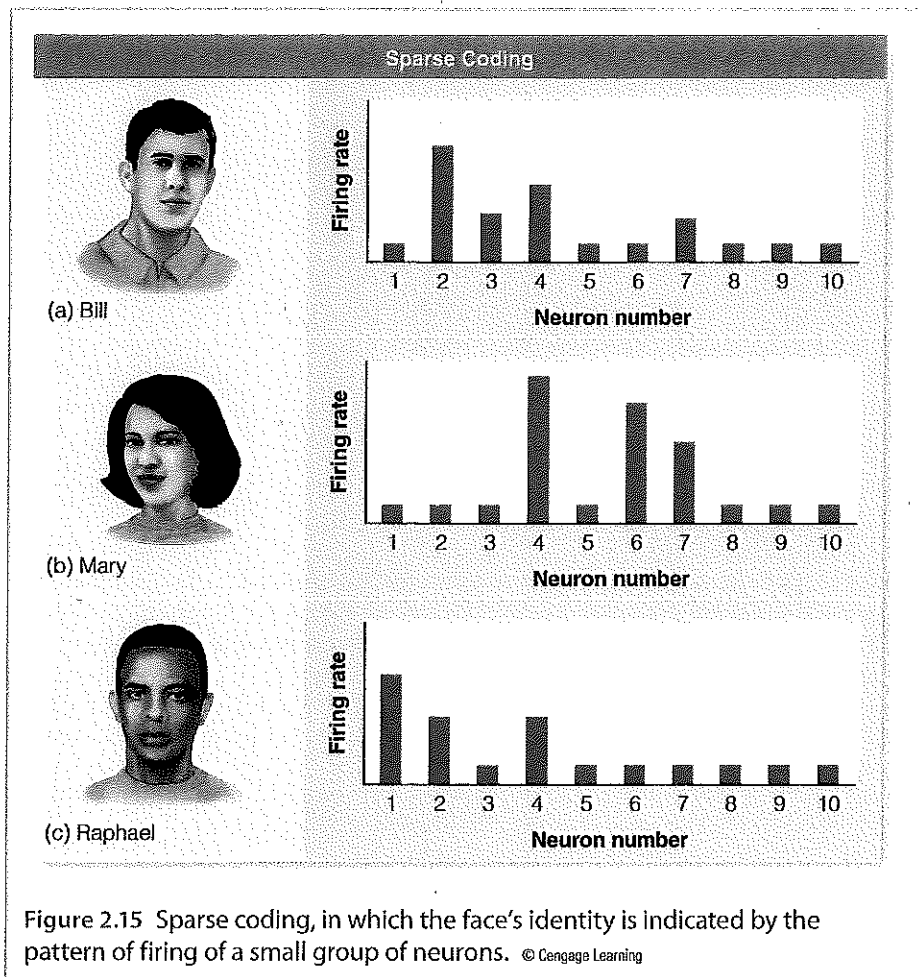


Figure 2.16 Records from a neuron in the temporal lobe that responded to different views of Steve Carell (top records) but did not respond to pictures of other well-known people (bottom records). (Source: R. Q. Quiroga, L. Reddy, G. Kreiman, C. Koch, & I. Fried, Sparse but not "grandmother-cell" coding in the medial temporal lobe, *Trends in Cognitive Sciences*, 12, 87–91, 2008. Reproduced by permission.)

associated with memory is associated with information about the past that has been stored in the brain, as when Gil *remembers* seeing Mary. We know less about the actual form of this stored information for memory, but it is likely that the basic principles of population and sparse coding also operate for memory, with specific memories being represented by particular patterns of stored information that result in a particular pattern of nerve firing when we experience the memory.

Saying that individual neurons and groups of neurons contain information for perception, memory, and other cognitive functions is the first step toward understanding representation. The next step involves looking at organization: how different types of neurons and functions are organized within the brain.

TEST YOURSELF 2.1

1. Describe the idea of levels of analysis. How does this relate to answering the question "Why study cognitive neuroscience?"
2. How did early brain researchers describe the brain in terms of a nerve net? How does the idea of individual neurons differ from the idea of a nerve net?
3. Describe the research that led Cajal to propose the neuron doctrine.

4. Describe the structure of a neuron. Describe the synapse and neural circuits.
5. How are action potentials recorded from a neuron? What do these signals look like, and what is the relation between action potentials and stimulus intensity?
6. How has the question of how different perceptions can be represented by neurons been answered? Consider both research involving recording from single neurons and ideas about sensory coding.
7. How is neural representation for memory different from representation for perception? How is it similar?

Organization: Neuropsychology and Recording From Neurons

One of the basic principles of brain organization is **localization of function**—specific functions are served by specific areas of the brain. Most of the cognitive functions are served by the cerebral cortex, which is a layer of tissue about 3 mm thick that covers the brain (Fischl & Dale, 2006). The cortex is the wrinkled covering you see when you look at an intact brain (Figure 2.17). Early evidence for localization of function came from **neuropsychology**—the study of the behavior of people with brain damage.

LOCALIZATION DEMONSTRATED BY NEUROPSYCHOLOGY

A great deal of neuropsychological research has involved the study of patients who have suffered brain damage caused by stroke—disruption of the blood supply to the brain, usually by a blood clot. An early report of localization of function based on a stroke patient was Paul Broca's (1861) proposal that an area in the left frontal lobe, now called **Broca's area**, is specialized for speech (Figure 2.17). His proposal was based on his study of a patient who had suffered damage to his frontal lobe and was called "Tan" because this was the only word he could say. In 1879, Carl Wernicke studied another group of patients with damage in an area of the temporal lobe, now called **Wernicke's area**, whose speech was fluent and grammatically correct but tended to be incoherent.

