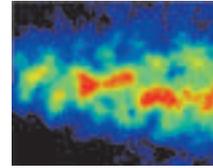


# Chapter 8



## 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

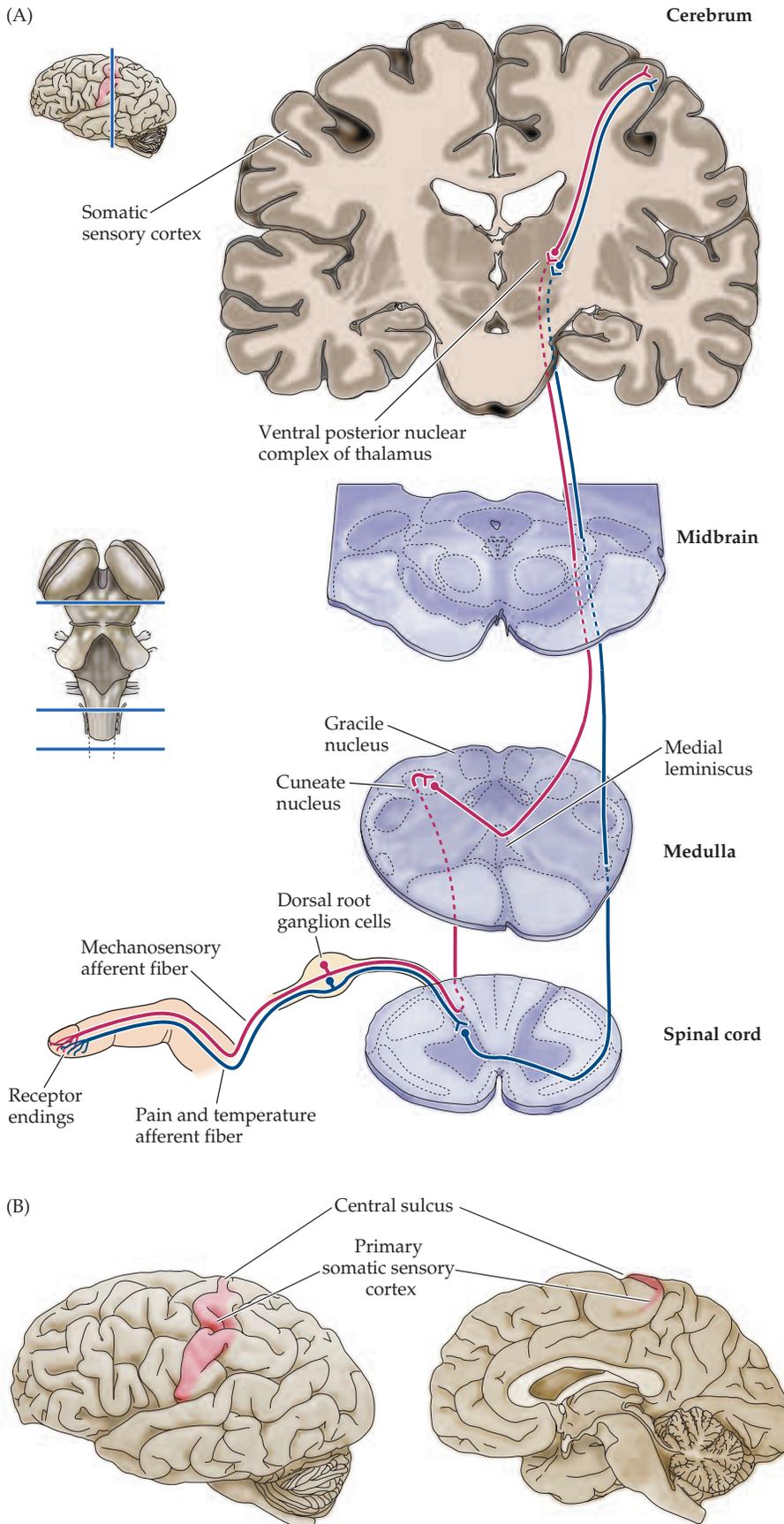
**TABLE 8.1**  
**The Major Classes of Somatic Sensory Receptors**

Receptor type	Anatomical characteristics	Associated axons <sup>a</sup> (and diameters)	Axonal conduction velocities	Location	Function	Rate of adaptation	Threshold of activation
Free nerve endings	Minimally specialized nerve endings	C, A $\delta$	2–20 m/s	All skin	Pain, temperature, crude touch	Slow	High
Meissner's corpuscles	Encapsulated; between dermal papillae	A $\beta$ 6–12 $\mu$ m		Principally glabrous skin	Touch, pressure (dynamic)	Rapid	Low
Pacinian corpuscles	Encapsulated; onionlike covering	A $\beta$ 6–12 $\mu$ m		Subcutaneous tissue, interosseous membranes, viscera	Deep pressure, vibration (dynamic)	Rapid	Low
Merkel's disks	Encapsulated; associated with peptide-releasing cells	A $\beta$		All skin, hair follicles	Touch, pressure (static)	Slow	Low
Ruffini's corpuscles	Encapsulated; oriented along stretch lines	A $\beta$ 6–12 $\mu$ 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

<sup>a</sup>In 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  $\alpha$  (the fastest),  $\beta$ , and  $\delta$  (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!

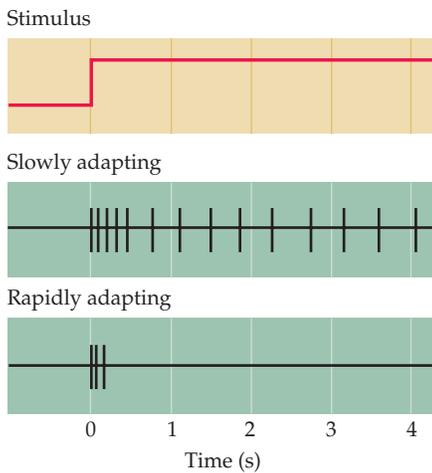
nerve endings, which in turn affects the ionic permeability of the receptor cell membrane. Changes in permeability generate a depolarizing current in the nerve ending, thus producing a **receptor** (or **generator**) **potential** that triggers action potentials, as described in Chapters 2 and 3. This 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.

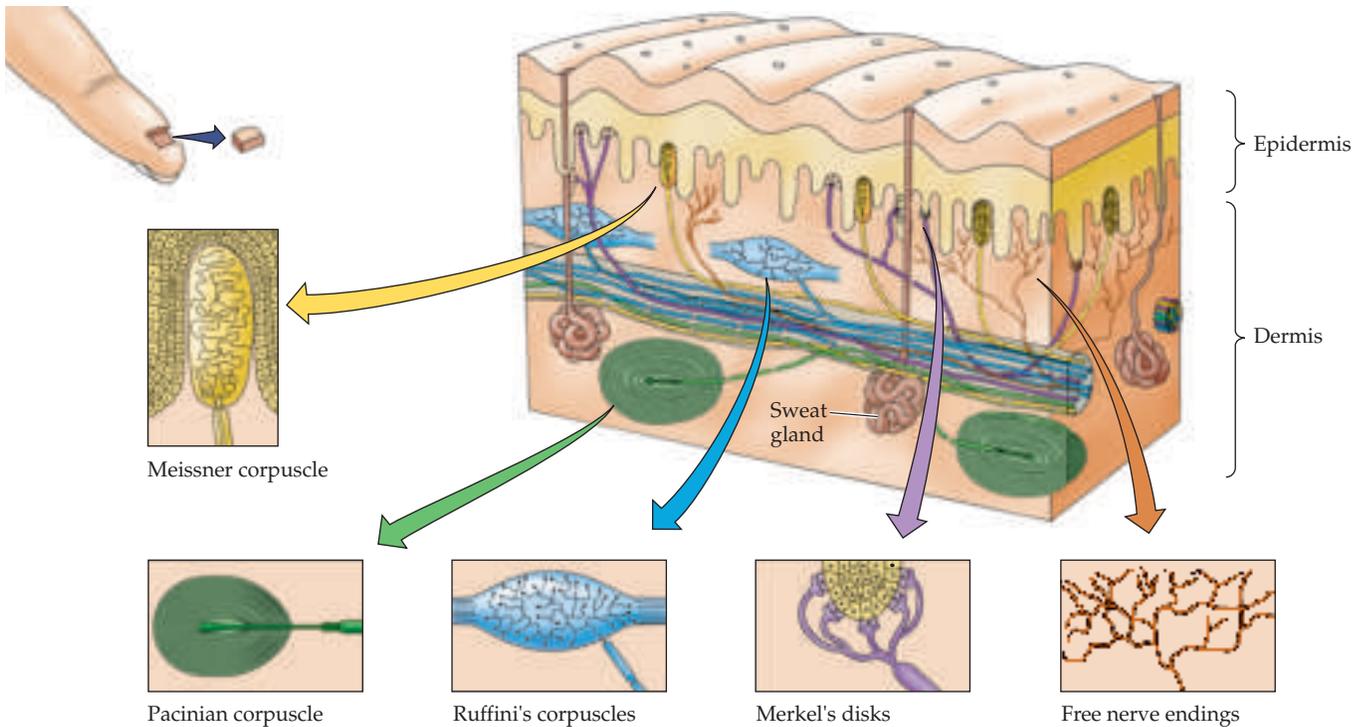
become quiescent are particularly effective in conveying information about changes in the information the receptor reports; conversely, receptors that continue to fire convey information about the persistence of a stimulus. Accordingly, somatic sensory receptors and the neurons that give rise to them 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 $\beta$ ; 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.)

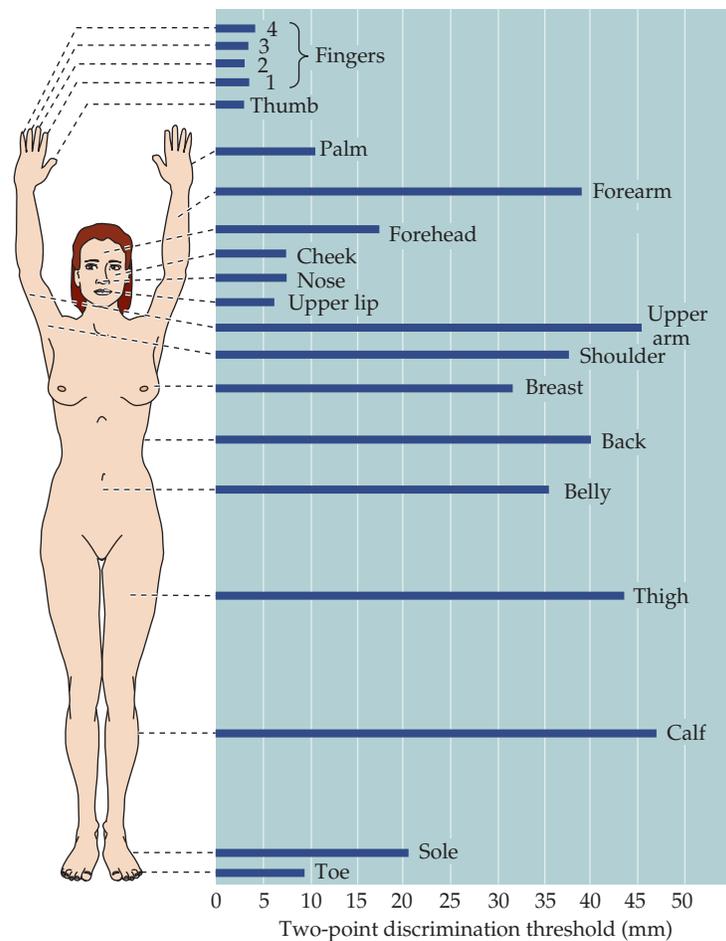
Slowly adapting cutaneous mechanoreceptors include **Merkel's disks** and **Ruffini's corpuscles** (see Figure 8.3 and Table 8.1). Merkel's disks are located in the epidermis, where they are precisely aligned with the papillae that lie beneath the dermal ridges. They account for about 25% of the mechanoreceptors 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

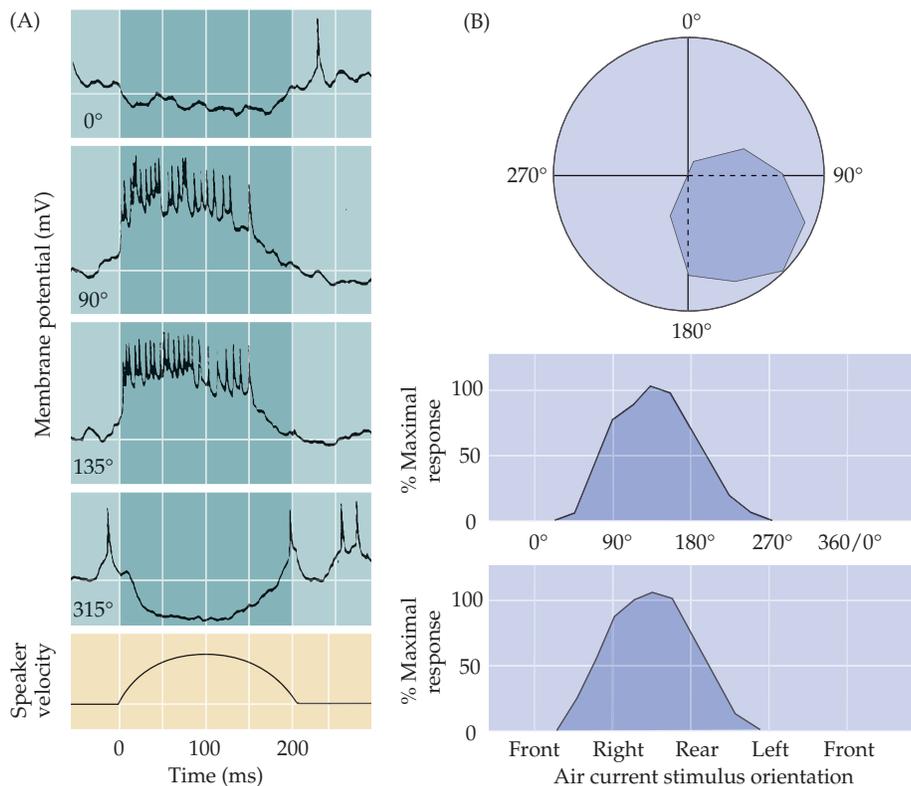
allow them to be displaced by air currents having different directions and speeds (Figure A). Accordingly, the peripheral sensory neurons associated with the hairs represent the full range of air current directions and velocities impinging on the animal. This information is carried centrally and is systematically 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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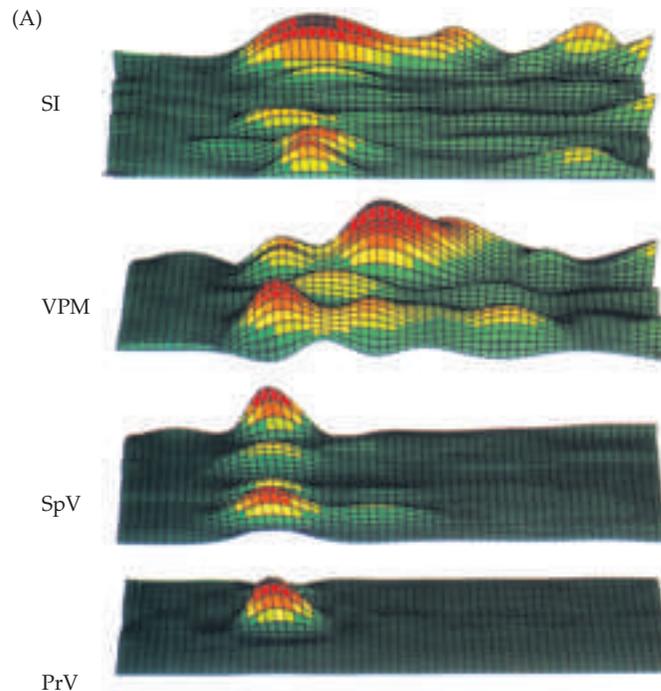
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## Box B

### Dynamic Aspects of Somatic Sensory Receptive Fields

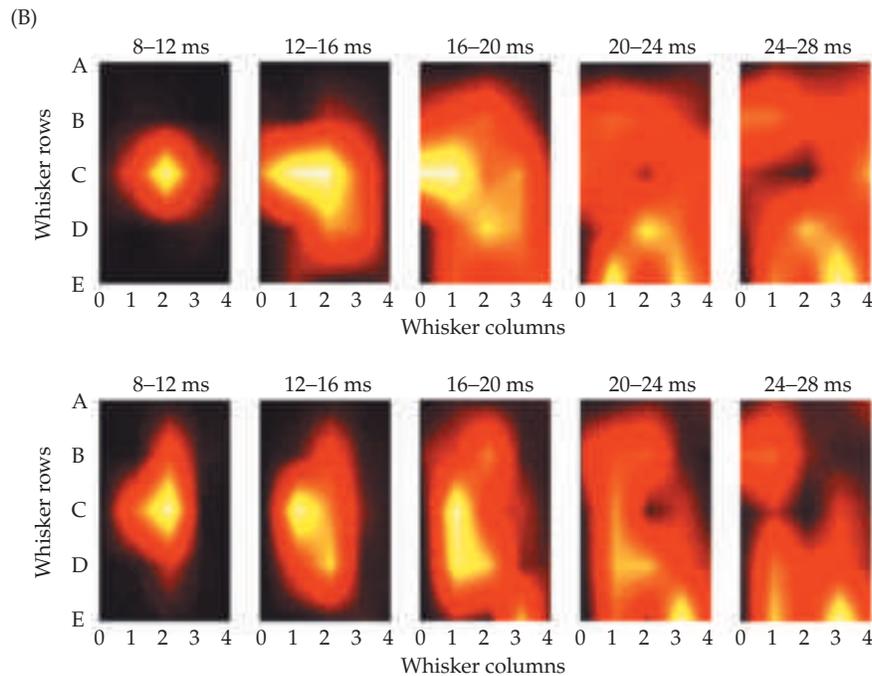
When humans explore objects with their hands, multiple contacts between the skin and the object surface generate extraordinarily complex patterns of tactile stimuli. As a consequence, the somatic sensory system must process signals that change continuously in time. Nonetheless, we routinely discriminate 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.

