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The Functional Organization of Perception and Movement

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The Thalamus Is an Essential Link Between Sensory Receptors and the Cerebral Cortex for All Modalities Except Olfaction

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An Overall View

THE HUMAN BRAIN IDENTIFIES OBJECTS and carries out actions in ways no current computer can even 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. The brain accomplishes these computational feats because its information processing units—its nerve cells—are wired together in very precise ways.

In this chapter we outline the neuroanatomical organization of perception and action. We focus on touch because the somatosensory system is particularly well understood and because touch clearly illustrates the interaction of sensory and motor systems—how information from the body surface ascends through the sensory relays of the nervous system to the cerebral cortex and is transformed into motor commands that descend to the spinal cord to produce movements.

We now have a fairly complete understanding of how the physical energy of a tactile stimulus is transduced by mechanoreceptors in the skin into electrical activity, and how this activity at different relays in the brain correlates with specific aspects of the experience of touch. Moreover, because the pathways from one relay to the next are well delineated, we can see how sensory information is coded at each relay.

Trying to comprehend the functional organization of the brain might at first seem daunting. But as we saw in the last 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 structure and serves a similar function. Second, neurons in the brain and spinal cord are clustered in discrete functional groups called nuclei, which are connected to form functional systems. Third, specific regions of the cerebral cortex are specialized for sensory, motor, or, as we shall learn in detail in Chapters 17 and 18, associational functions.

Sensory Information Processing Is Illustrated in the Somatosensory System

Complex behaviors, such as using touch alone to differentiate a ball from 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 and at each level of processing the information becomes increasingly 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 pathways in the brain.

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

Sensory information from the trunk and limbs enters the spinal cord, which has a core H-shape region of gray matter surrounded by white matter. The gray matter on each side of the cord is divided into dorsal (or posterior) and ventral (or anterior) horns (Figure 16–1). The dorsal horn contains groups of sensory neurons

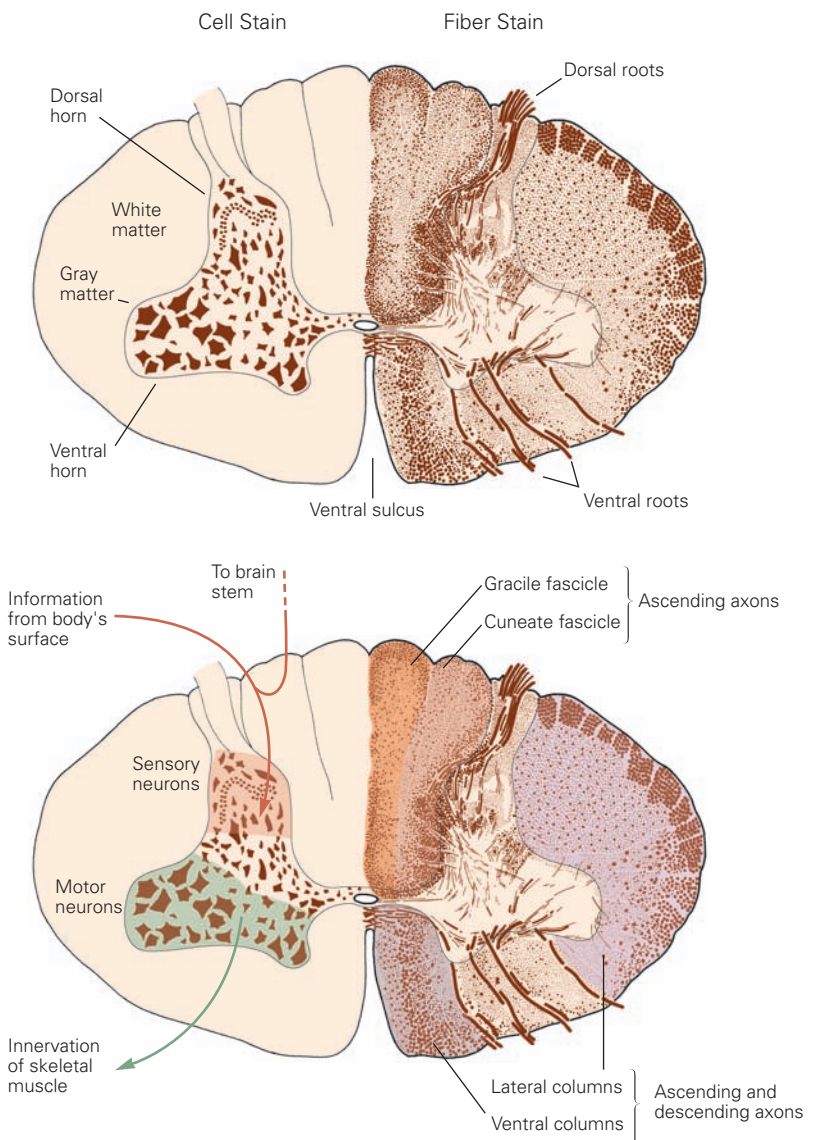


Figure 16–1 The major anatomical features of the spinal cord. **Top:** The left side depicts a cell stain of the gray matter and the right side a fiber-stained section. **Bottom:** The ventral horn (green) contains large motor neurons, whereas the dorsal horn (orange) contains smaller neurons. Fibers of the gracile fascicle carry somatosensory information from the lower limbs, whereas fibers of the cuneate fascicle carry somatosensory information from the upper body. Fiber bundles of the lateral and ventral columns include both ascending and descending fiber bundles.

(sensory nuclei) whose axons receive stimulus information from the body's surface. The ventral horn contains groups of motor neurons (motor nuclei) whose axons exit the spinal cord and innervate skeletal muscles.

Unlike the sensory nuclei, the motor nuclei form columns that run the length of the spinal cord. Interneurons of various types in the gray matter inhibit the output of the spinal cord neurons. These inhibitory interneurons thus 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.

The white matter surrounding the gray matter contains bundles of ascending and descending axons that are divided into dorsal, lateral, and ventral columns. The dorsal columns, which lie between the two dorsal horns of the gray matter, contain only ascending axons that carry somatic sensory information to the brain stem (Figure 16-1). The lateral columns include both ascending axons and axons descending from the brain stem and neocortex that innervate spinal interneurons and motor neurons. The ventral columns also include ascending and descending axons. The ascending somatic sensory axons in the lateral and ventral columns constitute parallel pathways that convey information about pain and thermal sensation to higher levels of the central nervous system. The descending axons control axial muscles and posture.

