

movement enhances the sensations produced by the dots. Because the Braille dots are spaced approximately 3 mm apart, a distance greater than the receptive field diameter of an SA1 fiber, each dot stimulates a different set of SA1 fibers. An SA1 fiber fires a burst of action potentials as a dot enters its receptive field and is silent once the dot leaves the field (Figure 19–7). Specific combinations of SA1 fibers that fire synchronously signal the spatial arrangement of the Braille dots. RA1 fibers also discriminate the dot patterns, enhancing the signals provided by SA1 fibers.

Although Pacinian corpuscles (RA2 fibers) respond to scanning Braille dots over the skin, their spike trains do not reflect the periodicity of dots in the Braille patterns. Instead, they signal the skin vibrations evoked by motion of the Braille dots over the skin. Sliman Bensmaia and colleagues recently found that when fine textures such as fabrics are tested with this method, RA2 afferents signal the periodicity of threads in the weave by generating their spike trains in phase with these surface features. SA1 fibers are less responsive to motion of textiles because the thread size is usually too small to indent the skin at sufficient amplitude. Nevertheless, all three types of tactile afferents contribute to human percepts of roughness and smoothness.

### Slowly Adapting Fibers Detect Object Pressure and Form

The most important function of SA1 and SA2 fibers is their ability to signal skin deformation and pressure. The sensitivity of SA1 receptors to edges, corners, points, and curvature provides information about an object's compliance, shape, size, and surface texture. We perceive an object as hard or rigid if it indents the skin when we touch it, and soft if we deform the object.

Paradoxically, as an object's size and diameter increase, its surface curvature decreases. The responses of individual SA1 fibers are weaker and the resulting sensations feel less distinct. For example, the tip of a pencil pressed 1 mm into the skin feels sharp, unpleasant, and highly localized at the contact point, whereas a 1-mm indentation by the eraser feels blunt and broad. The weakest sensation is evoked by a flat surface pressed against the finger pad.

To understand why these objects evoke different sensations, we need to consider the physical events that occur when the skin is touched. When a pencil tip is pressed against the skin, it dimples the surface at the contact point and forms a shallow, sloped basin in the surrounding region (approximately 4 mm in radius). Although the indentation force is concentrated in the center, the surrounding region is also perturbed by

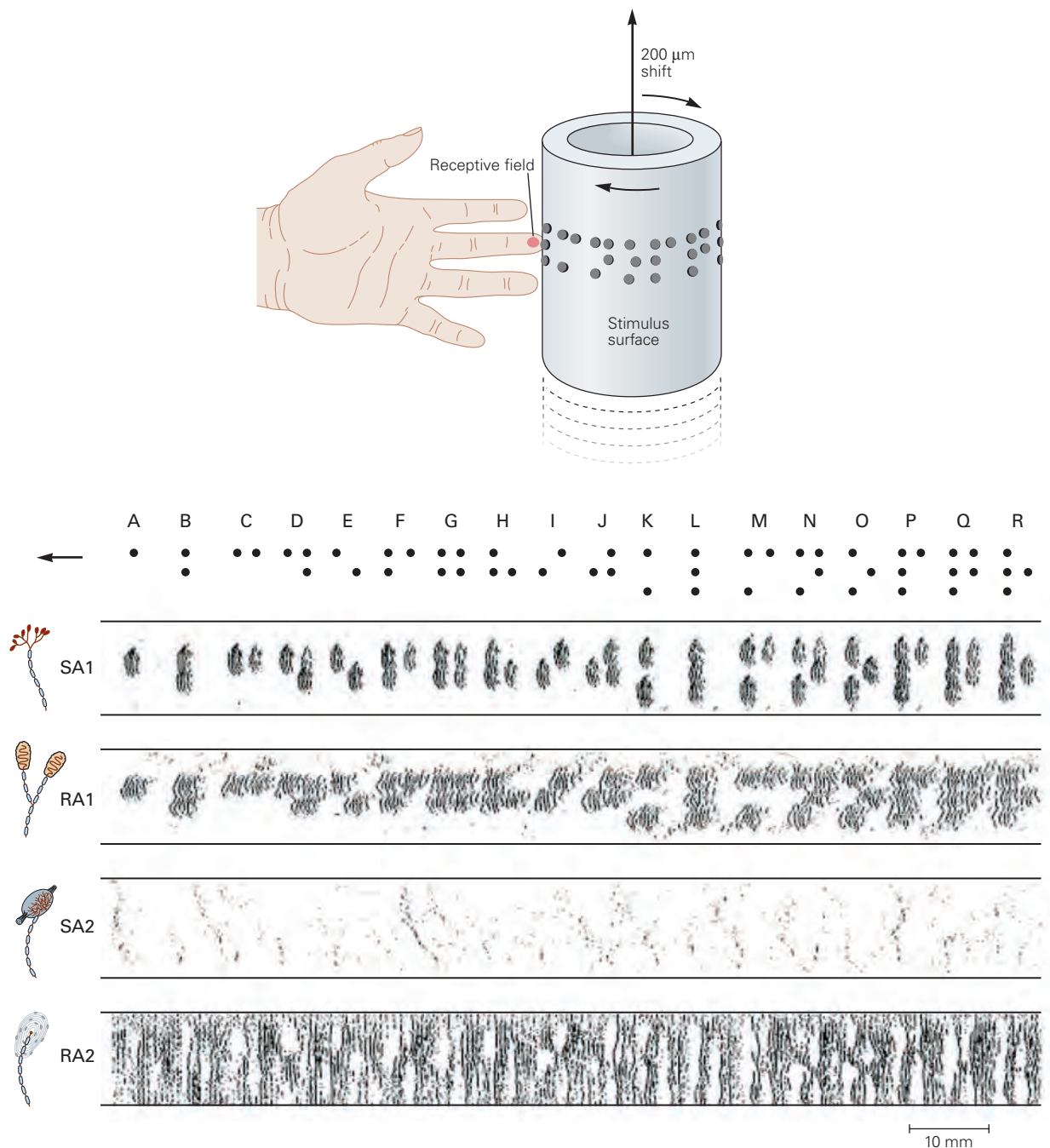
local stretch, called tensile strain. SA1 receptors at both the center and the surrounding "hillsides" of skin are stimulated, firing spike trains proportional to the degree of local stretch.