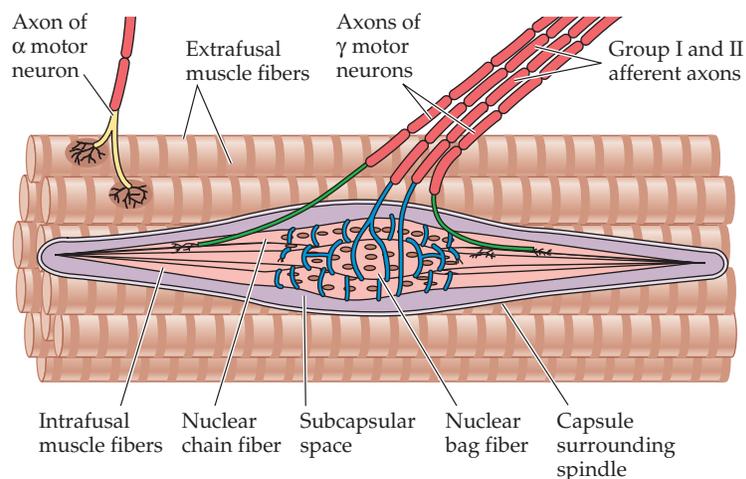
## Mechanoreceptors Specialized for Proprioception

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

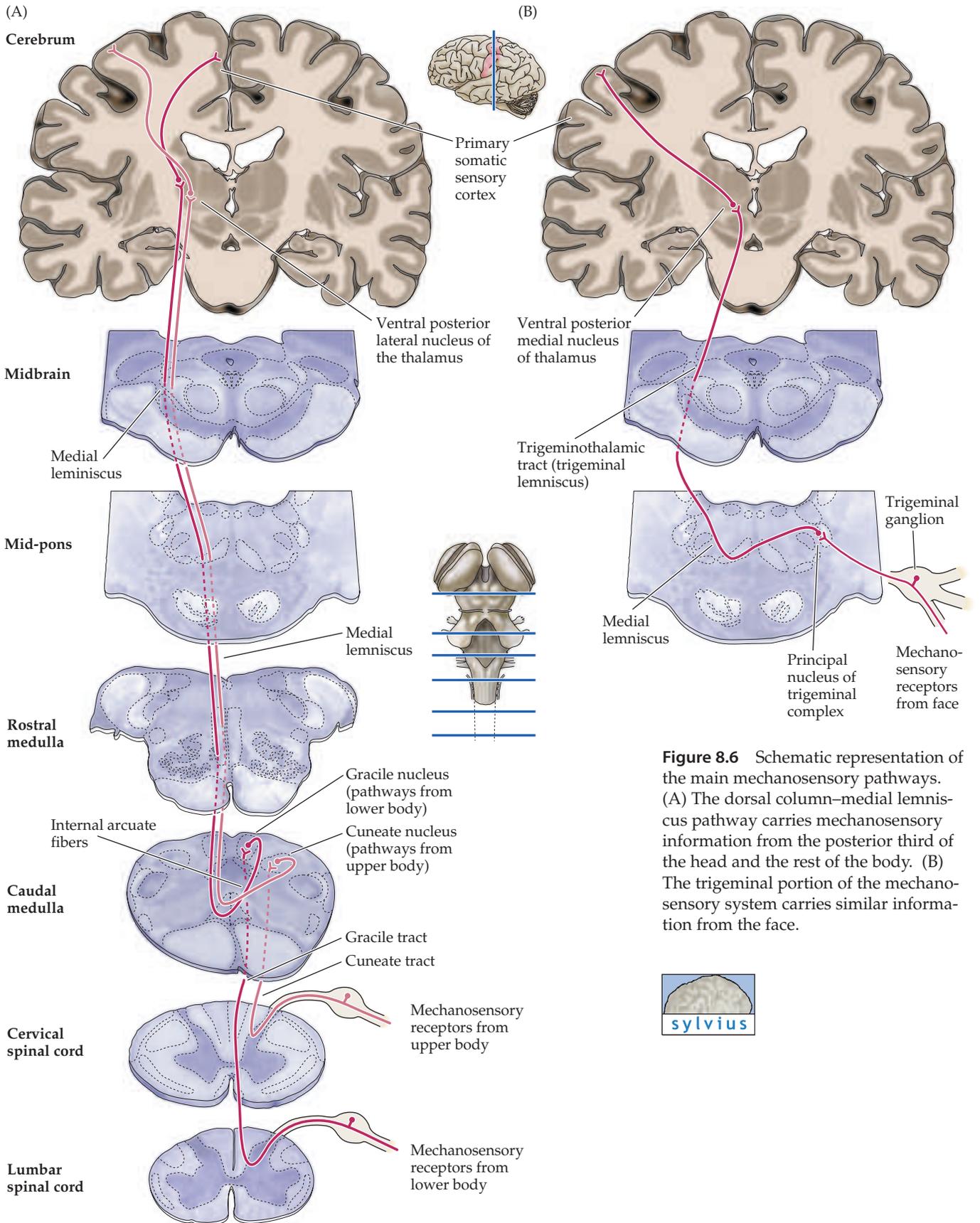
from somatic receptors have different patterns of termination in the spinal cord and define distinct somatic sensory pathways within the central nervous system (see Figure 8.1). The **dorsal column–medial lemniscus pathway** carries the majority of information from the mechanoreceptors that mediate tactile 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-

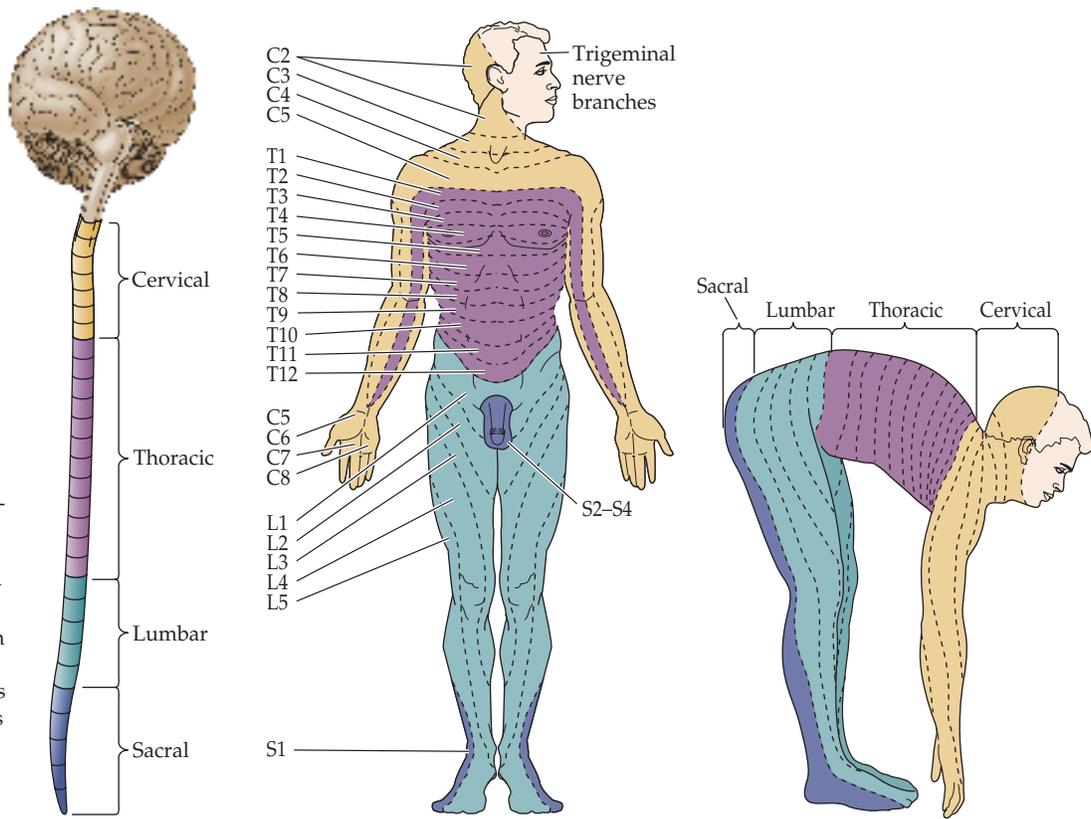


**Figure 8.6** Schematic representation of the main mechanosensory pathways. (A) The dorsal column–medial lemniscus pathway carries mechanosensory information from the posterior third of the head and the rest of the body. (B) The trigeminal portion of the mechanosensory system carries similar information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

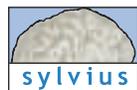
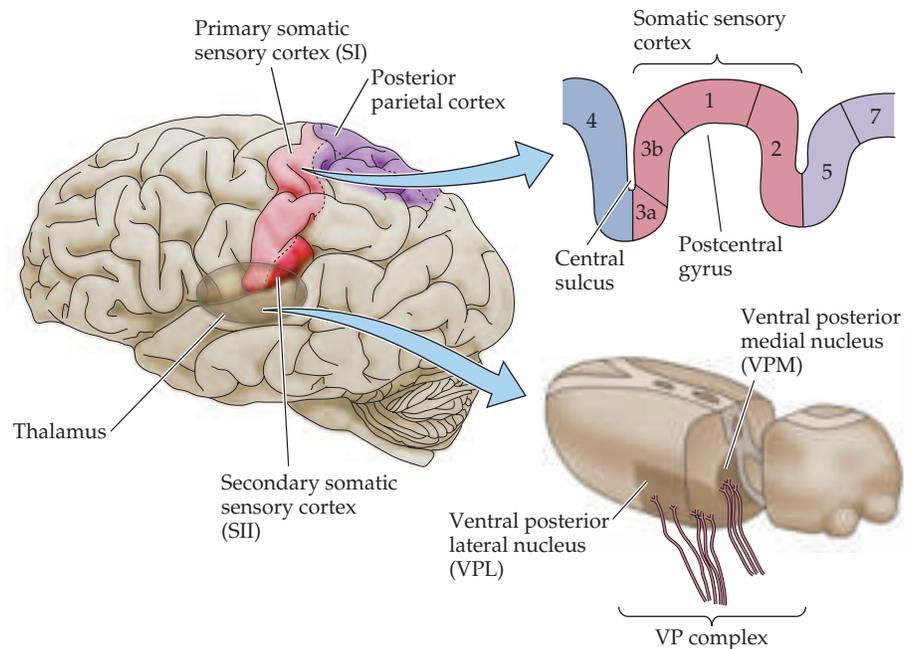
The trigeminal complex has two major components: the **principal nucleus** (responsible for processing mechanosensory stimuli), and the **spinal nucleus** (responsible for processing painful and thermal stimuli). Thus, most of the axons carrying information from low-threshold cutaneous mechanoreceptors 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

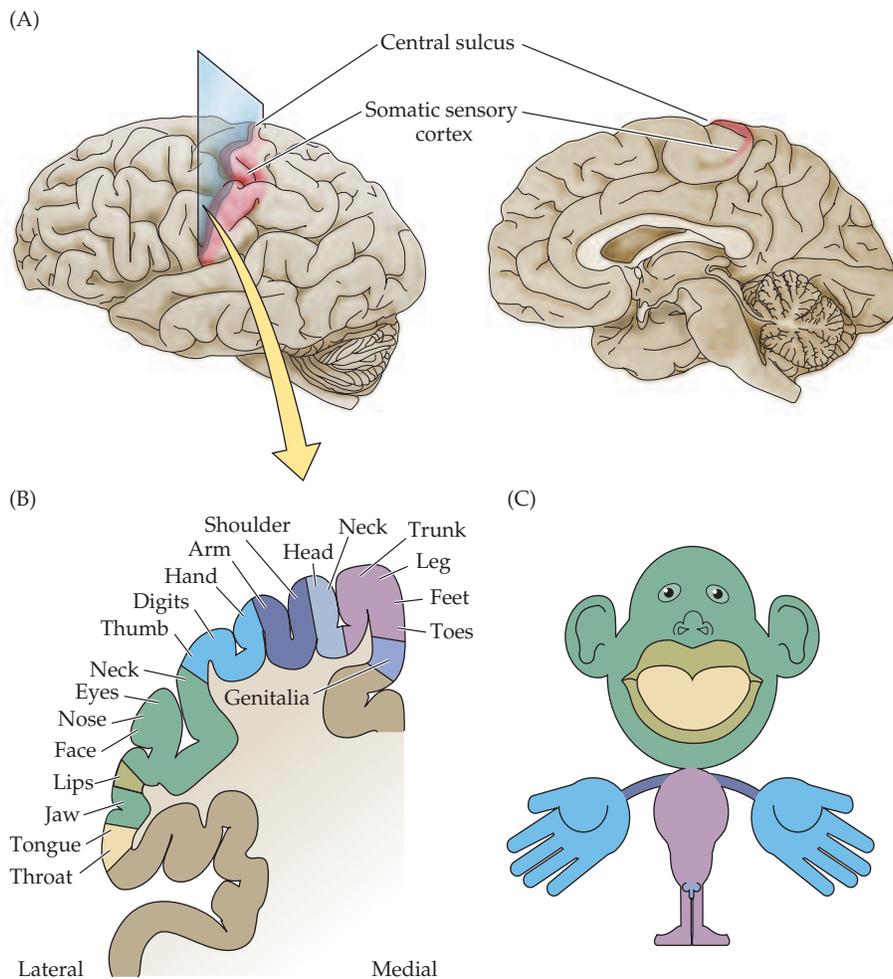


**Figure 8.7** Diagram of the somatic sensory portions of the thalamus and their cortical targets in the postcentral gyrus. The ventral posterior nuclear complex comprises the VPM, which relays somatic sensory information carried by the trigeminal system from the face, and the VPL, which relays somatic 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-



## 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).

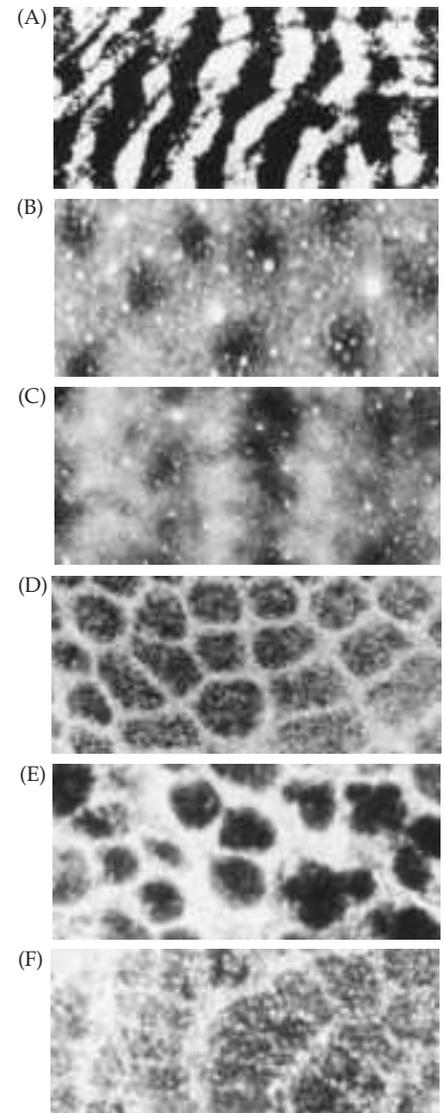
The observation that the somatic sensory cortex comprises elementary units of vertically linked cells was first noted in the 1920s by the Spanish neuroanatomist Rafael Lorente de Nó, based on his studies in the rat. The potential importance of cortical modularity remained largely unexplored until the 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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## Touch

Esther P. Gardner

Eric R. Kandel

INFORMATION TRANSMITTED to the brain from mech-anoreceptors in the fingers enables us to feel the shape and texture of objects and permits us to read braille, play musical instruments, type on computer keyboards, or perform fine surgical dissections. In this chapter we shall examine how neuronal activity of mechanoreceptors in the skin gives rise to perception of discriminative touch and why the fingertips are best suited to this task.