Broca and Wernicke thus identified one area for *producing* language (Broca's area) and one area for *comprehending* language (Wernicke's area). Although this straightforward categorization in terms of production and comprehension has been modified by the results of later research (see Novick et al., 2005, and page 308 in Chapter 11), the idea that these two areas of the brain serve different functions is still valid and was a major impetus to accepting the idea of localization of function.

Further evidence for localization of function came from studies of the effect of brain injury in wartime. Studies of Japanese soldiers in the Russo-Japanese war of 1904–1905 and Allied soldiers in World War I showed that damage to the **occipital lobe** of the brain, where the visual cortex is located (Figure 2.18), resulted in blindness, and that there was a connection between the area of the occipital lobe that was damaged and the place in visual space where the person was blind (Glickstein & Whitteridge, 1987; Holmes & Lister, 1916; Lanska, 2009). For example, damage to the left part of the occipital lobe caused an area of blindness in the upper right part of visual space.

As noted earlier, other areas of the brain have also been associated with specific functions. The auditory cortex, which receives signals from the ears, is in the upper **temporal lobe** and is responsible for hearing. The somatosensory cortex, which receives signals from the

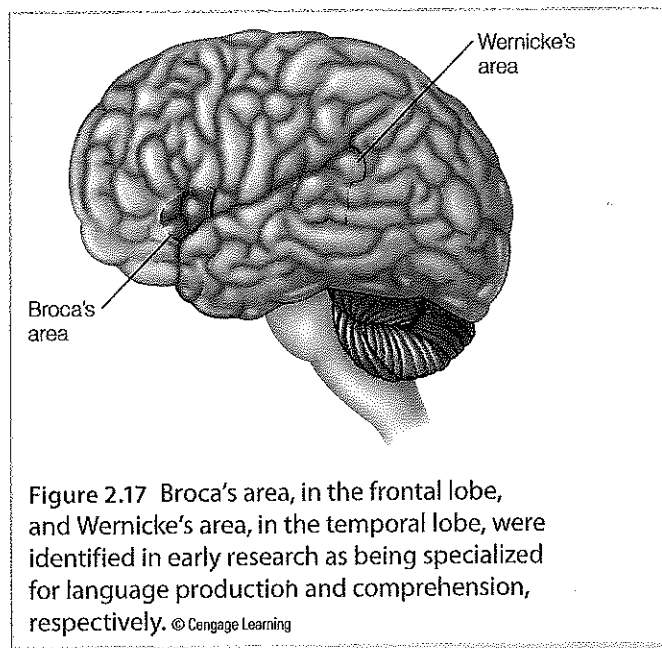


Figure 2.17 Broca's area, in the frontal lobe, and Wernicke's area, in the temporal lobe, were identified in early research as being specialized for language production and comprehension, respectively. © Cengage Learning

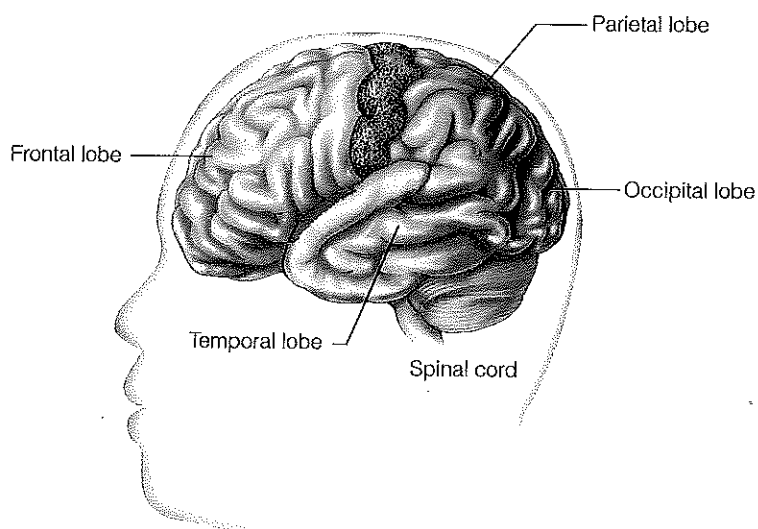


Figure 2.18 The human brain, showing the locations of the primary receiving areas for the senses: vision = occipital lobe; skin senses = parietal lobe (dotted blue area); hearing = temporal lobe (located within the temporal lobe, approximately under the dark shaded area). Areas for taste and smell are not visible. The frontal lobe responds to all of the senses and is involved in higher cognitive functioning. © Cengage Learning

skin, is in the parietal lobe and is responsible for perceptions of touch, pressure, and pain. The frontal lobe receives signals from all of the senses and is responsible for coordination of the senses, as well as higher cognitive functions like thinking and problem solving.

Another effect of brain damage on visual functioning, reported in patients who have damage to the temporal lobe on the lower right side of the brain, is **prosopagnosia**—an inability to recognize faces. People with prosopagnosia can tell that a face is a face, but can't recognize whose face it is, even for people they know well such as friends and family members. In some cases, people with prosopagnosia look into a mirror and, seeing their own image, wonder who the stranger is looking back at them (Burton et al., 1991; Hecaen & Angelergues, 1962; Parkin, 1996).

One of the goals of neuropsychology research is to determine whether a particular area of the brain is specialized to serve a particular cognitive function. Though it might be tempting to conclude, based on a single case of prosopagnosia, that the damaged brain area in the lower temporal lobe is responsible for recognizing faces, it is necessary to take further steps before reaching this conclusion. To reach more definite conclusions about the functions of a particular area, researchers usually test a number of different patients with damage to different brain areas, in order to demonstrate a *double dissociation*.

