Chapter 19: Touch

Introduction

IN THIS CHAPTER ON THE SENSE OF TOUCH, we focus on the hand because of its importance for this modality, in particular its role in the appreciation of object properties and in performance of skilled motor tasks. The human hand is one of evolution's great creations. The fine manipulative capacity provided by our fingers is possible because of their fine sensory capacity; if we lose tactile sensation in our fingers, we lose manual dexterity.

The softness and compliance of the glabrous skin play a major role in the sense of touch. When an object contacts the hand, the skin conforms to its contours, forming a mirror image of the object's surface. The resultant displacement and indentation of the skin stretches the tissue, thereby stimulating the sensory endings of mechanoreceptors at or near the region of contact.

These receptors are highly sensitive and are continually active as we manipulate objects and explore the world with our hands. They provide information to the brain about the object's position in the hand, its shape and surface texture, the amount of force applied at the contact points, and how these features change over time when the hand or the object moves. The fingertips are among the most densely innervated parts of the body, providing extensive and redundant somatosensory information about objects manipulated by the hand.

Moreover, the anatomical structure of the hand, with its multiple joints and apposable digits, enables humans to shape the hand in ways that mirror an object's overall shape, providing a hand-centered proprioceptive representation of the external world. This ability to internalize the shape of objects allows us to create tools that extend the abilities of our hands alone.

When we become skilled in the use of a tool, such as a scalpel or a pair of scissors, we feel conditions at the working surface of the tool as though our fingers were there because two groups of touch receptors monitor the vibrations and forces produced by those distant conditions. When we scan our fingers across a surface, we feel its form and texture because another group of mechanoreceptors has high spatial and temporal acuity. A blind person uses this capacity to read Braille at a hundred words per minute. When we grip and manipulate an object, we do so delicately, with only as much force as needed, because specific mechanoreceptors continually monitor slip and adjust our grip appropriately.

We are also able to recognize objects placed in the hand from touch alone. When we are handed a baseball, we recognize it instantly without having to look at it because of its shape, size, weight, density, and texture. We do not have to think about the information provided by each finger to deduce that the object must be a baseball; the information flows to memory and instantly matches previously stored representations of baseballs. Even if we have never previously handled a baseball, we perceive it as a single object, not as a collection of discrete features. The somatosensory pathways of the brain have the daunting task of integrating information from thousands of sensors in each hand and transforming it to a form suitable for cognition and action.

Sensory information is extracted for the purpose of motor control as well as cognition, and different kinds of information are extracted for those purposes. We can, for example, shift our attention from the baseball's shape to its location in the hand to readjust our grip for an effective throw or pitch. This selective attention to different aspects of the sensory information is brought about by cortical mechanisms.

Active and Passive Touch Have Distinct Goals

Touch is defined as direct contact between two physical bodies. In neuroscience, touch refers to the special sense by which contact with the body is perceived consciously. Touch can be active, as when you move your hand or some other part of the body against another surface, or passive, as when someone or something else touches you. Active touch is fundamentally a top-down process in which the subject has agency, seeks particular information, and controls what occurs. Subjects select relevant salient features of objects to determine subsequent behaviors. They choose which object to grasp and the most efficient hand shape needed to acquire it, and decide how to manipulate it to achieve particular goals. During active touch, somatosensory information depicts the physical properties of objects as well as the motor actions of the subject's hand and arm, and their

relation to the task goals. Importantly, active manipulation of objects is based upon the concept of touch as a three-dimensional modality designed to capture the volumetric, topographic, and elastic properties of objects, as first proposed by Roberta Klatzky and Susan Lederman. These three-dimensional qualities are best appreciated by active manipulation including grasping, rotation, and contour tracing by the hand.

