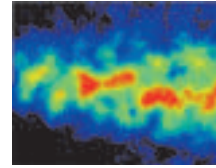


Chapter 8



The Somatic Sensory System

Overview

The somatic sensory system has two major components: a subsystem for the detection of mechanical stimuli (e.g., light touch, vibration, pressure, and cutaneous tension), and a subsystem for the detection of painful stimuli and temperature. Together, these two subsystems give humans and other animals the ability to identify the shapes and textures of objects, to monitor the internal and external forces acting on the body at any moment, and to detect potentially harmful circumstances. This chapter focuses on the mechanosensory subsystem; the pain and temperature subsystem is taken up in the following chapter.

Mechanosensory processing of external stimuli is initiated by the activation of a diverse population of cutaneous and subcutaneous mechanoreceptors at the body surface that relays information to the central nervous system for interpretation and ultimately action. Additional receptors located in muscles, joints, and other deep structures monitor mechanical forces generated by the musculoskeletal system and are called proprioceptors. Mechanosensory information is carried to the brain by several ascending pathways that run in parallel through the spinal cord, brainstem, and thalamus to reach the primary somatic sensory cortex in the postcentral gyrus of the parietal lobe. The primary somatic sensory cortex projects in turn to higher-order association cortices in the parietal lobe, and back to the subcortical structures involved in mechanosensory information processing.

Cutaneous and Subcutaneous Somatic Sensory Receptors

The specialized sensory receptors in the cutaneous and subcutaneous tissues are dauntingly diverse (Table 8.1). They include free nerve endings in the skin, nerve endings associated with specializations that act as amplifiers or filters, and sensory terminals associated with specialized transducing cells that influence the ending by virtue of synapse-like contacts. Based on function, this variety of receptors can be divided into three groups: **mechanoreceptors**, **nociceptors**, and **thermoceptors**. On the basis of their morphology, the receptors near the body surface can also be divided into **free** and **encapsulated** types. Nociceptor and thermoceptor specializations are referred to as **free nerve endings** because the unmyelinated terminal branches of these neurons ramify widely in the upper regions of the dermis and epidermis (as well as in some deeper tissues); their role in pain and temperature sensation is discussed in Chapter 9. Most other cutaneous receptors show some degree of **encapsulation**, which helps determine the nature of the stimuli to which they respond.

Despite their variety, all somatic sensory receptors work in fundamentally the same way: Stimuli applied to the skin deform or otherwise change the

TABLE 8.1
The Major Classes of Somatic Sensory Receptors

Receptor type	Anatomical characteristics	Associated axons ^a (and diameters)	Axonal conduction velocities	Location	Function	Rate of adaptation	Threshold of activation
Free nerve endings	Minimally specialized nerve endings	C, A δ	2–20 m/s	All skin	Pain, temperature, crude touch	Slow	High
Meissner's corpuscles	Encapsulated; between dermal papillae	A β 6–12 μ m		Principally glabrous skin	Touch, pressure (dynamic)	Rapid	Low
Pacinian corpuscles	Encapsulated; onionlike covering	A β 6–12 μ m		Subcutaneous tissue, interosseous membranes, viscera	Deep pressure, vibration (dynamic)	Rapid	Low
Merkel's disks	Encapsulated; associated with peptide-releasing cells	A β		All skin, hair follicles	Touch, pressure (static)	Slow	Low
Ruffini's corpuscles	Encapsulated; oriented along stretch lines	A β 6–12 μ m		All skin	Stretching of skin	Slow	Low
Muscle spindles	Highly specialized (see Figure 8.5 and Chapter 15)	Ia and II		Muscles	Muscle length	Both slow and rapid	Low
Golgi tendon organs	Highly specialized (see Chapter 15)	Ib		Tendons	Muscle tension	Slow	Low
Joint receptors	Minimally specialized	—		Joints	Joint position	Rapid	Low

^aIn the 1920s and 1930s, there was a virtual cottage industry classifying axons according to their conduction velocity. Three main categories were discerned, called A, B, and C. A comprises the largest and fastest axons, C the smallest and slowest. Mechanoreceptor axons generally fall into category A. The A group is further broken down into subgroups designated α (the fastest), β , and δ (the slowest). To make matters even more confusing, muscle afferent axons are usually classified into four additional groups—I (the fastest), II, III, and IV (the slowest)—with subgroups designated by lowercase roman letters!

nerve endings, which in turn affects the ionic permeability of the receptor cell membrane. Changes in permeability generate a depolarizing current in the nerve ending, thus producing a **receptor** (or **generator**) **potential** that triggers action potentials, as described in Chapters 2 and 3. This overall process, in which the energy of a stimulus is converted into an electrical signal in the sensory neuron, is called **sensory transduction** and is the critical first step in all sensory processing.

The *quality* of a mechanosensory (or any other) stimulus (i.e., what it represents and where it is) is determined by the properties of the relevant receptors and the location of their central targets (Figure 8.1). The quantity or strength of the stimulus is conveyed by the rate of action potential discharge triggered by the receptor potential (although this relationship is nonlinear and often quite complex). Some receptors fire rapidly when a stimulus is first presented and then fall silent in the presence of continued stimulation (which is to say they “adapt” to the stimulus), whereas others generate a sustained discharge in the presence of an ongoing stimulus (Figure 8.2). The usefulness of having some receptors that adapt quickly and others that do not is to provide information about both the *dynamic* and *static* qualities of a stimulus. Receptors that initially fire in the presence of a stimulus and then

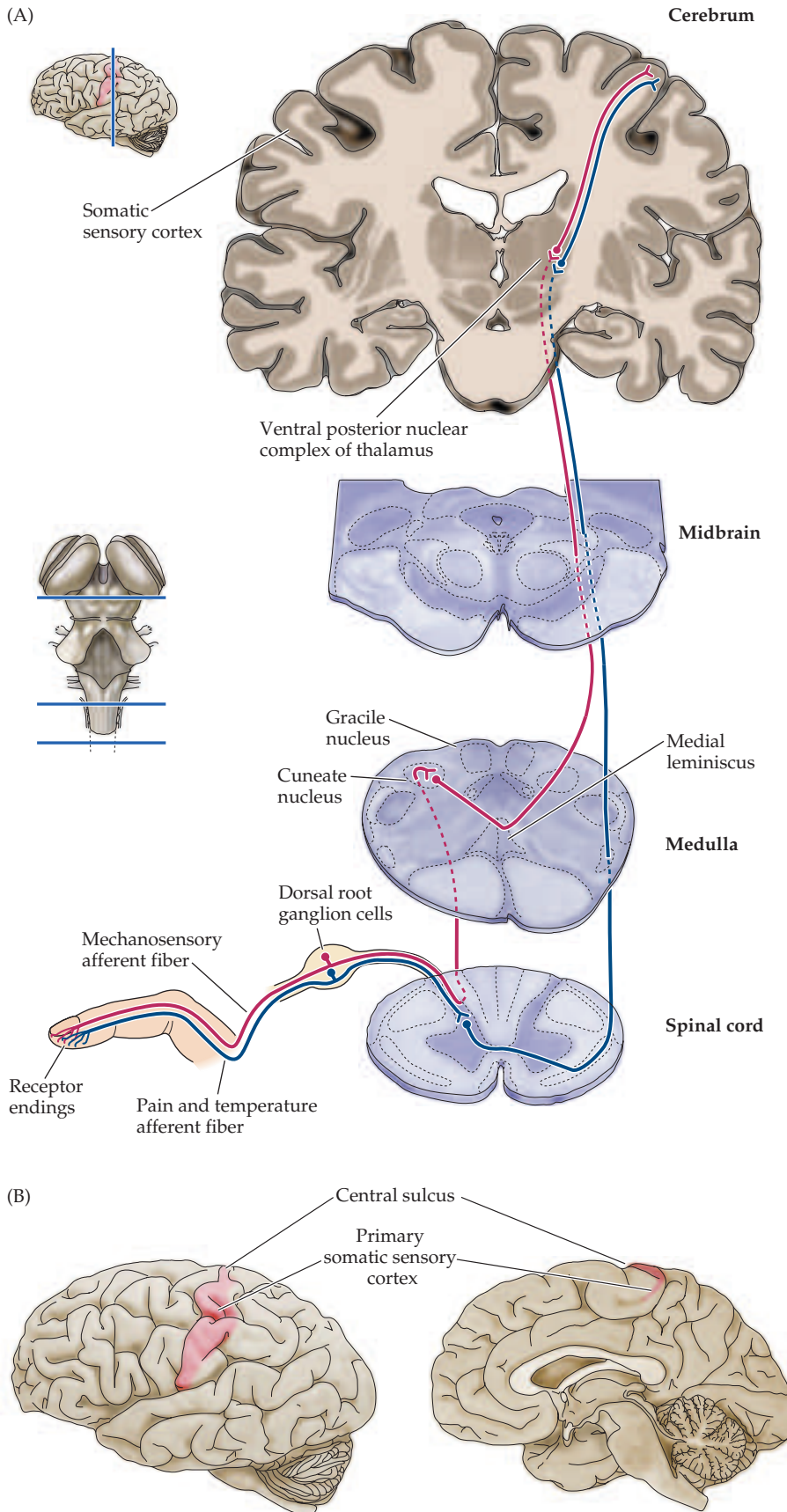


Figure 8.1 General organization of the somatic sensory system. (A) Mechanosensory information about the body reaches the brain by way of a three-neuron relay (shown in red). The first synapse is made by the terminals of the centrally projecting axons of dorsal root ganglion cells onto neurons in the brain-stem nuclei (the local branches involved in segmental spinal reflexes are not shown here). The axons of these second-order neurons synapse on third-order neurons of the ventral posterior nuclear complex of the thalamus, which in turn send their axons to the primary somatic sensory cortex (red). Information about pain and temperature takes a different course (shown in blue; the anterolateral system), and is discussed in the following chapter. (B) Lateral and midsagittal views of the human brain, illustrating the approximate location of the primary somatic sensory cortex in the anterior parietal lobe, just posterior to the central sulcus.