If a second probe is pressed close to the first one, more SA1 fibers are stimulated but the neural response of each fiber is reduced because the force needed to displace the skin is shared between the two probes. Ken Johnson and his colleagues have shown that as more probes are added within the receptive field, the response intensity at each sensory ending becomes progressively weaker because the displacement forces on the skin are distributed across the entire contact zone. Thus, the skin mechanics result in a case of "less is more." Individual SA1 fibers respond more vigorously to a small object than to a large one because the force needed to indent the skin is concentrated at a small contact point. In this manner, each SA1 fiber integrates the local skin indentation profile within its receptive field.

The sensitivity of SA1 receptors to local strain on the skin enables them to detect edges, the places where an object's curvature changes abruptly. SA1 firing rates are many times greater when a finger touches an edge than when it touches a flat surface because the force applied by an object boundary displaces the skin asymmetrically, beyond the edge as well as at the edge. This asymmetric distribution of force enhances responses from receptive fields located along the edges of an object. As edges are often perceived as sharp, we tend to grasp objects on flat or gently curved surfaces rather than by their edges.

The SA2 fibers that innervate Ruffini endings respond more vigorously to stretch of the skin than to indentation, because of their anatomical location along the palmar folds or at the finger joints. They provide information about the shape of large objects grasped with the entire hand, the "power grasp" in which an object is pressed against the palm.

The SA2 system may play a central role in stereognosis—the recognition of three-dimensional objects using touch alone—as well as other perceptual tasks in which skin stretch is a major cue. Benoni Edin has shown that SA2 innervation of the hairy skin on the dorsum of the hand plays a substantial role in the perception of hand shape and finger position. The SA2 fibers aid the perception of finger joint angle by detecting skin stretch over the knuckles, or in the webbing between the fingers. The Ruffini endings near these joints are aligned such that different groups of receptors are stimulated as the fingers move in specific directions (Figure 19–5A, bottom panel). In this manner, the SA2 system provides a neural representation



**Figure 19-7** Responses of touch receptors to Braille dots scanned by the fingers. The Braille symbols for the letters A through R were mounted on a drum that was repeatedly rotated against the fingertip of a human subject. Following each revolution, the drum was shifted upward so that another portion of the symbols was scanned across the finger. Microelectrodes placed in the median nerve of this subject recorded the responses of the mechanoreceptive fibers innervating the fingertip. The action potentials discharged by the nerve fibers as the Braille symbols moved over the receptive field are represented in these records by small dots; each horizontal row of dots represents the responses of the fiber to a single revolution of the drum. The SA1 receptors register the sharpest image of the Braille symbols,

representing each Braille dot with a series of action potentials and falling silent when the spaces between Braille symbols provide no stimulation. RA1 receptors provide a blurred image of the Braille symbols because their receptive fields are larger, but the individual dot patterns are still recognizable. Neither RA2 nor SA2 receptors are able to encode the spatial characteristics of the Braille patterns because their receptive fields are larger than the dot spacing. The high firing rate of the RA2 fibers reflects the keen sensitivity of Pacinian corpuscles to vibration. (Abbreviations: **RA1**, rapidly adapting type 1; **RA2**, rapidly adapting type 2; **SA1**, slowly adapting type 1; **SA2**, slowly adapting type 2.) (Reproduced, with permission, from Phillips, Johansson, and Johnson 1990. Copyright © 1990 Society for Neuroscience.)

of skin stretch over the entire hand, a proprioceptive rather than exteroceptive function.

The SA2 fibers also provide proprioceptive information about hand shape and finger movements when the hand is empty. If the fingers are fully extended and abducted, we feel the stretch in the palm and proximal phalanges as the glabrous skin is flattened. Similarly, if the fingers are fully flexed, forming a fist, we feel the stretch of the skin on the back of the hand, particularly over the metacarpal-phalangeal and proximal interphalangeal joints. Humans use this proprioceptive information to preshape their hand to grasp objects efficiently, opening the fingers just wide enough to clear the object and grasp it skillfully without too much force.