Passive touch engages a bottom-up process in which subjects react to external stimuli specified by the experimenter or clinician. The experimenter selects and controls the location, amplitude, force, timing, duration, and spatial spread of stimuli delivered to the skin. Subsequent behaviors are guided by instructions provided in the paradigm. Tactile stimuli are classified into experimenter-selected categories and/or rated along an intensive or hedonic scale. Subjects therefore need to analyze all of the transmitted somatosensory information and select specific features guided in part by the task instructions.

Active and passive modes of tactile stimulation excite the same population of receptors in the skin and evoke similar responses in afferent fibers. They differ somewhat in cognitive features that reflect attention and behavioral goals during the period of stimulation. Passive touch is tested by naming objects or describing sensations; active touch is used when the hand manipulates objects. The sensory and motor components of touch are intimately connected anatomically in the brain and are important functionally in guiding motor behavior.

During active touch, descending fibers from motor centers of the cerebral cortex terminate on interneurons in the medial dorsal horn that receive tactile information from the skin. Similar fibers from cortical motor areas terminate in the dorsal column nuclei, providing an *efference copy* (or corollary discharge) of the motor commands that generate behavior (Chapter 30). In this manner, tactile signals from the hand resulting from active hand movements may be distinguished centrally from passively applied stimuli in the neurological exam or in psychophysical tests.

The distinction between active and passive touch is important clinically when patients have deficits in hand use. Motor deficits such as weakness, stiffness, or clumsiness may result from sensory loss, which is why passive sensory testing is important in the neurological examination. Common neurological tests for touch include measurements of detection thresholds, vibration sense, two-point or texture discrimination, and the ability to recognize form through touch (*stereognosis*). These tests measure the sensitivity and function of various receptors for touch. Deviations from expected values may help diagnose sensory deficits or lesions that underlie somatosensory dysfunction. The neural mechanisms underlying these tests are discussed in this chapter. Other common tests of somatosensory function—tendon reflexes, pinprick, and thermal tests—are discussed in other chapters.

The Hand Has Four Types of Mechanoreceptors

Tactile sensations in the human hand arise from four kinds of mechanoreceptors: Meissner corpuscles, Merkel cells, Pacinian corpuscles, and Ruffini endings (Figure 19–1). Each receptor responds in a distinctive manner depending on its morphology, innervation pattern, and depth in the skin. The sense of touch can be understood as the combined result of the information provided by these four systems acting in concert.

Touch receptors are innervated by slowly adapting or rapidly adapting axons. Slowly adapting (SA) fibers respond to steady skin indentation with a sustained discharge, whereas rapidly adapting (RA) fibers stop firing when indentation becomes stationary (Figure 19–1 and Table 19–1). Sustained mechanical sensations from the hand must accordingly arise from the SA fibers; the sensation of motion on or across the skin is signaled primarily by RA fibers.

Figure 19–1

Four types of mechanoreceptors are responsible for the sense of touch in the human hand. The terminals of myelinated sensory nerves innervating the hand are surrounded by specialized structures that detect contact on the skin. The receptors differ in morphology, innervation patterns, location in the skin, receptive field size, and physiological responses to touch. (Adapted, with permission, from Johansson and Vallbo 1983.)

A. The superficial and deep layers of the glabrous (hairless) skin of the hand each contain distinct types of mechanoreceptors. The superficial layers contain small receptor cells: Meissner corpuscles (**RA1**, rapidly adapting type 1) and Merkel cells (**SA1**, slowly adapting type 1). The sensory nerve fibers that innervate these receptors have branching terminals that innervate multiple receptors of one type. The deep layers of the skin and subcutaneous tissue contain large receptors: Pacinian corpuscles (**RA2**, rapidly adapting type 2) and Ruffini endings (**SA2**, slowly adapting type 2). Each of these receptors is innervated by a single nerve fiber, and each fiber innervates only one receptor.

B. The receptive field of a mechanoreceptor reflects the location and distribution of its terminals in the skin. Touch receptors in the superficial layers

of the skin have smaller receptive fields than those in the deep layers.