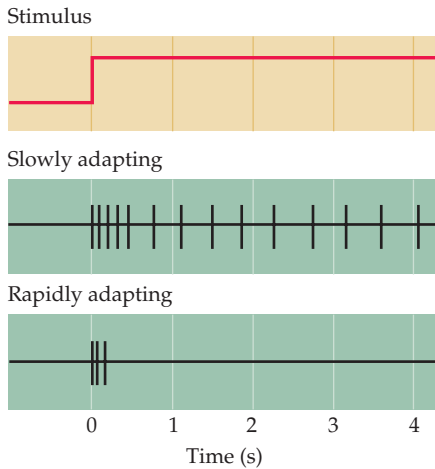


Figure 8.2 Slowly adapting mechanoreceptors continue responding to a stimulus, whereas rapidly adapting receptors respond only at the onset (and often the offset) of stimulation. These functional differences allow the mechanoreceptors to provide information about both the static (via slowly adapting receptors) and dynamic (via rapidly adapting receptors) qualities of a stimulus.

become quiescent are particularly effective in conveying information about changes in the information the receptor reports; conversely, receptors that continue to fire convey information about the persistence of a stimulus. Accordingly, somatic sensory receptors and the neurons that give rise to them are usually classified into rapidly or slowly adapting types (see Table 8.1). **Rapidly adapting**, or **phasic**, receptors respond maximally but briefly to stimuli; their response decreases if the stimulus is maintained. Conversely, **slowly adapting**, or **tonic**, receptors keep firing as long as the stimulus is present.

Mechanoreceptors Specialized to Receive Tactile Information

Four major types of encapsulated mechanoreceptors are specialized to provide information to the central nervous system about touch, pressure, vibration, and cutaneous tension: Meissner's corpuscles, Pacinian corpuscles, Merkel's disks, and Ruffini's corpuscles (Figure 8.3 and Table 8.1). These receptors are referred to collectively as **low-threshold** (or high-sensitivity) mechanoreceptors because even weak mechanical stimulation of the skin induces them to produce action potentials. All low-threshold mechanoreceptors are innervated by relatively large myelinated axons (type A β ; see Table 8.1), ensuring the rapid central transmission of tactile information.

Meissner's corpuscles, which lie between the dermal papillae just beneath the epidermis of the fingers, palms, and soles, are elongated receptors formed by a connective tissue capsule that comprises several lamellae of Schwann cells. The center of the capsule contains one or more afferent nerve fibers that generate rapidly adapting action potentials following minimal skin depression. Meissner's corpuscles are the most common mechanoreceptors of "glabrous" (smooth, hairless) skin (the fingertips, for instance), and their afferent fibers account for about 40% of the sensory innervation of the human hand. These corpuscles are particularly efficient in transducing information about the relatively low-frequency vibrations (30–50 Hz) that occur when textured objects are moved across the skin.

Pacinian corpuscles are large encapsulated endings located in the subcutaneous tissue (and more deeply in interosseous membranes and mesenteries of the gut). These receptors differ from Meissner's corpuscles in their morphology, distribution, and response threshold. The Pacinian corpuscle has an onion-like capsule in which the inner core of membrane lamellae is separated from an outer lamella by a fluid-filled space. One or more rapidly adapting afferent axons lie at the center of this structure. The capsule again acts as a filter, in this case allowing only transient disturbances at high frequencies (250–350 Hz) to activate the nerve endings. Pacinian corpuscles adapt more rapidly than Meissner's corpuscles and have a lower response threshold. These attributes suggest that Pacinian corpuscles are involved in the discrimination of fine surface textures or other moving stimuli that produce high-frequency vibration of the skin. In corroboration of this supposition, stimulation of Pacinian corpuscle afferent fibers in humans induces a sensation of vibration or tickle. They make up 10–15% of the cutaneous receptors in the hand. Pacinian corpuscles located in interosseous membranes probably detect vibrations transmitted to the skeleton. Structurally similar endings found in the bills of ducks and geese and in the legs of cranes and herons detect vibrations in water; such endings in the wings of soaring birds detect vibrations produced by air currents. Because they are rapidly adapting, Pacinian corpuscles, like Meissner's corpuscles, provide information primarily about the dynamic qualities of mechanical stimuli.

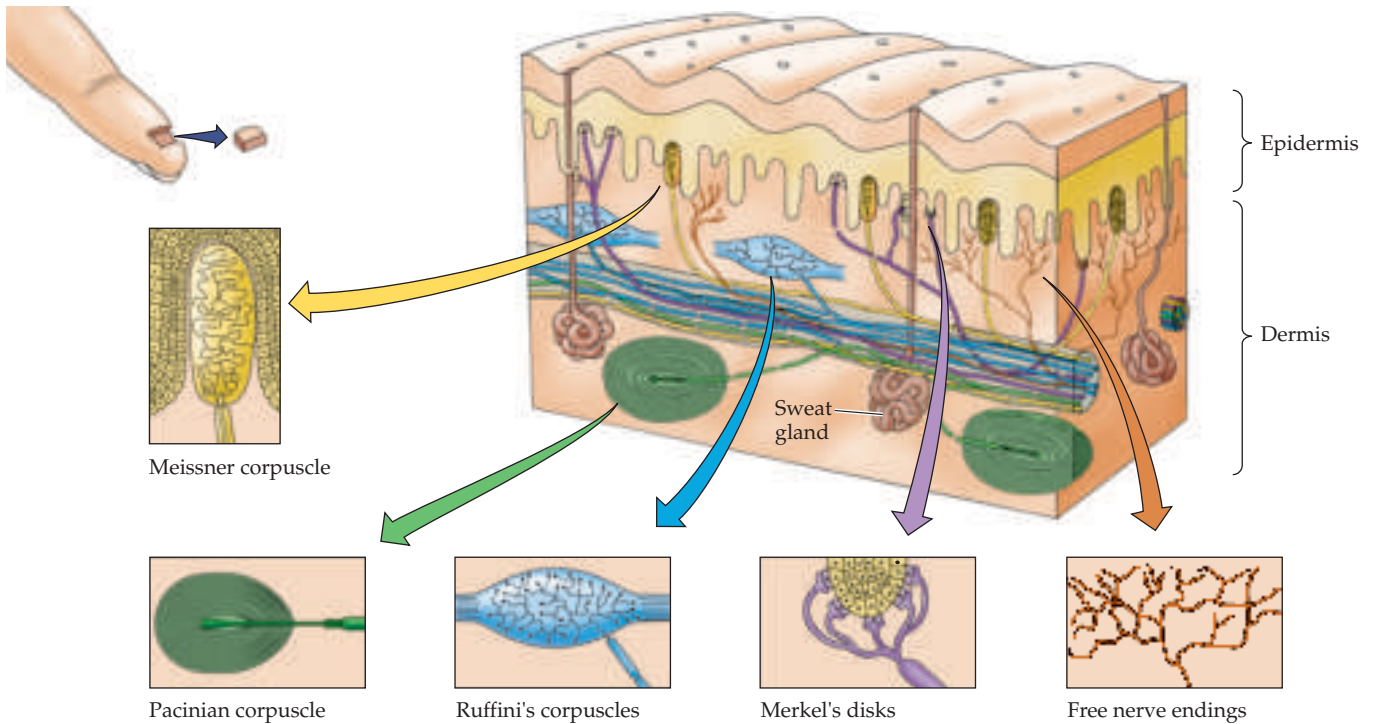


Figure 8.3 The skin harbors a variety of morphologically distinct mechanoreceptors. This diagram represents the smooth, hairless (also called glabrous) skin of the fingertip. The major characteristics of the various receptor types are summarized in Table 8.1. (After Darian-Smith, 1984.)