### **Rapidly Adapting Fibers Detect Motion and Vibration**

Tests of vibration sense form an important component of the neurological exam. Touching the skin with a tuning fork that oscillates at a particular frequency evokes a periodic buzzing sensation because most touch receptors fire synchronized, periodic trains of action potentials in phase with the stimulus frequency (Figure 19-8A2). Vibration sense is a useful measurement of dynamic sensitivity to touch, particularly in cases of localized nerve damage.

The RA2 receptor, the Pacinian corpuscle, is the most sensitive mechanoreceptor in the somatosensory system. It is exquisitely responsive to high-frequency (30–500 Hz) vibratory stimuli and can detect vibration of 250 Hz in the nanometer range (Figure 19-8B2). The ability of Pacinian corpuscles to filter and amplify high-frequency vibration allows us to feel conditions at the working surface of a tool in our hand as if our fingers themselves were touching the object under the tool. The clinician uses this exquisite sensitivity to guide a needle into a blood vessel and to probe tissue stiffness. The auto mechanic uses vibratory sense to position wrenches on unseen bolts. We can write in the dark because we feel the vibration of the pen as it contacts the paper and transmits the frictional forces from the surface roughness to our fingers.

Although Pacinian corpuscles have the lowest vibration thresholds for frequencies greater than 40 Hz (Figure 19-8B2), vibratory stimuli of higher amplitude also excite SA1 and RA1 fibers, even if their evoked spike trains are weaker than those of Pacinian afferents. Figure 19-9A illustrates the evoked firing patterns of 15 different peripheral nerve fibers stimulated at 20 Hz at weak, moderate, and high amplitudes. Although these fibers differ in sensitivity to vibration,

their spike trains have certain important characteristics in common. First, each neuron fires at a particular phase of the vibratory cycle, usually when the probe indents the skin, and its phasic pattern of spikes replicates the vibratory frequency: when stimulated at 20 Hz, the spike bursts recur at intervals of approximately 50 ms. The patterning of the spike trains is further reinforced because the population of fibers fires synchronously, enabling the frequency information to be preserved centrally due to synaptic integration.

The total number of spikes per burst also increases as the stimulus amplitude rises, allowing each fiber to multiplex signals of vibratory frequency and intensity: the frequency information is conveyed by the temporal pattern of the spike train, and the vibratory amplitude is encoded by the total number of spikes fired per second by each fiber, as well as the total spike output of the ensemble of activated fibers. Finally, note that the spike trains of each neuron are very similar in time course and spike count from trial to trial for each condition, indicating the high reliability of sensory signaling provided by tactile afferent fibers. This reliability and predictability of sensory coding make vibration a particularly useful technique for assessing the sense of touch.

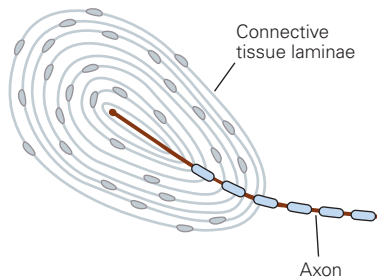
### **Both Slowly and Rapidly Adapting Fibers Are Important for Grip Control**

In addition to their role sensing the physical properties of objects, touch receptors provide important information concerning hand actions during skilled movements. Roland Johansson and Gören Westling used microneurography to determine the role of touch receptors when objects are grasped in the hand. By placing microelectrodes in the median nerve, they were able to record the firing patterns of touch fibers as an object was initially contacted by the fingers, and when it was grasped between the thumb and index finger, lifted, held above a table, lowered, and returned to rest.

They found that all four classes of touch fibers respond to grasp and that each fiber type monitors a particular function. The RA1, RA2, and SA1 fibers are normally silent in the absence of tactile stimuli. They detect contact when an object is first touched (Figure 19-10). The SA1 fibers signal the amount of grip force applied by each finger, and the RA1 fibers sense how quickly the grasp is applied. The RA2 fibers detect the small shock waves transmitted through the object when it is lifted from the table and when it is returned. We know when an object makes contact with the table top because of these vibrations and therefore can

## A Neural coding of vibration

## 1 Pacinian corpuscle



## 2 RA2 fiber

Steady pressure



Stimulus

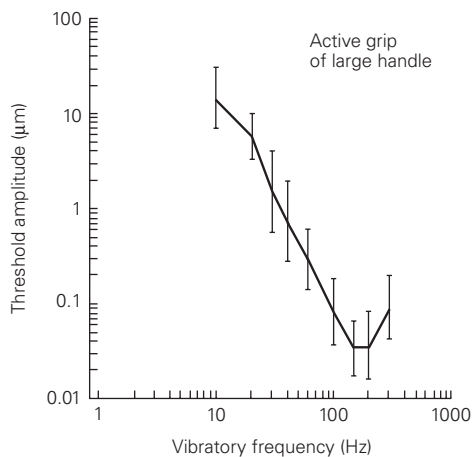
Sinusoidal vibration (110 Hz)