METHOD

DEMONSTRATING A DOUBLE DISSOCIATION

A **double dissociation** occurs if damage to one area of the brain causes function A to be absent while function B is present, and damage to another area causes function B to be absent while function A is present. To demonstrate a double dissociation, it is necessary to find two people with brain damage that satisfy the above conditions.

Double dissociations have been demonstrated for face recognition and object recognition, by finding patients who can't recognize faces (Function A) but who can recognize objects (Function B), and other patients, with damage in a different area, who can't recognize objects (Function B) but who can recognize faces (Function A) (McNeal & Warrington, 1993; Moscovitch et al., 1997). The importance of demonstrating a double dissociation is that it enables us to conclude that functions A and B are served by different mechanisms, which operate independently of one another.

The results of the neuropsychology studies described above indicate that face recognition is served by one area in the temporal lobe and that this function is separate from mechanisms associated with recognizing other types of objects, which is served by another area of the temporal lobe. Neuropsychological research has also identified areas that are important for perceiving motion and, as we will see later in this book, for different functions of memory, thinking, and language. In addition to neuropsychology, another tool for demonstrating localization of function is recording from single neurons.

LOCALIZATION DEMONSTRATED BY RECORDING FROM NEURONS

We previously discussed how visual stimuli can be represented by the firing of groups of neurons. We can also use single-neuron recording to demonstrate localization of function.

Most of this research has been done on animals. For example, Doris Tsao and coworkers (2006) found that 97 percent of neurons within a small area in the lower part of a monkey's temporal lobe responded to pictures of faces but not to pictures of other types of objects. This "face area," as it turns out, is located near the area in humans that is associated with prosopagnosia. The idea that our perception of faces is associated with a specific area of the brain is also supported by research using a technique called brain imaging, which makes it possible to determine which areas of the brains of humans are activated by different cognitions.

Organization: Brain Imaging

In the 1980s, a technique called magnetic resonance imaging (MRI), which made it possible to create images of structures within the brain, was introduced for clinical practice; since then, it has become a standard technique for detecting tumors and other brain abnormalities. This technique is excellent for revealing brain structures, but it doesn't indicate neural activity. Another technique, functional magnetic resonance imaging (fMRI), has enabled researchers to determine how various types of cognition activate different areas of the brain.

METHOD BRAIN IMAGING

Functional magnetic resonance imaging takes advantage of the fact that blood flow increases in areas of the brain activated by a cognitive task. The measurement of blood flow is based on the fact that hemoglobin, which carries oxygen in the blood, contains a ferrous (iron) molecule and therefore has magnetic properties. If a magnetic field is presented to the brain, the hemoglobin molecules line up like tiny magnets. fMRI indicates the presence of brain activity because the hemoglobin molecules in areas of high brain activity lose some of the oxygen they are transporting. This makes the hemoglobin more magnetic, so these molecules respond more strongly to the magnetic field. The fMRI apparatus determines the relative activity of various areas of the brain by detecting changes in the magnetic response of the hemoglobin.

The setup for an fMRI experiment is shown in Figure 2.19a, with the person's head in the scanner. As a person engages in a cognitive task such as perceiving an image, the activity of

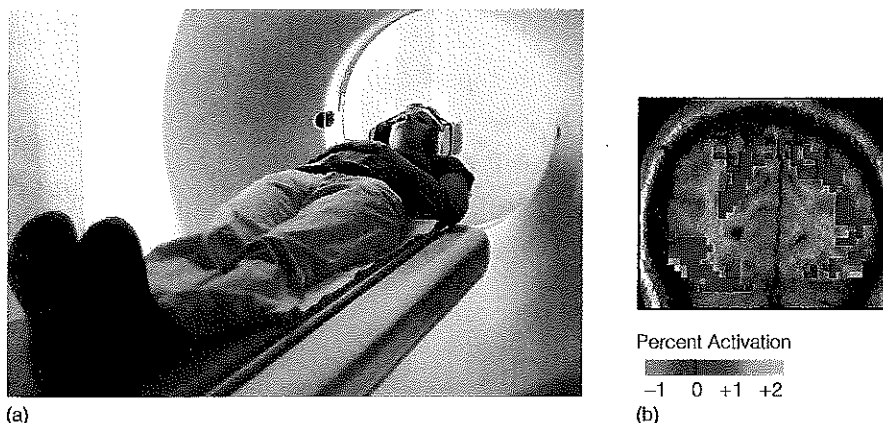


Figure 2.19 (a) Person in a brain scanner. (b) fMRI record. Colors indicate locations of increases and decreases in brain activity. Red and yellow indicate increases in brain activity; blue and green indicate decreases. (Source: Part b from Alumi Ishai, Leslie G. Ungerleider, Alex Martin, & James V. Haxby, *The representation of objects in the human occipital and temporal cortex*, *Journal of Cognitive Neuroscience*, 12: 2, 35–51. © 2000 by the Massachusetts Institute of Technology.)

the brain is determined. Activity is recorded in **voxels**, which are small cube-shaped areas of the brain about 2 or 3 mm on a side. Voxels are not brain structures but are simply small units of analysis created by the fMRI scanner. One way to think about voxels is that they are like the small square pixels that make up digital photographs or the image on your computer screen, but since the brain is three-dimensional, voxels are small cubes rather than small squares. Figure 2.19b shows the result of an fMRI scan. Increases or decreases in brain activity associated with cognitive activity are indicated by colors, with specific colors indicating the amount of activation.