C. The nerve fibers innervating each type of mechanoreceptor respond differently when activated. The schematic spike trains show responses of each type of nerve when its receptor is activated by slowly increasing and constant pressure against the skin. The rapidly adapting fibers respond to motion at the onset and end of a pressure stimulus and adapt rapidly to constant stimulation, whereas the slowly adapting fibers respond to both steady pressure and motion and adapt slowly.

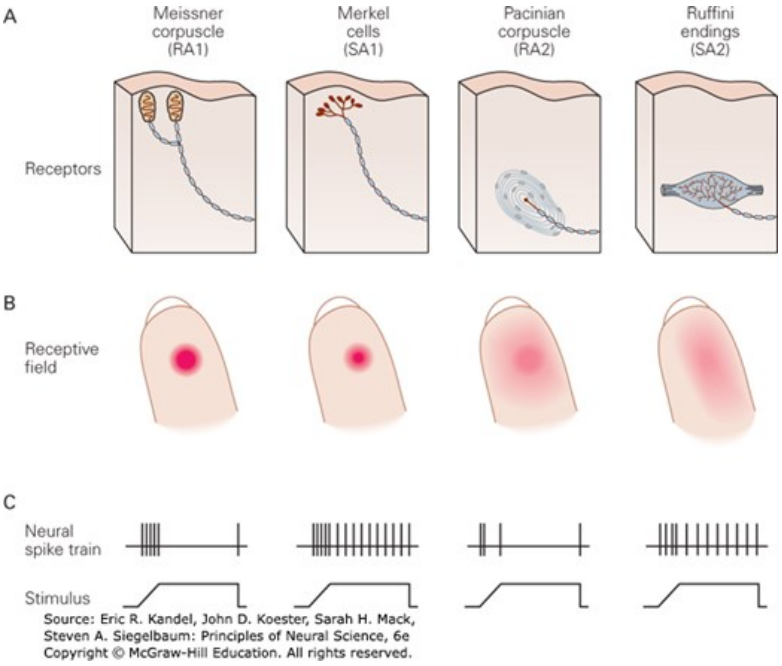


Table 19–1

Cutaneous Mechanoreceptors in Glabrous Skin

	Type 1		Type 2	
	SA1	RA1[1]	SA2	RA2[2]
Receptor	Merkel cell/neurite complex (multiple endings)	Meissner corpuscle (multiple endings)	Ruffini ending (single ending)	Pacinian corpuscle (single ending)
Location	Base of intermediate ridge surrounding sweat duct	Dermal papillae (adjacent to limiting ridge)	Skin folds, skin over joints, nail bed	Dermis (deep tissue)
Axon diameter (μm)	7–11	6–12	6–12	6–12
Conduction velocity (ms)	40–65	35–70	35–70	35–70
Best stimulus	Edges, points	Lateral motion	Skin stretch	Vibration
Response to sustained indentation	Sustained with slow adaptation (irregular firing pattern)	Phasic at stimulus onset	Sustained with slow adaptation (regular firing rate)	Phasic at stimulus onset
Frequency range (Hz)	0–100	1–300		5–1,000
Best frequency (Hz)	5	50		200
Threshold for rapid indentation or vibration (best) (μm)	8	2	40	0.01

[1]Also called RA, QA, or FA1.

[2]Also called PC or FA2.