The spinal cord is divided into four major regions: cervical, thoracic, lumbar, and sacral (Figure 16-2). These regions are related to the embryological somites from which muscles, bones, and other components of the body develop (see Chapters 52 and 53). Axons projecting from the spinal cord to body structures that develop at the same segmental level join together in the intervertebral foramen with axons entering the spinal cord to form spinal nerves. Spinal nerves at the cervical level are involved with sensory perception and motor function of the back of the head, neck, and arms; nerves at the thoracic level innervate the upper trunk; whereas lumbar and sacral spinal nerves innervate the lower trunk, back, and legs.

Each of the four regions of the spinal cord contains several segments; there are 8 cervical segments, 12 thoracic segments, 5 lumbar segments, and 5 sacral segments. Although the actual substance of the mature spinal cord does not look segmented, the segments of the four spinal regions are nonetheless defined by the number and location of the dorsal and ventral roots that enter or exit the cord. The spinal cord varies in size and shape along its rostrocaudal axis because of two organizational features.

First, relatively few sensory axons enter the cord at the sacral level. At higher levels (lumbar, thoracic, and cervical) the number of sensory axons entering the cord increases progressively. Conversely, most descending axons from the brain terminate at cervical levels, with progressively fewer descending to lower levels of the spinal cord. Thus the number of fibers in the white matter is highest at cervical levels (where there are the highest numbers of both ascending and descending fibers) and lowest at sacral levels. As a result, sacral levels of the spinal cord have much less white matter than gray matter, whereas the cervical cord has more white matter than gray matter (Figure 16-2).

The second organizational feature is variation in the size of the ventral and dorsal horns. The ventral horn is larger at the levels where the motor nerves that innervate the arms and legs exit the spinal cord. The number of ventral motor neurons dedicated to a body region roughly parallels the dexterity of movements of that region. Thus a larger number of motor neurons is needed to innervate the greater number of muscles and to regulate the greater complexity of movement in the limbs as compared with the trunk. Likewise, the dorsal horn is larger where sensory nerves from the limbs enter the cord. Limbs have a greater density of sensory receptors to mediate finer tactile discrimination and thus send more fibers to the cord. These regions of the cord are known as the lumbosacral and cervical enlargements.

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

The sensory neurons that convey information from the skin, muscles, and joints of the limbs and trunk to the spinal cord are clustered together in dorsal root ganglia within the vertebral column immediately adjacent to the spinal cord (Figure 16-3). These neurons are pseudo-unipolar in shape; they have a bifurcated axon with central and peripheral branches. The peripheral branch terminates in skin, muscle, or other tissue as a free nerve ending or in association with specialized receptors.

The central process enters the spinal cord. On entry the axon forms branches that either terminate within the spinal gray matter or ascend to nuclei located near the junction of the spinal cord with the medulla (Figure 16-3). These local and ascending branches provide two functional pathways for somatosensory information entering the spinal cord from dorsal root ganglion cells. The local branches can activate local reflex circuits while the ascending branches carry information into the brain, where this information becomes the raw material for the perception of touch, position sense, or pain.

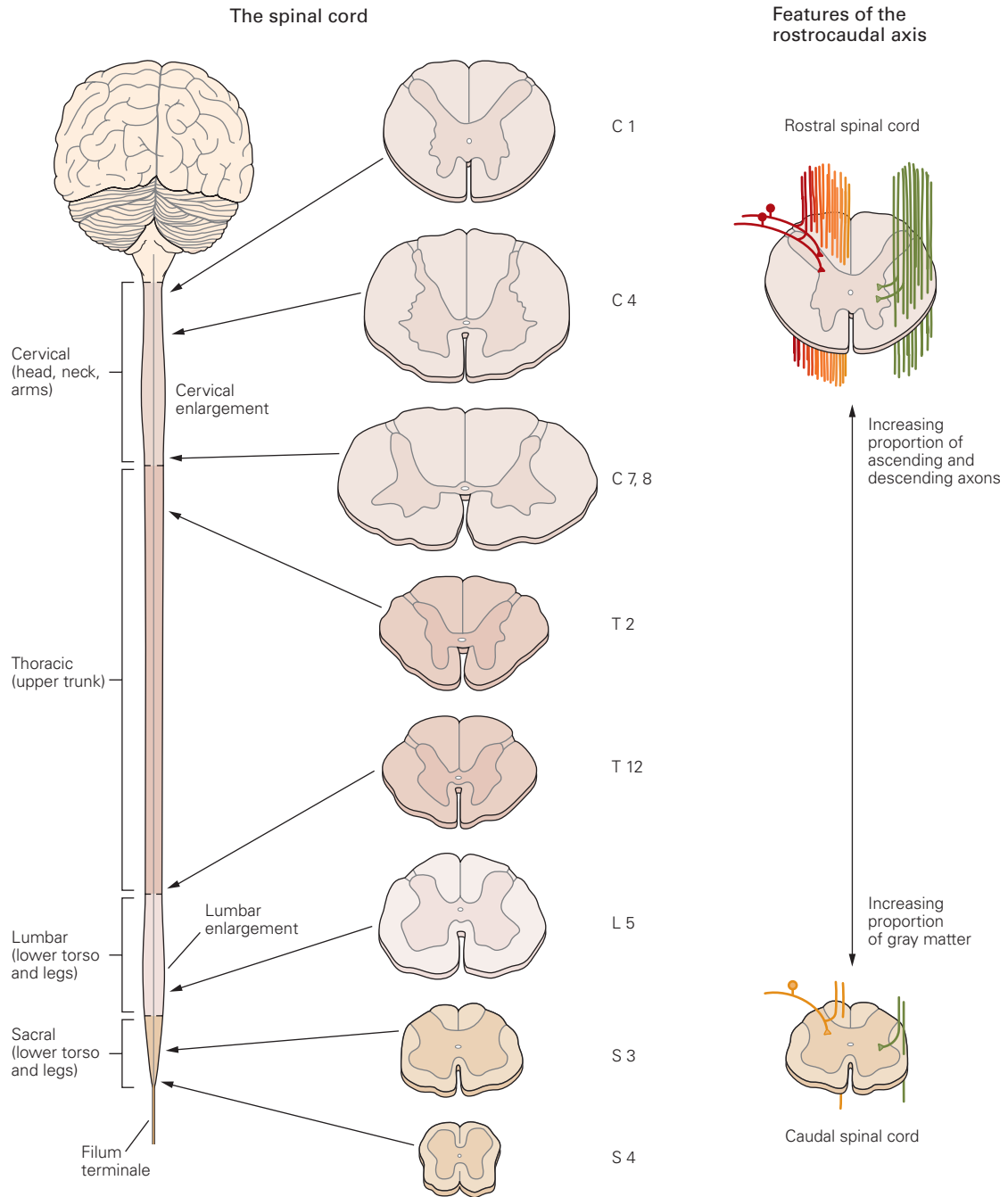


Figure 16–2 The internal and external appearances of the spinal cord vary at different levels. The proportion of gray matter (the H-shaped area within the spinal cord) to white matter is greater at sacral levels than at cervical levels. At sacral levels very few incoming sensory fibers have joined the spinal cord,

whereas most of the motor fibers have already terminated at higher levels of the spinal cord. The cross-sectional enlargements at the lumbar and cervical levels are regions where the large number of fibers innervating the limbs enter or leave the spinal cord.