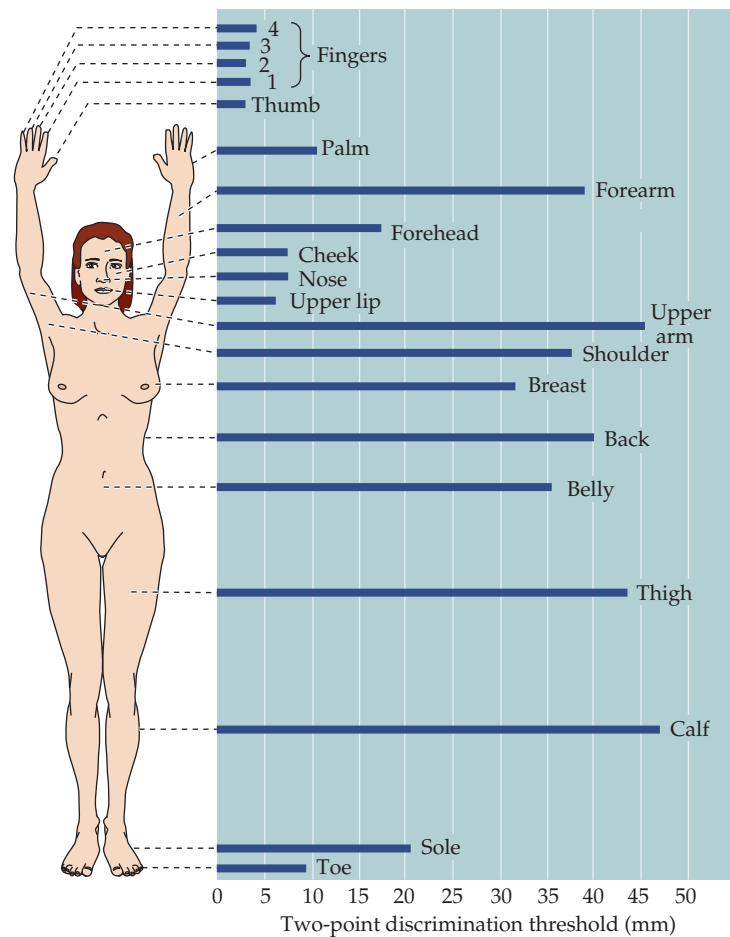
Slowly adapting cutaneous mechanoreceptors include **Merkel's disks** and **Ruffini's corpuscles** (see Figure 8.3 and Table 8.1). Merkel's disks are located in the epidermis, where they are precisely aligned with the papillae that lie beneath the dermal ridges. They account for about 25% of the mechanoreceptors of the hand and are particularly dense in the fingertips, lips, and external genitalia. The slowly adapting nerve fiber associated with each Merkel's disk enlarges into a saucer-shaped ending that is closely applied to another specialized cell containing vesicles that apparently release peptides that modulate the nerve terminal. Selective stimulation of these receptors in humans produces a sensation of light pressure. These several properties have led to the supposition that Merkel's disks play a major role in the static discrimination of shapes, edges, and rough textures.

Ruffini's corpuscles, although structurally similar to other tactile receptors, are not well understood. These elongated, spindle-shaped capsular specializations are located deep in the skin, as well as in ligaments and tendons. The long axis of the corpuscle is usually oriented parallel to the stretch lines in skin; thus, Ruffini's corpuscles are particularly sensitive to the cutaneous stretching produced by digit or limb movements. They account for about 20% of the receptors in the human hand and do not elicit any particular tactile sensation when stimulated electrically. Although there is still some question as to their function, they probably respond primarily to internally generated stimuli (see the section on proprioception, below).

Differences in Mechanosensory Discrimination across the Body Surface

The accuracy with which tactile stimuli can be sensed varies from one region of the body to another, a phenomenon that illustrates some further principles

Figure 8.4 Variation in the sensitivity of tactile discrimination as a function of location on the body surface, measured here by two-point discrimination. (After Weinstein, 1968.)



of somatic sensation. Figure 8.4 shows the results of an experiment in which variation in tactile ability across the body surface was measured by **two-point discrimination**. This technique measures the minimal interstimulus distance required to perceive two simultaneously applied stimuli as distinct (the indentations of the points of a pair of calipers, for example). When applied to the skin, such stimuli of the fingertips are discretely perceived if they are only 2 mm apart. In contrast, the same stimuli applied to the forearm are not perceived as distinct until they are at least 40 mm apart! This marked regional difference in tactile ability is explained by the fact that the encapsulated mechanoreceptors that respond to the stimuli are three to four times more numerous in the fingertips than in other areas of the hand, and many times more dense than in the forearm. Equally important in this regional difference are the sizes of the neuronal receptive fields. The **receptive field** of a somatic sensory neuron is the region of the skin within which a tactile stimulus evokes a sensory response in the cell or its axon (Boxes A and B). Analysis of the human hand shows that the receptive fields of mechanosensory neurons are 1–2 mm in diameter on the fingertips but 5–10 mm on the palms. The receptive fields on the arm are larger still. The importance of receptive field size is easy to envision. If, for instance, the receptive fields of all cutaneous receptor neurons covered the entire digital pad, it would be impossible to discriminate two spatially separate stimuli applied to the fingertip (since all the receptive fields would be returning the same spatial information).

Box A

Receptive Fields and Sensory Maps in the Cricket

Two principles of somatosensory organization have emerged from studies of the mammalian brain: (1) individual neurons are tuned to particular aspects of complex stimuli; and (2) these stimulus qualities are represented in an orderly fashion in relevant regions of the nervous system. These principles apply equally well to invertebrates, including the equivalent of the somatic sensory system in insects such as crickets, grasshoppers, and cockroaches.

In the cricket, the salient tactile stimulation for the animal comes from air currents that displace sensory hairs of bilaterally symmetric sensory structures called cerci (sing. *cercus*). The location and structure of specific cercal hairs

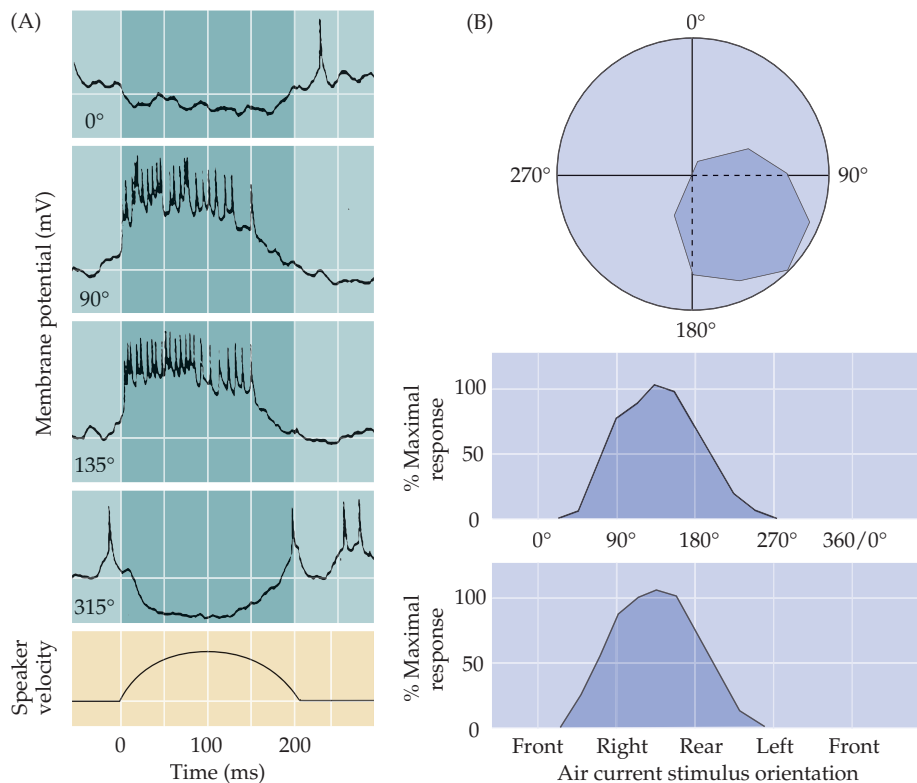
allow them to be displaced by air currents having different directions and speeds (Figure A). Accordingly, the peripheral sensory neurons associated with the hairs represent the full range of air current directions and velocities impinging on the animal. This information is carried centrally and is systematically represented in a region of the cricket central nervous system called the terminal ganglion.

Individual neurons in this ganglion correspond to the cercal hairs, and have receptive fields and response properties that represent a full range of directions and speeds for extrinsic mechanical forces, including air currents (Figure B). For the cricket, the significance of this

information is, among other things, detecting the direction and speed of oncoming objects to then execute motor programs for escape. (This is also the likely significance of this representation for cockroaches, which can therefore escape the consequences of a descending human foot.)

Much like the somatic sensory system in mammals, the primary sensory afferents project to the terminal ganglion in an orderly fashion, such that there is a somatotopic map of air current directions. And, like mammals, individual neurons within this representation are tuned to specific aspects of the mechanical forces acting on the cricket.

These facts about insects' mechanosensory system emphasize that somatic sensory functions are basically similar across a wide range of animals. Indeed, regardless of sensory modality, nervous system organization, or the identity of the organism, it is likely that stimulus specificity will be reflected in receptive fields of individual neurons and there will be orderly mapping of those receptive fields into either a topographic or computational map in the animal's brain.



(A) Intracellular recording of action potential activity of an individual sensory neuron's responses to different directions of wind current. (B) The plots indicate this neuron's receptive field for wind direction (top) and the tuning curve for the neuron's selective firing to its preferred direction. (After Miller et al., 1991.)

