

the intensity of sensation or speed of movement is the frequency of the action potentials. Likewise, the duration of a sensation or movement is determined by the period over which action potentials are generated.

In addition to the frequency of the action potentials, the pattern of action potentials also conveys important information. For example, some neurons are spontaneously active in the absence of stimulation. Some spontaneously active nerve cells (beating neurons) fire action potentials regularly; others (bursting neurons) fire in brief bursts of action potentials. These diverse cells respond differently to the same excitatory synaptic input. An excitatory synaptic potential may initiate one or more action potentials in a cell that is not spontaneously active, whereas that same input to spontaneously active cells will simply increase the existing rate of firing.

An even more dramatic difference is seen when the input signal is inhibitory. Inhibitory inputs have little information value in a silent cell. By contrast, in spontaneously active cells, inhibition can have a powerful sculpting role. By establishing periods of silence in otherwise ongoing activity, inhibition can produce a complex pattern of alternating firing and silence where none existed. Such subtle differences in firing patterns may have important functional consequences for the information transfer between neurons. Mathematical modelers of neuronal networks have attempted to delineate neural codes in which information is also carried by the fine-grained pattern of firing—the exact timing of each action potential.

If signals are stereotyped and reflect only the most elementary properties of the stimulus, how can they carry the rich variety of information needed for complex behavior? How is a message that carries visual information about a bee distinguished from one that carries pain information about the bee's sting, and how are these sensory signals distinguished from motor signals for voluntary movement? The answer is simple and yet is one of the most important organizational principles of the nervous system: Interconnected neurons form anatomically and functionally distinct pathways—labeled lines—and it is these pathways of connected neurons, these labeled lines, not individual neurons, that convey information. The neural pathways activated by receptor cells in the retina that respond to light are completely distinct from the pathways activated by sensory cells in the skin that respond to touch.

### The Output Component Releases Neurotransmitter

When an action potential reaches a neuron's terminal, it stimulates the release of chemical substances from the cell. These substances, called *neurotransmitters*, can be

small organic molecules, such as L-glutamate and acetylcholine, or peptides like substance P or LHRH (luteinizing hormone-releasing hormone).

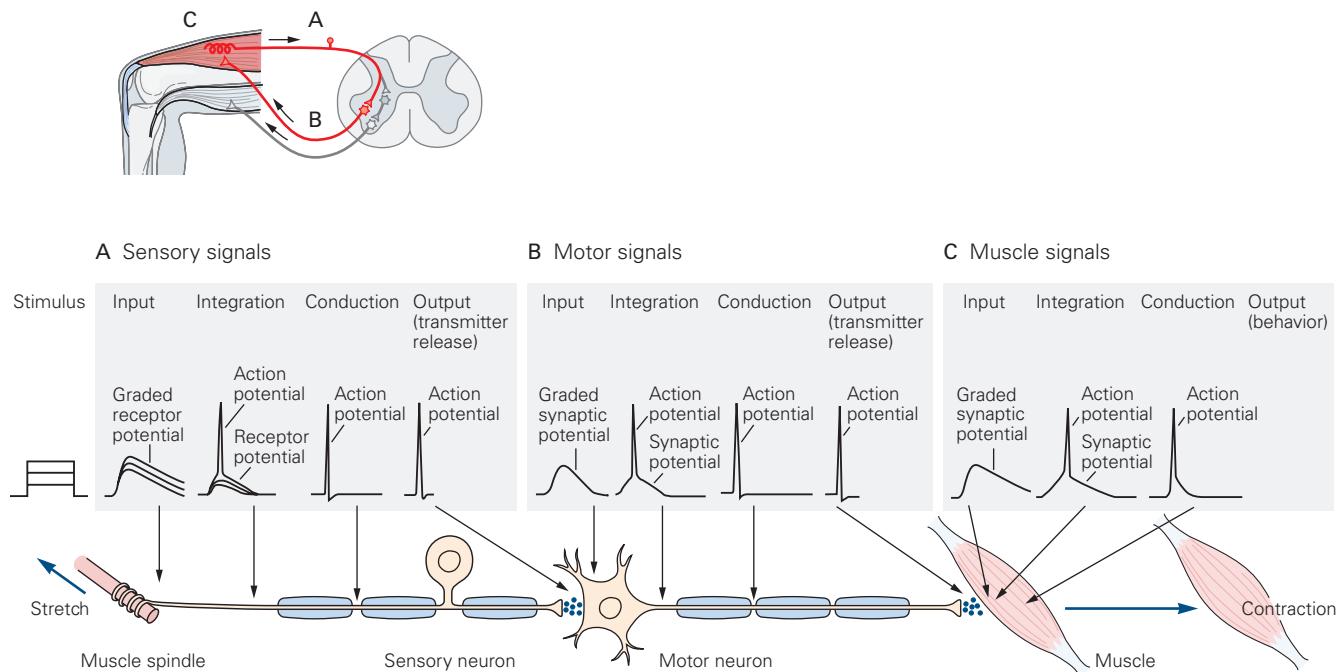
Neurotransmitter molecules are held in subcellular organelles called *synaptic vesicles*, which accumulate in the terminals of the axon at specialized release sites called *active zones*. To eject their transmitter substance into the synaptic cleft, the vesicles move up to and fuse with the neuron's plasma membrane, then burst open to release the transmitter into the synaptic cleft (the extracellular space between the pre- and postsynaptic cell) by a process known as *exocytosis*. The molecular machinery of neurotransmitter release is described in Chapters 14 and 15.