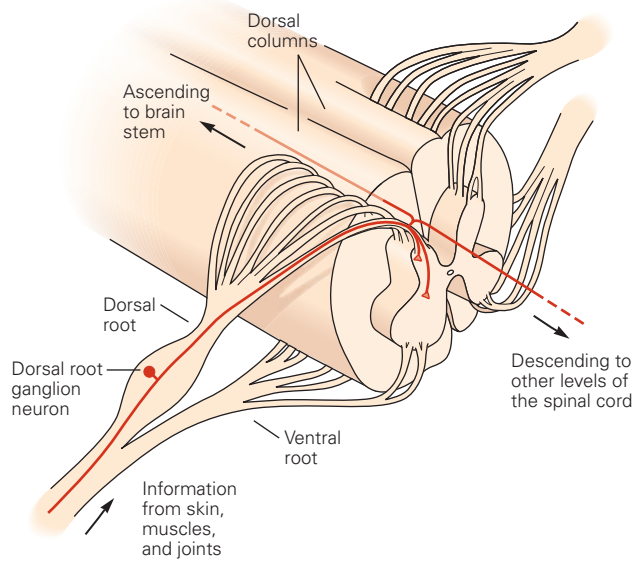


Figure 16-3 Dorsal root ganglia and spinal nerve roots. The cell bodies of neurons that bring sensory information from the skin, muscles, and joints lie in the dorsal root ganglia, clusters of cells that lie adjacent to the spinal cord. The axons of these neurons are bifurcated into peripheral and central branches. The central branch enters the dorsal portion of the spinal cord.

The Central Axons of Dorsal Root Ganglion Neurons Are Arranged to Produce a Map of the Body Surface

The central axons of the dorsal root ganglion cells form a neural map of the body surface when they terminate in the spinal cord. This orderly somatotopic distribution of inputs from different portions of the body surface is maintained throughout the entire ascending somatosensory pathway.

Axons that enter the cord in the sacral region ascend in the dorsal column near the midline, whereas those that enter at successively higher levels ascend at progressively more lateral positions within the dorsal columns. Thus, in the cervical cord, where axons from all portions of the body have already entered, sensory fibers from the lower body are located medially in the dorsal column, while fibers from the trunk, the arm and shoulder, and finally the neck occupy progressively more lateral areas. At cervical levels of the cord the axons forming the dorsal columns are divided into two bundles: a medially situated gracile fascicle and a more laterally situated cuneate fascicle (Figure 16-4).

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

The submodalities of somatic sensation—touch, pain, and position sense—are processed in the brain through different pathways that end in different brain regions. To illustrate the specificity of these parallel pathways, we will follow the path of information for the submodality of touch.

The primary afferent fibers that carry information about touch enter the ipsilateral dorsal column and, without crossing to the contralateral column, ascend to the medulla. Fibers from the lower body run in the gracile fascicle and terminate in the gracile nucleus, whereas fibers from the upper body run in the cuneate fascicle and terminate in the cuneate nucleus. Neurons in the gracile and cuneate nuclei give rise to axons that cross to the other side of the brain and ascend to the thalamus in a long fiber bundle called the medial lemniscus (Figure 16-4).

As in the dorsal columns of the spinal cord, the fibers of the medial lemniscus are arranged somatotopically. Because the sensory fibers cross the midline to the other side of the brain, the right side of the brain receives sensory information from the left side of the body, and vice versa. The fibers of the medial lemniscus end in a specific subdivision of the thalamus called the ventral posterior nucleus (Figure 16-4). There the fibers maintain their somatotopic organization such that those carrying information from the lower body end laterally and those carrying information from the upper body and face end medially.

The Thalamus Is an Essential Link Between Sensory Receptors and the Cerebral Cortex for All Modalities Except Olfaction

The thalamus is an egg-shaped structure that constitutes the dorsal portion of the diencephalon. It conveys sensory input to the primary sensory areas of the cerebral cortex but is more than simply a relay. It acts as a gatekeeper for information to the cerebral cortex, preventing or enhancing the passage of specific information depending on the behavioral state of the animal.

The thalamus is a good example of a brain region made up of several well-defined nuclei. As many as 50 thalamic nuclei have been identified. Some nuclei receive information specific to a sensory modality and project to a specific area of the neocortex. Cells in the ventral posterior lateral nucleus (where the medial lemniscus terminates) process somatosensory information,