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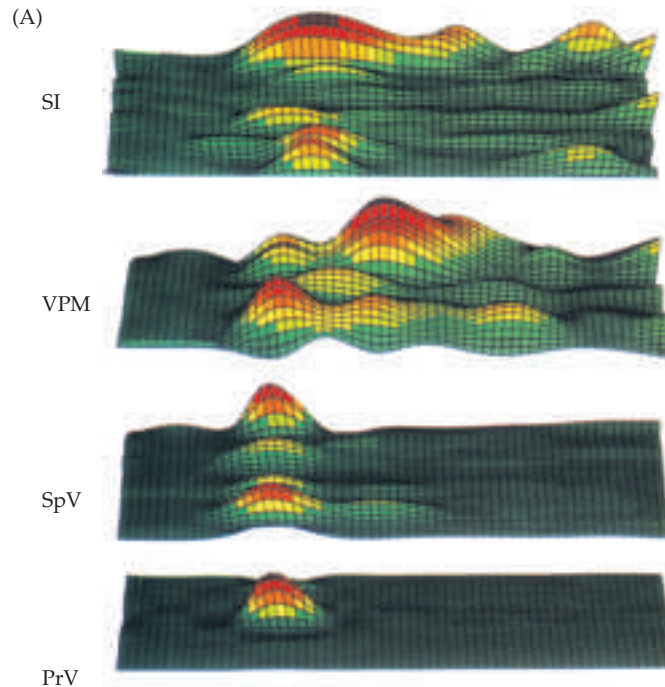
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Box B

Dynamic Aspects of Somatic Sensory Receptive Fields

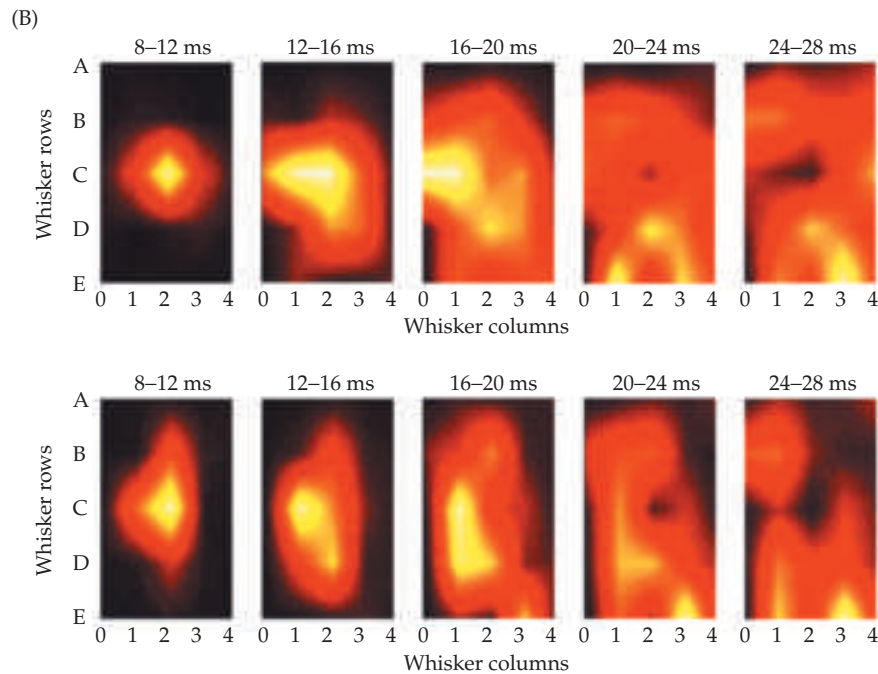
When humans explore objects with their hands, multiple contacts between the skin and the object surface generate extraordinarily complex patterns of tactile stimuli. As a consequence, the somatic sensory system must process signals that change continuously in time. Nonetheless, we routinely discriminate the size, texture and shape of objects with great accuracy. Until recently, the temporal structure of such stimuli was not considered a major variable in characterizing the physiological properties of somatic sensory neurons. For instance, the classical definition of the receptive field of a somatic sensory neuron takes into account only the overall area of the body surface that elicits significant variation in the neuron's firing rate. By the same token, the topographic maps in the somatic sensory system have been interpreted as evidence that tactile information processing involves primarily spatial criteria.

The advent of multiple electrode recording to simultaneously monitor the activity of large populations of single neurons has begun to change this "static" view of the somatic sensory system. In both primates and rodents, this approach has shown that the receptive fields of cortical and subcortical neurons



(A) Simultaneous electrode recordings in behaving rats allow monitoring of the spatiotemporal spread of neuronal activation across several levels of the somatic sensory system following stimulation (of a single facial whisker, in this example). These 3-D graphs represent patterns of neuronal ensemble activity at each level of the pathway. The x axis represents the poststimulus time in ms, the y axis the number of neurons recorded at each level; the color-coded gradient in the z axis shows the response of the neurons, with red the highest firing and green the lowest. SI, somatic sensory cortex; VPM, ventral posterior medial nucleus of the thalamus; SpV, spinal nucleus of the trigeminal brainstem complex; PrV, principal nucleus of the brainstem trigeminal complex. (From Nicholelis et al., 1997.)

Receptor density and receptive field sizes in different regions are not the only factors determining somatic sensation. Psychophysical analysis of tactile performance suggests that something more than the cutaneous periphery is needed to explain variations in tactile perception. For instance, sensory thresholds in two-point discrimination tests vary with practice, fatigue, and stress. The contextual significance of stimuli is also important in determining what we actually feel; even though we spend most of the day wearing clothes, we usually ignore the tactile stimulation that they produce. Some aspect of the mechanosensory system allows us to filter out this information and pay attention to it only when necessary. The fascinating phenomenon of "phantom limb" sensations after amputation (see Box C in Chapter 9) provides further evidence that tactile perception is not fully explained by the



(B) Receptive fields of two cortical neurons from two different animals. Each panel represents the matrix of whiskers on the animals' snout (whisker columns are on the x axis and whisker rows on the y axis) for a 4-ms epoch of poststimulus time. Within a particular time period, the center of the receptive field is defined as the whisker eliciting the greatest response magnitude (yellow). Note that the receptive field centers shift as a function of time. (From Ghazanfar and Nicholelis, 1998.)

vary as a function of time: The neuron responds differently to a spatially defined stimulus as the period of stimulation proceeds (see Figures A and B).

This coupling of space and time can

also be demonstrated at level of somatotopic maps. By recording the activity of single neurons located in different regions of the map simultaneously, it is apparent that the stimulation of a small

area of the skin tends to excite more and more neurons as time goes by. Thus, many more neurons than those located in the area of the map directly representing the stimulated skin actually respond to the stimulus, albeit at longer latencies.

The end result of these more complex neuronal responses is the emergence of spatiotemporal representations at all levels of the somatic sensory system. Thus, contrary to the classical notion of receptive fields, the somatic sensory system processes information in a dynamic way. Such processing is not only relevant for the normal operation of the system, but may also account for some aspects of adult plasticity (see Chapter 24).

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peripheral information that travels centrally. The central nervous system clearly plays an active role in determining the perception of the mechanical forces that act on us.

Mechanoreceptors Specialized for Proprioception

Whereas cutaneous mechanoreceptors provide information derived from external stimuli, another major class of receptors provides information about mechanical forces arising from the body itself, the musculoskeletal system in particular. These are called **proprioceptors**, roughly meaning “receptors for self.” The purpose of proprioceptors is primarily to give detailed and continuous information about the position of the limbs and other body parts in

space (specialized mechanoreceptors also exist in the heart and major vessels to provide information about blood pressure, but these neurons are considered to be part of the visceral motor system; see Chapter 20). Low-threshold mechanoreceptors, including muscle spindles, Golgi tendon organs, and joint receptors, provide this kind of sensory information, which is essential to the accurate performance of complex movements. Information about the position and motion of the head is particularly important; in this case, proprioceptors are integrated with the highly specialized vestibular system, which is considered separately in Chapter 13.

The most detailed knowledge about proprioception derives from studies of **muscle spindles**, which are found in all but a few striated (skeletal) muscles. Muscle spindles consist of four to eight specialized **intrafusal muscle fibers** surrounded by a capsule of connective tissue. The intrafusal fibers are distributed among the ordinary (extrafusal) fibers of skeletal muscle in a parallel arrangement (Figure 8.5). In the largest of the several intrafusal fibers, the nuclei are collected in an expanded region in the center of the fiber called a bag; hence the name *nuclear bag fibers*. The nuclei in the remaining two to six smaller intrafusal fibers are lined up single file, with the result that these fibers are called *nuclear chain fibers*. Myelinated sensory axons belonging to group Ia innervate muscle spindles by encircling the middle portion of both types of intrafusal fibers (see Figure 8.5 and Table 8.1). The Ia axon terminal is known as the **primary sensory ending** of the spindle. Secondary innervation is provided by group II axons that innervate the nuclear chain fibers and give off a minor branch to the nuclear bag fibers. The intrafusal muscle fibers contract when commanded to do so by motor axons derived from a pool of specialized motor neurons in the spinal cord (called **γ motor neurons**). The major function of muscle spindles is to provide information about muscle length (that is, the degree to which they are being stretched). A detailed account of how these important receptors function during movement is given in Chapters 15 and 16.