Since this chapter is the first in which we discuss, in cell-physiological detail, the central projections of a sensory system to the cerebral cortex, we also address two key questions about the cerebral cortex. How does it work on the cellular level? How does it integrate and transform sensory information coming from the periphery? Thus, we describe how the cortex constructs an image of objects we touch from the fragmented information provided by the receptors of the skin. Moreover, in this chapter we use the sense of touch as a model for deriving principles of cortical organization that give rise to conscious perception. Specifically, we examine the degree to which the various somatic modalities are functionally segregated in the central nervous system and how they are recombined for coherent perception of tactile information. We have chosen the modality of touch to introduce the principles of cortical function because these principles were first established for the somatosensory cortex and later extended to other sensory and motor cortical areas, as we shall see in subsequent chapters.

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P.452

### Tactile Information About an Object is Fragmented by Peripheral Sensors and Must Be Integrated by the Brain

The ability to recognize objects placed in the hand on the basis of touch alone is one of the most important and complex functions of the somatosensory system. By holding an object in the hand we can perceive its size, shape, texture, mass, and temperature. These properties together give rise to the percept of a coherent object. Neurologists call the ability to perceive form through touch *stereognosis*. Stereognosis not only tests the ability of the dorsal column-medial lemniscal system to transmit sensations from the hand but also measures the ability of cognitive processes in the brain to integrate that information.

Many familiar objects such as an apple, a screwdriver, or a set of keys are much larger than the receptive field of any one receptor in the hand. These objects stimulate a large population of sensory nerve fibers, each of which scans a small portion of the object. The peripheral sensory apparatus deconstructs the object into tiny segments because, as we saw in [Chapter 22](#), a sensory nerve fiber conveys information from only a small area of the receptor sheet. When a particular nerve fiber fires an action potential, it signals that its territory has been contacted at an intensity sufficient to cause it to fire. By analyzing which nerve fibers have been excited, the brain reconstructs the pattern made by the object.

In addition, objects excite more than one kind of receptor. For example, a textured surface such as an array of Braille dots stimulates Merkel disk receptors, Meissner's corpuscles, and Pacinian corpuscles but evokes a different discharge pattern in each type of receptor because each signals a special feature of the stimulus. Similarly, the shape of an object is signaled by the firing patterns of Merkel disk receptors, which sense the curvature of the object's surface; by Meissner's corpuscles, which signal edges (where the curvature changes abruptly); and by the postural information provided by receptors in the muscles and joints of the hand.

Thus, no single sensory axon, or even class of sensory axons, signals all of the relevant information. Spatial properties are processed by populations of receptors that form many parallel pathways to the brain. It is the job of the central nervous system to construct a coherent image of an object from fragmented information conveyed in multiple pathways. In this chapter we shall examine how neural circuits in the dorsal column-medial lemniscal system and the somatosensory areas of the cerebral cortex integrate information from neighboring areas of skin and different populations of receptors in order to form a *percept*.

### The Primary Somatic Sensory Cortex Integrates Information About Touch

The anatomical plan of the somatic sensory system reflects an organizational principle common to all sensory systems: Sensory information is processed in a series of relay regions within the brain. We learned in [Chapter 22](#) that there are only three synaptic relay sites between sensory receptors in the skin and the cerebral cortex (see [Figure 22-14](#)). Mechanoreceptors in the skin send their axons to the caudal medulla, where they terminate in the gracile or cuneate nuclei. These second-order neurons project directly to the contralateral thalamus, terminating in the ventral posterior lateral nucleus. A parallel pathway from the principal trigeminal nucleus, which represents the face, ascends to the ventral posterior medial nucleus. The third-order neurons in the thalamus send axons to the primary somatic sensory cortex (S-I), located in the postcentral gyrus of the parietal lobe.

As we learned in [Chapter 20](#), the primary somatic cortex S-I contains four cytoarchitectural areas: Brodmann's areas 3a, 3b, 1, and 2 ([Figure 23-1](#)). Most thalamic fibers terminate in areas 3a and 3b, and the cells in areas 3a and 3b project their axons to areas 1 and 2. Thalamic neurons also send a small projection directly to Brodmann's areas 1 and 2. These four regions of the cortex differ functionally. Areas 3b and 1 receive information from receptors in the skin, whereas areas 3a and 2 receive proprioceptive information from receptors in muscles and joints. However, the four areas of the cortex are extensively interconnected, so that both serial and parallel processing are involved in higher-order elaboration of sensory information.

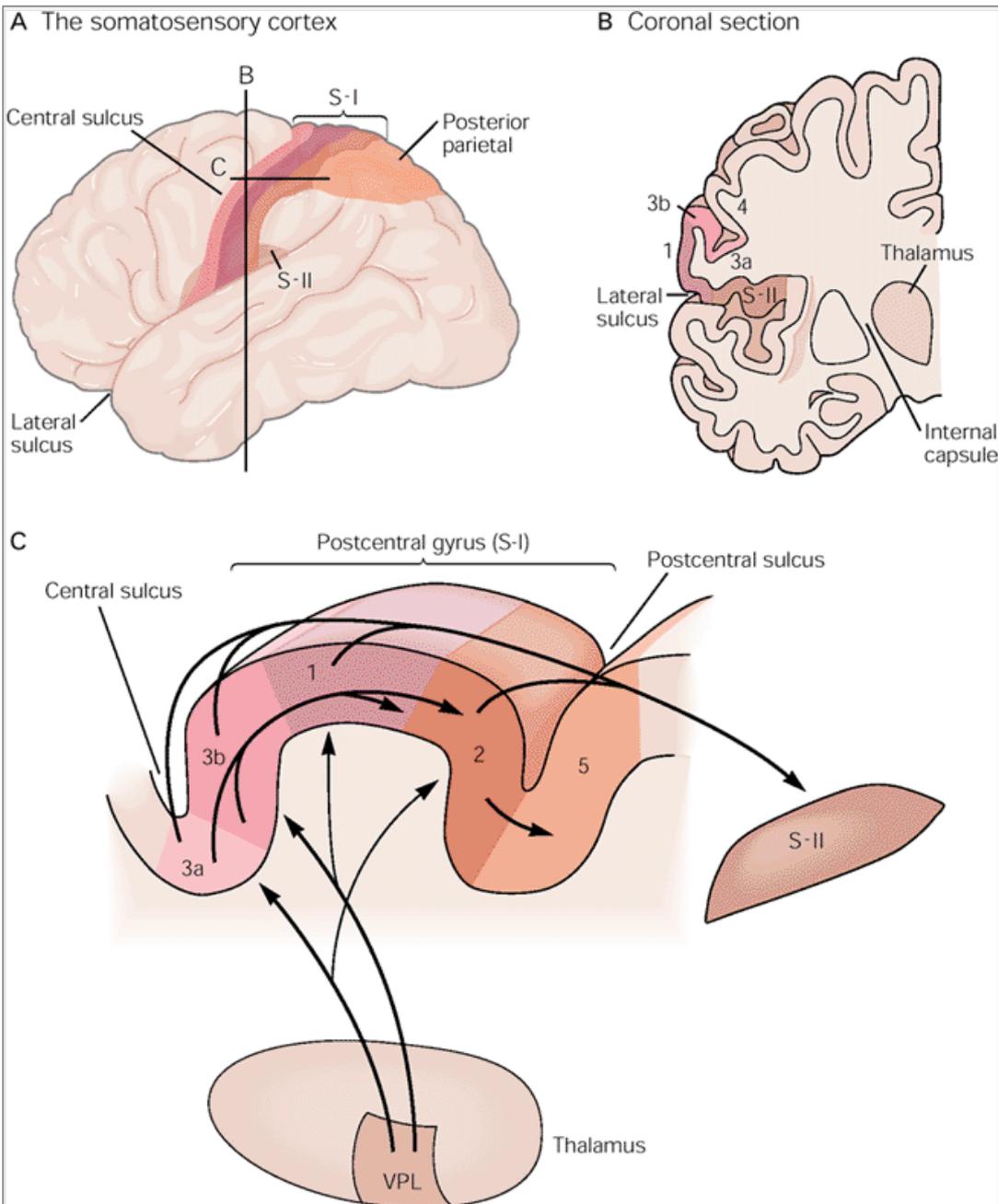
The *secondary somatic sensory cortex* (S-II), located on the superior bank of the lateral fissure, is innervated by neurons from each of the four areas of S-I ([Figure 23-1C](#)). The projections from S-I are required for the function of S-II. For example, when the neural connections from the hand area of S-I are removed, stimuli applied to the skin of the hand do not activate neurons in S-II. In contrast, removal of parts of S-II has no effect on the response of neurons in S-I. The S-II cortex projects to the *insular cortex*, which in turn innervates regions of the temporal lobe believed to be important for tactile memory.

Finally, as we have seen in [Chapters 19](#) and [20](#), other important somatosensory cortical areas are located in the *posterior parietal cortex* (Brodmann's areas 5 and 7). These areas receive input from S-I as well as input from the pulvinar and thus have an associational function. They are also connected bilaterally through the corpus callosum. Area 5 integrates tactile information from mechanoreceptors in the skin with proprioceptive

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P.453

inputs from the underlying muscles and joints. This region also integrates information from the two hands. Area 7 receives visual as well as tactile and proprioceptive inputs, allowing integration of stereognostic and visual information. The posterior parietal cortex projects to the motor areas of the frontal lobe and plays an important role in sensory initiation and guidance of movement.



**Figure 23-1 The somatic sensory cortex has three major divisions: the primary and secondary somatosensory cortices and the posterior parietal cortex.**

**A.** The anatomical location of the three divisions of the somatic sensory cortex is seen best from a lateral perspective of the surface of the cerebral cortex. The *primary somatic sensory cortex* (S-I) forms the most rostral portion of the parietal lobe. It covers the postcentral gyrus, beginning at the bottom of the central sulcus and extending posteriorly to the postcentral and intraparietal sulci. The postcentral gyrus also extends into the medial wall of the hemisphere to the cingulate gyrus. The *posterior parietal cortex* (Brodmann's areas 5 and 7) lies immediately posterior to S-I. The *secondary somatic sensory cortex* (S-II) is located on the parietal operculum of the lateral sulcus (fissure of Sylvius).

**B.** The relationship of the S-I to the S-II cortex is illustrated in a coronal section through the cortex. The S-II cortex lies lateral to S-I, and extends laterally to the insular cortex, forming the superior bank of the lateral sulcus. The numbers on the section indicate Brodmann's cytoarchitectural areas.

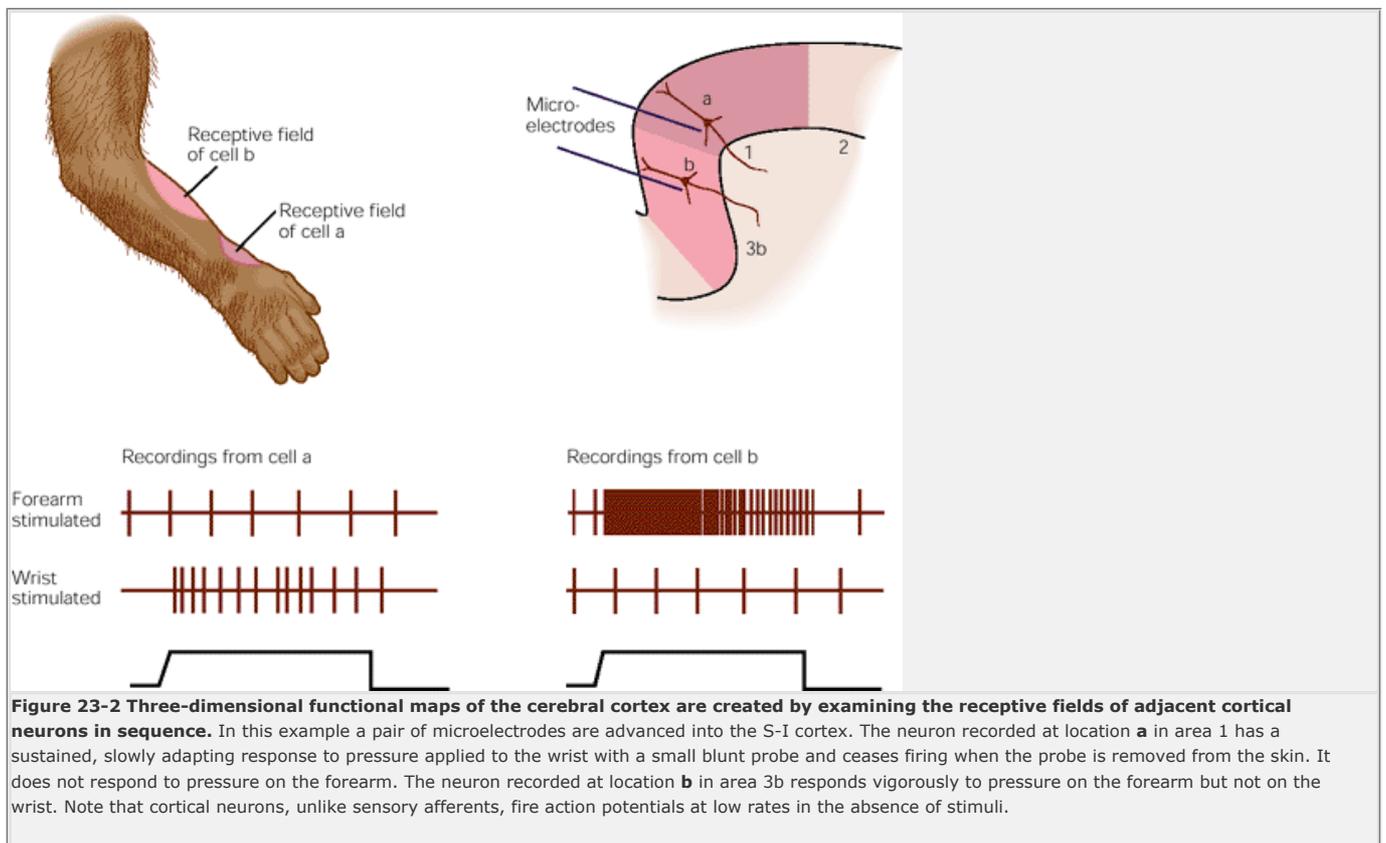
**C.** S-I is subdivided into four distinct cytoarchitectonic regions (Brodmann's areas). This sagittal section illustrates the spatial relationship of these four regions to area 5 of the posterior parietal cortex. Somatosensory input to the cortex originates from the ventral posterior lateral nucleus of the thalamus. Neurons in this nucleus project to all areas in S-I, mainly to Brodmann's areas 3a and 3b but also to areas 1 and 2. In turn, neurons in areas 3a and 3b project to areas 1 and 2, and all of these project to S-II and to posterior parietal cortex. These higher-order somatosensory areas also contain distinct cytoarchitectonic and functional subregions that are not illustrated here. (Modified from [Jones and Friedman 1982](#).)