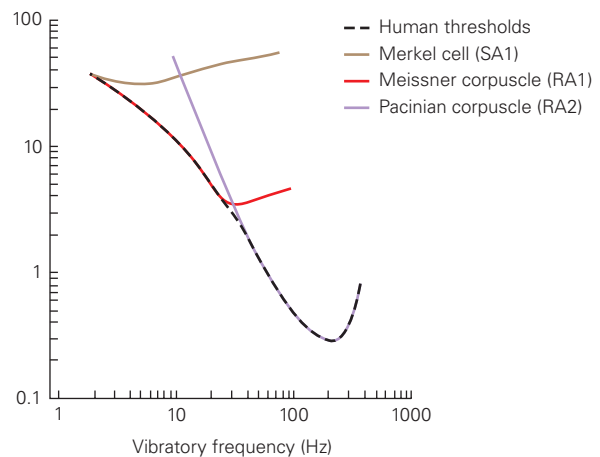
Stimulus

## B Thresholds for detection of vibration

## 1 Human perceptual thresholds



## 2 Neural thresholds

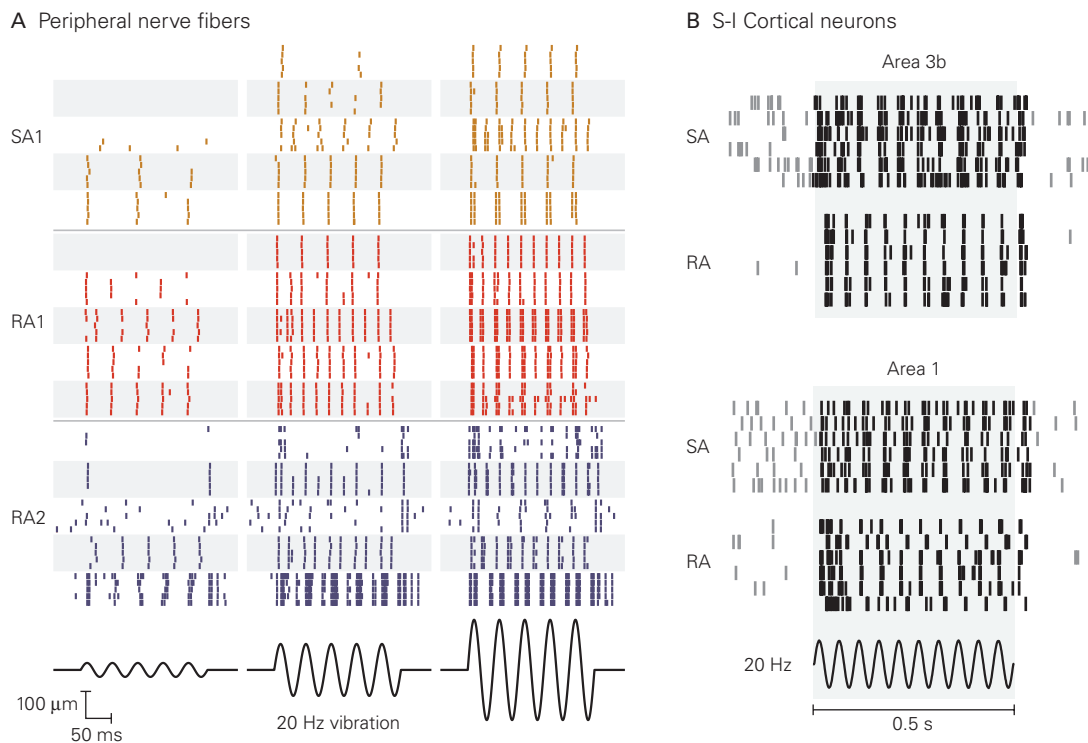


**Figure 19–8** Rapidly adapting type 2 (RA2) fibers have the lowest threshold for vibration. Vibration is the sensation produced by sinusoidal stimulation of the skin, as by the hum of an electric motor, the strings of a musical instrument, or a tuning fork used in the neurological examination.

**A. 1.** The Pacinian corpuscle consists of concentric, fluid-filled lamellae of connective tissue that encapsulate the terminal of an RA2 fiber. This structure is uniquely suited to the detection of motion. Sensory transduction in the RA2 fiber occurs in stretch-sensitive cation channels linked to the inner lamellae of the capsule. **2.** When steady pressure is applied to the skin, the RA2 fiber fires a burst at the start and end of stimulation. In response to sinusoidal stimulation (vibration), the fiber fires at regular intervals such that each action potential signals one cycle of the stimulus. Our perception of vibration as a rhythmically repeating event results from the simultaneous activation

of many RA2 units, which fire in synchrony. (Adapted from Talbot et al. 1968.)

**B. 1.** Psychophysical thresholds for detection of vibration depend on the stimulation frequency. As shown here, humans can detect vibrations as small as 30 nm at 200 Hz when grasping a large object; the threshold is higher at other frequencies and when tested with small probes. (Adapted, with permission, from Brisben, Hsiao, and Johnson 1999.) **2.** Human thresholds for vibration, measured by a small probe tip indenting the skin, match those of the most sensitive touch fibers in each frequency range. Each type of mechanosensory fiber is most sensitive to a specific range of frequencies. Slowly adapting type 1 (SA1) fibers are the most sensitive population below 5 Hz, rapidly adapting type 1 (RA1) fibers between 10 Hz and 50 Hz, and RA2 fibers above 50 Hz and 400 Hz. (Adapted, with permission, from Mountcastle, LaMotte, and Carli 1972, and Johansson, Landström, and Lundström 1982.)