The density of spindles in human muscles varies. Large muscles that generate coarse movements have relatively few spindles; in contrast, extraocular muscles and the intrinsic muscles of the hand and neck are richly supplied with spindles, reflecting the importance of accurate eye movements, the need to manipulate objects with great finesse, and the continuous demand for precise positioning of the head. This relationship between receptor den-

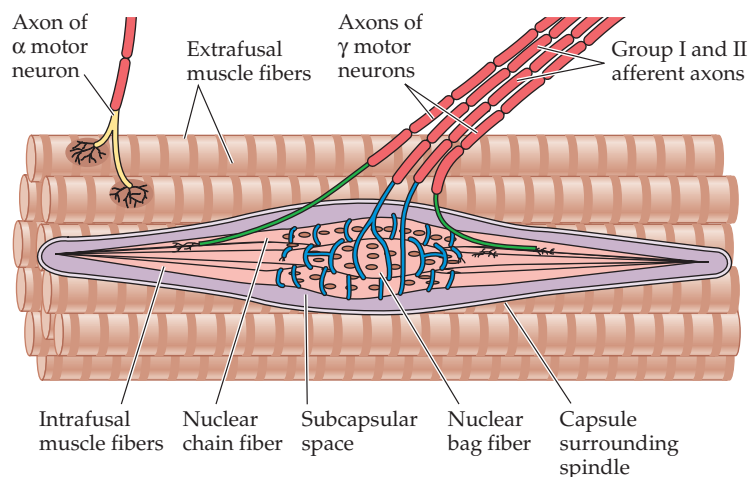


Figure 8.5 A muscle spindle and several extrafusal muscle fibers. See text for description. (After Matthews, 1964.)

sity and muscle size is consistent with the generalization that the sensory motor apparatus at all levels of the nervous system is much richer for the hands, head, speech organs, and other parts of the body that are used to perform especially important and demanding tasks. Spindles are lacking altogether in a few muscles, such as those of the middle ear, which do not require the kind of feedback that these receptors provide.

Whereas muscle spindles are specialized to signal changes in muscle *length*, low-threshold mechanoreceptors in tendons inform the central nervous system about changes in muscle *tension*. These mechanoreceptors, called **Golgi tendon organs**, are innervated by branches of group Ib afferents and are distributed among the collagen fibers that form the tendons (see Chapter 15).

Finally, rapidly adapting mechanoreceptors in and around joints gather dynamic information about limb position and joint movement. The function of these **joint receptors** is not well understood.

Active Tactile Exploration

Tactile discrimination—that is, perceiving the detailed shape or texture of an object—normally entails active exploration. In humans, this is typically accomplished by using the hands to grasp and manipulate objects, or by moving the fingers across a surface so that a sequence of contacts between the skin and the object of interest is established. Psychophysical evidence indicates that relative movement between the skin and a surface is the single most important requirement for accurate discrimination of texture. Animal experiments confirm the dependence of tactile discrimination on active exploration. Rats, for instance, discriminate the details of texture by rhythmically brushing their facial whiskers across surfaces. Active touching, which is called **haptics**, involves the interpretation of complex spatiotemporal patterns of stimuli that are likely to activate many classes of mechanoreceptors. Haptics also requires dynamic interactions between motor and sensory signals, which presumably induce sensory responses in central neurons that differ from the responses of the same cells during passive stimulation of the skin (see Box B).

The Major Afferent Pathway for Mechanosensory Information: The Dorsal Column–Medial Lemniscus System

The action potentials generated by tactile and other mechanosensory stimuli are transmitted to the spinal cord by afferent sensory axons traveling in the peripheral nerves. The neuronal cell bodies that give rise to these first-order axons are located in the **dorsal root** (or **sensory**) **ganglia** associated with each segmental spinal nerve (see Figure 8.1 and Box C). Dorsal root ganglion cells are also known as **first-order neurons** because they initiate the sensory process. The ganglion cells thus give rise to long peripheral axons that end in the somatic receptor specializations already described, and shorter central axons that reach the dorsolateral region of the spinal cord via the **dorsal** (**sensory**) **roots** of each spinal cord segment. The large myelinated fibers that innervate low-threshold mechanoreceptors are derived from the largest neurons in these ganglia, whereas the smaller ganglion cells give rise to smaller afferent nerve fibers that end in the high-threshold nociceptors and thermoreceptors (see Table 8.1).

Depending on whether they belong to the mechanosensory system or to the pain and temperature system, the first-order axons carrying information

from somatic receptors have different patterns of termination in the spinal cord and define distinct somatic sensory pathways within the central nervous system (see Figure 8.1). The **dorsal column–medial lemniscus pathway** carries the majority of information from the mechanoreceptors that mediate tactile discrimination and proprioception (Figure 8.6); the **spinothalamic (anterolateral) pathway** mediates pain and temperature sensation and is described in Chapter 9. This difference in the afferent pathways of these modalities is one of the reasons that pain and temperature sensation is treated separately here.

Upon entering the spinal cord, the first-order axons carrying information from peripheral mechanoreceptors bifurcate into ascending and descending branches, which in turn send collateral branches to several spinal segments. Some collateral branches penetrate the dorsal horn of the cord and synapse on neurons located mainly in a region called Rexed's laminae III–V. These synapses mediate, among other things, segmental reflexes such as the “knee-jerk” or myotatic reflex described in Chapter 1, and are further considered in Chapters 15 and 16. The major branch of the incoming axons, however, ascends ipsilaterally through the **dorsal columns** (also called the *posterior funiculi*) of the cord, all the way to the lower medulla, where it terminates by contacting **second-order neurons** in the **gracile** and **cuneate nuclei** (together referred to as the **dorsal column nuclei**; see Figures 8.1 and 8.6A). Axons in the dorsal columns are topographically organized such that the fibers that convey information from lower limbs are in the medial subdivision of the dorsal columns, called the **gracile tract**, a fact of some significance in the clinical localization of neural injury. The lateral subdivision, called the **cuneate tract**, contains axons conveying information from the upper limbs, trunk, and neck. At the level of the upper thorax, the dorsal columns account for more than a third of the cross-sectional area of the human spinal cord.

Despite their size, lesions limited to the dorsal columns of the spinal cord in both humans and monkeys have only a modest effect on the performance of simple tactile tasks. Such lesions, however, do impede the ability to detect the direction and speed of tactile stimuli, as well as degrading the ability to sense the position of the limbs in space. Dorsal column lesions may also reduce a patient's ability to initiate active movements related to tactile exploration. For instance, such individuals have difficulty recognizing numbers and letters drawn on their skin. The relatively mild deficit that follows dorsal column lesions is presumably explained by the fact that some axons responsible for cutaneous mechanoreception also run in the spinothalamic (pain and temperature) pathway, as described in Chapter 9.

The second-order relay neurons in the dorsal column nuclei send their axons to the somatic sensory portion of the thalamus (see Figure 8.6A). The axons from dorsal column nuclei project in the dorsal portion of each side of the lower brainstem, where they form the **internal arcuate tract**. The internal arcuate axons subsequently cross the midline to form another named tract that is elongated dorsoventrally, the **medial lemniscus**. (The crossing of these fibers is called the *decussation* of the medial lemniscus, from the roman numeral “X,” or *decem*; the word *lemniscus* means “ribbon.”)

In a cross-section through the medulla, such as the one shown in Figure 8.6A, the medial lemniscal axons carrying information from the lower limbs are located ventrally, whereas the axons related to the upper limbs are located dorsally (again, a fact of some clinical importance). As the medial lemniscus ascends through the pons and midbrain, it rotates 90° laterally, so that the upper body is eventually represented in the medial portion of the tract, and the lower body in the lateral portion. The axons of the medial lem-