### Box 23-1 Extracellular Recordings Are Used to Study Neurons in the Central Nervous System

Much of what we know about the processing of somatic sensory information in the brain, particularly in the cerebral cortex, has been learned from studies of monkeys. The monkey has proven so useful because primates have sensory receptors identical to those of humans. Furthermore, psychophysical measurements of somatosensory discriminative abilities indicate that humans and monkeys experience the same tactile sensations in their hands when they feel vibration, palpate objects, or touch a textured surface.

The techniques for studying the physiology of the cerebral cortex at the cellular level were developed by Vernon Mountcastle and his colleagues in the 1950s. Using extracellular microelectrodes (which had just become available) they recorded the electrical responses of individual neurons. Extracellular recordings reveal only the action potentials of the cell and thus, do not show synaptic activity except under certain circumstances. (Extracellular recording, however, is much simpler than intracellular recording in the intact brain because the brain pulsates, making it difficult to maintain intracellular penetrations.) Nevertheless, extracellular recording has been a useful tool in defining how sensory stimuli modulate the firing patterns of single cells.

Microelectrode recording allows the receptive fields of several neurons at adjacent locations in the brain to be examined in sequence ([Figure 23-2](#)). By systematically moving the electrode in steps of thousandths of a millimeter, one can reconstruct a three-dimensional map of the cerebral cortex. This technique, termed micromapping, forms the experimental foundation for what we know about the columnar and somatotopic organization of the cortex.



P.454

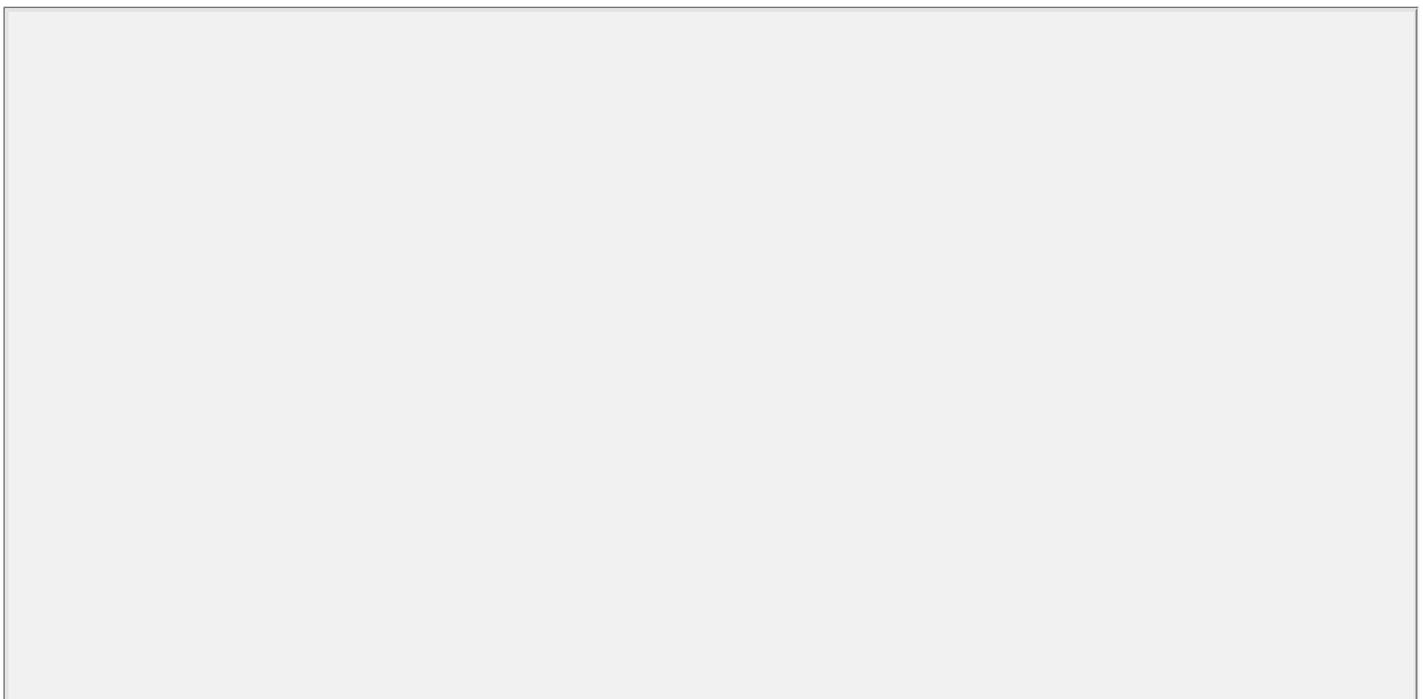
### Cortical Neurons Are Defined by Their Receptive Fields As Well As by Modality

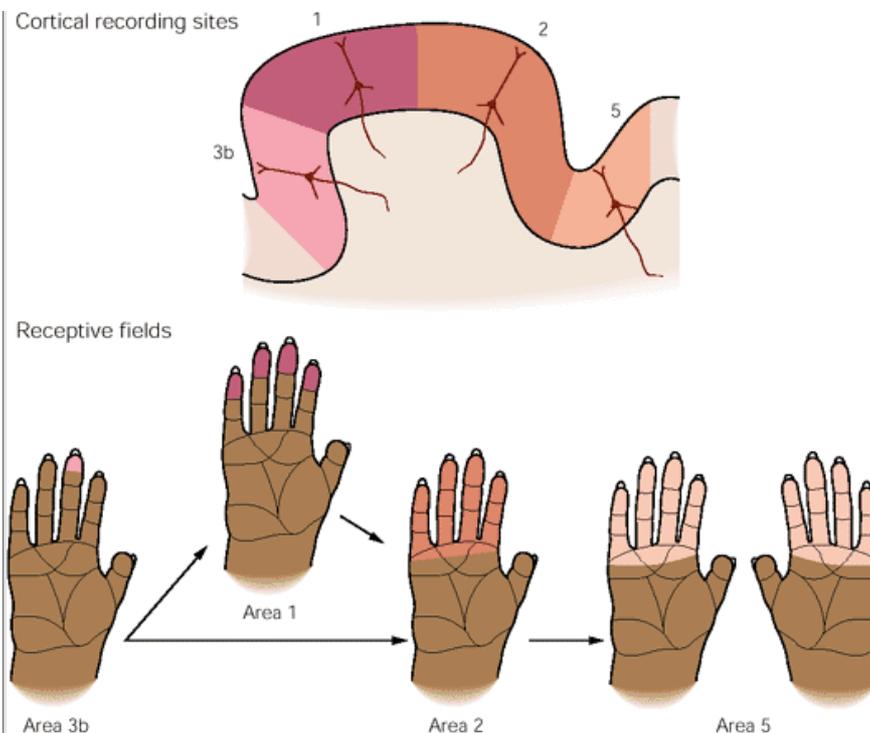
To understand the function of these different regions of the cortex, we begin by examining the properties of individual cortical neurons. The neurons in the primary somatic sensory cortex are at least three synapses beyond the peripheral receptors. Thus their response properties reflect information processing in the dorsal column nuclei, the thalamus, and in the cortex itself. Cortical neurons, like neurons elsewhere in the brain, are usually studied using the technique of extracellular recording (see [Box 23-1](#)). Microelectrodes are inserted into the cortex to record both the spike trains that occur spontaneously and those evoked by appropriate stimuli.

Like mechanoreceptors, the cortical neurons receiving sensory information from the skin are either slowly adapting or rapidly adapting neurons, signaling either

P.455

the amplitude or rate of the peripheral skin indentation. Moreover, since each cortical neuron receives inputs from receptors in a specific area of the skin, central neurons also have receptive fields. Thus, each cortical neuron is defined by its receptive field as well as by its sensory modality. Any point on the skin is represented in the cortex by a population of cortical cells connected to the afferent fibers that innervate that point on the skin. When a point on the skin is touched, the population of cortical neurons connected to the receptors at that location is excited. Stimulation of another point on the skin activates another population of cortical neurons. We perceive contact at a particular location on the skin because a specific population of neurons in the brain is activated. Conversely, as we saw in [Chapter 19](#), when a point on the cortex is stimulated electrically, we experience tactile sensations on a specific part of the skin. We shall show later in this chapter that cortical neurons are grouped by function and that their receptive fields are arranged in an orderly topographic sequence that forms a map of the body.





**Figure 23-3 The receptive fields of neurons in the primary somatic sensory cortex are larger than those of the sensory afferents.** Each of the hand figurines shows the receptive field of an individual neuron in areas 3b, 1, 2, and 5 of the primary somatic sensory cortex, based on recordings made in alert monkeys. The colored regions indicate the region of the hand where light touch elicits action potentials from the neuron. Neurons that participate in later stages of cortical processing (Brodmann's areas 1 and 2) have larger receptive fields and more specialized inputs than neurons in area 3b. The neuron illustrated from area 2 is directionally sensitive to motion toward the fingertips. Neurons in area 5 often have symmetric bilateral receptive fields at mirror image locations on the contralateral and ipsilateral hand. (Adapted from [Gardner 1988](#), [Iwamura et al. 1994](#).)

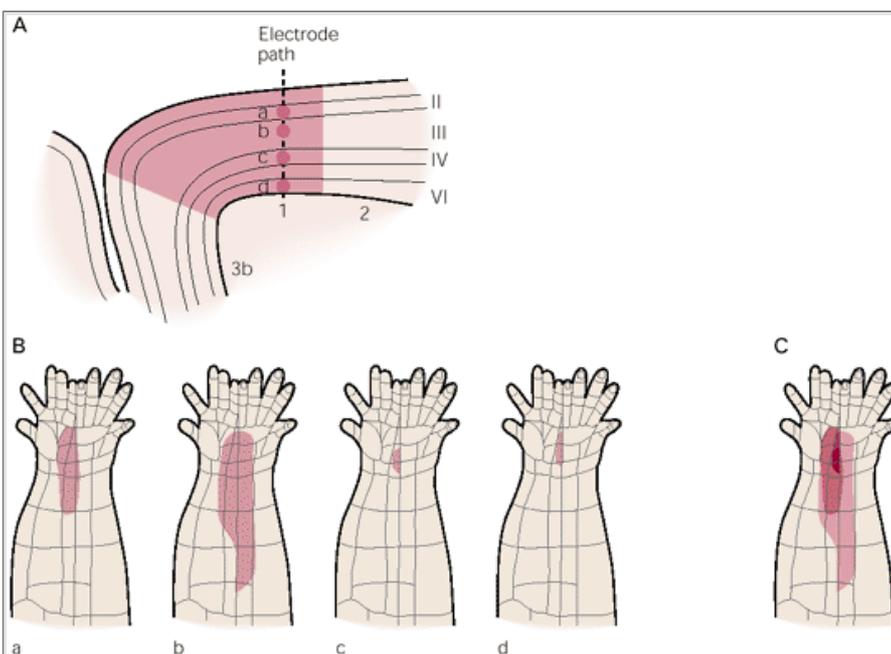
The receptive fields of cortical neurons are much larger than those of dorsal root ganglion neurons. For example, the receptive fields of sensory neurons innervating a finger cover tiny spots on the skin, while those of the cortical cells receiving these inputs are large areas covering an entire fingertip, or several adjacent fingers, or the palmar surface of the contralateral hand (Figure 23-3). The receptive field of a neuron in area 3b represents a composite of inputs from about 300-400 mechanoreceptive afferents. Receptive fields in higher cortical areas are even larger. In the posterior parietal cortex, receptive fields are often bilateral, located at symmetric positions on the contralateral and ipsilateral hands.

Cortical receptive fields encompass functional regions of skin that are activated simultaneously during motor activity. The size and position of cortical receptive fields on the skin are not fixed permanently but can be modified by experience or by injury to sensory nerves. Cortical receptive fields appear to be formed during development and maintained by simultaneous activation of the input pathways.

Although the receptive fields of cortical neurons cover a large area of skin, a cortical neuron is nevertheless able to discriminate fine detail because it responds best to excitation in the middle of its receptive field. As the stimulation site is moved toward the periphery of the field, responses become progressively weaker until eventually no spikes are recorded. Thus, a stimulus applied to the tip of the index finger strongly excites some neurons, while others fire weakly or not at all. If a more proximal spot on the finger is touched, many of the same cells are activated but in different proportions. Information

P.456

provided by the entire population of excited cells localizes a stimulus on the skin.



**Figure 23-4** The receptive fields of cells in a column in Brodmann's area 1 share a common central location on the skin. The columns representing a given skin location are approximately 300-600  $\mu\text{m}$  wide. (Adapted from [Favorov and Whitsel 1988.](#))

**A.** Sagittal section through S-I cortex illustrating the recording sites of a group of neurons located in a single column. The most superficial neuron (**a**) is located in layer II, and the deepest neuron (**d**) is located in layer VI. Neuron **b** is located in layer III, and neuron **c** is situated in layer IV.

**B.** Receptive fields of the four neurons shown in A. The neurons in this column share receptive fields on the ulnar portion of the forearm, wrist, and hand. The dorsal and volar surfaces of the hand and arm have been juxtaposed to illustrate the continuity of receptive fields along the ulnar margin. The receptive fields are labeled according to depth in the cortex. Neuron **c** has the smallest receptive field, localized near the wrist; it is located in layer IV where the thalamic afferents terminate. Pyramidal neurons in layers II and III have larger receptive fields because their large basal dendritic fields extend into the neighboring columns.

**C.** Superimposition of the receptive fields illustrated in **B**. The darkest region in the center is shared by all receptive fields of the neurons in the column; this region is used to reconstruct the representation area of the column in the somatotopic map. The skin areas surrounding the central focus are shared by most, but not all, of the neurons in the column. The skin locations at the outer margins of the column's global receptive field are represented in only a few cells' receptive fields.