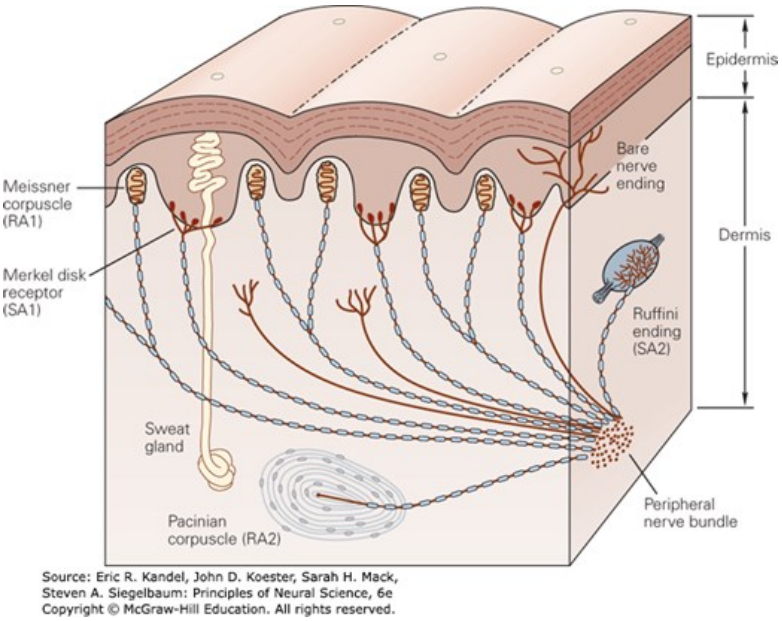
RA1, rapidly adapting type 1; **RA2**, rapidly adapting type 2; **SA1**, slowly adapting type 1; **SA2**, slowly adapting type 2.

Touch receptors in the hand are further subdivided into two types based on size and location in the skin. Type 1 touch fibers terminate in clusters of small receptor organs (Meissner corpuscles or Merkel cells) in the superficial layers of the skin at the margin between the dermis and epidermis (Figure 19–2, Box 19–1.). RA1 fibers are the most numerous tactile afferents in the hand, reaching a density of approximately 150 per cm^2 at the fingertip in man and monkey; SA1 fibers are also widely distributed in the hand, at densities of 70 per cm^2 in the fingertips.

Figure 19–2

Tactile innervation of the glabrous skin in humans. A cross section of the glabrous skin shows the principal receptors for touch in the human hand. All of these receptors are innervated by large-diameter Aβ myelinated fibers. The Meissner corpuscles and Merkel cells lie in the superficial layers of the skin at the base of the epidermis, 0.5 to 1.0 mm below the skin surface. The Meissner corpuscles are located in the dermal papillae that border the edges of each papillary ridge. The Merkel cells form dense bands below the intermediate ridge surrounding the sweat gland ducts along the center of the papillary ridges. The RA1 and SA1 fibers that innervate these receptors branch at their terminals so that each fiber innervates several nearby receptor organs. The Pacinian and Ruffini corpuscles lie within the dermis (2–3 mm thick) and in deeper tissues. The RA2 and SA2 fibers that

innervate these receptors each innervate only one receptor organ. (Abbreviations: **RA1**, rapidly adapting type 1; **RA2**, rapidly adapting type 2; **SA1**, slowly adapting type 1; **SA2**, slowly adapting type 2.)



Box 19–1 Fingerprint Structure Enhances Touch Sensitivity in the Hand

The histological structure of glabrous skin—the smooth, hairless skin of the palm and fingertips—plays a crucial role in the hand's sensitivity to touch. The fingerprints are formed by a regular array of parallel ridges in the epidermis, the papillary ridges (Figure 19–3). Regularly spaced Merkel cells below sweat ducts that emerge from the center of each ridge provide a spatial grid that allows us to localize stimuli precisely on our fingertips.

Each ridge is bordered by epidermal folds—the limiting ridges—that are visible as thin lines on the fingers, palms, and feet. The limiting ridges increase the stiffness and rigidity of the skin, protecting it from damage when contacting objects or when walking barefooted. Meissner corpuscles are typically located in dermal papillae adjacent to the limiting ridges; each dermal papilla contains several Meissner corpuscles and is innervated by two to five RA1 axons (Figure 19–4A).

Merkel cells, innervated by an SA1 fiber, are densely clustered in the center of each papillary ridge, at the base of the intermediate ridge surrounding the epidermal sweat ducts (Figure 19–4A), placing them in an excellent position to detect deformation of the epidermis from pressure or lateral stretch. They perform similar tactile receptive functions as Merkel cells in the touch domes of hairy skin (Chapter 18).