It bears emphasizing that these colored areas do not appear as the brain is being scanned. They are determined by a calculation in which brain activity that occurred during the cognitive task is compared to baseline activity that was recorded prior to the task. The results of this calculation, which indicate increases or decreases in activity in specific areas of the brain, are then converted into colored displays like those in Figure 2.19b.

BRAIN IMAGING EVIDENCE FOR LOCALIZATION OF FUNCTION

Most of the brain imaging experiments that have provided evidence for localization of function have involved determining which brain areas were activated when people observed pictures of different objects.

LOOKING AT PICTURES As shown in Figures 2.20a and 2.20b, faces activate a specific area in the brain (Kanwisher et al., 1997; Kanwisher & Dilks, 2013). This area, called the **fusiform face area (FFA)** because it is in the fusiform gyrus on the underside of the temporal lobe (Kanwisher et al., 1997), is the same part of the brain that is damaged in cases of prosopagnosia.

Further evidence for localization of function comes from fMRI experiments that have shown that perceiving pictures representing indoor and outdoor scenes like those shown in Figure 2.21a activates the **parahippocampal place area (PPA)** (Aguirre et al., 1998; R. Epstein et al., 1999). Apparently, what is important for this area is information about spatial layout, because increased activation occurs when viewing pictures both of empty rooms and of rooms that are completely furnished (Kanwisher, 2003). The other specialized area, the **extrastriate body area (EBA)**, is activated by pictures of bodies and parts of bodies (but not by faces), as shown in Figure 2.21b (Downing et al., 2001).

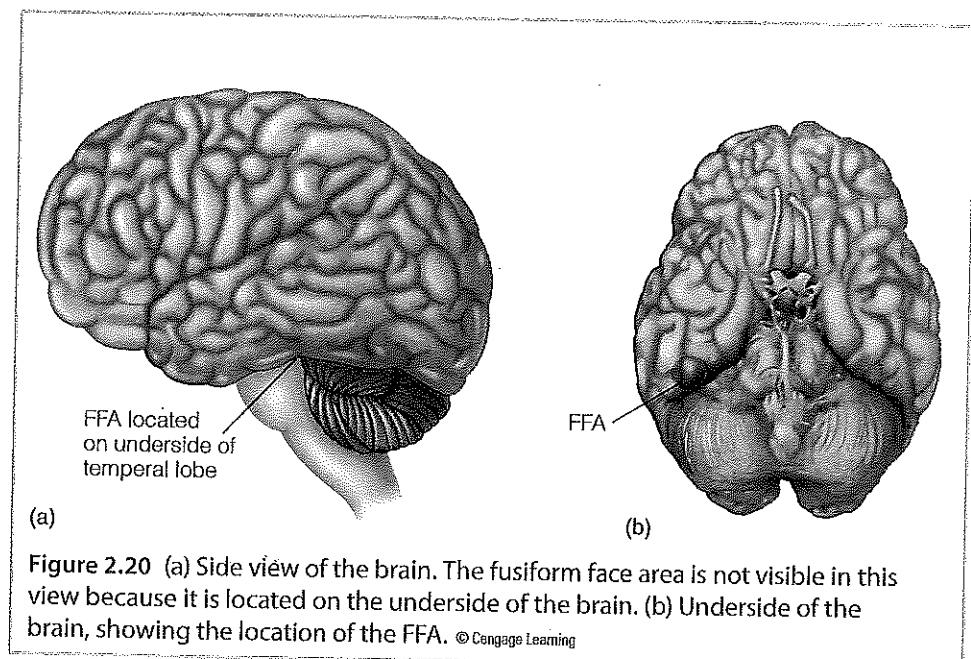


Figure 2.20 (a) Side view of the brain. The fusiform face area is not visible in this view because it is located on the underside of the brain. (b) Underside of the brain, showing the location of the FFA. © Cengage Learning

LOOKING AT MOVIES In everyday life, our usual experience involves seeing scenes that contain many different objects, some of which are moving. Therefore, Alex Huth and coworkers (2012) conducted an fMRI experiment using stimuli similar to what we see in the environment, by having subjects view film clips. Huth's subjects viewed 2 hours of film clips while in a brain scanner. To analyze how the voxels in these subjects' brains responded to different objects and actions in the films, Huth created a list of 1,705 different objects and action categories and determined which categories were present in each film scene.

Figure 2.22 shows four scenes and the categories (labels) associated with them. By determining how each voxel responded to each scene and then analyzing his results using a complex statistical procedure, Huth was able to determine what kinds of stimuli each voxel responded to. For example, one voxel responded well when streets, buildings, roads, interiors, and vehicles were present.

Figure 2.23 shows the types of stimuli that cause voxels across the surface of the brain to respond. Objects and actions similar to each other are located near each other in the brain. The reason there are two areas for humans and two for animals is that each area represents different features related to humans or animals. For example, the area labeled "human" at the bottom of the brain (which is actually on the underside of the brain) corresponds to the fusiform face area (Figure 2.20b), which responds to all aspects of faces. The human area higher on the brain responds specifically to facial expressions. The areas labeled "talking" correspond to Broca's and Wernicke's areas.