Ascending dorsal column–medial lemniscal pathway to primary sensory cortex

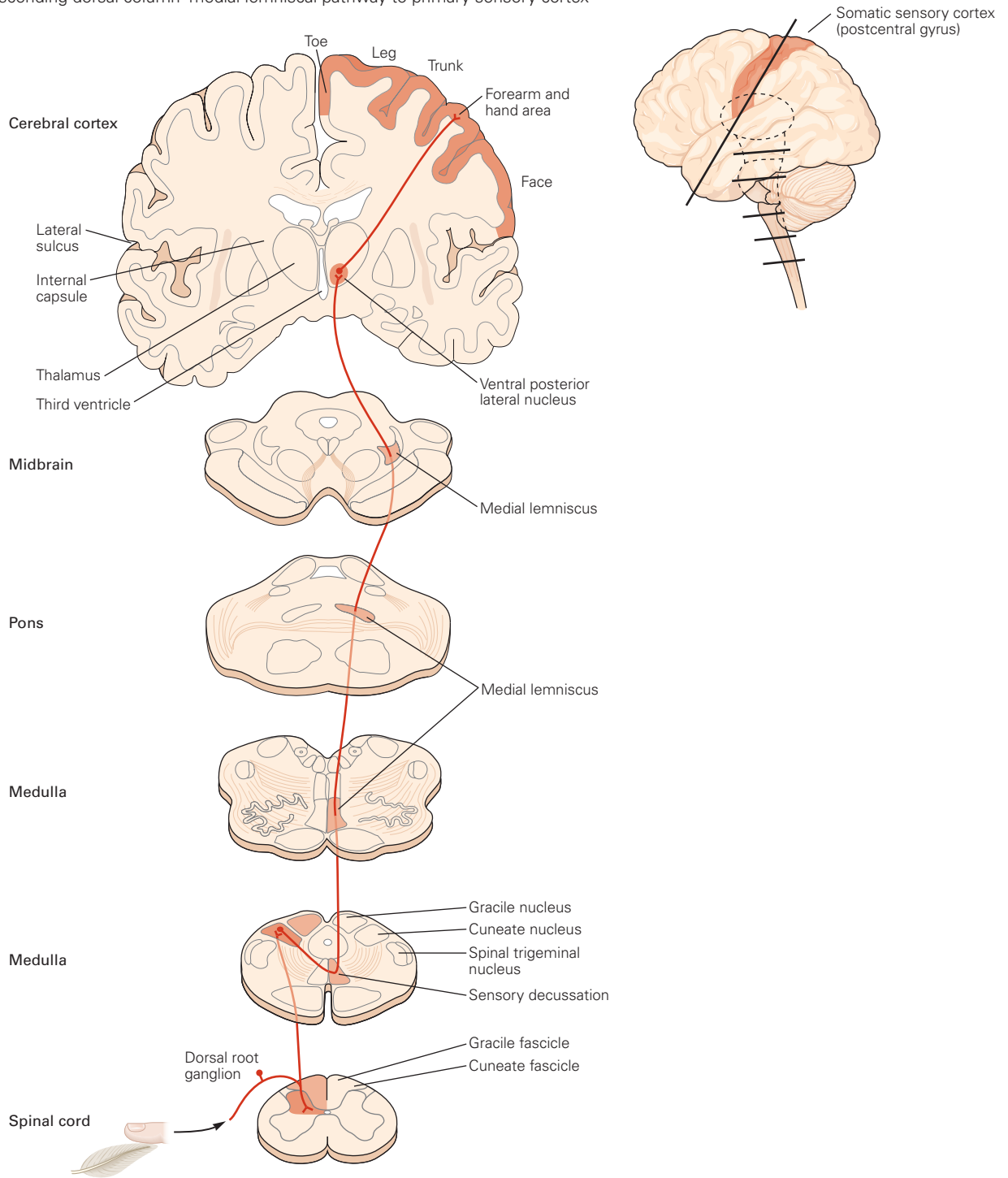


Figure 16–4 The medial lemniscus is a major afferent pathway for somatosensory information. Somatosensory information enters the central nervous system through the dorsal root ganglion cells. The flow of information ultimately leads

to excitation of 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.

and their axons project to the primary somatosensory cortex (Figure 16–4). Other portions of the thalamus participate in motor functions, transmitting information from the cerebellum and basal ganglia to the motor regions of the frontal lobe.

Axons from cells of the thalamus that project to the neocortex travel in the internal capsule, a large fiber bundle that carries most of the axons running to and from the cerebral hemispheres. Through its connections with the frontal lobe, the thalamus may also play a role in cognitive functions, such as memory. Some nuclei that may play a role in attention project diffusely to large but distinctly different regions of cortex. The reticular nucleus, which forms the outer shell of the thalamus, does not project to the neocortex at all. Its largely inhibitory neurons receive inputs from other fibers as they exit the thalamus en route to the neocortex and in turn to the other thalamic nuclei.

The nuclei of the thalamus are most commonly classified into four groups—*anterior*, *medial*, *ventrolateral*, and *posterior*—with respect to the internal medullary lamina, a sheet-like bundle of fibers that runs the rostro-caudal length of the thalamus (Figure 16–5). Thus the medial group of nuclei is located medial to the internal medullary lamina, whereas the ventral and posterior

groups are located lateral to it. At the rostral pole of the thalamus the internal medullary lamina splits and surrounds the anterior group. The caudal pole of the thalamus is occupied by the posterior group, dominated by the pulvinar nucleus. Groups of neurons are also located within the fibers of the internal medullary lamina and are collectively referred to as the *intralaminar nuclei*.

The *anterior group* receives its major input from the mammillary nuclei of the hypothalamus and from the presubiculum of the hippocampal formation. The role of the anterior group is uncertain but thought to be related to memory and emotion. The anterior group is also interconnected with regions of the cingulate and frontal cortices.

The *medial group* consists mainly of the mediodorsal nucleus. This large thalamic nucleus has three subdivisions, each of which is connected to a particular portion of the frontal cortex. The nucleus receives inputs from portions of the basal ganglia, the amygdala, and midbrain and has been implicated in memory.

The nuclei of the *ventral group* are named according to their position within the thalamus. The ventral anterior and ventral lateral nuclei are important for motor control and carry information from the basal

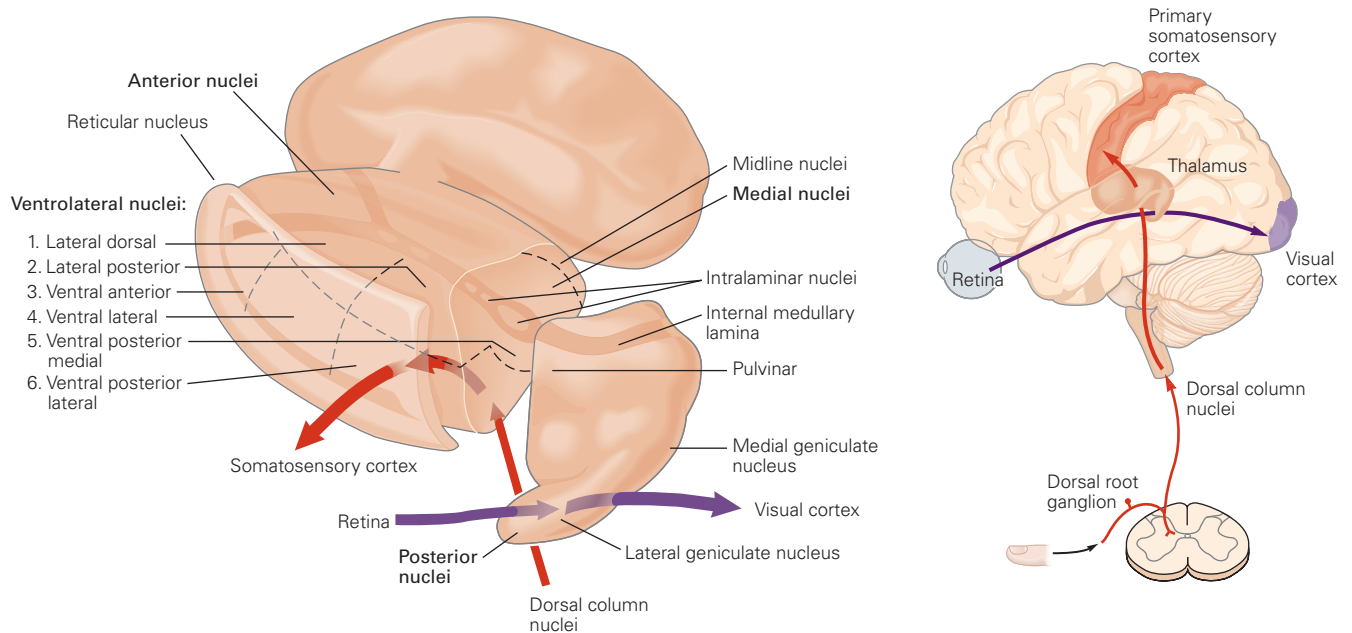


Figure 16–5 The major subdivisions of the thalamus. The thalamus is the critical relay for the flow of sensory information from peripheral receptors to the neocortex. Somatosensory information is conveyed from dorsal root ganglia to the ventral posterior lateral nucleus and from there to the primary