The fingerprints give the glabrous skin a corrugated, rough structure that increases friction, allowing us to grasp objects without slippage. Frictional forces are augmented further when these ridges contact the textured surfaces of objects. Smooth surfaces slide easily underneath the fingers and thus require greater grip force to maintain stability in the hand; the screw caps on bottles are often ridged to make them easy to turn. Frictional forces between the limiting ridges and objects also amplify our sensations of surface features when we palpate objects, generating vibrations that allow us to detect small irregularities such as the grain of wood and threads of fabrics.

The regular spacing of the papillary ridges—and the precise localization of specific receptors within this grid—allows us to repeatedly scan surfaces with back-and-forth hand movements while preserving a constant spatial alignment of adjacent surface features. They also provide an anatomical grid for referencing the precise location of tactile stimuli.

Figure 19–3

The skin of the human fingertip.

A. Scanning electron micrograph of the fingerprints in the human index finger. The glabrous skin of the hand is structured as arrays of papillary ridges and intervening sulci (limiting ridges) that recur at regular intervals. Globules of sweat exude from ducts at the center of the papillary ridges, forming a regularly spaced grid-like pattern along the center of each ridge. The Merkel cells are located in dense clusters below the sweat ducts at the base of the epidermis along the center of the papillary ridges (see Figure 19–2). (Adapted, with permission, from Quilliam 1978.)

B. Histological section of the glabrous skin cut parallel to the skin surface. The Meissner corpuscles, here immunostained for cholinesterase, form regularly spaced chains along both sides of each papillary ridge adjacent to the limiting ridge. Thus, Meissner corpuscles and Merkel cells form alternating bands of rapidly adapting type 1 (RA1) and slowly adapting type 1 (SA1) touch receptors that span each fingerprint ridge. (Adapted, with permission, from Bolanowski and Pawson 2003.)

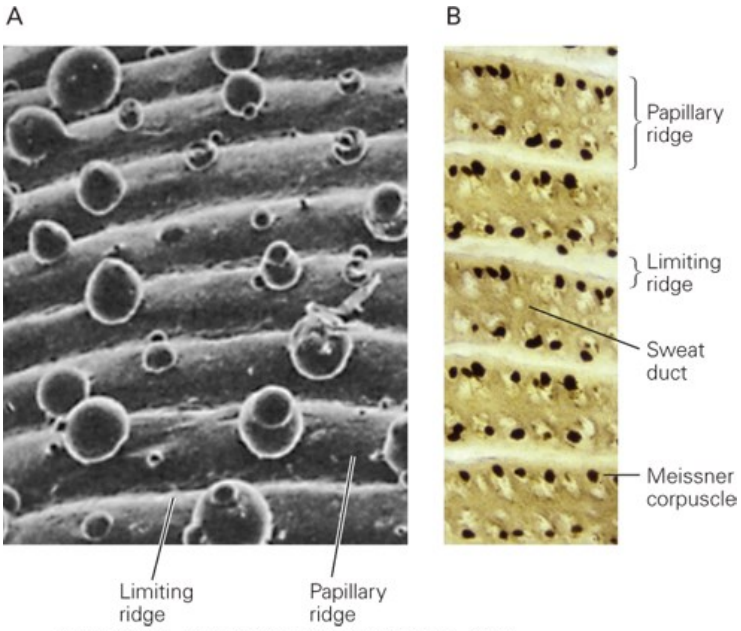


Figure 19–4

Innervation pattern of Meissner corpuscles and Merkel cells in glabrous and hairy skin.