## The Properties of Cortical Receptive Fields Are Due to Convergent and Divergent Connections in the Relay Nuclei

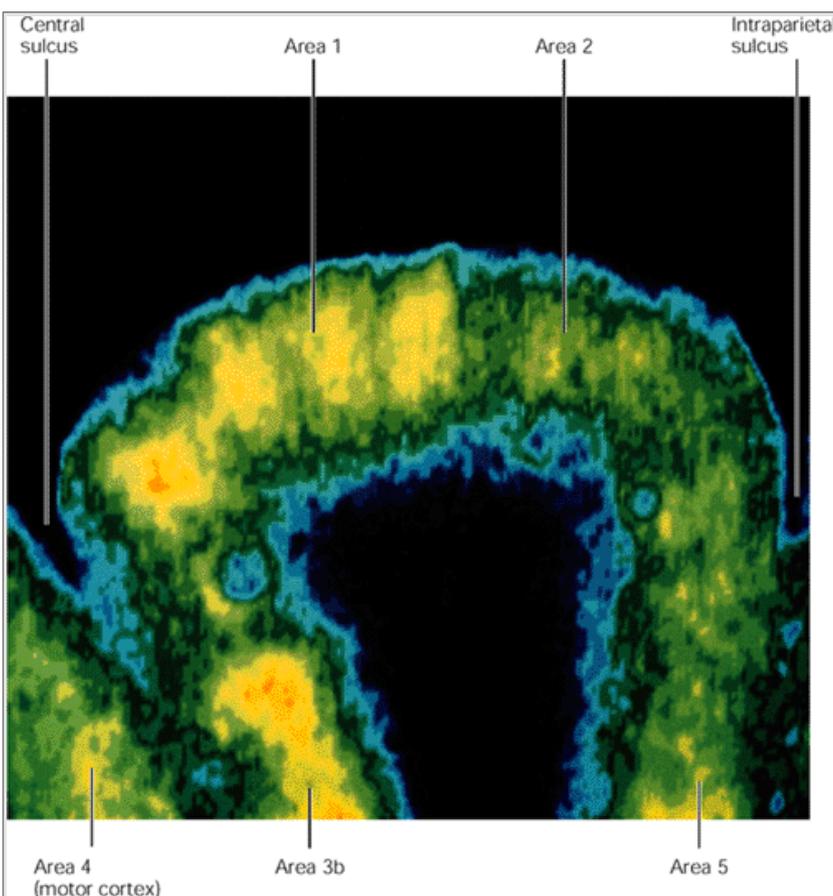
The increase in area of the receptive fields of cortical neurons reflects the anatomical circuitry within the relay nuclei. Relay nuclei, such as the dorsal column or thalamic nuclei, are composed of projection (or relay) neurons that send their axons to the next nucleus in the pathway and inhibitory interneurons that terminate upon relay neurons. Sensory inputs to the relay nucleus are characterized by extensive convergence and divergence. Each sensory afferent has a branched terminal that innervates several postsynaptic neurons, so that each projection neuron receives synaptic input from many sensory axons. This pattern of divergent pre-synaptic connections and convergent postsynaptic connections is repeated at each relay in the pathway.

## Inputs to the Somatic Sensory Cortex Are Organized in Columns by Receptive Field and Modality

Although convergence of sensory afferents enlarges the receptive fields of projection neurons at successive relay nuclei, the topographic arrangement of the receptive fields is preserved. In a series of pioneering studies Mountcastle discovered that the cortex is organized into vertical columns or slabs, 300-600  $\mu\text{m}$  wide, spanning all six layers from the cortical surface to the white matter. All of the neurons within a column receive inputs

P.457

from the same local area of skin and respond to a single class of receptors. Although the receptive fields of the neurons comprising a column are not precisely congruent, they do share a common center, which is most clearly evident in layer IV ([Figure 23-4](#)). A column therefore provides an anatomical structure that preserves the properties of location and modality. Neurons lying within a column comprise an elementary functional module of the cortex ([Figure 23-5](#)). We shall see in later chapters that columnar organization is a basic organizational and structural principle of the cerebral cortex.



**Figure 23-5** Columns of neurons in the primary somatic sensory cortex comprise the elementary functional modules of cortical processing of somatosensory information. This autoradiograph shows the pattern of  $^{14}\text{C}$  2-deoxyglucose (2-DG) labeling of neurons in a sagittal section through the hand area of the S-I cortex after 45 minutes of stroking the hand and wrist with a brush. Uptake of 2-DG in the brain is proportional to neuronal activity. Stimulation of the hand produces dense patches of labeled neurons in both area 3b and in area 1. Active neurons are found in vertical columns extending from layer II through layer V, with the strongest responses seen in layer IV (pale red). Columns are continuous in area 3b, but form distinct modules in area 1. Very little activity is seen in area 2, which receives input from deep receptors. (Photograph courtesy of S. Juliano, P. Hand, and B. Whitsel.)

The columnar organization of the cortex is a direct consequence of cortical circuitry. The pattern of intrinsic connections within the cerebral cortex is oriented vertically, perpendicular to the surface of the cortex ([Figure 23-6](#)). Thalamic afferents to the cortex terminate mainly on clusters of stellate cell neurons in layer IV. The axons of the stellate cells project vertically toward the surface of the cortex. Similarly, both the apical dendrites and axons of the pyramidal cells are oriented

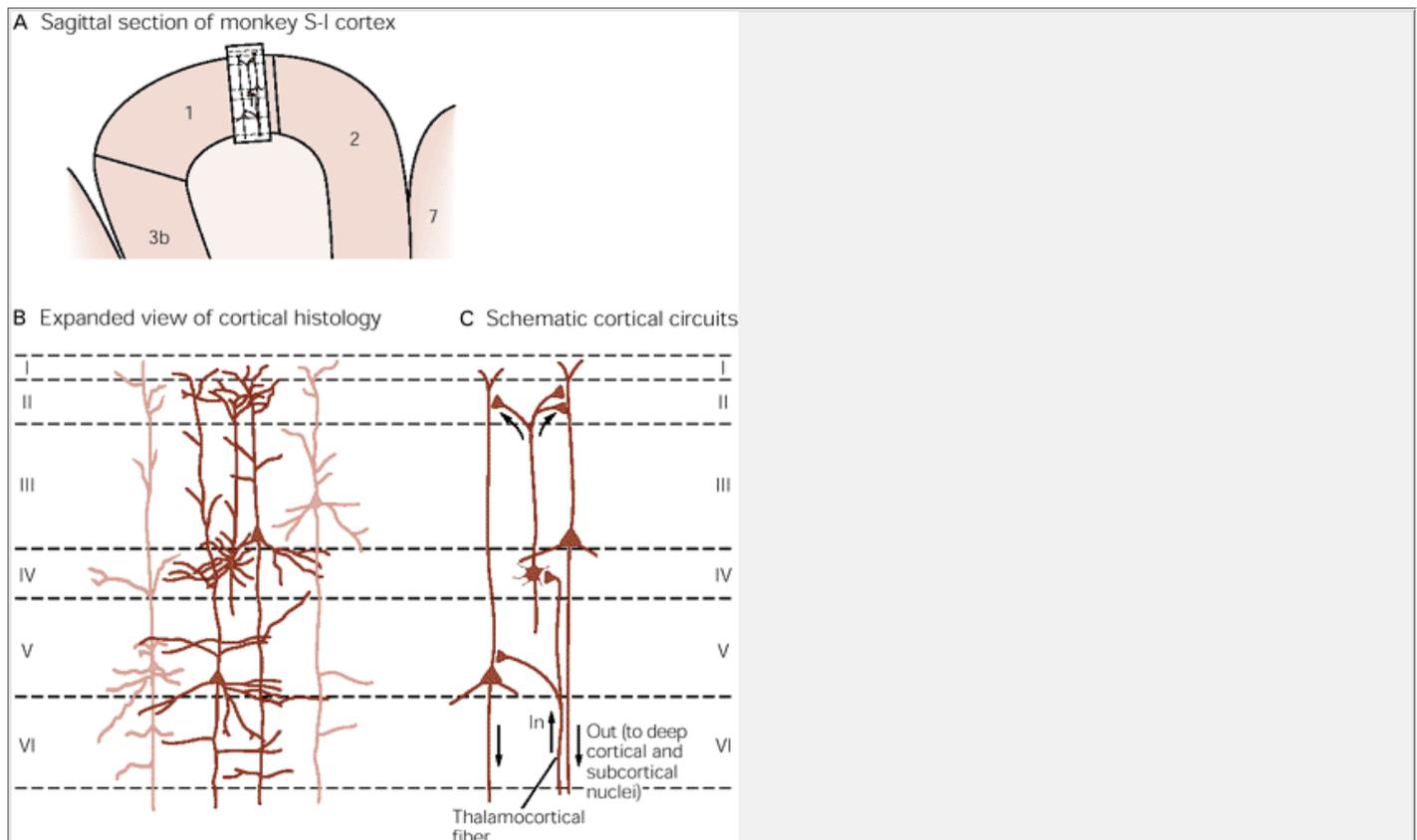
vertically, parallel to the stellate cell axons. The thalamocortical input is therefore relayed to a narrow vertical column of pyramidal cells whose apical dendrites are contacted by the stellate cell axons. This means that the same information is relayed up and down through the thickness of the cortex in columnar fashion.

In addition to sharing a common focal location on the skin, all of the neurons in a column usually respond to only one modality: touch, pressure, temperature, or pain. This is not surprising, as we have seen that the various somatosensory modalities are conveyed by anatomically separate pathways. The cells that make up these pathways have distinctive response properties inasmuch as each pathway conveys information from a different class of receptor. Sensory receptors and primary sensory neurons responsive to one submodality, such as pressure or vibration, are connected to clusters of cells in the dorsal column nuclei and thalamus that receive inputs only for that submodality. These relay neurons in turn project to modality-specific cells in the cortex.

Although each of the four areas of the primary somatic sensory cortex (3a, 3b, 1, and 2) receives input from all areas of the body surface, one modality tends to dominate in each area. In area 3a the dominant input is from proprioceptors signaling muscle stretch. Area 3b receives input primarily from cutaneous mechanoreceptors. Here the inputs from a discrete site on the skin are

P.458

divided into two sets of columns, one each for inputs from rapidly adapting and slowly adapting receptors (Figure 23-7). In area 1 rapidly adapting cutaneous receptors predominate, and the receptive fields of these cells are considerably larger than those of cells in area 3b, often covering several adjacent fingers. In area 2 and higher cortical areas the modality segregation is much weaker. Columns of neurons in area 2 receive convergent input from slowly and rapidly adapting cutaneous receptors or from cutaneous receptors and proprioceptors in the underlying muscles and joints. Thus, the receptive fields and response properties of neurons in areas 1 and 2 represent convergent input from regions of the hand and fingers that are represented separately in areas 3a and 3b.



**Figure 23-6 The columnar organization of cortical neurons is a consequence of the pattern of connections between neurons in different layers of cortex.** (Modified from Jones 1981.)

**A.** The dendrites and axons of most cortical neurons extend vertically from the surface to white matter, forming the anatomical basis of the columnar structure of the cortex.

**B.** Morphology of the relay neurons of layers III-V. Stellate neurons (small spiny cell) are located in layer IV. These neurons are the principal target of thalamocortical axons. The axons of the stellate neurons project vertically toward the surface of the cortex, terminating on the apical dendrites of a narrow beam of pyramidal cells whose somas lie in layers II, III, and V above or below them. Stellate cell axons also terminate on the basal branches of pyramidal cells in layers II and III. The axons of pyramidal neurons project vertically to deeper layers of the cortex and to other cortical or subcortical regions; they also send horizontal branches within the same cortical region to activate columns of neurons sharing similar physiological properties.

**C.** Schematic diagram of intracortical excitatory circuits. The principal connections are made vertically between neurons in different layers.

How does the layering of the cortex contribute to the functional organization of the cortex? As described in Chapter 19, each layer of cells has connections with different parts of the brain: Layer IV receives input from the thalamus; layer VI projects back to the thalamus; layers II and III project to other cortical regions; and layer V projects to subcortical structures. As a result, the information on stimulus location and modality processed in each column is conveyed to different regions of the brain.

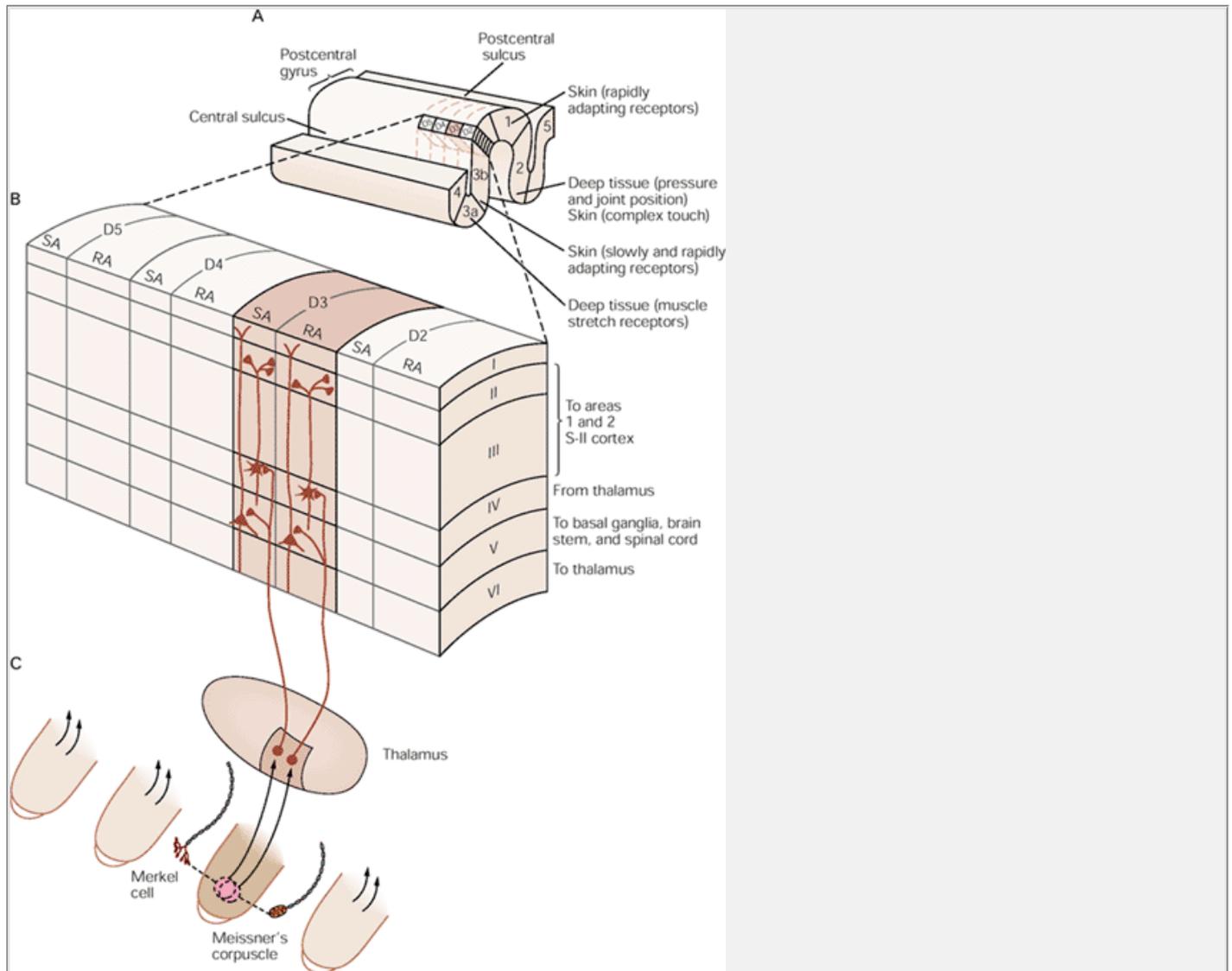
## The Body Surface Is Represented in the Brain by the Somatotopic Arrangement of Sensory Inputs

The columns of neurons in the somatic sensory cortex are arranged such that there is a complete topographic representation of the body in each of the four areas (3a, 3b, 1, and 2). The cortical map of the body corresponds to the spinal dermatomes defined by the afferent fibers entering the spinal cord at successively rostral levels (see Box 22-2). Sacral segments are represented medially, lumbar and thoracic segments centrally, cervical segments more laterally, and the trigeminal representation at the most lateral portion of the S-I cortex (Figure 23-8). The maps in adjacent cytoarchitectonic areas are rough mirror images of the distal-proximal or dorsal-ventral axes of each dermatome.

Topographic maps of the human parietal cortex have been constructed from measurements of sensory-evoked potentials or by using electrical stimulation of the cortex. These techniques, together with more modern noninvasive diagnostic tools such as magnetoencephalography (MEG), functional magnetic resonance imaging (fMRI), and positron emission tomography

P.459

(PET scan), allow neurologists to image the somatotopic functioning of the cortex in individual patients. While these imaging methods are less precise than the microelectrode maps made in animals, they are useful diagnostic tools in clinical neurology.