somatosensory cortex. Likewise, visual information from the retina reaches the lateral geniculate nucleus, which conveys it to the primary visual cortex in the occipital lobe. Each of the sensory systems, except olfaction, has a similar processing step within a distinct region of the thalamus.

ganglia and cerebellum to the motor cortex. The ventral posterior lateral nucleus conveys somatosensory information to the neocortex.

The *posterior group* includes the medial and lateral geniculate nucleus, lateral posterior nucleus, and the pulvinar. The medial and lateral geniculate nuclei are located near the posterior part of the thalamus. The medial geniculate nucleus is a component of the auditory system; it is organized tonotopically, and conveys auditory information to the superior temporal gyrus of the temporal lobe. The lateral geniculate nucleus receives information from the retina and conveys it to the primary visual cortex in the occipital lobe. The pulvinar is most enlarged in the primate brain, especially in the human brain, and its development seems to parallel the enlargement of the association regions of the parietal-occipital-temporal cortex (see Chapter 18). It has been divided into at least three subdivisions and is extensively interconnected with widespread regions of the parietal, temporal, and occipital lobes, as well as with the superior colliculus and other nuclei of the brain stem related to vision.

The thalamus not only projects to the visual areas of the neocortex but also receives extensive return inputs back from the neocortex. In fact, in the lateral geniculate nucleus the number of synapses formed by axons from the return projection from the occipital cortex is greater than the number of synapses that the lateral geniculate nucleus receives from the retina. Most nuclei of the thalamus receive a similarly prominent return projection from the cerebral cortex, although the functional significance of these projections is unclear.

The thalamic nuclei described thus far are called the *relay* (or *specific*) *nuclei* because they have a specific and selective relationship with a particular portion of the neocortex. Other thalamic nuclei, called *nonspecific nuclei*, project to several cortical and subcortical regions. These nuclei are located either on the midline of the thalamus (the midline nuclei) or within the internal medullary lamina (the intralaminar nuclei). The largest of the midline nuclei are the paraventricular, parataenial, and reuniens nuclei; the largest of the intralaminar cell groups is the centromedian nucleus. The intralaminar nuclei project to medial temporal lobe structures, such as the amygdala and hippocampus, but also send projections to components of the basal ganglia. These nuclei receive inputs from a variety of sources in the spinal cord, brain stem, and cerebellum and are thought to mediate cortical arousal and perhaps to participate in the integration of sensory submodalities that we shall learn about in Chapters 21 and 22.

Finally, the outer covering of the thalamus is formed by a unique sheet-like structure, the *reticular*

nucleus. The majority of its neurons use the inhibitory transmitter γ -aminobutyric acid (GABA), whereas most of the neurons in the other thalamic nuclei use the excitatory transmitter glutamate. Moreover, the neurons of the reticular nucleus are not interconnected with the neocortex. Rather, their axons terminate on the other nuclei of the thalamus. These other nuclei also provide the input to the reticular nucleus via collaterals of their axons that exit the thalamus through the reticular nucleus. Thus the reticular nucleus modulates activity in other thalamic nuclei based on its monitoring of the entirety of the thalamocortical stream of information. This portion of the thalamus thus acts like a filter that gates information flow to the neocortex.

We see, then, that the thalamus is not a passive relay station where information is simply passed on to the neocortex. Rather it is a complex brain region where substantial information processing is possible. To give but one example, the output of somatosensory information from the ventral posterior lateral nucleus is subject to four types of processing: (1) local processing within the nucleus; (2) modulation by brain stem inputs, such as the noradrenergic and serotonergic systems; (3) inhibitory feedback from the reticular nucleus; and (4) excitatory feedback from the neocortex.

Sensory Information Processing Culminates in the Cerebral Cortex

Somatosensory information from the ventral posterior lateral nucleus is conveyed mainly to the primary somatosensory cortex (Brodmann's area 3b). The neurons here are exquisitely sensitive to tactile stimulation of the skin surface. As in subcortical synaptic centers of the somatosensory system, the neurons in different parts of the cortex are somatotopically organized.

When the neurosurgeon Wilder Penfield stimulated the surface of the somatic sensory cortex in patients undergoing brain surgery, he found that sensation from the lower limbs is mediated by neurons located near the midline of the brain, whereas sensations from the upper body, hands and fingers, the face, lips, and tongue are mediated by neurons located laterally. As we shall learn in more detail in Chapter 17, Penfield found that although all parts of the body are represented in the cortex somatotopically, the area of cortex devoted to each body part is not proportional to its mass. Instead, it is proportional to the density of innervation, which translates to the fineness of discrimination in the body part. Thus the area of cortex devoted to the fingers is larger than that for the arms.

Likewise, the representation of the lips and tongue occupies more cortical surface than that of the remainder of the face (Figure 16–6).

The cerebral cortex is organized functionally into columns of cells extend from the white matter to the surface of the cortex. The cells in each column comprise a computational module with a highly specialized function. The larger the area of cortex dedicated to a function, the greater the number of computational columns that are dedicated to that function (see Chapter 19). The highly discriminative sense of touch in the fingers is a result of the large area of cortex dedicated to processing somatosensory information from the hand.

A second major insight from the early electrophysiological studies was that the somatosensory cortex contains not one but several somatotopic arrays of inputs from the skin and therefore several neural maps of the body surface. The primary somatosensory cortex (anterior parietal cortex) has four complete maps of the skin, one each in areas 3a, 3b, 1, and 2. Basic processing of tactile information takes place in area 3, whereas more complex or higher-order processing occurs in area 1. In area 2 tactile information is combined with

information concerning limb position to mediate the tactile recognition of objects. Neurons in the primary somatosensory cortex project to neurons in adjacent areas, and these neurons in turn project to other adjacent cortical regions (Figure 16–7). At higher levels in the hierarchy of cortical connections somatosensory information is used in motor control, eye–hand coordination, and memory related to touch.