The released neurotransmitter molecules are the neuron's output signal. The output signal is thus graded according to the amount of transmitter released, which is determined by the number and frequency of the action potentials that reach the presynaptic terminals (Figure 3–9C,D). After release, the transmitter molecules diffuse across the synaptic cleft and bind to receptors on the postsynaptic neuron. This binding causes the postsynaptic cell to generate a synaptic potential. Whether the synaptic potential has an excitatory or inhibitory effect depends on the type of receptor in the postsynaptic cell, not on the particular chemical neurotransmitter. The same transmitter substance can have different effects at different receptors.

### The Transformation of the Neural Signal From Sensory to Motor Is Illustrated by the Stretch-Reflex Pathway

As we have seen, the properties of a signal are transformed as the signal moves from one component of a neuron to another or between neurons. In the stretch reflex, when a muscle is stretched, the amplitude and duration of the stimulus are reflected in the amplitude and duration of the receptor potential generated in the sensory neuron (Figure 3–10A). If the receptor potential exceeds the threshold for an action potential in that cell, the graded signal is transformed at the trigger zone into an action potential. Although individual action potentials are all-or-none signals, the more the receptor potential exceeds threshold, the greater the depolarization and consequently the greater the frequency of action potentials in the axon. The duration of the input signal also determines the duration of the train of action potentials.

The information encoded by the frequency and duration of firing is faithfully conveyed along the axon to its terminals, where the firing of action potentials determines the amount of transmitter released.



**Figure 3–10** The sequence of signals that produces a reflex action.

A. The stretching of a muscle produces a receptor potential in the specialized receptor (the muscle spindle). The amplitude of the receptor potential is proportional to the intensity of the stretch. This potential spreads passively to the integrative or trigger zone at the first node of Ranvier. If the receptor potential is sufficiently large, it triggers an action potential that then propagates actively and without change along the axon to the axon terminal. At specialized sites in the terminal, the action potential leads to the release of a chemical neurotransmitter, the output signal. The transmitter diffuses across the synaptic

cleft between the axon terminal and a target motor neuron that innervates the stretched muscle; it then binds to receptor molecules on the external membrane of the motor neuron.

B. This interaction initiates a synaptic potential that spreads passively to the trigger zone of the motor neuron's axon, where it initiates an action potential that propagates actively to the terminal of the motor neuron's axon. At the axon terminal, the action potential leads to release of a neurotransmitter near the muscle fiber.

C. The neurotransmitter binds receptors on the muscle fiber, generating a synaptic potential. The synaptic potential triggers an action potential in the muscle, which causes a contraction.

These stages of signaling have their counterparts in the motor neuron (Figure 3–10B) and in the muscle (Figure 3–10C).