A. A confocal transverse section of a papillary ridge in the human fingertip skin shows the innervation pattern of mechanoreceptors. Meissner corpuscles are located in dermal papillae just below the epidermis (**blue**) bordering the limiting ridge and are innervated by two or more rapidly adapting type 1 (**RA1**) fibers. The fibers lose their myelin sheaths (**orange**) when entering the receptor capsule, exposing broad terminal bulbs (**green**) at which sensory transduction occurs. Individual slowly adapting type 1 (**SA1**) fibers innervate groups of Merkel cells clustered at the base of the intermediate ridge, providing localized signals of pressure applied to that ridge. Scale bar = 50 µm. (Adapted, with permission, from Nolano et al. 2003. Copyright © 2003 American Neurological Association.)

B. A higher-magnification micrograph portrays keratin-8 antibody-labeled Merkel cells (**red**) innervated by an SA1 fiber (**green**) labeled with neurofilament heavy polypeptide (NFH^+). Each nerve fiber extends multiple branches parallel to the surface of the skin that allow it to integrate tactile information from multiple receptor cells in a small zone of skin. The diameter of each Merkel cell is approximately 10 µm. (Adapted, with permission, from Snider 1998. Copyright © 1998 Springer Nature.)

Type 2 fibers innervate the skin sparsely and terminate in single large receptors (Pacinian corpuscles and Ruffini endings) located in the dermis or in subcutaneous tissue. These receptors are larger and less numerous than the receptor organs of the type 1 fibers. The large size of type 2 receptors allows them to sense mechanical displacement of the skin at some distance from the sensory nerve endings. The density of RA2 fibers in human fingers is only 21 per cm^2; SA2 fibers are the least abundant, providing only 9 fibers per cm^2.

A Cell's Receptive Field Defines Its Zone of Tactile Sensitivity

Individual mechanoreceptor fibers convey information from a limited area of skin called the *receptive field* (Chapter 18). Tactile receptive fields in the human hand were first studied by Åke Vallbo and Roland Johansson using microneurography. They inserted microelectrodes through the skin into the median or ulnar nerves in the human forelimb and recorded the responses of individual afferent fibers. They found that in humans, as in other primates, there are important differences between touch receptors, both in their physiological responses and in the structure of their receptive fields.

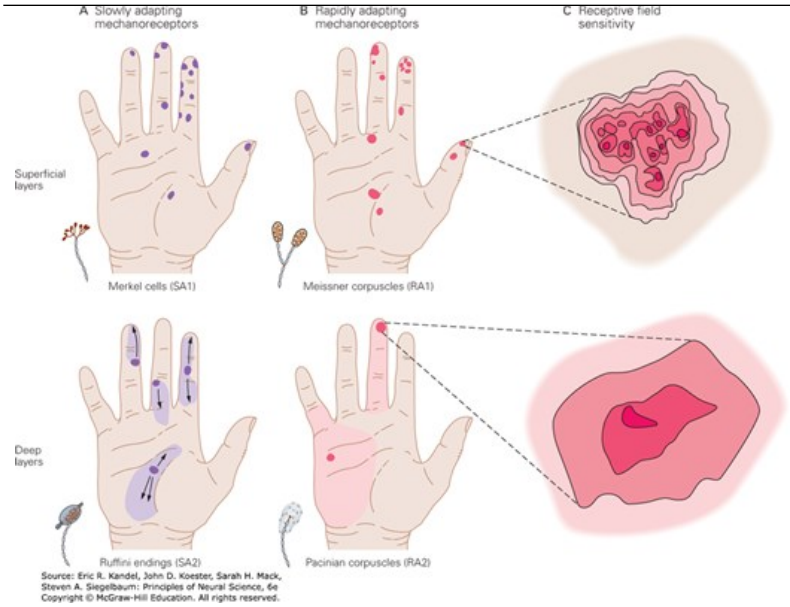
Type 1 fibers have small, highly localized receptive fields with multiple spots of high sensitivity that reflect the branching patterns of their axon terminals in the skin (Figure 19–5). An RA1 axon typically innervates 10 to 20 Meissner corpuscles, integrating information from several adjacent fingerprint ridges. An SA1 fiber innervates approximately 20 Merkel cells in young adults (Figure 19–4B); the number of Merkel cells drops significantly as we age.