The cortical areas involved in the early stages of sensory processing are concerned only (or primarily) with a single modality. Such regions are called unimodal association areas. Information from the unimodal association areas converges on multimodal association areas of the cortex concerned with combining sensory modalities. As we shall learn in the next two chapters and again in Chapter 62, these multimodal associational areas, which are heavily interconnected with the hippocampus, appear to be particularly important for two tasks: (1) the production of a unified percept and (2) the representation of the percept in memory.

Thus, from the mechanical pressure on a receptor in the skin to the perception that a finger has been touched by a friend shaking your hand, somatosensory

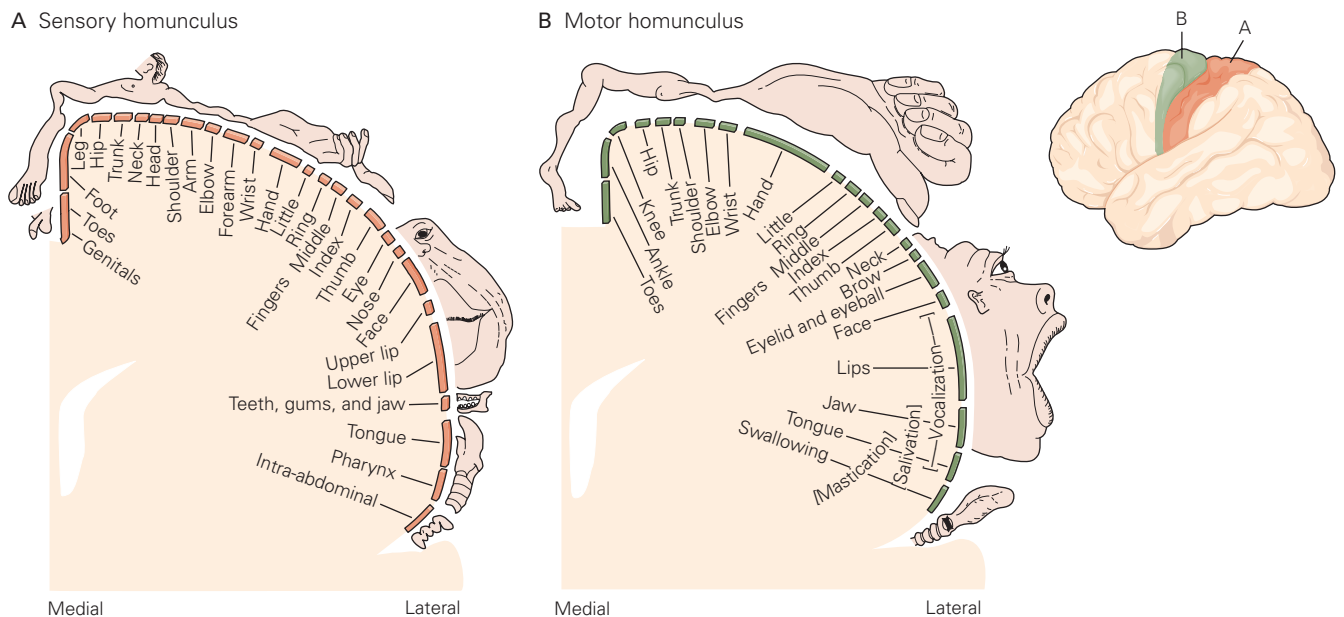


Figure 16–6 A homunculus illustrates the relative amounts of cortical area dedicated to individual parts of the body. (Adapted, with permission, from Penfield and Rasmussen 1950.)

A. The entire body surface is represented in an orderly array of somatosensory inputs in the cortex. The area of cortex dedicated to processing information from a particular part of the body is not proportional to the mass of the body part but

instead reflects the density of sensory receptors in that part. Thus sensory input from the lips and hands occupies more area of cortex than, say, that from the elbow.

B. Output from the motor cortex is organized in similar fashion. The amount of cortical surface dedicated to a part of the body is related to the degree of motor control of that part. Thus in humans much of the motor cortex is dedicated to moving the muscles of the fingers and the muscles related to speech.

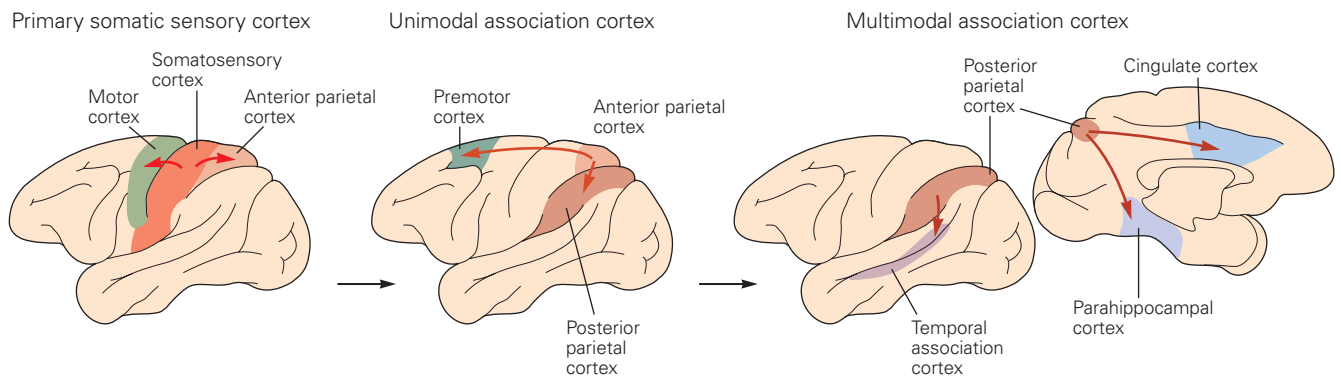


Figure 16-7 The processing of sensory information in the cerebral cortex begins with primary sensory areas, continues in unimodal association areas, and is completed in multimodal association areas. Sensory systems also communicate with portions of the motor cortex. For example, the primary somatosensory cortex projects to the motor area in the frontal lobe and to the somatosensory association area

in the parietal cortex. The somatosensory association area, in turn, projects to higher-order somatosensory association areas and to the premotor cortex. Information from different sensory systems converges in the multimodal association areas, which include the parahippocampal, temporal association, and cingulate cortices.

information is processed in serial and parallel pathways from the dorsal root ganglia to the somatosensory cortex, to unimodal association areas, and finally to multimodal association areas. One of the primary purposes of somatosensory information is to guide directed movement. As one might imagine, there is a close linkage between the somatosensory and motor functions of the cortex.