### Nerve Cells Differ Most at the Molecular Level

The model of neuronal signaling we have outlined is a simplification that applies to most neurons, but there are some important variations. For example, some neurons do not generate action potentials. These are typically local interneurons without a conductive component; they have no axon or such a short one that regeneration of the signal is not required. In these neurons, the input signals are summed and spread passively to the presynaptic terminal region near where transmitter is released. Neurons that are spontaneously active do not require sensory or synaptic inputs

to fire action potentials because they have a special class of ion channels that permit  $\text{Na}^+$  current flow even in the absence of excitatory synaptic input.

Even cells that are similar morphologically can differ importantly in molecular details. For example, they can have different combinations of ion channels. As we shall learn in Chapter 10, different ion channels provide neurons with various thresholds, excitability properties, and firing patterns. Such neurons can encode synaptic potentials into different firing patterns and thereby convey different information.

Neurons also differ in the chemical substances they use as transmitters and in the receptors that receive transmitter substances from other neurons. Indeed, many drugs that act on the brain do so by modifying the actions of specific chemical transmitters or receptors. Because of physiological differences among neurons, a disease may affect one class of neurons but

not others. Certain diseases strike only motor neurons (amyotrophic lateral sclerosis and poliomyelitis), whereas others affect primarily sensory neurons (leprosy and tabes dorsalis, a late stage of syphilis). Parkinson disease, a disorder of voluntary movement, damages a small population of neurons that use dopamine as a neurotransmitter. Some diseases are selective even within the neuron, affecting only the receptive elements, the cell body, or the axon. In Chapter 57, we describe how research into myasthenia gravis, a disease caused by a faulty transmitter receptor in the muscle membrane, has provided important insights into synaptic transmission. Indeed, because the nervous system has so many cell types and variations at the molecular level, it is susceptible to more diseases (psychiatric as well as neurological) than any other organ system of the body.

Despite the morphological differences among nerve cells, the molecular mechanisms of electrical signaling are surprisingly similar. This simplicity is fortunate, for understanding the molecular mechanisms of signaling in one kind of nerve cell aids the understanding of these mechanisms in many other nerve cells.

### The Reflex Circuit Is a Starting Point for Understanding the Neural Architecture of Behavior

The stretch reflex illustrates how interactions between just a few types of nerve cells can constitute a functional circuit that produces a simple behavior, even though the number of neurons involved is large (the stretch reflex circuit has perhaps a few hundred sensory neurons and a hundred motor neurons). Some invertebrate animals are capable of behavior as sophisticated as reflexes using far fewer neurons. Moreover, in some instances, just one critical command neuron can trigger a complex behavior such as the withdrawal of a body part from a noxious stimulus.

For more complex behaviors, especially in higher vertebrates, many neurons are required, but the basic neural structure of the simple reflex is often preserved. First, there is often an identifiable group of neurons whose firing rate changes in response to a particular type of environmental stimulus, such as a tone of a certain frequency, or the juxtaposition of light and dark at a particular angle. Just as the firing rate of the stretch receptor neurons encodes the degree of muscle tension, the firing rates of cortical neurons in sensory areas of the cortex encode the intensity of a sensory feature (eg, the degree of contrast of the contour). As we shall see in later chapters, it is possible to change

the features of a percept just by changing the firing rate of small groups of neurons.

Second, there is often an identifiable group of neurons whose firing rate changes before an animal performs a motor act. Just as the spike rate of motor neurons controls the magnitude of the contraction of the quadriceps muscle—hence the knee jerk—so does the firing rate of neurons in the motor cortex affect the latency and type of movement that will be performed. Exactly what aspect of the movement is encoded by such neurons remains an area of active inquiry, but it is well established that groups of neurons affect the ensuing action in a graded fashion by adjusting their firing rate. In other association areas of the cerebral cortex, the graded firing rates of neurons encode quantities that are essential for thought processes, such as the amount of evidence bearing on a choice (Chapter 56).