**Figure 23-7 Each region of the somatic sensory cortex receives inputs from primarily one type of receptor.**

**A.** In each of the four regions of the somatic sensory cortex—Brodmann's areas 3a, 3b, 1, and 2—inputs from one type of receptor in specific parts of the body are organized in columns of neurons that run from the surface to the white matter. (Adapted from [Kaas et al. 1981.](#))

**B.** Detail of the columnar organization of inputs from digits 2, 3, 4, and 5 in a portion of Brodmann's area 3b. Alternating columns of neurons receive inputs from rapidly adapting (RA) and slowly adapting (SA) receptors in the superficial layers of skin. (Adapted from [Sur et al. 1984.](#))

**C.** Overlapping receptive fields from RA and SA receptors project to distinct columns of neurons in area 3b.

## Spatial Resolution in the Cortex Is Correlated With the Innervation Density of the Skin

The somatotopic arrangement of somatosensory inputs in the human cortex is called a *homunculus*; it corresponds closely to the somatotopic maps of cortical columns determined by single neuron recordings in monkeys. However, the internal representation of the body within the homunculus does not duplicate the spatial topography of the skin exactly. Rather, the image of the body in the brain exaggerates certain body regions, particularly the hand, foot, and mouth and compresses more proximal body parts.

Each part of the body is represented in the brain in proportion to its relative importance to sensory perception. The map represents the *innervation density* of the skin rather than its total surface area. In humans a large number of cortical columns receive input from the hands, particularly from the fingers. About 100 times as much cortical tissue is devoted to a square centimeter of

P.460

skin on the fingers as to a square centimeter of skin on the abdomen. Similarly, large numbers of cortical neurons receive input from the foot and face. More than any other part of the body, the hands, face, and feet are important sensors of the properties of objects and thus have the highest density of touch receptors. The proximal portions of the limbs and trunk are much less densely innervated; correspondingly, fewer cortical neurons receive inputs from these regions.



**Figure 23-8** Each of the four regions of the primary somatic sensory cortex contains a complete map of the body surface. (Adapted from Nelson et al. 1980.)

**A.** Location of the primary somatosensory cortex in the brain of the macaque monkey. The body surface is mapped to the surface of the cortex as rostrocaudal strips arranged in the order of the spinal dermatomes.

**B.** Enlarged view of the body maps in areas 3b and 1 of the macaque primary somatic sensory cortex. The cortex is unfolded in this diagram along the central sulcus (**dotted line**, which parallels the border between 3b and 1), and at the medial wall of the hemisphere (**dashed line** at the edge of the foot representation). The sacral and lower lumbar segments are represented on the medial wall of the hemisphere. More rostral segments are mapped more laterally; the most lateral portions of the cortical map are devoted to the glabrous surface of the hand and foot; each finger has its own separate representation along the medial-to-lateral axes of the cortex. The maps in areas 3b and 1 form mirror images of the distal-proximal or dorsal-ventral axes of each dermatome. (**M** = mandible or lower jaw, **V** = maxilla or upper jaw.)

In lower species the hand representation in the brain is smaller than in primates, as these animals use other body parts to probe the environment. For example, rodents use their whiskers for tactile exploration rather than their hands. The representation of the whisker fields in the cortex is larger than that of the paw, forming distinct morphological structures called barrels (Box 23-2).

An important consequence of the magnification of the hand representation in the cortex is that the size of individual peripheral receptive fields on the hand cover a much smaller area of skin than receptive fields on the arm, which are smaller than receptive fields on the trunk. For example, receptive fields in the hand region may cover the tips of one or more fingers (Figure 23-3)

P.461

P.462

whereas receptive fields on the forearm may span the entire ulnar surface (Figure 23-4). The large receptive fields for proximal portions of the body (due to the low innervation density) grow proportionally greater at each successive relay.

### Box 23-2 The Cortical Representation of Whiskers in Rodents Is Precisely the Same From Animal to Animal

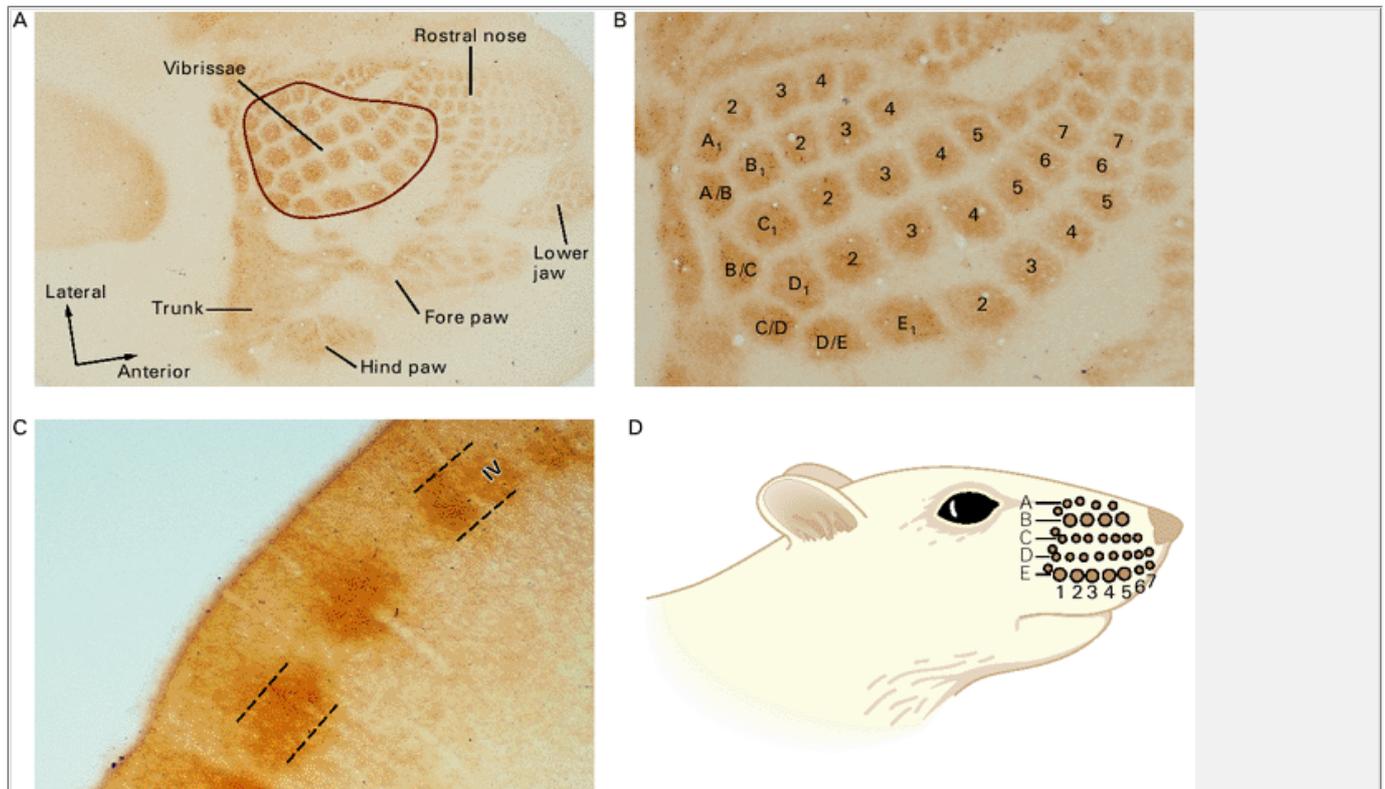
In rodents the whiskers are the principal tactile receptors. Thus the region surrounding the mouth is more extensively represented in the cortex than are the paws. Each whisker is innervated by a separate vibrissal nerve containing about 100 myelinated fibers, which are activated by movements of the whiskers in specific directions.

The cortical representation of the whiskers has a unique structure. The neurons of layer IV are arranged in discrete functional units called barrels, so-called

because when the cortex is cut tangentially, parallel to the cortical surface, the cell bodies of layer IV appear to form barrel-shaped arrays around a neuropil of axons and dendrites (Figure 23-9). Each barrel processes tactile input principally from a single whisker. The number of barrels is the same as the number of vibrissae on the contralateral side of the face, and the barrels are arranged in a pattern that corresponds to the topography of the whiskers.

The fact that each barrel represents a morphologically distinct group of tactile receptors makes it useful for studying plasticity of the cortical maps. Selective removal of vibrissae or vibrissal follicles, or distinctive patterns of stimulation of specific vibrissae, result in alterations in neuronal firing patterns in both the test and adjacent barrel fields. There is also a dynamic interaction between adjacent whiskers in the supragranular and infragranular layers of the cortex.

The unique morphology of the rodent barrel fields allows experimenters to correlate specific cortical locations with function without having to perform direct electrophysiological recordings. Thus measurements can be made of cytochemical, morphological, and metabolic changes related to altered sensory input.



**Figure 23-9** The representation of whiskers in the somatosensory cortex of the rat. (Adapted from Bennett-Clarke et al. 1997).

- A.** Photomicrograph of a horizontal section through layer IV of the somatosensory cortex of a juvenile rat that has been stained for serotonin. The dark immunoreactive patches correspond to the cortical representations of specific parts of the body. The largest part of the cortical map is devoted to the face representation (whiskers, nose, and lower jaw).
- B.** Enlarged view of the whisker representation. Neurons that receive projections from the whisker fields are arranged in discrete circular units called *barrels*. Each barrel is most responsive to a single whisker.
- C.** Coronal section through the rat somatosensory cortex. The barrels form dense patches localized to layer IV of the cortex.
- D.** The topographic arrangement of the barrels in the cortex corresponds to the spatial arrangement of the whiskers in discrete rows and columns on the face.

## Cortical Receptive Fields Are Altered by Use of the Hand

An important feature of somatotopic maps is that they are not fixed but can be altered by experience. While the general medial-to-lateral and rostral-to-caudal arrangement of cortical columns is the same in all individuals, the details of the map vary between individuals. A tennis champion will develop a larger proportion of cortical neurons devoted to sensory inputs from the arm than a pianist, who needs to differentiate inputs from individual fingers. As we saw in Chapter 20, the configuration of the map in individual animals can be altered experimentally by fusing adjacent digits or by increased stimulation of a particular finger.

## Inhibitory Networks Sharpen Spatial Resolution by Restricting the Spread of Excitation

For somatotopic mapping of cortical function it is enough to know which neurons respond to a stimulus at a particular site on the body. For this purpose the receptive fields of individual neurons are identified by touching the skin with a small probe. A more complex receptive field structure emerges when the skin is touched at two or more points simultaneously. Stimulation of regions of skin surrounding the excitatory region of the receptive field of a cortical neuron may reduce the responsiveness of the neuron to an excitatory stimulus because afferent inputs surrounding the excitatory region are inhibitory. These regions of the receptive field of a cortical neuron are called the *inhibitory surround*. This spatial distribution of excitatory and inhibitory activity serves to sharpen the peak of activity within the brain.

The inhibitory responses observed in the cortex are generated by interneurons in the dorsal column nuclei, the ventral posterior lateral nucleus of the thalamus, and the cortex itself. Inhibitory interneurons in relay nuclei form circuits that tend to limit the spatial spread of excitation through divergent connections (see Figure 21-12). Peripheral receptors in the somatic sensory system are not themselves inhibited (Figure 23-10A). At the first relay point in the somatic sensory system the afferent fibers inhibit the activity of cells in the dorsal column nuclei that surround the cells they excite (Figure 23-10B). Inhibition generated by activity of the most intensely activated receptors reduces the output of projection neurons that are less strongly excited. It permits a winner-take-all strategy, which ensures that the strongest of two or more competing responses is expressed. In addition, the most active output neurons use recurrent collateral fibers to limit the activity of adjacent neurons. This lateral inhibition further sharpens the contrast between the active cells and their neighbors (Figure 23-10C).

## Lateral Inhibition Can Aid in Two-Point Discrimination

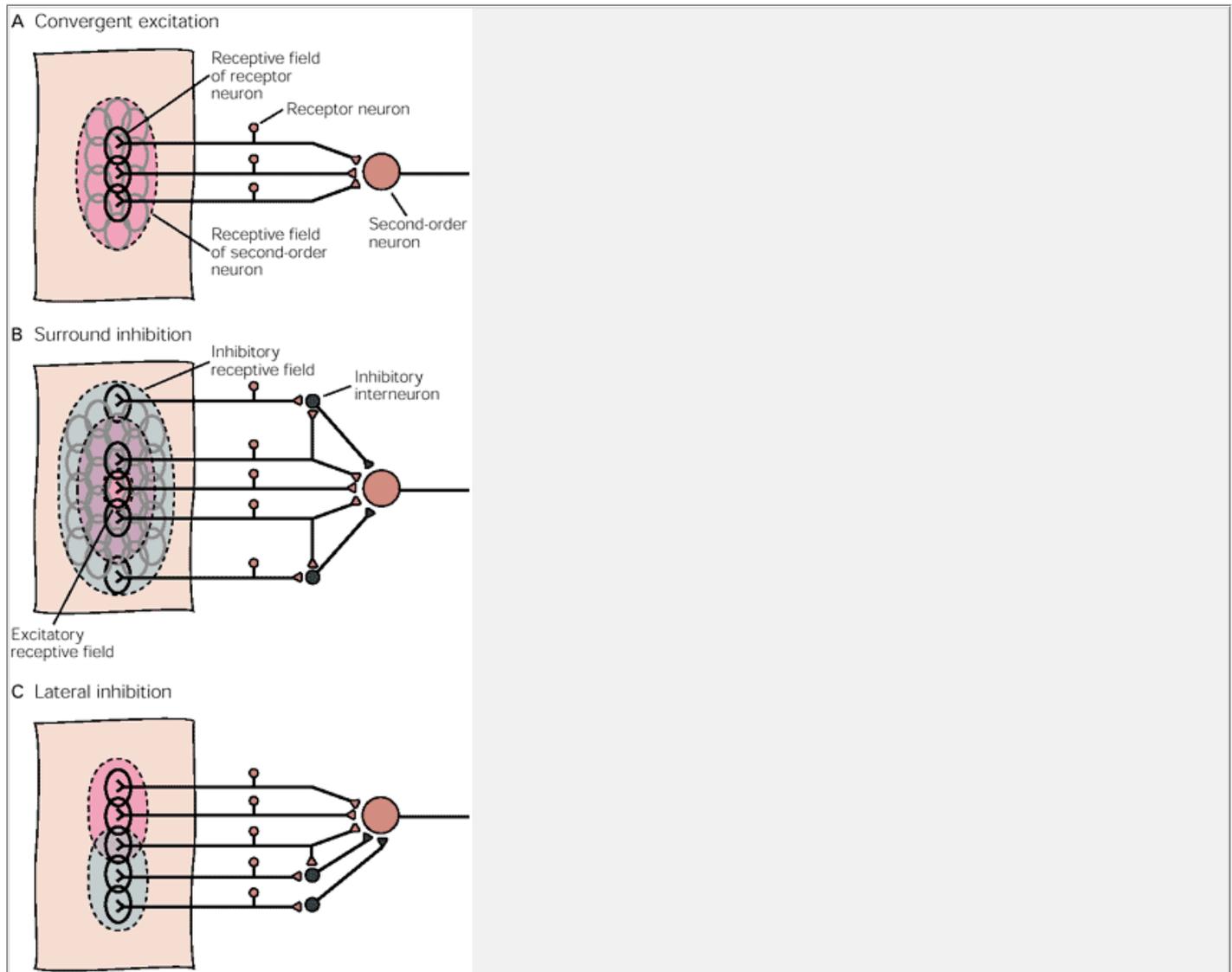
Inhibitory interactions are particularly important for fine tactile discrimination such as reading Braille. We can understand how this is accomplished by considering the simplest example of spatial discrimination: the ability to distinguish two closely placed point stimuli. We are able to perceive two points rather than one because two

distinct populations of neurons are activated. Stimuli applied to two widely spaced positions on the skin set up excitatory gradients of activity in two cell populations at every relay nucleus.

If the two stimuli are brought close together, the activity in the two populations tends to overlap, and the distinction between the two peaks might become blurred. However, the inhibition produced by each stimulus also summates in the zone of overlap. As a result of this more effective inhibition, the peaks of activity in the two responding populations become sharpened, thereby separating the two active populations spatially (Figure 23-11B). This sculpturing role of the inhibition thus preserves the spatial distinction between the two stimuli.