The results in Figure 2.23 present an interesting paradox. On one hand, the results confirm the earlier research that identified specific areas of the brain responsible for the perception of specific types of stimuli like faces, places, and bodies. On the other hand,

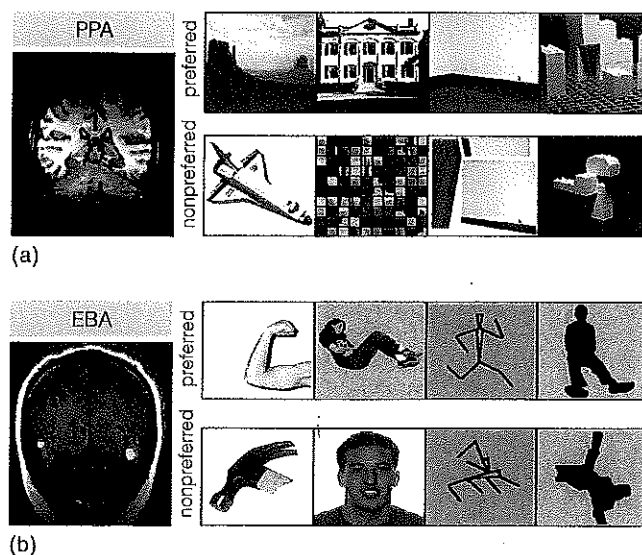
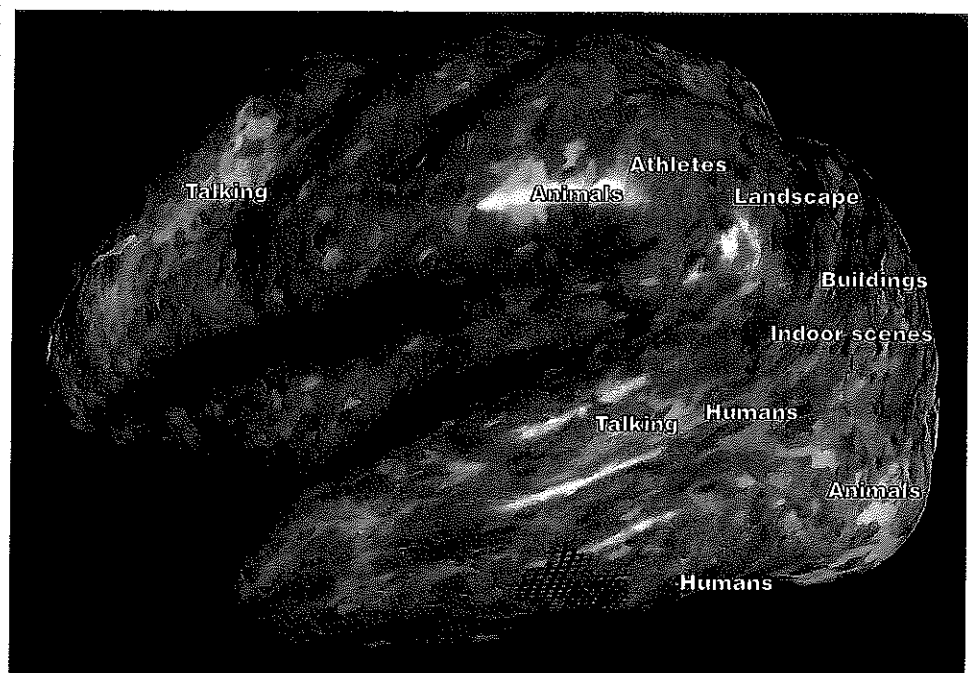


Figure 2.21 (a) The parahippocampal place area (PPA) is activated by places (top row) but not by other stimuli (bottom row). (b) The extrastriate body area (EBA) is activated by bodies (top), but not by other stimuli (bottom). (Source: From L. M. Chalupa & J. S. Werner, eds., *The Visual Neurosciences*, 2-vol. set, figure from pp. 1179–1189, © 2003 Massachusetts Institute of Technology, by permission of The MIT Press.)

Movie Clip	Labels	Movie Clip	Labels
	butte.n desert.n sky.n cloud.n brush.n		city.n expressway.n skyscraper.n traffic.n sky.n
	woman.n talk.v gesticulate.v book.n		bison.n walk.v grass.n stream.n

Figure 2.22 Four frames from the movies viewed by subjects in Huth et al.'s (2012) experiment. The words on the right indicate categories that appear in the frames (n = noun, v = verb). (Source: From A. G. Huth et al., *A continuous semantic space describes the representation of thousands of object and action categories across the human brain*, *Neuron*, 76, 1210–1224, Figure S1, Supplemental materials, 2012.)



Courtesy of Alex Huth

Figure 2.23 The results of Huth et al.'s (2012) experiment, showing locations on the brain where the indicated categories are most likely to activate the brain.

these new results reveal a map that stretches over a large area of the cortex. As we will now see, even though there is a great deal of evidence for localization of function, we need to consider the brain as a whole in order to understand the physiological basis of cognition.

DISTRIBUTED REPRESENTATION ACROSS THE BRAIN

We have seen that brain imaging research has made it possible to zero in on specific areas in the brain that are specialized to serve specific functions. We will now describe research in which brain imaging has been used to show that specific cognitions can affect many structures in the brain. The idea that specific cognitive functions activate many areas of the brain is called *distributed representation*. Although the idea of distributed representation might at first seem to contradict the idea of localization of function described above, we will see that these two ideas actually complement each other.

Consider, for example, the localization of face perception in the brain. We saw that brain imaging experiments have identified an area called the FFA that is strongly activated by faces and responds more weakly to other types of stimuli. But just because there is an area that is specialized to respond to faces doesn't mean that faces activate *only* that area. Faces strongly activate the FFA, *plus* other areas as well.