**Figure 19-9** Suprathreshold vibration activates multiple classes of touch receptors.

**A.** Rasters of spike trains recorded from 15 different somatosensory fibers in macaque monkeys stimulated by 20-Hz vibratory stimuli with amplitudes of 35 (left), 130 (center), and 250 μm (right). The alternating shaded and white bands indicate the responses of individual slowly adapting type 1 (SA1), rapidly adapting type 1 (RA1), and rapidly adapting type 2 (RA2) touch fibers to five presentations of the same stimulus. Neural responses are grouped in bursts of one or more spikes that occur in phase with the indentation phase of each vibratory cycle. The total number of spikes per cycle in each fiber is correlated with the amplitude of the vibration; the total number of spikes fired across this population also reflects the vibratory amplitude. Although the individual neurons differ in the intensity of their responses, the spike

trains of each touch fiber are very similar from trial to trial and occur synchronously between neurons. (Adapted, with permission, from Muniak et al. 2007. Copyright © 2007 Society for Neuroscience.)

**B.** S-I cortical responses to 20-Hz vibration. Rasters of spike trains evoked in two neurons in area 3b (top) and two neurons in area 1 (bottom) of S-I cortex of a macaque monkey. The shaded area indicates the period of vibratory stimulation. As in the peripheral nerves, S-I cortical neurons respond to low-frequency vibration with bursts of impulses in phase with the stimulation rate. Note that the spike trains vary somewhat from trial to trial and are less periodic in area 1 than in area 3b. The periodicity of firing is even less pronounced in S-II cortex (see Figure 19-21) than in S-I. (Abbreviations: RA, rapidly adapting; SA, slowly adapting.) (Adapted, with permission, from Salinas et al. 2000. Copyright © 2000 Society for Neuroscience.)

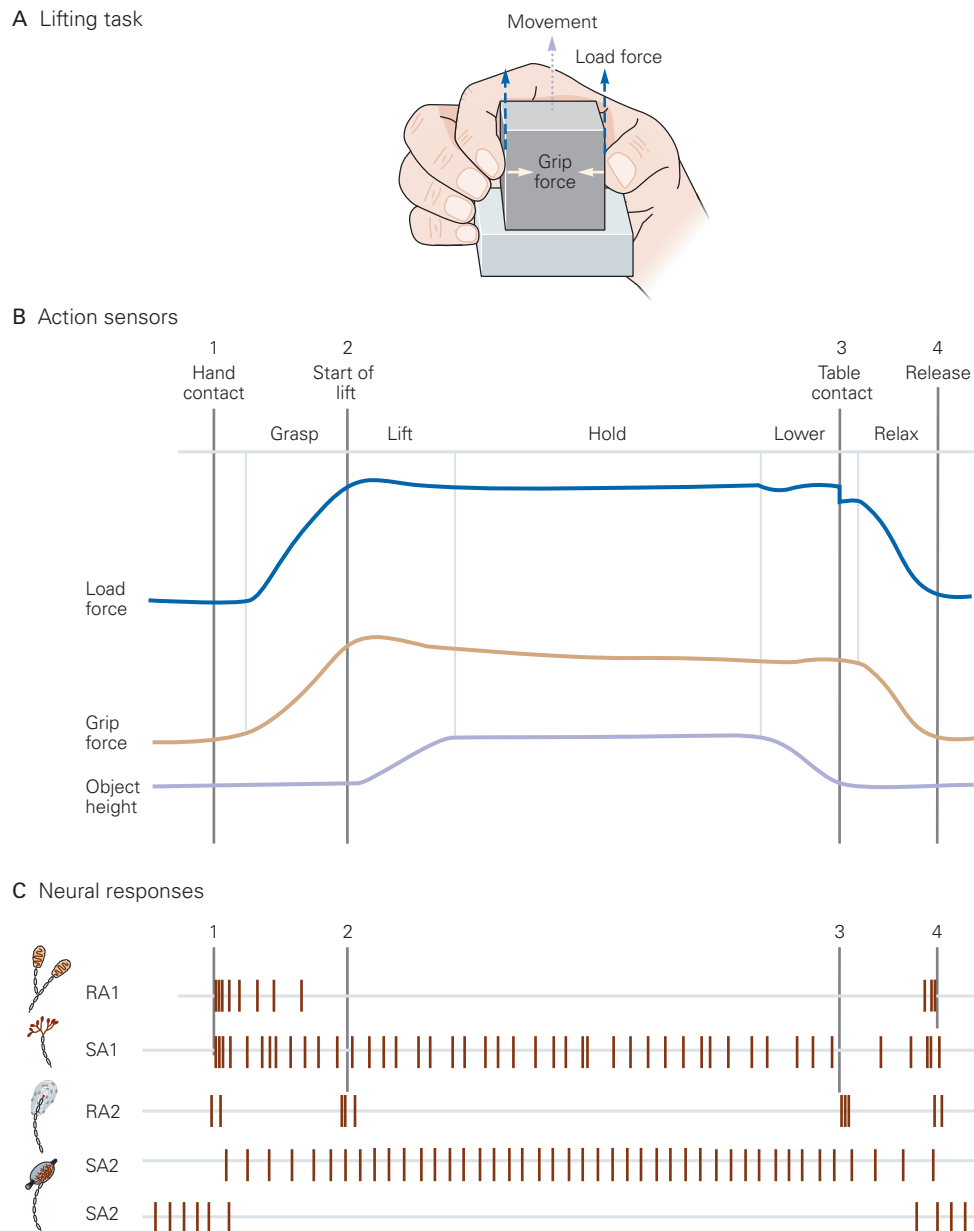
manipulate the object without looking at it. The RA1 and RA2 fibers cease responding after grasp is established. The SA2 fibers signal flexion or extension of the fingers during grasp or release of the object and thereby monitor the hand posture as these movements proceed.