Although sophisticated mental operations are far more complicated than a simple stretch reflex, it may nevertheless prove useful to consider the extent to which cognitive functions are supported by neural mechanisms that are organized in any way that resembles a simple reflex. What types of elaborations might be required to mediate a sophisticated behavior and thought? Unlike a simple reflex, with a sophisticated behavior, activation of sensory neurons would not give rise to an immediate reflexive action. There is more contingency to the process. Although simple reflexes are modulated by context, mental functions are more deeply shaped by a complex repertoire of contingencies, allowing for many possible effects of any one stimulus and many possible precipitants of any one action. In light of these contingencies, we are forced to conceive of a flexible routing between the brain's data acquisition systems—not just the sensory systems but also the memory systems—and effector systems. As we shall see in later chapters, this is the role of the higher association areas of the cerebral cortex, acting in concert with several subcortical brain structures.

Perhaps a more salient difference between a complex mental function and a reflex is the timing of action. Once activated, a reflex circuit leads to action almost immediately after the sensory stimulus. Any delay depends mainly on the conduction velocity of the action potentials in the afferent and efferent limbs of the reflex (eg, the ankle jerk is slower than the knee jerk because the spinal cord is further from the stretch receptors of the calf muscles than it is from the thigh extensors). For more complex behaviors, action need not occur more or less instantaneously with the arrival of sensory information. It might be delayed to await additional information or be expressed only when specific circumstances occur.

Interestingly, the neurons in the association areas of the cortex of primates have the capacity to sustain graded firing rates for durations of many seconds. These neurons are abundant in the parts of the brain that mediate the flexible linkage between sensory and motor areas. They afford a freedom from the instantaneous nature of reflexive behavior and therefore may furnish the essential circuit properties that distinguish cognitive functions from more straightforward sensorimotor transformations like a reflex.

## Neural Circuits Can Be Modified by Experience

Learning can result in behavioral changes that endure for years, even a lifetime. But even simple reflexes can be modified, albeit for a much briefer period of time. The fact that much behavior can be modified by learning raises an interesting question: How is it that behavior can be modified if the nervous system is wired so precisely? How can changes in the neural control of behavior occur when connections between the signaling units, the neurons, are set during early development?

Several solutions for this dilemma have been proposed. The proposal that has proven most farsighted is the *plasticity hypothesis*, first put forward at the turn of the 20th century by Ramón y Cajal. A modern form of this hypothesis was advanced by the Polish psychologist Jerzy Konorski in 1948.

The application of a stimulus leads to changes of a twofold kind in the nervous system ... [T]he first property, by virtue of which the nerve cells *react* to the incoming impulse ... we call *excitability*, and ... changes arising ... because of this property we shall call *changes due to excitability*. The second property, by virtue of which certain permanent functional transformations arise in particular systems of neurons as a result of appropriate stimuli or their combination, we shall call *plasticity* and the corresponding changes *plastic changes*.

There is now considerable evidence for functional plasticity at chemical synapses. These synapses often have a remarkable capacity for short-term physiological changes (lasting seconds to hours) that increase or decrease synaptic effectiveness. Long-term physiological changes (lasting days or longer) can give rise to anatomical alterations, including pruning of synapses and even growth of new ones. As we shall see in later chapters, chemical synapses are functionally and anatomically modified during critical periods of early development but also throughout life. This functional plasticity of neurons endows each of us with a characteristic manner of interacting with the surrounding world, both natural and social.

## Highlights

1. Nerve cells are the signaling units of the nervous system. The signals are mainly electrical within the cell and chemical between cells. Despite variations in size and shape, nerve cells share certain common features. Each has specialized receptors or transducers that receive input from other nerve cells or from the senses respectively; a mechanism to convert input to electrical signals; a threshold mechanism to generate an all-or-none electrical impulse, the action potential, which can be regenerated along the axon that connects the nerve cell to its synaptic target (another nerve cell, a muscle, or gland); and the ability to produce the release of a chemical (neurotransmitter) that affects the target.
2. Glial cells support nerve cells. One type provides the insulation that speeds propagation of the action potential along the axon. Others help establish the chemical milieu for the nerve cells to operate, and still others couple nerve activity to the vascular supply of the nervous system.
3. Nerve cells differ in their morphology, the connections they make, and where they make them. This is clearest in specialized structures like the retina. Perhaps the largest difference between neurons is at the molecular level. Examples of molecular diversity include expression of different receptors, enzymes for synthesis of different neurotransmitters, and different expressions of ion channels. Differences in gene expression furnish the starting point for understanding why certain diseases affect some neurons and not others.
4. Each nerve cell is part of a circuit that has one or more behavioral functions. The stretch reflex circuit is an example of a simple circuit that produces a behavior in response to a stimulus. Its simplicity belies integrative functions, such as relaxation of muscles that oppose the stretched muscle.
5. Modern neural science aspires to explain mental processes far more complex than reflexes. A natural starting point is to understand the ways that circuits must be elaborated to support sensory-motor transformations, which unlike a reflex, are contingent, flexible and not beholden to the immediacy of sensory processing and movement control.
6. Neural connections can be modified by experience. In simple circuits, this process is a simple change in the strength of connections between neurons. A working hypothesis in modern neuroscience is that the “plastic” mechanisms at play