While a number of areas of the brain participate in *perception* of a face, other areas also respond to various *reactions* to a face. For example, when you see someone walking down the street, looking at the person's face activates many neurons in your FFA, plus neurons in other areas that are responding to the face's form. But your response to that person's face may go beyond simply "That's a person's face." You may also be affected by whether the person is looking at you, how attractive you think the person is, any emotions the face may elicit, and your reactions to the person's facial expression. As it turns out, different areas in the brain are activated by each of these responses to a face (see Figure 2.24). Looking at a face thus activates a number of areas involved in perceiving the face, plus other areas associated with reactions elicited by the face.

But what about an encounter with a much simpler stimulus—one that doesn't look at you, have emotional expressions, or elicit emotional responses? How about perceiving a

rolling red ball, as the person is doing in Figure 2.25? Even this simple, neutral stimulus causes a wide distribution of activity in the brain, because each of the ball's qualities—color (red), movement (to the right), shape (round), depth, location—is processed in a different area of the brain.

What is remarkable about the rolling red ball is that even though it causes activity in a number of separated areas in the brain, our experience contains little or no evidence of this widely distributed activity. We just see the ball! The importance of this observation extends beyond perceiving a rolling red ball to other cognitive functions, such as memory, language, making decisions, and solving problems, all of which involve distributed activity in the brain.

For example, research on the physiology of memory, which we will consider in detail in Chapters 5 and 7, has revealed that multiple areas in every lobe of the brain are involved in storing memories for facts and events and then remembering them later. Recalling a fact or remembering an event not only elicits associations with other facts or events but can also elicit visual, auditory, smell, or taste perceptions associated with the memory; emotions elicited by the memory; and other thought processes as well. Additionally, there are different types of memory—short-term memory, long-term memory, memories about events in a person's life, memories for facts, and so on—all of which activate different, although sometimes partially overlapping, areas of the brain.

The idea that the principle of distributed representation holds for perception, memory, and other cognitive processes reflects the generality of the mechanisms responsible for cognition. Even though this book contains separate chapters on various types of cognitions, this separation does not always occur in the mind or the brain. The mind is, after all, not a textbook; it does not necessarily subdivide our experiences or cognitions into neat categories. Instead, the mind creates cognitive processes that can involve a number of different functions. Just as a symphony is created by many different instruments, all working together in an orchestra to create the harmonies and melodies of a particular composition, cognitive processes are created by many specialized brain areas, all working together to create a distributed pattern of activity that creates all of the different components of that particular cognition.

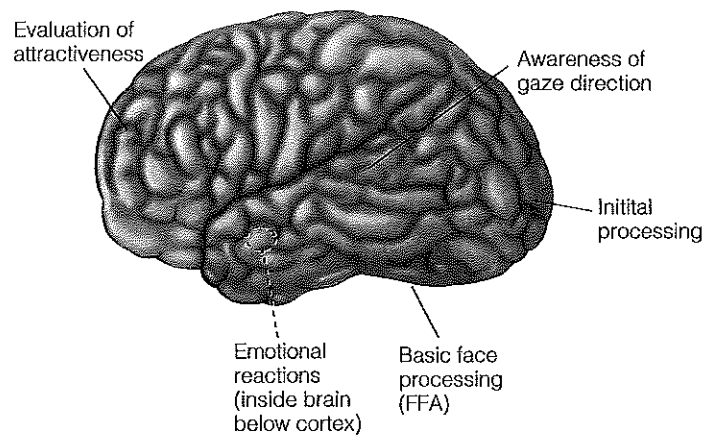


Figure 2.24 Areas of the brain that are activated by different aspects of faces. (Source: Adapted from Ishai, 2008; based on data from Calder et al., 2007; Gobbini & Haxby, 2007; Grill-Spector et al., 2004; Haxby et al., 2000; Ishai et al., 2004.) © Cengage Learning

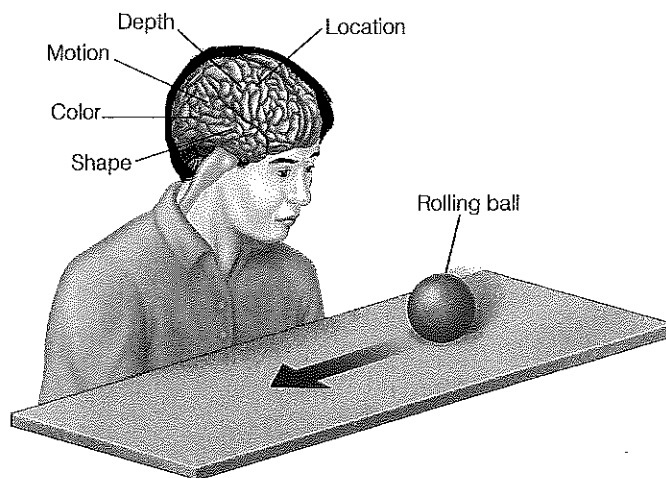


Figure 2.25 As this person watches the red ball roll by, different properties of the ball activate different areas of his cortex. These areas are in separate locations, although there is communication between them. © Cengage Learning

All Together Now: Neural Networks

The idea that the brain is like a symphony in which many different brain areas work together to create various cognitions is suggested not only by the discovery of different brain areas that relate to different aspects of cognition, but also by research on **neural networks**—groups of neurons or structures that are connected together.