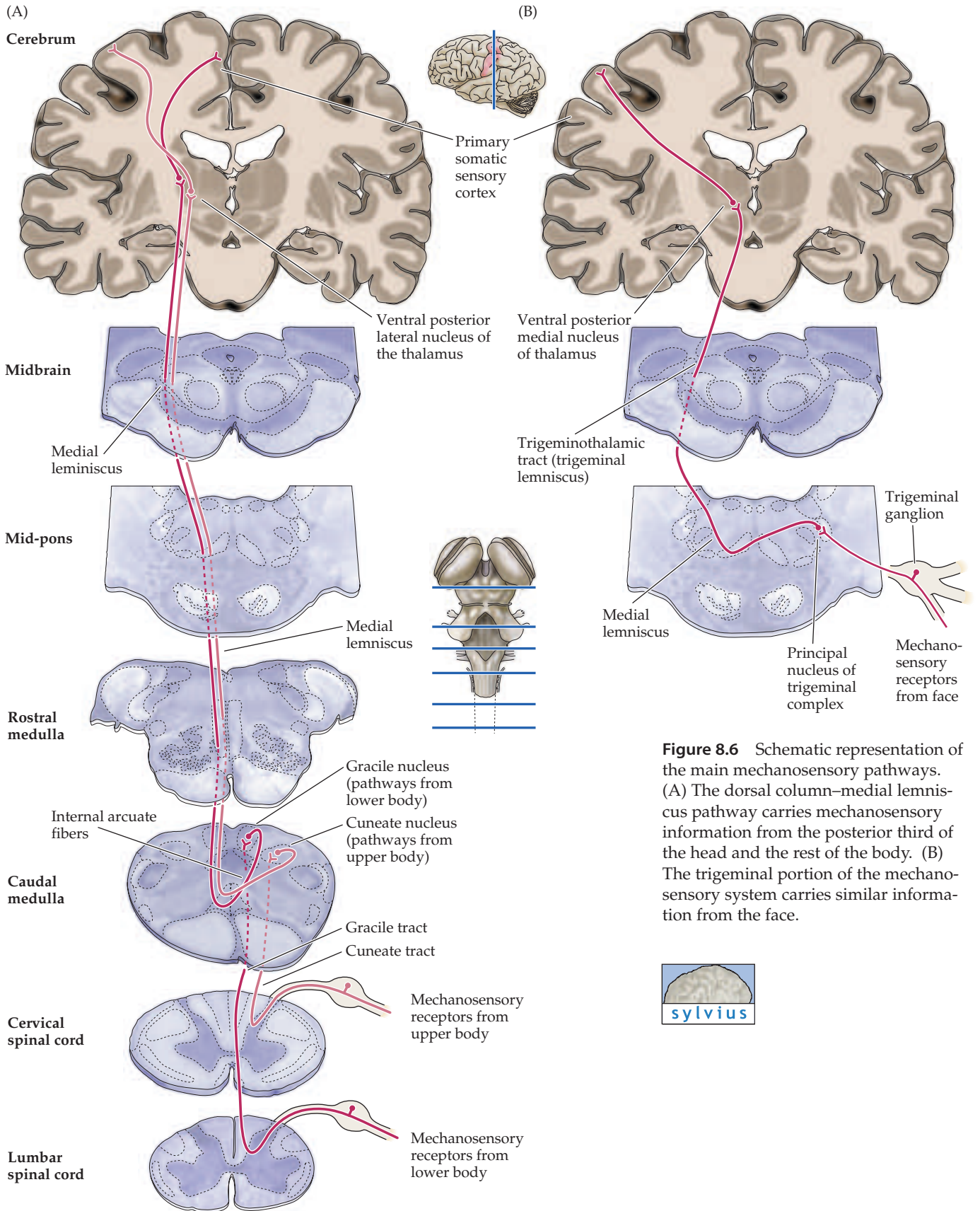
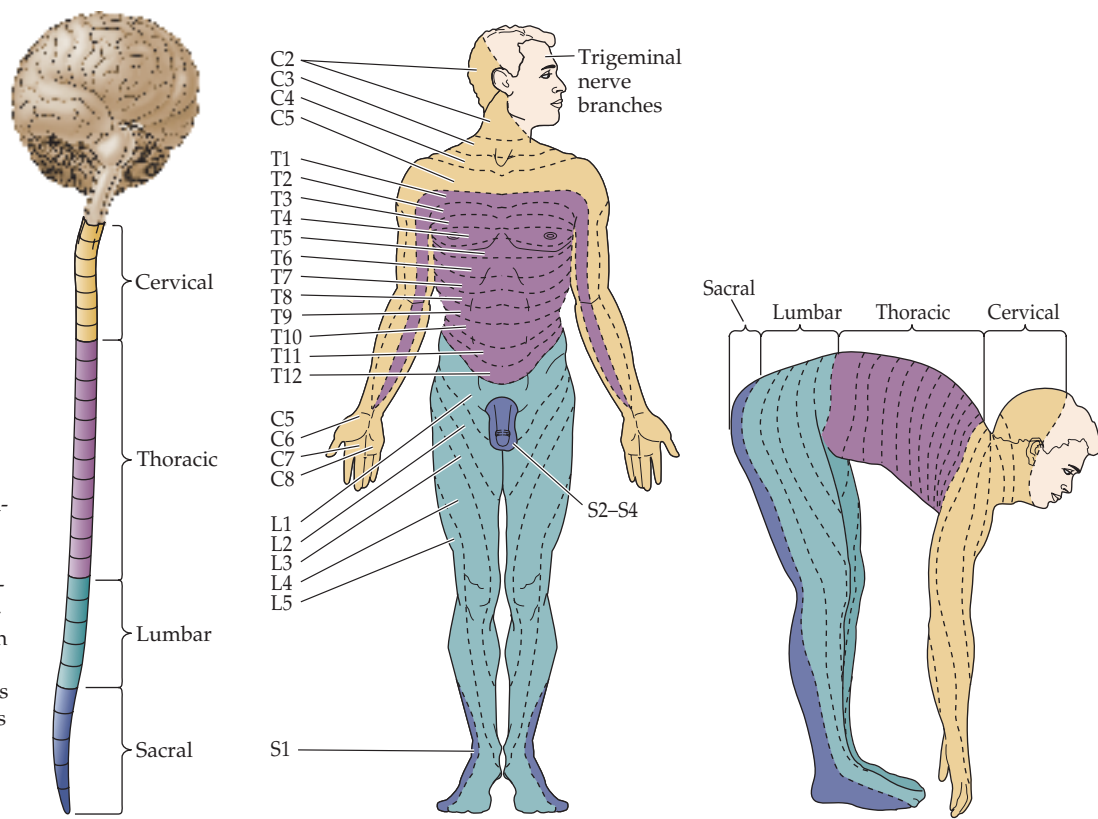


Figure 8.6 Schematic representation of the main mechanosensory pathways. (A) The dorsal column–medial lemniscus pathway carries mechanosensory information from the posterior third of the head and the rest of the body. (B) The trigeminal portion of the mechanosensory system carries similar information from the face.



Box C Dermatomes

The innervation arising from a single dorsal root ganglion and its spinal nerve is called a dermatome. The full set of sensory dermatomes is shown here for a typical adult. Knowledge of this arrangement is particularly important in defining the location of suspected spinal (and other) lesions. The numbers refer to the spinal segments by which each nerve is named. (After Rosenzweig et al., 2002.)



Each dorsal root (or sensory) ganglion and associated spinal nerve arises from an iterated series of embryonic tissue masses called somites. This fact of development explains the overall segmental arrangement of somatic nerves (and the targets they innervate) in the adult (see figure). The territory innervated by each spinal nerve is called a dermatome. In humans, the cutaneous area of each dermatome has been defined in patients in whom specific dorsal roots were affected

(as in herpes zoster, or “shingles”) or after surgical interruption (for relief of pain or other reasons). Such studies show that dermatomal maps vary among individuals. Moreover, dermatomes overlap substantially, so that injury to an individual dorsal root does not lead to complete loss of sensation in the relevant skin region, the overlap being more extensive for touch, pressure, and vibration than for pain and temperature. Thus, testing for pain sensation provides

a more precise assessment of a segmental nerve injury than does testing for responses to touch, pressure, or vibration. Finally, the segmental distribution of proprioceptors does not follow the dermatomal map but is more closely allied with the pattern of muscle innervation. Despite these limitations, knowledge of dermatomes is essential in the clinical evaluation of neurological patients, particularly in determining the level of a spinal lesion.

niscus thus reach the ventral posterior lateral (VPL) nucleus of the thalamus, whose cells are the **third-order neurons** of the dorsal column–medial lemniscus system (see Figure 8.7).

The Trigeminal Portion of the Mechanosensory System

As noted, the dorsal column–medial lemniscus pathway described in the preceding section carries somatic information from only the upper and lower body and from the posterior third of the head. Tactile and propriocep-

tive information from the face is conveyed from the periphery to the thalamus by a different route. Information derived from the face is transmitted to the central nervous system via the **trigeminal somatic sensory system** (Figure 8.6B). Low-threshold mechanoreception in the face is mediated by first-order neurons in the trigeminal (cranial nerve V) ganglion. The peripheral processes of these neurons form the three main subdivisions of the **trigeminal nerve** (the **ophthalmic**, **maxillary**, and **mandibular branches**), each of which innervates a well-defined territory on the face and head, including the teeth and the mucosa of the oral and nasal cavities. The central processes of trigeminal ganglion cells form the sensory roots of the trigeminal nerve; they enter the brainstem at the level of the pons to terminate on neurons in the subdivisions of the **trigeminal brainstem complex**.

The trigeminal complex has two major components: the **principal nucleus** (responsible for processing mechanosensory stimuli), and the **spinal nucleus** (responsible for processing painful and thermal stimuli). Thus, most of the axons carrying information from low-threshold cutaneous mechanoreceptors in the face terminate in the principal nucleus. In effect, this nucleus corresponds to the dorsal column nuclei that relay mechanosensory information from the rest of the body. The spinal nucleus corresponds to a portion of the spinal cord that contains the second-order neurons in the pain and temperature system for the rest of the body (see Chapter 9). The second-order neurons of the trigeminal brainstem nuclei give off axons that cross the midline and ascend to the ventral posterior medial (VPM) nucleus of the thalamus by way of the **trigeminothalamic tract** (also called the trigeminal lemniscus).

The Somatic Sensory Components of the Thalamus

Each of the several ascending somatic sensory pathways originating in the spinal cord and brainstem converge on the thalamus (Figure 8.7). The **ventral posterior complex** of the thalamus, which comprises a lateral and a medial nucleus, is the main target of these ascending pathways. As already mentioned, the more laterally located **ventral posterior lateral (VPL) nucleus** receives projections from the medial lemniscus carrying all somatosensory information from the body and posterior head, whereas the more medially located **ventral posterior medial (VPM) nucleus** receives axons from the trigeminal lemniscus (that is, mechanosensory and nociceptive information from the face). Accordingly, the ventral posterior complex of the thalamus contains a complete representation of the somatic sensory periphery.