Signals from the hand that report on the shape, size, and texture of an object are important factors governing the application of force during grasping. Johansson and his colleagues found that we lift and manipulate an object with delicacy—with grip forces that just exceed the forces that result in overt slip—and that the grip force is adjusted automatically to compensate for differences in the frictional coefficient between the

fingers and object surface. Subjects predict how much force is required to grasp and lift an object and modify these forces based on tactile information provided by SA1 and RA1 afferents. Objects with smooth surfaces are grasped more firmly than those with rough textures, properties coded by RA1 afferents during initial contact of the hand with an object. The significance of the tactile information in grasping is seen in cases of nerve injury or during local anesthesia of the hand; patients apply unusually high grip forces, and coordination between the grip and load forces applied by the fingers is poor.

The information supplied by the RA1 receptors to monitor grasping actions is critical for grip control,





**Figure 19–10** Sensory information from the hand during grasping and lifting. (Adapted, with permission, from Johansson 1996.)

**A.** The subject grasps and lifts a block between the thumb and fingertips, holds it above a table, and then returns it to the resting position. The normal (grip) force secures the object in the hand, and the tangential (load) force overcomes gravity. The grip force is adapted to the surface texture and weight of the object.

**B.** The grip and load forces are monitored with sensors in the object. These forces are coordinated following contact with

the object, stabilize as lift begins, and relax in concert after the object is returned to the table.

**C.** All four mechanoreceptors detect hand contact with the object, but each monitors a different aspect of the action as the task progresses. SA1 fibers encode the grip force and SA2 fibers the hand posture. RA1 fibers encode the rate of force application and movement of the hand on the object. RA2 fibers sense vibrations in the object during each task phase: at hand contact, lift-off, table contact, and release of grasp. (Abbreviations: **RA1**, rapidly adapting type 1; **RA2**, rapidly adapting type 2; **SA1**, slowly adapting type 1; **SA2**, slowly adapting type 2.)

allowing us to hold on to objects when perturbations cause them to slip unexpectedly. RA1 fibers are silent during steady grasp and usually remain quiet until the object is returned to rest and the grasp released. However, if the object is unexpectedly heavy or jolted by external forces and begins to slip from the hand, the RA1 fibers fire in response to the small tangential slip movements of the object. The net result of this RA1 activity is that grip force is increased by signals from the motor cortex.

### Tactile Information Is Processed in the Central Touch System

Sensory afferent fibers innervating the hand transmit tactile and other somatosensory information to the central nervous system through the median, ulnar, and superficial radial nerves. These nerves terminate ipsilaterally in spinal segments C6 to T1; other branches of these fibers project through the ipsilateral dorsal columns directly to the medulla, where they make synaptic connections to neurons in the cuneate nucleus, the lateral division of the dorsal column nuclei (Figure 19–11).

### Spinal, Brain Stem, and Thalamic Circuits Segregate Touch and Proprioception

Fibers in the dorsal columns, and neurons in the dorsal column nuclei, are organized topographically, with the upper body (including the hand) represented laterally in the cuneate fascicle and nucleus and the lower body represented medially in the gracile fascicle and nucleus. The somatosensory submodalities of touch and proprioception are also segregated functionally

in these regions, as individual spinal and brain stem neurons receive synaptic inputs from afferents of a single type, and neurons of distinct types are spatially separated. The rostral third of the dorsal column nuclei is dominated by neurons that process proprioceptive information from muscle afferents; tactile inputs predominate more caudally. Modality segregation is a consistent feature of the projection pathways to the primary somatosensory cortex.

Neurons in the dorsal column nuclei project their axons across the midline in the medulla to form the *medial lemniscus*, a prominent fiber tract that transmits tactile and proprioceptive information from the contralateral side of the body through the pons and midbrain to the thalamus. As a result of this crossing (or decussation) of sensory fibers, the left side of the brain receives somatosensory input from mechanoreceptors on the right side of the body, and vice versa. In transit, the somatotopic representation of the body in the medial lemniscus and within the thalamus becomes inverted; the topographic map of the body displays the face medially, the lower body laterally, and the upper body and hands in between.