Figure 2.26 shows the network we introduced in Chapter 1 to illustrate structural models (see Figure 1.15, page 19). This network, called the **pain matrix**, consists of a number of connected structures that are involved in the perception of pain. In this figure, we have replaced the names of structures with some of the functions these structures serve. Thus, one area is involved in determining the location of pain and its sensory aspects (described by words like *throbbing*, *prickly*, and *intense*); some areas are involved in emotional aspects

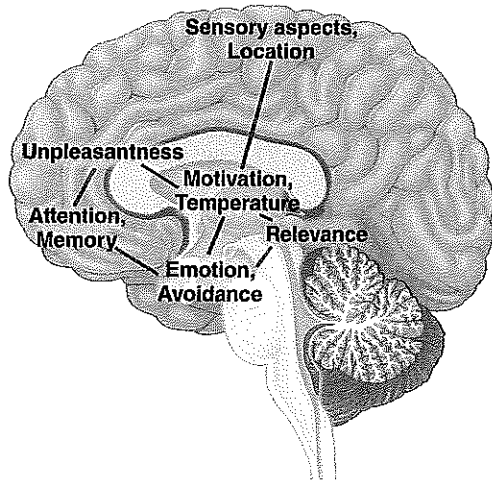


Figure 2.26 The perception of pain is caused by the activation of a network called the pain matrix, consisting of a number of different connected structures. Many structures have multiple functions. Some of the functions associated with structures in the pain matrix are indicated here. © 2015 Cengage Learning

of pain (described by words such as *unpleasant*, *torturing*, and *frightful*); other areas are involved in evaluating the significance of a pain stimulus for ongoing behavior, directing attention to or away from a painful stimulus, and recording memories of the stimulus. All of the structures in this network, working together, determine the nature of the overall experience of pain.

The network in Figure 2.26 is just one example of many networks that have been proposed based on research involving all of the methods we have described in this chapter: recording from single neurons, neuropsychology, and brain imaging. In addition, a new generation of anatomical techniques has been developed to trace the pathways of the nerve fibers that create communication between different structures. One technique, called **diffusion tensor imaging (DTI)**, is based on detection of how water diffuses along the length of nerve fibers. Figure 2.27 shows nerve tracts determined by this technique (Calamante, 2013). New techniques like this are constantly being developed, in order to determine more precisely how areas of the brain communicate with each other.

Earlier in this chapter, we introduced the ideas of *levels of analysis*—studying a topic at different levels—and *neural representation*—how experience is determined by representations in the nervous system. The way various structures in the brain communicate and interact with each other illustrates both of these ideas. To understand the neural basis of cognition, we need to consider levels ranging from individual neurons to structures created from these neurons to groups of structures working together. We also need to realize that all of this activity taken together is what creates representations of our cognitions in the nervous system.

In the next chapter, on perception, we will encounter evidence for these interactions when we see how knowledge we bring to a situation can combine with information provided by signals received from our sensory receptors to create our perception of the environment.

Something to Consider

WHAT NEUROSCIENCE TELLS US ABOUT COGNITION

We have seen that one of the contributions of neuroscience has been to determine where different capacities occur in the brain—a continuing research project that we could call the study of the *geography of the brain*. But the contribution of neuroscience extends beyond just determining where different functions are located. Much neuroscience research has focused on dynamic processes that are happening within the brain, and on determining the mechanisms responsible for cognitive behaviors. In Chapter 4, Attention, we will describe an impressive demonstration of a dynamic process when we revisit the cortical map shown in Figure 2.23. As it turns out, this map is not static but can expand or contract. Thus, when you are looking for a cat, aspects of the map relevant to cats expand and aspects distant from cats contract. In other words, the geography of the brain becomes tuned to enable you to more effectively find cats (Çukur, 2013)!

We will also encounter experiments in which proposals based on behavioral observations are supported by the results of physiological research. Consider, for example, Endel Tulving's (1985) distinction, which we introduced in Chapter 1 (page 19) and will consider in detail in Chapter 7, between two types of long-term memory, *episodic memory* and *semantic memory*. Episodic memory, according to Tulving, is

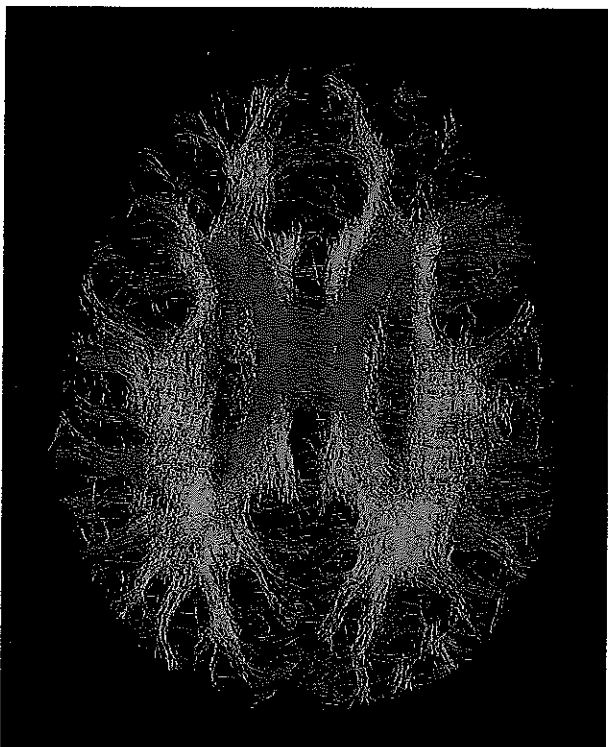


Figure 2.27 Nerve tracts in the human brain determined by diffusion tensor imaging. (Source: From F. Calamante, et al., *Track-weighted functional connectivity [TW-FC]: A tool for characterizing the structural-functional connections in the brain*, *NeuroImage* 70, 199–210, Figure 2a, page 202, 2013.)