in simple circuits also play a critical role in the learning of more complex behavior and cognitive function.

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# 4

## The Neuroanatomical Bases by Which Neural Circuits Mediate Behavior

### Local Circuits Carry Out Specific Neural Computations That Are Coordinated to Mediate Complex Behaviors

#### Sensory Information Circuits Are Illustrated in the Somatosensory System

Somatosensory Information From the Trunk and Limbs Is Conveyed to the Spinal Cord

The Primary Sensory Neurons of the Trunk and Limbs Are Clustered in the Dorsal Root Ganglia

The Terminals of Central Axons of Dorsal Root Ganglion Neurons in the Spinal Cord Produce a Map of the Body Surface

Each Somatic Submodality Is Processed in a Distinct Subsystem From the Periphery to the Brain

#### The Thalamus Is an Essential Link Between Sensory Receptors and the Cerebral Cortex

#### Sensory Information Processing Culminates in the Cerebral Cortex

#### Voluntary Movement Is Mediated by Direct Connections Between the Cortex and Spinal Cord

#### Modulatory Systems in the Brain Influence Motivation, Emotion, and Memory

#### The Peripheral Nervous System Is Anatomically Distinct From the Central Nervous System

#### Memory is a Complex Behavior Mediated by Structures Distinct From Those That Carry Out Sensation or Movement

The Hippocampal System Is Interconnected With the Highest-Level Polysensory Cortical Regions

The Hippocampal Formation Comprises Several Different but Highly Integrated Circuits

The Hippocampal Formation Is Made Up Mainly of Unilateral Connections

### Highlights

**T**HE HUMAN BRAIN carries out actions in ways no current computer can begin to approach.

Merely to see—to look onto the world and recognize a face or facial expression—entails amazing computational achievements. Indeed, all our perceptual abilities—seeing, hearing, smelling, tasting, and touching—are analytical triumphs. Similarly, all of our voluntary actions are triumphs of engineering. Sensation and movement, while wondrous in their own right, pale in comparison to complex cognitive behaviors such as forming memories or understanding social conventions.

The brain accomplishes these computational feats because its nerve cells are wired together in very precise functional circuits. The brain is hierarchically organized such that information processed at one level is passed to higher-level circuits for more complex and refined processing. In essence, the brain is a network of networks. Different brain areas work in an integrated fashion to accomplish purposeful behavior.

In this chapter, we outline the neuroanatomical organization of some of the circuits that enable the brain to process sensory input and produce motor output. We focus on touch as a sensory modality because the somatosensory system is particularly well understood and because touch clearly illustrates the interaction of sensory processing circuits at several levels, from the spinal cord to the cerebral cortex. Our purpose here is to illustrate the basic principles of how circuits control behavior. In the next chapter, we consider the functional properties of these circuits, including the computations by which they process information. In subsequent chapters, we consider in more detail the

anatomy and function of the various sensory modalities and how sensory input regulates movement.

Finally, we provide a preview of the brain circuits that are instrumental in producing the memories of our daily lives, called explicit memory (see Chapters 52 and 54). We do this to make the point that while many of the neurons in the memory circuits are similar to those in the sensory and motor circuits, not all are. Moreover, the organization of the pathways between circuits is different in the memory system than it is in the motor and sensory systems. This highlights a basic neurobiological tenet that different circuits of the brain have evolved an organization to most efficiently carry out specific functions.