## Spatial Detail Is Accurately Represented in the Cortex

How far does this fidelity of the sensory stimulus extend? Studies of cortical neurons using Braille dot patterns, or embossed letters touched by the fingers, indicate that the signal transmitted to the cortex faithfully reproduces the stimulus features encoded by the receptors in the skin. As we saw in Chapter 22, both Merkel disk receptors and Meissner's corpuscles transmit a faithful neural image of such patterns (see Figure 22-8). These sharp sensory images are preserved up to the first stage of cortical processing in area 3b of the somatic sensory cortex. Neurons in area 3b fire bursts as each line segment of a letter is scanned across the receptive field and together faithfully signal its shape (Figure 23-12).



**Figure 23-10** The receptive field of a higher-order neuron in the dorsal column nuclei has a characteristic pattern of excitation and inhibition that increases spatial resolution.

**A.** Many peripheral receptors converge onto a single second-order sensory neuron in the dorsal column nuclei. As a consequence, the excitatory receptive field of the central neuron is made up of the receptive fields of all the presynaptic cells.

**B.** The receptive field of a neuron in the dorsal column nuclei and in the ventral posterior nuclei of the thalamus typically has a central excitatory receptive field surrounded or flanked by an inhibitory region. The addition of inhibitory interneurons (**gray**) narrows the discharge zone. Feed-forward inhibition sharpens the representation of a punctate stimulus by limiting the spread of excitation through convergent neural networks. On either side of the excitatory region the discharge rate is driven below the resting level by inhibition.

**C.** The asymmetric distribution of inhibitory interneurons produces lateral inhibition. In this schematic network, stimulation in the upper portion of the receptive field produces strong excitation of the relay neuron. Stimulation of the lower portion of the receptive field inhibits firing because the interneurons produce feed-forward inhibition. Stimulation in the zone of overlap of excitation and inhibition reduces the responsiveness of the relay neuron to the stimulus. Lateral inhibition is particularly important for feature detection.

The cortical representation of each letter is further sharpened by a pause in firing as the moving edges exit the excitatory receptive field and enter its inhibitory surround. The contrast between the spike bursts and subsequent silent intervals permits the letters to stand out from the noisy background activity.

Neurons in area 3b are able to signal the precise shape of the letters moved over the finger because their receptive fields are smaller than the letters. The individual line segments that characterize each letter are viewed one at a time as they cross the neuron's receptive field. The spatial arrangement of stimulated and unstimulated regions of skin is represented in the cortex in columns of active and silent neurons.

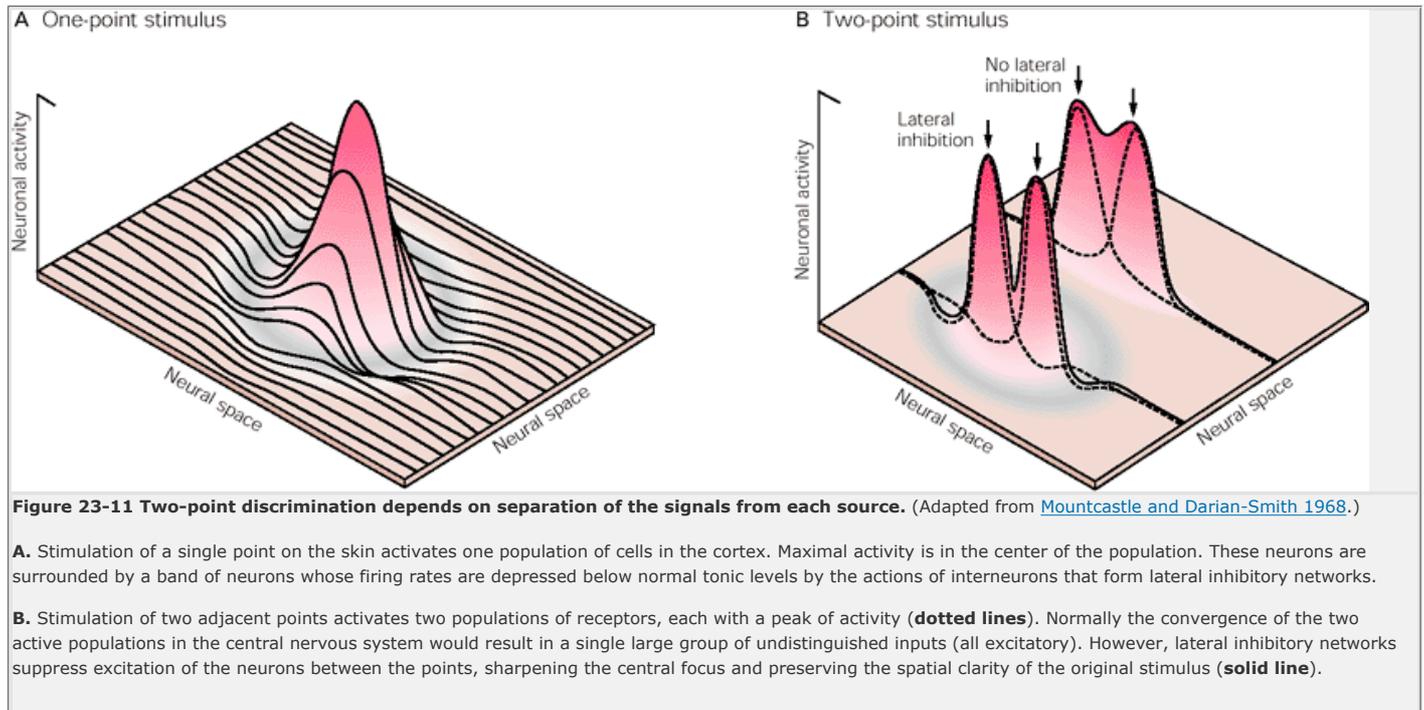
In later stages of cortical processing, however, the responses are more abstract. For example, activity in neurons in area 1 does not reproduce the shape of the letters but instead signals specific features common to groups of letters, such as the presence of vertical or horizontal line segments. Since certain cortical neurons represent letter stimuli faithfully and neurons at a later stage do not, it should be possible to determine the intermediate step by which the initial representation becomes abstracted.

## Neurons in Higher Cortical Areas Have Complex Feature-Detecting Properties

To produce a coherent sensation of an object the nervous system must integrate information from a large number and variety of receptors as well as the modalities of touch, proprioception, and temperature. How is this integration accomplished? At least four factors are involved:

P.464

- (1) The size of the receptive field becomes larger at each level of processing, so that eventually the entire object rather than a single edge is sensed by a neuron.
- (2) The profile of activity in the active population of neurons changes through the action of inhibitory networks.
- (3) At successive levels of sensory processing in the cortex individual neurons respond to more complex inputs.
- (4) The submodalities converge on individual neurons in association cortical areas.



We have seen that neurons in area 3b provide a detailed representation of the properties of an individual object such as an embossed letter. They respond to a particular form and amount of energy at a specific location in space and together reproduce its shape. As information flows from the initial stages of cortical processing toward higher-order cortical areas, specific combinations of stimuli or stimulus patterns are needed to excite individual neurons. Neurons in areas 1 and 2 are concerned with more abstract properties of tactile stimuli than simply the site of stimulation. These cells ignore many of the myriad details of a stimulus and instead detect regularities amid the confusion. Their firing patterns signal features such as the orientation of edges, the direction of motion across the skin, the surface curvature of objects, or the spatial arrangement of repeated patterns that form textures. Feature detection is a basic principle of cortical processing that allows the brain to find patterns common to stimuli of a particular class.

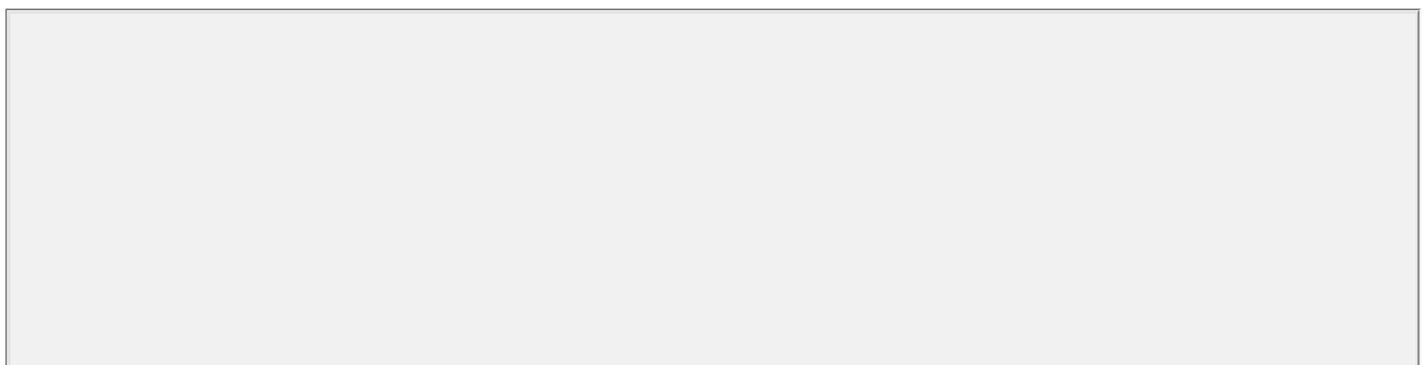
Experiments using alert animals have revealed a variety of feature-detection neurons in the cortex. Some cortical neurons in area 2 respond preferentially to specific combinations of simultaneously stimulated receptors. Such *orientation-sensitive* neurons sense the angle of edges contacted by the skin (Figure 23-13A). This information is extremely important in reconstructing the shapes of objects. Other cells are *direction sensitive*. They respond vigorously when the skin is stroked in a preferred direction and are unresponsive when the same region of skin is stroked in the opposite direction (Figure 23-13B). Some neurons in area 2 are even more specialized, sensing the spacing or alignment of ridges in a grating when the hand is rubbed over its surface.

The ability of a cortical neuron to detect the orientation of an edge or direction of motion results from the spatial arrangement of its input neurons (Figure 23-14). The excitatory receptive fields of the input neurons are aligned along the preferred axis and produce a strong excitatory response when the stimulus orientation matches that of the receptive fields. In addition, the inhibitory receptive fields are placed to one side of the excitatory fields, suppressing inputs with the "wrong" orientation or approaching from the "wrong" direction.

The convergent projections from areas 3a and 3b onto areas 1 and 2 permit neurons in area 2 to respond

P.465

to other complex features, such as the shape of objects. Whereas neurons in 3b and 1 respond only to touch, and neurons in areas 3a respond only to position sense, certain neurons in area 2 have both inputs. These neurons respond best when an object of a specific shape is grasped by the hand. Some of these cells respond more vigorously to round objects than to objects with distinct edges, while others are activated selectively by rectangular objects. As we shall see below, this information is thought to provide the necessary tactile clues for skilled movement of the fingers.





**Figure 23-12** The spatial characteristics of embossed letters are accurately represented by neurons in area 3b of the primary somatic sensory cortex but not in area 1. (Adapted from Phillips et al. 1988.)

**A.** Spatial event plots (see Figure 22-8A) for the principal tactile afferent fibers of the hand: the slowly adapting (**SA**) Merkel disk receptors and rapidly adapting (**RA**) Meissner's corpuscles. Both SA and RA receptors accurately encode the shape of each letter.

**B.** Spatial event plots for neurons in areas 3b and 1 of an awake monkey. In area 3b slowly adapting (SA) receptors continue to signal the shape of the letters, but rapidly adapting (RA) neurons are more sensitive to the vertical leading edges. In area 1 SA neurons sense particular features of the letter (in this case the vertical but not horizontal components) while the RA neuron illustrated failed to represent form.

Detection of the direction of movement and of other features of the stimulus is not apparent in neurons in the dorsal column nuclei, in the thalamus, or even in areas 3a and 3b. Feature-detecting neurons sensitive to stimulus direction and orientation are first found in area 1 and are represented more extensively in area 2, the areas concerned with stereognosis (the three-dimensional perception of objects) and with discriminating the direction of movement of objects on the skin. Thus, these complex stimulus properties arise not from thalamic input but from cortical processing of more elementary inputs.

In the posterior parietal cortex (areas 5 and 7) the somatosensory responses are even more complex and are often integrated with other sensory modalities. These association cortical areas play an important role in the sensory guidance of movement and are consequently organized functionally rather than topographically (Chapter 19). Many neurons in area 5 receive inputs from several adjacent joints or groups of muscles that provide information about the posture of the entire hand or arm, particularly when monkeys reach out their hands to grasp objects. Other cells integrate tactile and postural information and are most vigorously activated when the monkey preshapes the hand to grasp and acquire objects, or plucks food morsels from a small container.

Neurons in area 7 of the posterior parietal cortex integrate tactile and visual stimuli that overlap in space and play an important role in eye-hand coordination. They respond more vigorously when the monkey is able to observe its hand while manipulating objects of interest than when simply looking at the object or handling it in the dark. Such neurons are used to monitor visually guided hand movements rather than to convey detailed sensory information concerning the exact position or intensity of touch.

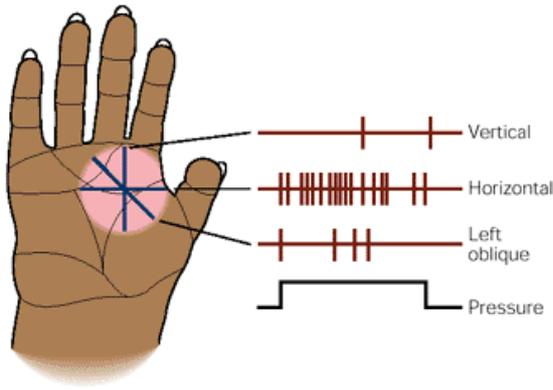
## Stimulus Features Are Processed in Parallel by Distinct Areas of Cortex

We have seen that specific stimulus features are represented in discrete somatosensory cortical areas. Neurons

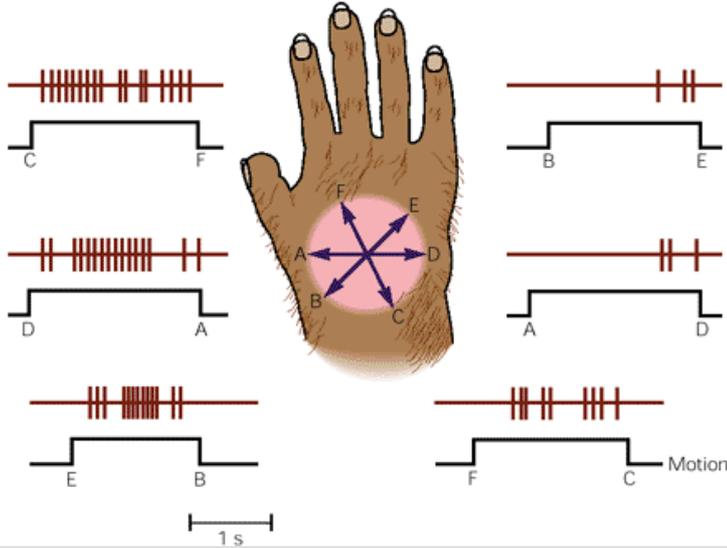
P.466

in area 3b with small receptive fields sense which finger is contacted and indeed which individual phalanx touches the object. Neurons in area 1 with multi-finger receptive fields sense the object size; they fire at higher rates if several fingers are touched and at lower rates if only a small portion of the receptive field is contacted. Neurons in area 2 sense even more complex features, such as the direction of motion across the hand, the curvature of surfaces, the orientation of edges, or the spacing of ridges on textured surfaces. Neurons in area 5 integrate tactile inputs from the skin with proprioceptive postural information from the fingers to encode the shape of objects grasped in the hand. Neurons in the posterior parietal cortex integrate the tactile and proprioceptive information with visual properties of the objects touched.