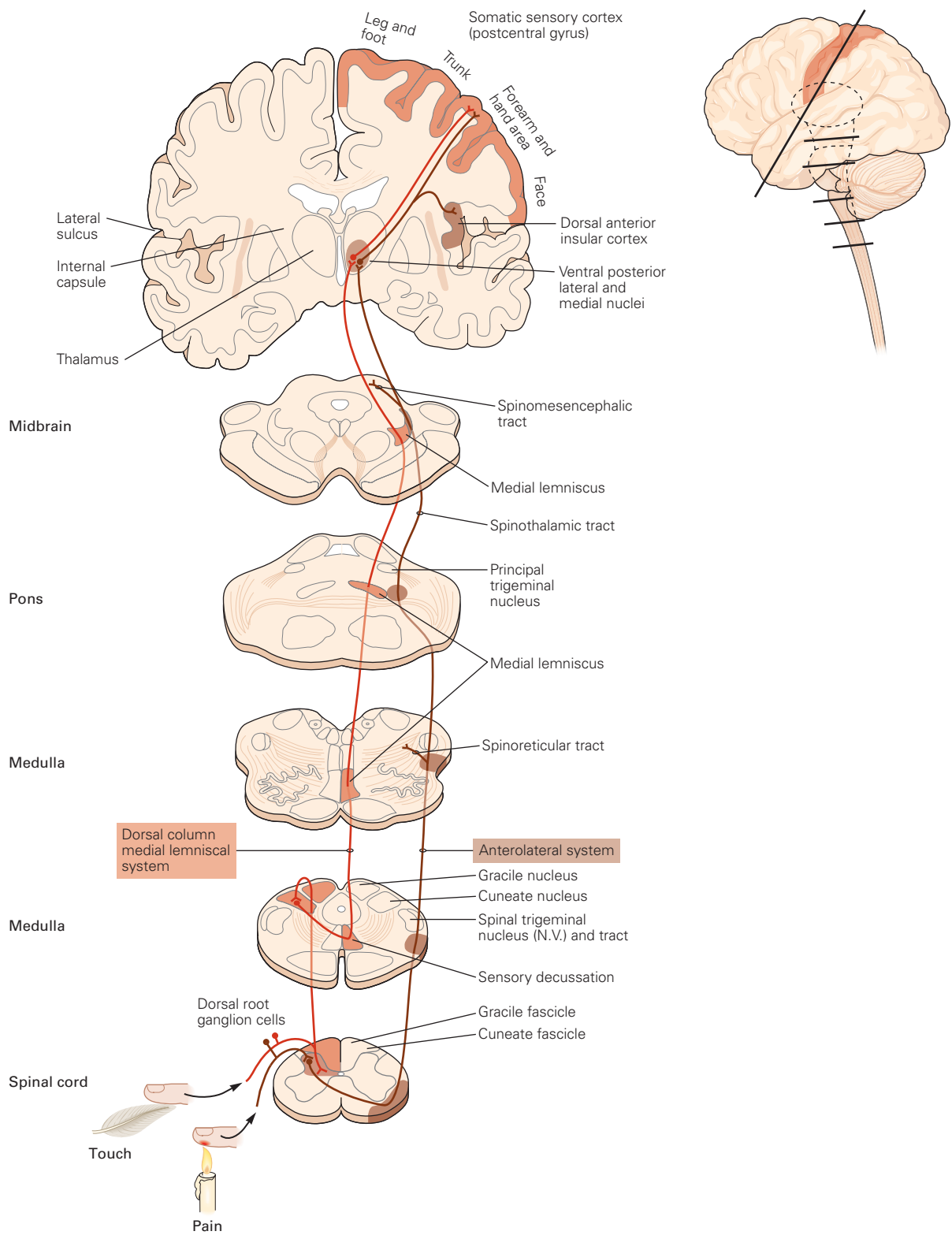
Tactile and proprioceptive information from the hand and other regions of the body is processed in distinct subnuclei of the thalamus. Touch signals from the limbs and trunk are sent via the medial lemniscus to the ventral posterior lateral (VPL) nucleus, while those from the face and mouth are conveyed to the ventral posterior medial (VPM) nucleus. Proprioceptive information from muscles and joints, including those of the hand, is transmitted to the ventral posterior superior (VPS) nucleus. These nuclei send their outputs to different subregions of the parietal lobe of the cerebral cortex. The VPL and VPM nuclei transmit cutaneous information primarily to area 3b of the primary somatosensory

**Figure 19–11** (Opposite) Somatosensory information from the limbs and trunk is conveyed to the thalamus and cerebral cortex by two ascending pathways. Brain slices along the neuraxis from the spinal cord to the cerebrum illustrate the anatomy of the two principal pathways conveying somatosensory information to the cerebral cortex. The two pathways are separated until they reach the pons, where they are juxtaposed.

**Dorsal column—medial lemniscal system (orange).** Touch and limb proprioception signals are conveyed to the spinal cord and brain stem by large-diameter myelinated nerve fibers and transmitted to the thalamus in this system. In the spinal cord, the fibers for touch and proprioception divide, one branch going to the ipsilateral spinal gray matter and the other ascending in the ipsilateral dorsal column to the medulla. The second-order fibers from neurons in the dorsal column nuclei cross the

midline in the medulla and ascend in the contralateral medial lemniscus toward the thalamus, where they terminate in the lateral and medial ventral posterior nuclei. Thalamic neurons in these nuclei convey tactile and proprioceptive information to the primary somatosensory cortex.