Comprehending the functional organization of the brain might at first seem daunting. But as we saw in the previous chapter, the organization of the brain is simplified by three anatomical considerations. First, there are relatively few types of neurons. Each of the many thousands of spinal motor neurons or millions of neocortical pyramidal cells has a similar anatomical structure and serves a similar function. Second, neurons in the brain and spinal cord are clustered in functional groups called nuclei or discrete areas of the cerebral cortex, which form networks or functional systems. Third, the discrete areas of the cerebral cortex are specialized for sensory, motor, or associative functions such as memory.

### **Local Circuits Carry Out Specific Neural Computations That Are Coordinated to Mediate Complex Behaviors**

Neurons are interconnected to form functional circuits. Within the spinal cord, for example, simple reflex circuits receive sensory information from stretch receptors and send output to various muscle groups. For more complex behavioral functions, different stages of information processing are carried out in networks in different regions of the nervous system. Connections between neurons within the nervous system can be of different lengths.

Within a brain region, local connections, which may be excitatory or inhibitory, integrate many of the neurons into functional networks. Such local networks may then provide outputs to one or more other brain regions through longer projections. Many of these longer pathways have names. For example, projections from the lateral geniculate nucleus of the thalamus to the visual cortex are called the optic radiations. Connections from the neocortex—the region of the cerebral cortex nearest the surface of the brain—of one side of the brain to the other side of the brain form the corpus

callosum. Information carried by these long pathways integrates the output of many local circuits (Figure 4–1).

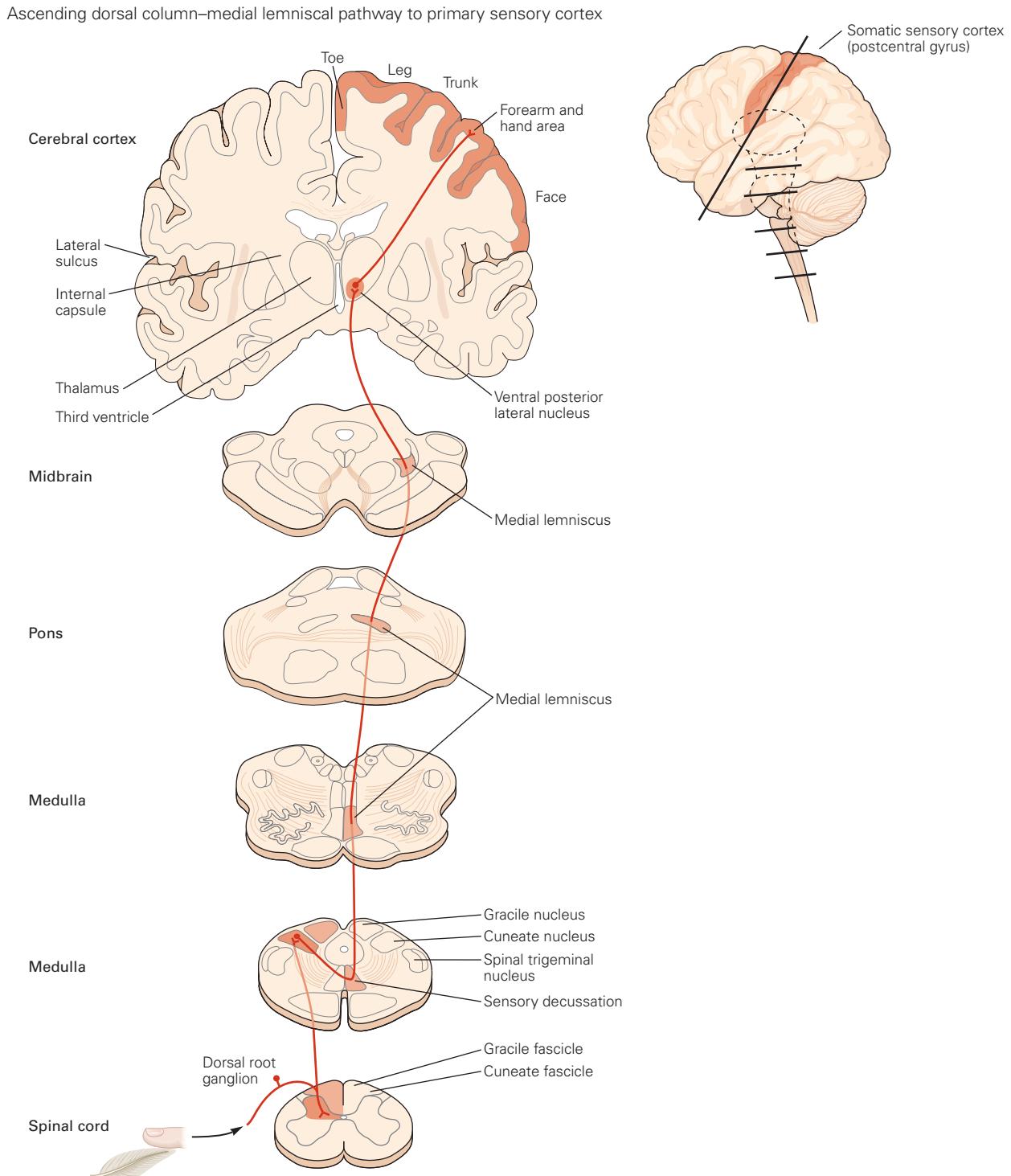
Consider the simple act of hitting a tennis ball (Figure 4–2). Visual information about the motion of the approaching ball is analyzed in the visual system, which is itself a hierarchically organized system extending from the retina to the lateral geniculate nucleus of the thalamus to dozens of cortical areas in the occipital and temporal lobes (Chapter 21). This information is combined in the motor cortex with proprioceptive information about the position of the arms, legs, and trunk to calculate the movement necessary to intercept the ball. Once the swing is initiated, many minor adjustments of the motor program are made by other brain regions dedicated to movement, such as the cerebellum, based on a steady stream of sensory information about the trajectory of the approaching ball and the position of the arm.