The Somatic Sensory Cortex

The axons arising from neurons in the ventral posterior complex of the thalamus project to cortical neurons located primarily in layer IV of the somatic sensory cortex (see Figure 8.7; also see Box A in Chapter 25 for a more detailed description of cortical lamination). The **primary somatic sensory cortex** in humans (also called **SI**), which is located in the postcentral gyrus of the parietal lobe, comprises four distinct regions, or fields, known as **Brodman's areas 3a**, **3b**, **1**, and **2**. Experiments carried out in nonhuman primates indicate that neurons in areas 3b and 1 respond primarily to cutaneous stimuli, whereas neurons in 3a respond mainly to stimulation of proprioceptors; area 2 neurons process both tactile and proprioceptive stimuli. Mapping studies in humans and other primates show further that each

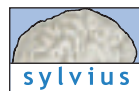
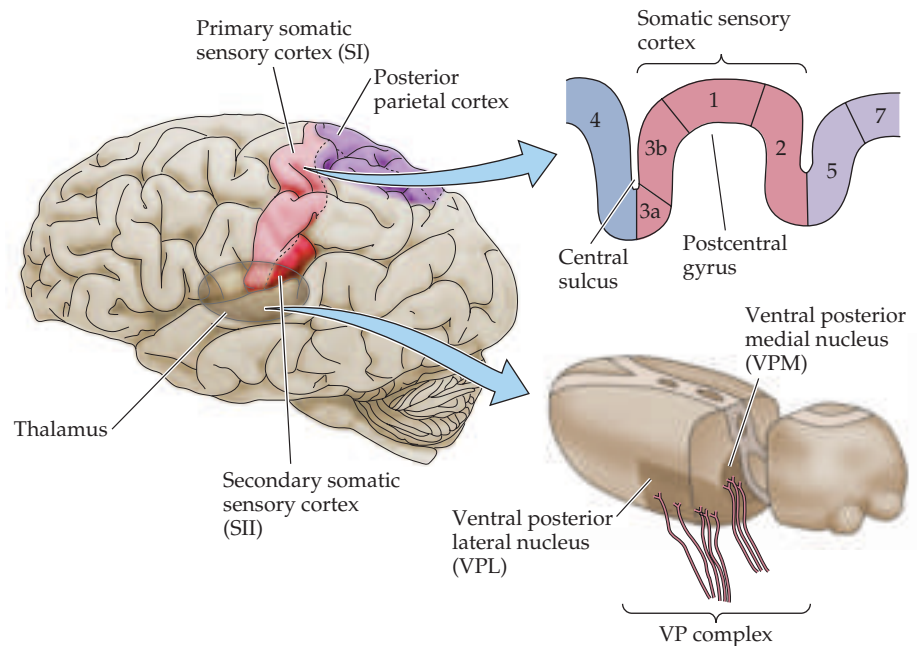


Figure 8.7 Diagram of the somatic sensory portions of the thalamus and their cortical targets in the postcentral gyrus. The ventral posterior nuclear complex comprises the VPM, which relays somatic sensory information carried by the trigeminal system from the face, and the VPL, which relays somatic sensory information from the rest of the body. Inset above shows organization of the primary somatosensory cortex in the postcentral gyrus, shown here in a section cutting across the gyrus from anterior to posterior. (After Brodal, 1992, and Jones et al., 1982.)

of these four cortical areas contains a separate and complete representation of the body. In these **somatotopic maps**, the foot, leg, trunk, forelimbs, and face are represented in a medial to lateral arrangement, as shown in Figures 8.8A,B and 8.9.

Although the topographic organization of the several somatic sensory areas is similar, the functional properties of the neurons in each region and their organization are distinct (Box D). For instance, the neuronal receptive fields are relatively simple in area 3b; the responses elicited in this region are generally to stimulation of a single finger. In areas 1 and 2, however, the majority of the receptive fields respond to stimulation of multiple fingers. Furthermore, neurons in area 1 respond preferentially to particular directions of skin stimulation, whereas many area 2 neurons require complex stimuli to activate them (such as a particular shape). Lesions restricted to area 3b produce a severe deficit in both texture and shape discrimination. In contrast, damage confined to area 1 affects the ability of monkeys to perform accurate texture discrimination. Area 2 lesions tend to produce deficits in finger coordination, and in shape and size discrimination.

A salient feature of cortical maps, recognized soon after their discovery, is their failure to represent the body in actual proportion. When neurosurgeons determined the representation of the human body in the primary sensory (and motor) cortex, the homunculus (literally, “little man”) defined by such mapping procedures had a grossly enlarged face and hands compared to the torso and proximal limbs (Figure 8.8C). These anomalies arise because

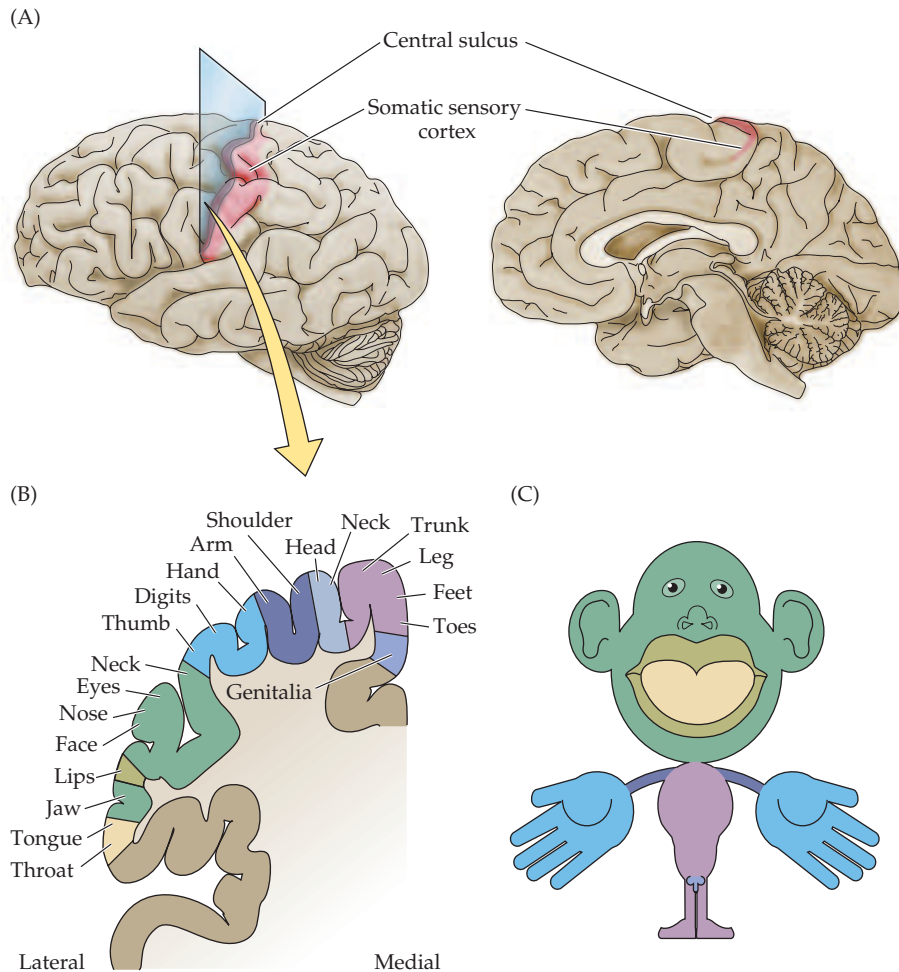
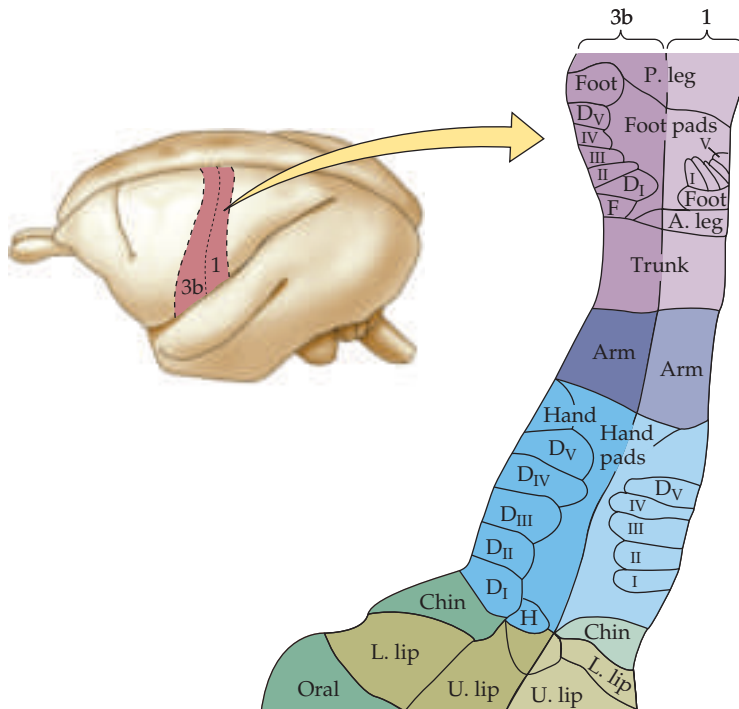