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

As we shall see in Chapter 18 a major function of the perceptual systems is to provide the sensory information necessary for the actions mediated by the motor systems. The primary motor cortex is organized somatotopically like the somatic sensory cortex (Figure 16-6B). Specific regions of the motor cortex influence the activity of specific muscle groups.

The axons of neurons in layer V of the primary motor cortex project through the corticospinal tract to the ventral horn of the spinal cord. The human corticospinal tract consists of approximately one million axons, of which approximately 40% originate in the motor cortex. These axons descend through the subcortical white matter, the internal capsule, and the cerebral peduncle in the midbrain (Figure 16-8). In the medulla the fibers form prominent protuberances on the ventral surface called the medullary pyramids, and thus the entire projection is sometimes called the pyramidal tract.

Like the ascending somatosensory system, the descending corticospinal tract crosses to the opposite side of the spinal cord. Most of the corticospinal fibers cross the midline in the medulla at a location known as the pyramidal decussation. However, approximately 10% of the fibers do not cross until they reach the level of the spinal cord at which they will terminate. The corticospinal fibers make monosynaptic connections with motor neurons, connections that are particularly important for individuated finger movements. They also form synapses with interneurons in the spinal cord. These indirect connections are important for coordinating larger groups of muscles in behaviors such as reaching and walking.

The motor information carried in the corticospinal tract is significantly modulated by both sensory information and information from other motor regions. A continuous stream of tactile, visual, and proprioceptive information is needed to make voluntary movement both accurate and properly sequenced. In addition, the output of the motor cortex is under the substantial influence of other motor regions of the brain, including the cerebellum and basal ganglia, structures that are essential for smoothly executed movements. These two subcortical centers provide feedback essential for the smooth execution of skilled movements and thus are also important for motor learning, the improvement in motor skills through practice (Figure 16-9, and see Chapter 65).

The cerebellum receives somatosensory information directly from primary afferents originating in the spinal cord as well as from corticospinal axons descending

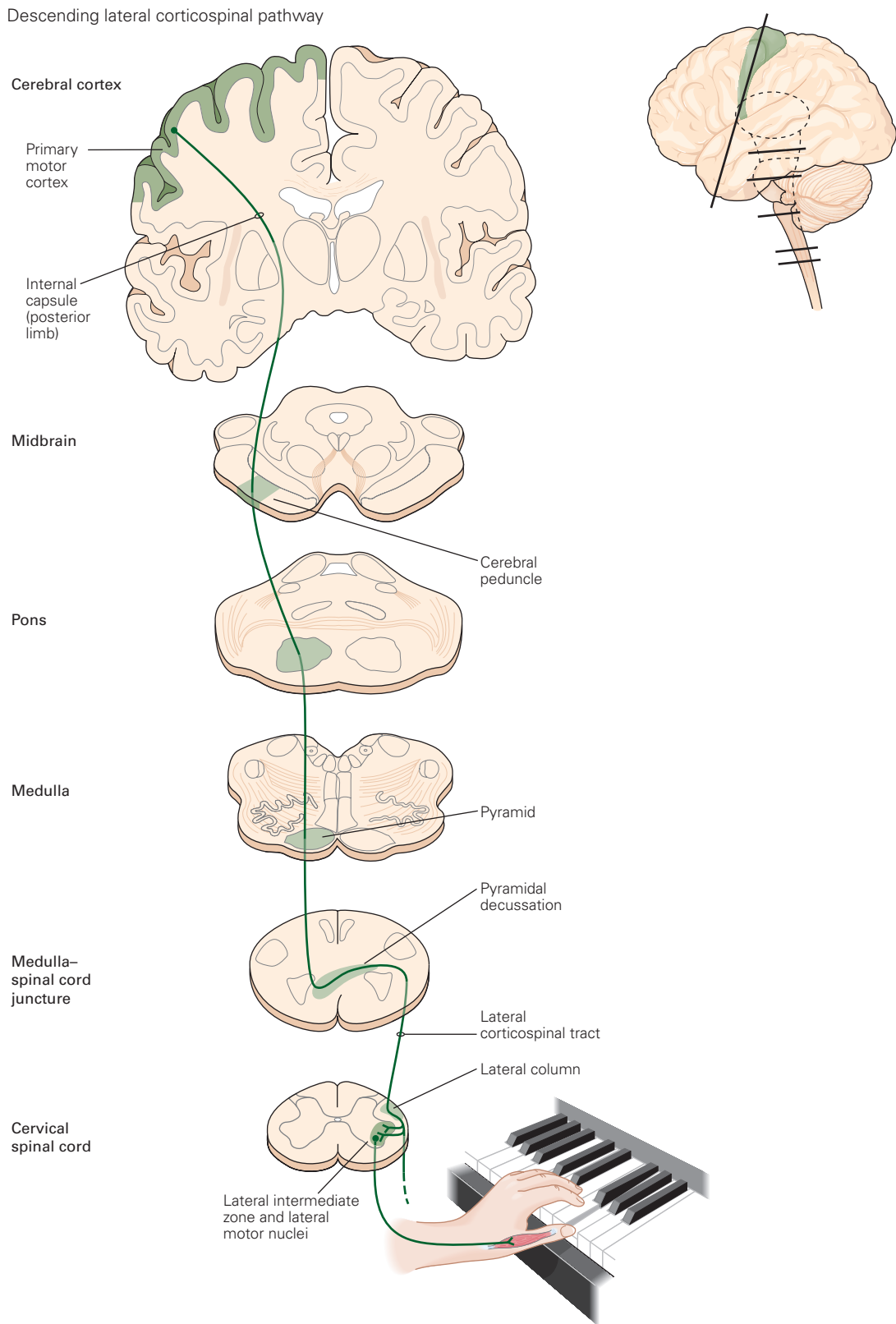


Figure 16–8 Fibers that originate in the primary motor cortex and terminate in the ventral horn of the spinal cord constitute a significant part of the corticospinal tract.

The same axons are at various points in their projection part of the internal capsule, the cerebral peduncle, the medullary pyramid, and the lateral corticospinal tract.