Like most motor behaviors, hitting a tennis ball is not hardwired into brain circuits but requires learning and memory. The memory for motor tasks, termed procedural or implicit memory, requires modifications to circuits in motor cortex, the basal ganglia, and the cerebellum. Finally, this entire act is accessible to consciousness and may elicit conscious recall of past similar experiences, termed explicit memory, and emotions. Explicit memory depends on circuits in the hippocampus (Chapters 52 and 54), whereas emotions are regulated by the amygdala (Chapters 42 and 53) and portions of the orbitofrontal, cingulate, and insular cortices. Of course, as the swing is being executed, the brain is also engaged in coordinating the player's heart rate, respiration, and other homeostatic functions through equally complex networks.

### **Sensory Information Circuits Are Illustrated in the Somatosensory System**

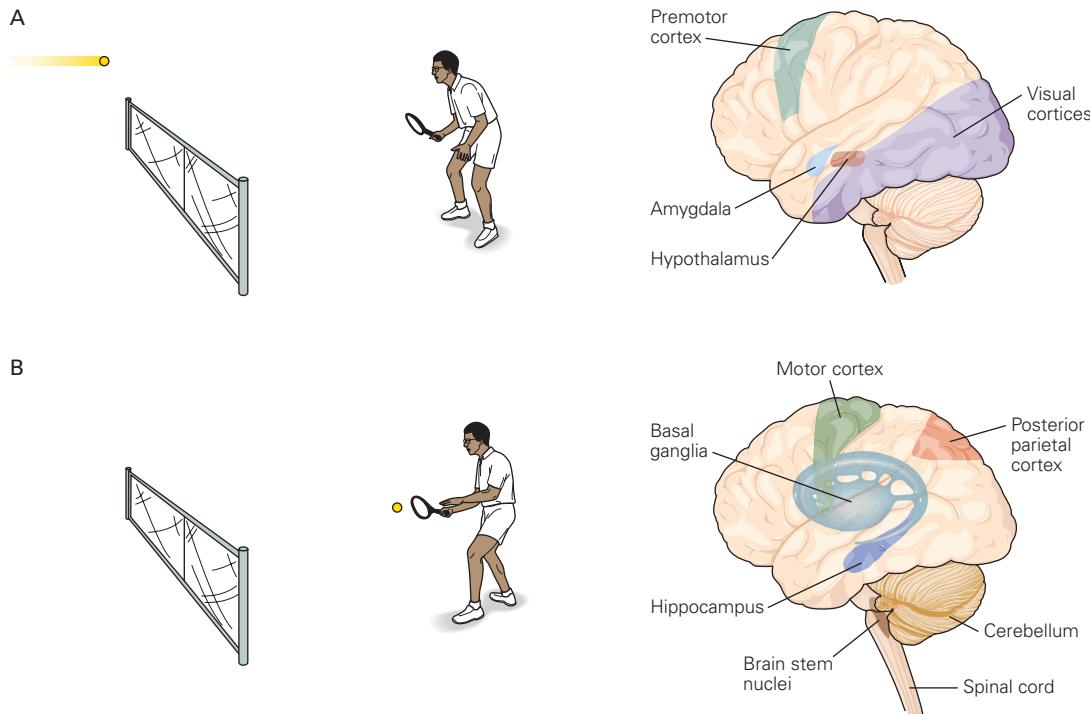
Complex behaviors, such as differentiating the motor acts required to grasp a ball versus a book, require the integrated action of several nuclei and cortical regions. Information is processed in the brain in a hierarchical fashion. Thus, information about a stimulus is conveyed through a succession of subcortical and then cortical regions; at each level of processing, the information becomes increasingly more complex.