**Anterolateral system (brown).** Pain, itch, temperature, and visceral information is conveyed to the spinal cord by small-diameter myelinated and unmyelinated fibers that terminate in the ipsilateral dorsal horn. This information is conveyed across the midline by neurons within the spinal cord and transmitted to the brain stem and the thalamus in the contralateral anterolateral system. Anterolateral fibers terminating in the brain stem compose the spinoreticular and spinomesencephalic tracts; the remaining anterolateral fibers form the spinothalamic tract.





cortex (S-I), whereas the VPS nucleus conveys proprioceptive information principally to area 3a.

### The Somatosensory Cortex Is Organized Into Functionally Specialized Columns

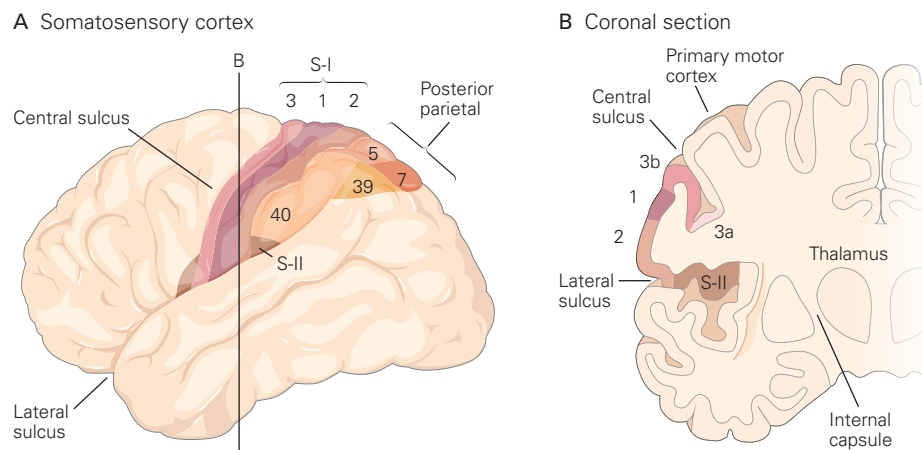
Conscious awareness of touch is believed to originate in the cerebral cortex. Tactile information enters the cerebral cortex through the primary somatosensory cortex (S-I) in the postcentral gyrus of the parietal lobe. The primary somatic sensory cortex comprises four cytoarchitectural areas: Brodmann's areas 3a, 3b, 1, and 2 (Figure 19–12). These areas are interconnected such that processing of sensory information in S-I involves both serial and parallel processing.

In a series of pioneering studies of the cerebral cortex, Vernon Mountcastle discovered that S-I cortex is organized into vertical columns or slabs. Each column is 300 to 600  $\mu\text{m}$  wide and spans all six cortical layers from the pial surface to the white matter (Figure 19–13). Neurons within a column receive inputs from the same local area of skin and respond to the same class or classes of touch receptors. A column therefore comprises an elementary functional module of

the neocortex; it provides an anatomical structure that organizes sensory inputs to convey related information about location and modality.

The columnar organization of the cortex is a direct consequence of intrinsic cortical circuitry, the projection patterns of thalamocortical axons, and migration pathways of neuroblasts during cortical development. The pattern of connections within a column is oriented vertically, perpendicular to the cortical surface. Thalamocortical axons terminate primarily on clusters of stellate cells in layer IV, whose axons project vertically toward the surface of the cortex, as well as on star pyramid cells. Thus, thalamocortical inputs are relayed to a narrow column of pyramidal cells that are contacted by the layer IV cell axons. The apical dendrites and axons of cortical pyramidal cells in other cortical layers are also largely oriented vertically, parallel to the thalamocortical axons and stellate cell axons (Figure 19–14). This allows the same information to be processed by a column of neurons throughout the thickness of the cortex.

Pyramidal neurons form the principal excitatory class of somatosensory cortex; they compose approximately 80% of S-I neurons. Pyramidal neurons in



**Figure 19–12** The somatosensory areas of the cerebral cortex in the human brain.

**A.** The somatosensory areas of cortex lie in the parietal lobe and consist of three major divisions. The *primary somatosensory cortex (S-I)* forms the anterior part of the parietal lobe. It extends throughout the postcentral gyrus beginning at the bottom of the central sulcus, extending posteriorly to the postcentral sulcus, and into the medial wall of the hemisphere to the cingulate gyrus (not shown). The S-I cortex comprises four distinct cytoarchitectonic regions: Brodmann's areas 3a, 3b, 1, and 2. The *secondary somatosensory cortex (S-II)* is located on the upper bank of the lateral sulcus (Sylvian fissure) and on the parietal operculum; it covers Brodmann's

area 43. The *posterior parietal cortex* surrounds the intraparietal sulcus on the lateral surface of the hemisphere, extending from the postcentral sulcus to the parietal-occipital sulcus and medially to the precuneus. The superior parietal lobule (Brodmann's areas 5 and 7) is a somatosensory area; the inferior parietal lobule (areas 39 and 40) receives both somatosensory and visual inputs.

**B.** A coronal section through the postcentral gyrus illustrates the anatomical relationship of S-I, S-II, and the primary motor cortex (area 4). S-II lies adjacent to area 2 in S-I and extends medially along the upper bank of the lateral sulcus to the insular cortex. The primary motor cortex lies rostral to area 3a within the anterior wall of the central sulcus.