Courtesy of Fernando Calamante and Elsevier

memory for personal experiences. Your memory for your trip to New York City and the things you did there would be episodic memories. Semantic memories are stored knowledge and memory for facts. Your knowledge that New York City is in New York State, that throngs of people converge on Times Square every New Year's Eve, and the layout of the New York City subway map are examples of semantic memories.

But although we can distinguish between these two types of memory based on the types of things we remember, can we say that they are served by different mechanisms? One answer to this question is provided by neuropsychological research that has demonstrated a double dissociation between episodic and semantic memory (see Method: Demonstrating a Double Dissociation, page 40). As we will describe in Chapter 7, there are people with brain damage who have lost the ability to remember personal experiences (episodic memory) but still retain memory for facts about the world (semantic memory). There are also people with the opposite problem: Their brain damage has taken away their ability to access their knowledge for facts, but they can still remember personal experiences. These two types of people, taken together, create a double dissociation and enable us to conclude that episodic and semantic memories are served by independent mechanisms. This is just one example of how a proposal based on behavioral observations has been supported and expanded by the results of physiological experiments.

Our description of cognitive neuroscience in this chapter has taken us from the firing of single neurons to maps covering the brain, from linking brain areas to specific cognitions to linking many brain areas together to create more complex cognitions. But let's not lose sight of the purpose of these physiological mechanisms, which is to determine cognitions ranging from recognizing your friend to having a conversation. Although it may be nice to know how neurons work or where brain structures are located, we are not really interested in studying just the properties of neurons or brain structures. We are interested in determining how neurons and brain structures determine cognition. In other words, our main focus is on explaining behaviors related to cognition, and the approach in this book is based on the idea that the best way to explain these behaviors is by conducting both behavioral and physiological experiments. As you read this book, you will encounter many examples of the results of behavioral and physiological experiments combining to provide a richer understanding of the mind than would be provided by either alone.

TEST YOURSELF 2.2

1. What is localization of function? Describe how localization has been demonstrated by neuropsychology and recording from neurons. Be sure you understand the principle of double dissociations.
2. Describe the basic principles behind functional magnetic resonance imaging.
3. Describe brain imaging evidence for localization of function. Describe experiments that involved looking at still pictures and that involved looking at movies. What does each type of experiment tell us about localization of function?
4. What is distributed representation? How is distributed processing illustrated by how the brain responds to faces? By how it responds to a rolling red ball?
5. What is a neural network? What is the connection between the network called the pain matrix and our perception of pain?
6. Describe two things that neuroscience can tell us about cognition.

CHAPTER SUMMARY

1. Cognitive neuroscience is the study of the physiological basis of cognition. Taking a levels-of-analysis approach to the study of the mind involves research at both behavioral and physiological levels.
2. Ramon y Cajal's research resulted in the abandonment of the neural net theory in favor of the neuron doctrine, which states that individual cells called neurons transmit signals in the nervous system.
3. Signals can be recorded from neurons using microelectrodes. Adrian, who recorded the first signals from single neurons, determined that action potentials remain the same size as they travel down an axon and that increasing stimulus intensity increases the rate of nerve firing.
4. The principle of neural representation states that everything that a person experiences is based not on direct contact with stimuli, but on representations in the person's nervous system.
5. Representation by neurons can be explained by considering feature detectors, neurons that respond to complex stimuli, and how neurons are involved in specificity coding, population coding, and sparse coding.
6. The idea of localization of function in perception is supported by the existence of a separate primary receiving area for each sense, by the effects of brain damage on perception (for example, prosopagnosia), by recording from single neurons, and from the results of brain imaging experiments.
7. Brain imaging measures brain activation by measuring blood flow in the brain. Functional magnetic resonance imaging (fMRI) is widely used to determine brain activation during cognitive functioning. Brain imaging experiments have measured the response to still pictures to identify areas in the human brain that respond best to faces, places, and bodies, and the response to movies to create a brain map indicating the kinds of stimuli that activate different areas of the brain.
8. The idea of distributed processing is that specific functions are processed by many different areas in the brain. This principle is illustrated by the finding that faces activate many areas of the brain and by the simpler example of the rolling red ball, which also activates a number of areas.
9. Distributed processing also occurs for other cognitive functions, such as memory, decision making, and problem solving. A basic principle of cognition is that different cognitive functions often involve similar mechanisms.
10. Neural networks are groups of neurons or structures that are connected together. The structures that create the pain matrix are, together, an example of a neural network.
11. One of the contributions of neuroscience to the understanding of the mind is determining where different capacities occur in the brain. In addition, proposals based on behavioral research can be supported by the results of physiological research. One example is how the proposal of different types of long-term memory, based on behavior, has been supported by neuropsychological research, studying patients with different types of brain damage.

THINK ABOUT IT

1. Some cognitive psychologists have called the brain the mind's computer. What are computers good at that the brain is not? How do you think the brain and computers compare in terms of complexity? What advantage does the brain have over a computer?
2. People generally feel that they are experiencing their environment directly, especially when it comes to sensory experiences such as seeing, hearing, or feeling the texture of a surface. However, our knowledge of how the nervous system operates indicates that this is not the case. Why would a physiologist say that all of our experiences are indirect?
3. When brain activity is being measured in an fMRI scanner, the person's head is surrounded by an array of magnets and must be kept perfectly still. In addition, the operation of the machine is very noisy. How do these characteristics of brain scanners limit the types of behaviors that can be studied using brain scanning?
4. It has been argued that we will never be able to fully understand how the brain operates because doing this involves using the brain to study itself. What do you think of this argument?