In addition, different types of information, even within a single sensory modality, are processed in several anatomically discrete pathways. In the somatosensory system, a light touch and a painful pin prick to the same area of skin are mediated by different sensory receptors in the skin that connect to distinct pathways



**Figure 4–1** The dorsal column-medial lemniscal pathway is the major afferent pathway for somatosensory information. Somatosensory information enters the central nervous system through the dorsal root ganglion cells. The flow of information

ultimately leads to the somatosensory cortex. Fibers that relay information from different parts of the body maintain an orderly relationship to each other and form a neural map of the body surface in their pattern of termination at each synaptic relay.



**Figure 4–2** A simple behavior is mediated by many parts of the brain.

**A.** A tennis player watching an approaching ball uses the visual cortex to judge the size, direction, and velocity of the ball. The premotor cortex develops a motor program to return the ball. The amygdala acts in conjunction with other brain regions to adjust the heart rate, respiration, and other homeostatic mechanisms and also activates the hypothalamus to motivate the player to hit well.

**B.** To execute the shot, the player must use all of the structures illustrated in part **A** as well as others. The motor cortex sends signals to the spinal cord that activate and inhibit many

in the brain. The system for fine touch, pressure, and proprioception is called the epicritic system, whereas the system for pain and temperature is called the protopathic system.

### Somatosensory Information From the Trunk and Limbs Is Conveyed to the Spinal Cord

All forms of somatosensory information from the trunk and limbs enter the spinal cord, which has a core H-shaped region of gray matter where neuronal cell bodies are located. The gray matter is surrounded by white matter formed by myelinated axons that make up both short and long connections. The gray matter on each side of the cord is divided into dorsal (or posterior) and ventral (or anterior) horns (Figure 4–3).

The dorsal horn contains groups of secondary sensory neurons (sensory nuclei) whose dendrites

muscles in the arms and legs. The basal ganglia become involved in initiating motor patterns and perhaps recalling learned movements to hit the ball properly. The cerebellum adjusts movements based on proprioceptive information from peripheral sensory receptors. The posterior parietal cortex provides the player with a sense of where his body is located in space and where his racket arm is located with respect to his body. Brain stem neurons regulate heart rate, respiration, and arousal throughout the movement. The hippocampus is not involved in hitting the ball but is involved in storing the memory of the return so that the player can brag about it later.

receive stimulus information from primary sensory neurons that innervate the body's skin, muscles, and joints. The ventral horn contains groups of motor neurons (motor nuclei) whose axons exit the spinal cord and innervate skeletal muscles. The spinal cord has circuits that mediate behaviors ranging from the stretch reflex to coordination of limb movements.

As we discussed in Chapter 3, when considering the knee-jerk reflex, interneurons of various types in the gray matter regulate the output of the spinal cord motor neurons (see Figure 3–5). Some of these interneurons are excitatory, whereas others are inhibitory. These interneurons modulate both sensory information flowing toward the brain and motor commands descending from the brain to the spinal motor neurons. Motor neurons can also adjust the output of other motor neurons via the interneurons. These