Figure 8.8 Somatotopic order in the human primary somatic sensory cortex. (A) Diagram showing the region of the human cortex from which electrical activity is recorded following mechanosensory stimulation of different parts of the body. The patients in the study were undergoing neurosurgical procedures for which such mapping was required. Although modern imaging methods are now refining these classical data, the human somatotopic map first defined in the 1930s has remained generally valid. (B) Diagram along the plane in (A) showing the somatotopic representation of body parts from medial to lateral. (C) Cartoon of the homunculus constructed on the basis of such mapping. Note that the amount of somatic sensory cortex devoted to the hands and face is much larger than the relative amount of body surface in these regions. A similar disproportion is apparent in the primary motor cortex, for much the same reasons (see Chapter 17). (After Penfield and Rasmussen, 1950, and Corsi, 1991.)



manipulation, facial expression, and speaking are extraordinarily important for humans, requiring more central (and peripheral) circuitry to govern them. Thus, in humans, the cervical spinal cord is enlarged to accommodate the extra circuitry related to the hand and upper limb, and as stated earlier, the density of receptors is greater in regions such as the hands and lips. Such distortions are also apparent when topographical maps are compared across species. In the rat brain, for example, an inordinate amount of the somatic sensory cortex is devoted to representing the large facial whiskers that pro-

Figure 8.9 The primary somatic sensory map in the owl monkey based, as in Figure 8.8, on the electrical responsiveness of the cortex to peripheral stimulation. Much more detailed mapping is possible in experimental animals than in neurosurgical patients. The enlargement on the right shows areas 3b and 1, which process most cutaneous mechanosensory information. The arrangement is generally similar to that determined in humans. (After Kaas, 1983.)



vide a key component of the somatic sensory input for rats and mice (see Boxes B and D), while raccoons overrepresent their paws and the platypus its bill. In short, the sensory input (or motor output) that is particularly significant to a given species gets relatively more cortical representation.

Higher-Order Cortical Representations

Somatic sensory information is distributed from the primary somatic sensory cortex to “higher-order” cortical fields (as well as to subcortical structures). One of these higher-order cortical centers, the secondary somatosensory cortex (sometimes called SII and adjacent to the primary cortex; see Figure 8.7), receives convergent projections from the primary somatic sensory cortex and sends projections in turn to limbic structures such as the amygdala and hippocampus (see Chapters 28 and 30). This latter pathway is believed to play an important role in tactile learning and memory. Neurons in motor cortical areas in the frontal lobe also receive tactile information from the anterior parietal cortex and, in turn, provide feedback projections to several cortical somatic sensory regions. Such integration of sensory and motor information is considered in Chapters 19 and 25, where the role of these “association” regions of the cerebral cortex are discussed in more detail.

Finally, a fundamental but often neglected feature of the somatic sensory system is the presence of massive descending projections. These pathways originate in sensory cortical fields and run to the thalamus, brainstem, and spinal cord. Indeed, descending projections from the somatic sensory cortex outnumber ascending somatic sensory pathways! Although their physiological role is not well understood, it is generally assumed (with some experimental support) that descending projections modulate the ascending flow of sensory information at the level of the thalamus and brainstem.

Box D

Patterns of Organization within the Sensory Cortices: Brain Modules

Observations over the last 40 years have made it clear that there is an iterated substructure within the somatic sensory (and many other) cortical maps. This substructure takes the form of units called *modules*, each involving hundreds or thousands of nerve cells in repeating patterns. The advantages of these iterated patterns for brain function remain largely mysterious; for the neurobiologist, however, such iterated arrangements have provided important clues about cortical connectivity and the mechanisms by which neural activity influences brain development (see Chapters 22 and 23).

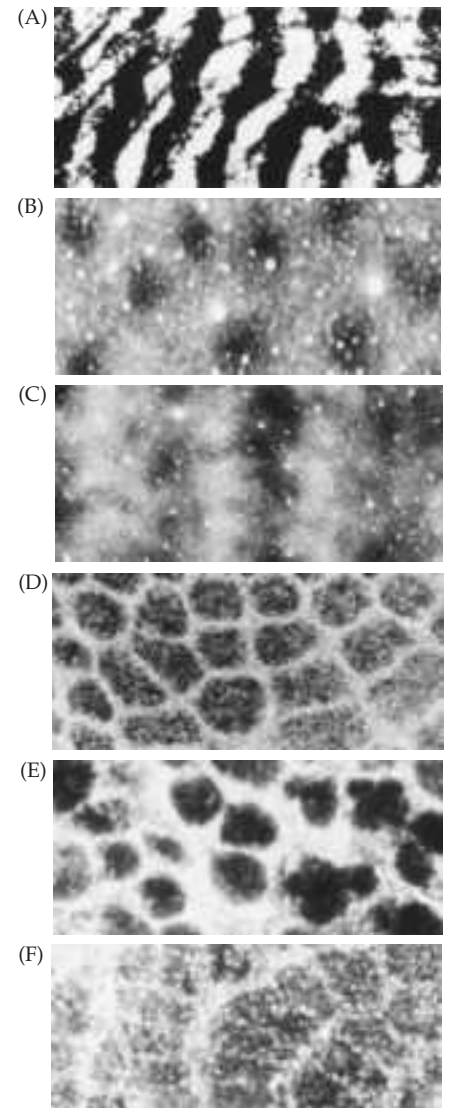
The observation that the somatic sensory cortex comprises elementary units of vertically linked cells was first noted in the 1920s by the Spanish neuroanatomist Rafael Lorente de Nó, based on his studies in the rat. The potential importance of cortical modularity remained largely unexplored until the 1950s, however, when electrophysiological experiments indicated an arrangement of repeating units in the brains of cats and, later, monkeys. Vernon Mountcastle, a neurophysiologist at Johns Hopkins, found that vertical microelectrode penetrations in the primary somatosensory cortex of these animals encountered cells that responded to the same sort of mechanical stimulus presented at the same location on the body surface. Soon after Mountcastle's pioneering work, David Hubel and Torsten Wiesel discovered a similar arrangement in the cat primary visual cortex. These and other observations led Mountcastle to the general view that "the elementary pattern of organization of the cerebral cortex is a vertically oriented column or cylinder of cells capable of input-output functions of considerable complexity." Since these discoveries in the late 1950s and early 1960s, the view that modular circuits represent a fundamental feature of the mammalian cerebral cortex has gained wide acceptance, and many such entities

have now been described in various cortical regions (see figure).

This wealth of evidence for such patterned circuits has led many neuroscientists to conclude, like Mountcastle, that modules are a fundamental feature of the cerebral cortex, essential for perception, cognition, and perhaps even consciousness. Despite the prevalence of iterated modules, there are some problems with the view that modular units are universally important in cortical function. First, although modular circuits of a given class are readily seen in the brains of some species, they have not been found in the same brain regions of other, sometimes closely related, animals. Second, not all regions of the mammalian cortex are organized in a modular fashion. And third, no clear function of such modules has been discerned, much effort and speculation notwithstanding. This salient feature of the organization of the somatic sensory cortex and other cortical (and some subcortical) regions therefore remains a tantalizing puzzle.

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Examples of iterated, modular substructures in the mammalian brain. (A) Ocular dominance columns in layer IV in the primary visual cortex (V1) of a rhesus monkey. (B) Repeating units called "blobs" in layers II and III in V1 of a squirrel monkey. (C) Stripes in layers II and III in V2 of a squirrel monkey. (D) Barrels in layer IV in primary somatic sensory cortex of a rat. (E) Glomeruli in the olfactory bulb of a mouse. (F) Iterated units called "barreloids" in the thalamus of a rat. These and other examples indicate that modular organization is commonplace in the brain. These units are on the order of one hundred to several hundred microns across. (From Purves et al., 1992.)

Summary

The components of the somatic sensory system considered in this chapter process information conveyed by mechanical stimuli that impinge upon the body surface or that are generated within the body itself (proprioception). This processing is performed by neurons distributed across several brain structures that are connected by both ascending and descending pathways. Transmission of afferent mechanosensory information from the periphery to the brain begins with a variety of receptor types that initiate action potentials. This activity is conveyed centrally via a chain of neurons, referred to as the first-, second-, and third-order cells. First-order neurons are located in the dorsal root and cranial nerve ganglia. Second-order neurons are located in brainstem nuclei. Third-order neurons are found in the thalamus, from whence they project to the cerebral cortex. These pathways are topographically arranged throughout the system, the amount of cortical and subcortical space allocated to various body parts being proportional to the density of peripheral receptors. Studies of non-human primates show that specific cortical regions correspond to each functional submodality; area 3b, for example, processes information from low-threshold cutaneous receptors, and area 3a from proprioceptors. Thus, at least two broad criteria operate in the organization of the somatic sensory system: modality and somatotopy. The end result of this complex interaction is the unified perceptual representation of the body and its ongoing interaction with the environment.

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