**A Orientation-sensitive neuron**



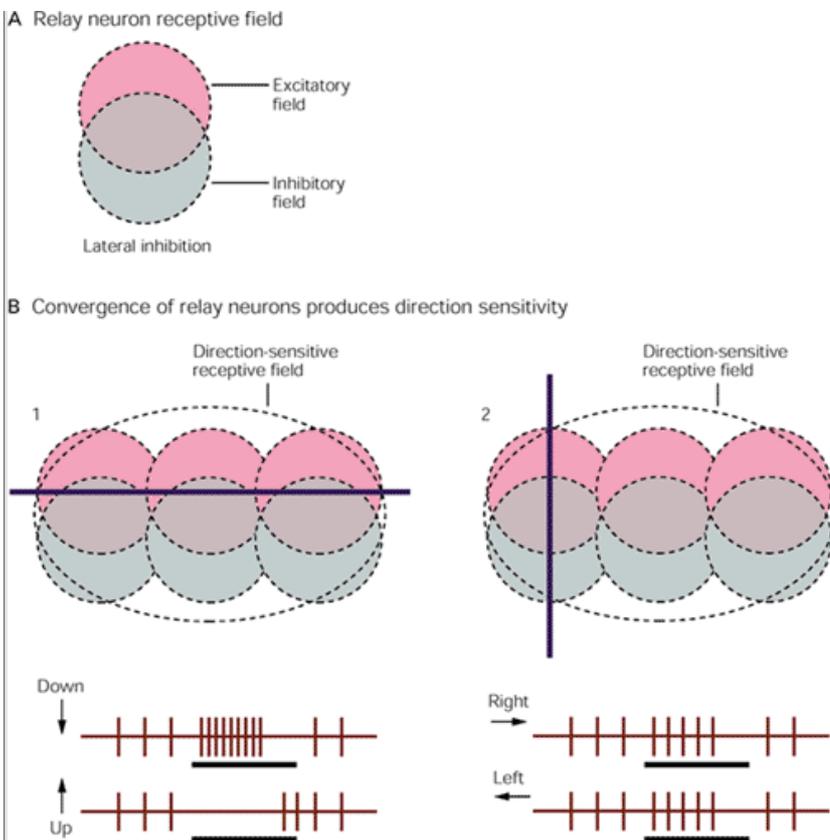
**B Direction-sensitive neuron**



**Figure 23-13 Feature-detection neurons in area 2 of the primary somatic sensory cortex respond to highly specific features of a stimulus.** The examples shown here are from a macaque monkey.

**A.** This orientation-sensitive neuron distinguishes horizontal and vertical edges pressed on the palm. The neuron responds vigorously when the edge is oriented horizontally but is nearly silent when the edge is oriented vertically. Responses to the oblique orientation are weaker than those to the horizontal position. (Adapted from [Hyvärinen and Poranen 1978](#).)

**B.** This direction-sensitive neuron responds most vigorously to movement across the hand toward the thumb and index finger. The neuron displays its strongest responses to motion in the radial direction (D to A and E to B); the weakest responses occur in the ulnar direction (A to D and B to E). Responses to distal movements toward the fingers (C to F) are more vigorous than responses to proximal movements toward the wrist (F to C). The trace below each cell record shows the duration of motion and the start and end points of the path. (Adapted from [Costanzo and Gardner 1980](#).)



**Figure 23-14** The spatial arrangement of presynaptic inputs to a cortical neuron determined which specific features of a stimulus will activate the neuron.

**A.** Stimuli moving across the receptive field of a relay neuron receiving lateral inhibition (see [Figure 23-10](#)) are more effective when the excitatory field is stimulated first because the inhibitory responses are longer in duration than the excitatory responses. Stimuli starting from the excitatory field produce a burst of action potentials followed by inhibition as the stimulus moves into the inhibitory field. Motion in the opposite direction is less effective because the long-lasting inhibitory postsynaptic potential evoked from the inhibitory field decreases the ability of the cell to respond when the stimulus moves into the excitatory field.

**B.** Convergence of three relay neurons with the same arrangement of excitatory and inhibitory fields confers direction sensitivity on a cortical neuron. In this example the preferred stimulus is a horizontal bar moving downward. **1.** Motion of a horizontal bar across the cortical receptive field (**solid line** below the spike trace). Downward motion of the bar produces a strong excitatory response because it crosses the excitatory fields of all three relay neurons simultaneously. Upward motion of the bar strongly inhibits firing because it enters all three inhibitory fields first. The neuron responds poorly to upward motion through the excitatory field because the initial inhibition outlasts the stimulus. **2.** Motion of a vertical bar across the cortical receptive field evokes a weak response because it crosses excitatory and inhibitory fields of the relay neurons simultaneously. Motion to the left and right are not distinguished in this example.

P.467

The somatosensory information necessary for stereognosis is processed in parallel in these areas because palpation involves repetitive touching of the object for several seconds. Such information is not simply relayed from point to point in the brain, as are the somatosensory evoked potentials after a brief shock to the nerve. Instead, tactile sensory information transmitted to higher cortical areas must be compared with more recent information being processed at the early stages. Thus, the activity that occurs simultaneously in different cortical areas is produced by events that happen at different moments in time. Responses in areas 3a and 3b occur 20 ms after touch or movement and therefore reflect stimuli in the immediate past. The more posterior cortical areas receive sensory information at longer latencies, processing stimuli presented 30-100 ms earlier.

P.468

How does the brain put together all of these features to form a coherent percept of an object? The firing patterns of neurons in separate cortical areas interact in ways we do not fully understand. The problem of binding together activity in different regions of the cerebral cortex has been studied more extensively for vision than for touch. Those studies of the visual system indicate that the brain may bind together the various stimulus features by synchronizing firing in different cortical areas.

## The Behavioral Relevance of a Tactile Stimulus Modifies Cortical Responses

Selective attention can modify firing patterns at the higher stages of cortical processing. Although neurons in S-II are activated by embossed letters scanned across their receptive fields, they do not signal the spatial properties of the letters as do neurons in area 3b. Instead, neuronal responses in S-II depend on behavioral context or motivational state. For example, the firing rates can be altered by varying the letters that are reinforced with rewards or by distracting the monkey with an unrelated visual or auditory discrimination task. These same changes in circumstance have little effect on the spatial information conveyed by neurons in S-I.

The S-II cortex provides the gateway to the temporal lobe via the insular cortex. We shall learn in a later chapter that regions of the medial temporal lobe, particularly the hippocampus, are vital to the formation of memories. We do not store in memory every scintilla of tactile information that enters the nervous system, only information that has some behavioral significance. The demonstration that the firing patterns of S-II neurons are modified by selective attention suggests that S-II serves as a decision point for determining whether a particular bit of tactile information is remembered.

## Lesions in Somatosensory Areas of the Brain Produce Specific Sensory Deficits

The earliest information about the function of the somatic sensory system came from the analysis of disease states and traumatic injuries of the spinal cord. For example, one of the late consequences of syphilitic infection in the nervous system is a syndrome called *tabes dorsalis*, which destroys the large-diameter neurons in the dorsal root ganglia, causing degeneration of myelinated afferent fibers in the dorsal columns. Patients who have this degeneration as a result of *tabes dorsalis* have severe deficits in touch and position sense but often little loss of temperature perception and of nociception.

Additional information about the somatic afferent system has come from studies of the behavioral defects produced by transection of the dorsal columns of the spinal cord in experimental animals or by trauma in humans. Injury to the afferent somatosensory pathways in the dorsal columns results in a chronic deficit in certain

tactile discriminations, such as detecting the direction of movement across the skin, the frequency of vibration, the relative position of two cutaneous stimuli, and two-point discrimination. The deficit is ipsilateral to the lesion and occurs at levels below the lesion. Interestingly, some simple spatial discriminations, such as differentiating the size of probes pressed on the skin, can be recovered after extensive retraining and rehabilitative therapy. However, perception of stimuli with complex spatio-temporal patterns, such as distinguishing letters drawn on the skin (*graphesthesia*), is permanently impaired.

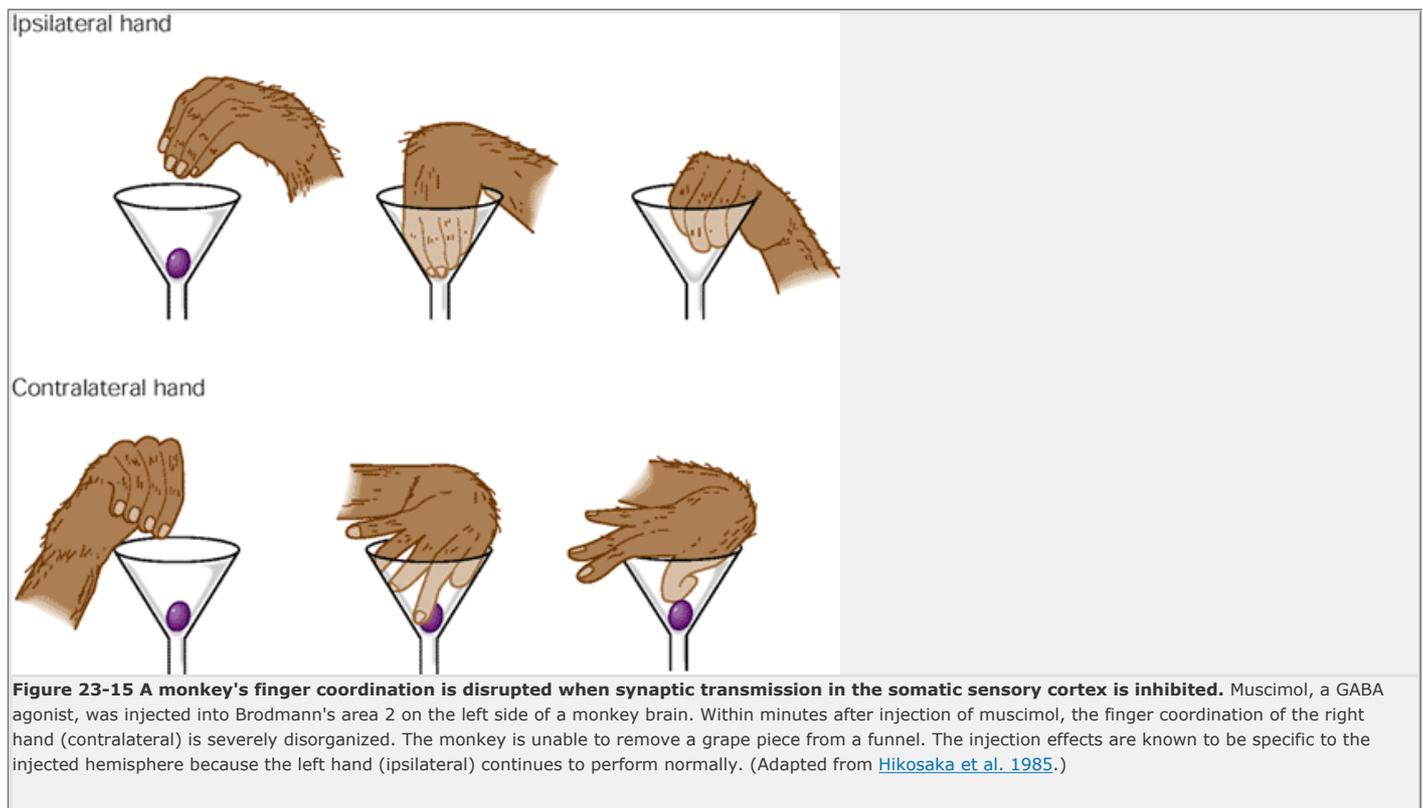
In addition to sensory deficits, lesions of the dorsal columns distort natural hand movements. For example, macaque monkeys with a lesion of the cuneate fascicle show major deficits in the control of fine finger movements during grooming, scratching, and manipulation of objects. A similar but reversible deficit in the execution of skilled movements can be produced experimentally in monkeys by pharmacological inhibition of neural activity in area 2 of the cortex. When muscimol (a GABA agonist that inhibits cortical cells) is applied to the hand representation of area 2, the monkey is unable to assume normal functional postures of the hand or coordinate the fingers for picking up small objects ([Figure 23-15](#)).

Experimental lesions of the various somatic areas of the cortex have also provided valuable information about the function of different Brodmann's areas concerned with somatic sensibility. Total removal of S-I (areas 3b, 3a, 1, and 2) produces deficits in position sense and the ability to discriminate size, texture, and shape. Thermal and pain sensibilities usually are not abolished, but are altered. In addition, serious motor deficits in hand function occur following major lesions in S-I.

Small lesions in the cortical representation of the hand in Brodmann's area 3b produce deficits in the discrimination of the texture of objects as well as their size and shape. Lesions in area 1 produce a defect in the assessment of the texture of objects, whereas lesions in area 2 alter the ability to differentiate the size and shape of objects. This is consistent with the idea that area 3b receives information about texture as well as size and shape (area 3b, together with 3a, is the principal target for the afferent projections from the ventral posterior lateral nucleus of the thalamus). Area 3b projects to both areas 1 and 2. The projection to area 1 is concerned primarily

P.469

with texture, whereas the projection to area 2 is concerned with size and shape.



Because S-II receives inputs from all areas of S-I, removal of S-II causes severe impairment in the discrimination of both shape and texture and prevents monkeys from learning new tactile discriminations based on the shape of an object.

Finally, as we saw in [Chapter 20](#), damage to the posterior parietal cortex produces complex sensorimotor abnormalities. These include the inability to accurately process stimuli in the contralateral visual field or contralateral half of the body. Poor motor coordination and poor eye-hand coordination during reaching, grasping, and hand orientation lead to neglect in usage of the hand.

## An Overall View

To perceive how the world impinges on our bodies, the brain is organized to represent the tactile sensory system of the skin. The receptive fields of cortical neurons become progressively more complex with each stage of information processing, thus extracting more cohesive features of a stimulus at each stage. Cortical receptive fields are larger than those of peripheral receptors due to convergence of inputs from simultaneously stimulated areas of skin.

Cortical neurons are functionally organized in columns, so that all six layers of the cortex in any column receive information representing the same location and modality. The columns are arranged topographically, projecting a precise representation of the external body surface onto the cortical surface. Somatotopy, the orderly projection of the sensory sheet in the brain, permits orderly intracortical connections. However, the somatosensory map or homunculus is not an exact representation of the body surface but is distorted. The finger tips, for example, are represented by a much greater cortical area than are regions like the back. The cortical map represents the density of innervation, hence the functional importance of different areas of the skin.

The body surface has at least eight distinct neural maps in the parietal cortex, four in S-I, two in S-II, and two in the posterior parietal cortex. Each of the four subregions in S-I contains its own map of the body surface, specific to a particular somatic sensory modality. Area 3a receives input primarily from muscle stretch receptors; area 3b receives cutaneous receptor input; area 1 receives input from rapidly adapting receptors; and area 2 contains a map of both cutaneous and deep receptors. As a result, these different regions are responsible for different aspects of somatic sensation. Areas 3b and 1 are involved in sensing surface texture, while area 2 is responsible for sensing the size and shape of objects.

Neurons in areas 2, 5, and 7 are involved in the later stages of somatosensory processing, have more complex feature-detecting properties, receive convergent input from several submodalities, and have larger receptive fields than first-order cortical neurons. At least four types of higher-order somatosensory cells have been found: direction-sensitive, orientation-sensitive, texture-sensitive, and shape-sensitive neurons. Even more complicated processing seems to be carried out by neurons activated when the hand is manipulating an object; these neurons project to the motor cortex for sensory-motor integration. Finally, the S-I cortex sends outputs to the posterior parietal cortex, where integration with other senses and the opposite limb occurs and where an overall picture of the body is formed.

Why are there so many representations of the body surface? Somatic sensation involves the parallel analysis of different stimulus attributes in different cortical areas. Parallel processing in the brain is a form of processing that we shall encounter repeatedly in the sensory systems. It is designed not to achieve multiplication of

P.470

identical circuitry but to allow different neuronal pathways and brain relays to deal with sensory information in slightly different ways.

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P.471

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