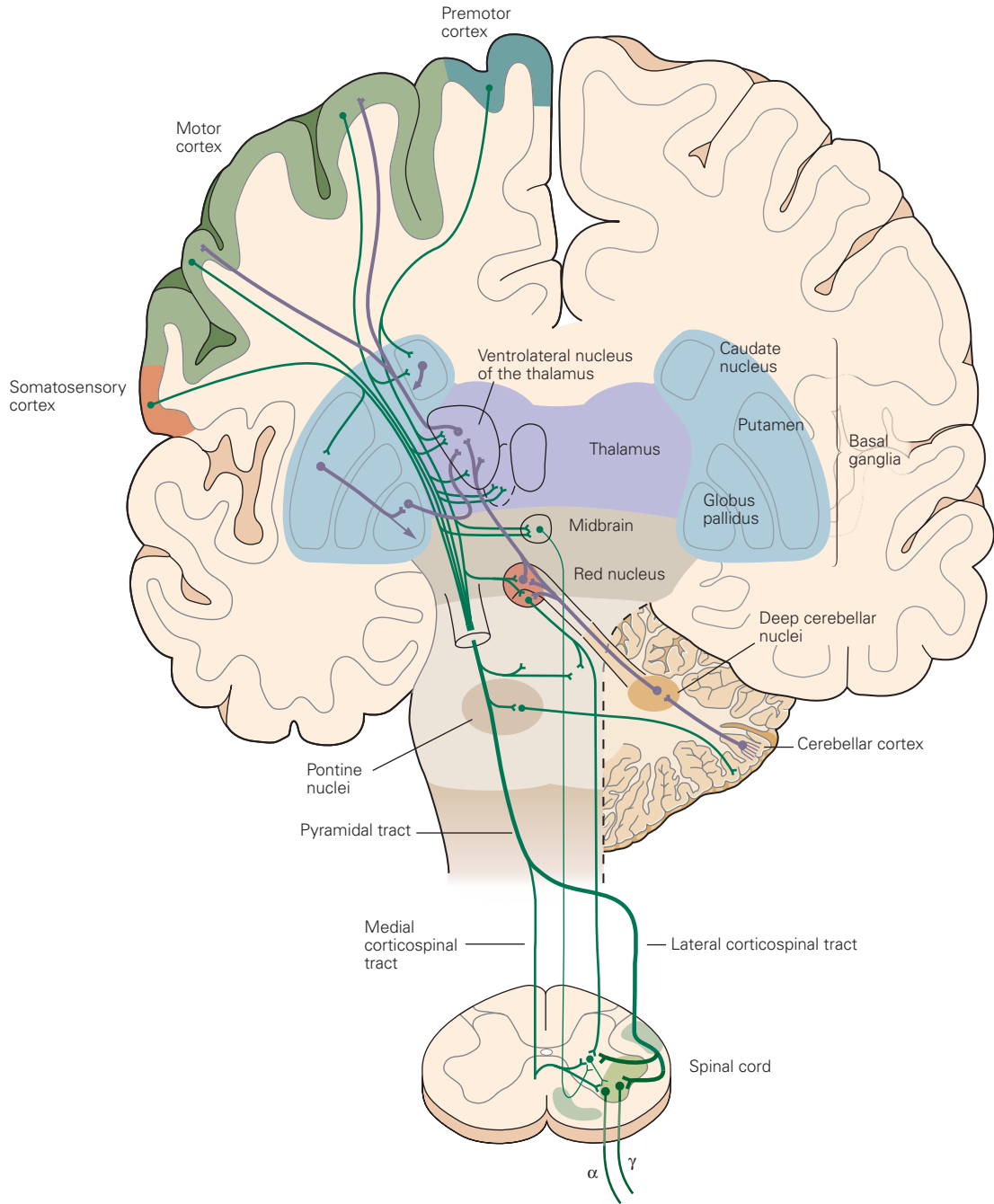


Figure 16–9 Voluntary movement requires coordination of all components of the motor system. The principal components are the motor cortex, basal ganglia, thalamus, midbrain, cerebellum, and spinal cord. The principal descending projections are shown in green; feedback projections and local connections are shown in purple. All of this processing is

incorporated in the inputs to the motor neurons of the ventral horn of the spinal cord, the so-called “final common pathway” that innervates muscle and elicits movements. (This figure is a composite view made from sections of the brain taken at different angles.)

from the neocortex. The cerebellum is thought to be part of an error-correcting mechanism for movements because it can compare movement commands from the cortex with somatic sensory information about what actually happened. Thus the cerebellum is thought to be important in “predictive control” of movements, in which commands for movements are adjusted based on information about the effectiveness of prior movement. In addition, as muscles get stronger with exercise and as our bodies grow, the neural signals for a particular movement must change, as they must if muscles are damaged. The cerebellum enables motor control systems to adapt motor commands to the changing condition of the musculature so that, for example, a weakened arm will not undershoot its goal or a stronger arm overshoot.

The cerebellum can influence posture and movement through its connections in the brain stem motor nuclei, which can directly modulate spinal motor circuits. However, the major influence of the cerebellum on movement is through its connections in the ventrolateral nuclei of the thalamus, which connect directly to the motor and premotor cortex.

The basal ganglia are a collection of subcortical nuclei (see Figure 16–9) that receive direct projections from much of the neocortex, including sensory, motor, and premotor areas, and those parts of association cortex that are important for motivation, cognition, and emotion. The output nuclei of the basal ganglia send signals to regions of the thalamus that project to the cerebral cortex. Although the functions of the basal ganglia have remained surprisingly elusive, dysfunction of the basal ganglia results in particularly striking disorders of movement characteristic of Parkinson disease (tremor at rest, rigidity, and disinclination to move) and of Huntington disease (choreiform movements).

Thus an important consequence of basal ganglia dysfunction is that the abnormal signals sent to cortical motor areas have a major, negative, impact on motor output. Indeed, cortical lesions that limit voluntary movement also abolish the involuntary movements associated with disorders of the basal ganglia. This capacity of the basal ganglia to create marked disorders of movement when they are functioning abnormally must in some way be matched by a similar profound influence over normal motor function.

An Overall View

Sensory and motor information is processed in the brain in a variety of discrete pathways that are active simultaneously. A functional pathway is formed by

the serial connection of identifiable groups of neurons, and each group processes more complex or specific information than the preceding group. Thus different pathways that run through the spinal cord, brain stem, and into the cortex mediate the sensations of touch and pain. All sensory and motor systems follow the pattern of hierarchical and parallel processing.

As we shall see in later chapters, contrary to an intuitive analysis of our personal experience, perceptions are not precise copies of the world around us. Sensation is an abstraction, not a replication, of reality. The brain constructs an internal representation of external physical events after first analyzing various features of those events. When we hold an object in the hand, the shape, movement, and texture of the object are simultaneously but separately analyzed according to the brain’s own rules, and the results are integrated in a conscious experience.

How this integration occurs—the *binding problem*—and how conscious experience emerges from the brain’s selective attention to incoming sensory information are two of the most pressing questions in cognitive neural science.

David G. Amaral

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