Figure 19–5

Receptive fields in the human hand are smallest at the fingertips. Each colored area on the hands indicates the receptive field of an individual sensory nerve fiber. (Adapted, with permission, from Johansson and Vallbo 1983.)

A–B. In the superficial layers of skin, the receptive fields of type 1 receptors encompass spot-like patches of skin. In the deep layers, type 2 receptive fields extend across wide regions of skin (**light shading**), but responses are strongest in the skin directly over the receptor (**dark spots**). The **arrows** indicate the directions of skin stretch that activate slowly adapting type 2 (**SA2**) fibers.

C. Pressure sensitivity throughout the receptive field is shown as a contour map. The most sensitive regions are indicated in **deep red** and the least sensitive areas in **pale pink**. The receptive field of a rapidly adapting type 1 (**RA1**) fiber (**above**) has many points of high sensitivity, marking the positions of the group of Meissner corpuscles innervated by the fiber. The receptive field of a rapidly adapting type 2 (**RA2**) fiber (**below**) has a single point of maximum sensitivity overlying the Pacinian corpuscle. The receptive field contour map of slowly adapting type 1 (**SA1**) fibers is similar to that of RA1 fibers. Likewise, the receptive field map of SA2 fibers resembles that of RA2 fibers.



In contrast, type 2 fibers innervating the deep layers of skin are connected to only a single Pacinian corpuscle or Ruffini ending. As these receptors are large, they collect information from a broader area of skin. Their receptive fields typically contain a single "hot spot" where sensitivity to touch is greatest; this point is located directly above the receptor (Figure 19–5).

Receptive fields on the fingertips are the smallest on the body, averaging 11 mm^2 for SA1 fibers and 25 mm^2 for RA1 fibers. The small fields complement the high density of receptors in the fingertips. Receptive fields become progressively larger on the proximal phalanges and the palm, consistent with the lower density of mechanoreceptors in these regions. Importantly, the receptive fields of type 1 fibers are significantly smaller than most objects that contact the hand, and therefore signal the spatial properties of only a limited portion of an object. As in the visual system, the spatial features of objects are distributed across a population of stimulated receptors whose responses are integrated in the brain to form a unified percept.

Each RA2 axon terminates without branching in a single Pacinian corpuscle, and each Pacinian corpuscle receives but a single RA2 axon. Pacinian corpuscles are large onion-like structures in which successive layers of connective tissue are separated by fluid-filled spaces (see Figure 19–8A1). These layers surround the unmyelinated RA2 ending and its myelinated axon up to one or more nodes of Ranvier. The capsule amplifies high-frequency vibration, a role that is important for tool use. Estimates of the number of Pacinian corpuscles in the human hand range from 2,400 in the young to 300 in the elderly.

The SA2 fibers innervate Ruffini endings concentrated at the finger and wrist joints, the skin surrounding the fingernails, and along the skin folds in the palm. The Ruffini endings are elongated fusiform structures that enclose collagen fibrils extending from the subcutaneous tissue to folds in the skin at the joints, in the palm, or at the fingernail borders. The SA2 nerve endings are intertwined between the collagen fibers in the capsule, as in Golgi tendon organs (Box 32–4), and are excited by stimuli that stretch the skin along its long axis.

Two-Point Discrimination Tests Measure Tactile Acuity

The ability of humans to resolve spatial details of textured surfaces depends on which region of the body is contacted. When a pair of probes is spaced several millimeters apart on the hand, each probe is perceived as a distinct point because it produces a separate dimple in the skin and stimulates nonoverlapping populations of receptors. As the probes are moved closer together, the two sensations become blurred because both probes are contained within the same receptive fields. The spatial interactions between tactile stimuli form the basis of neurological tests of *two-point discrimination* and texture recognition.

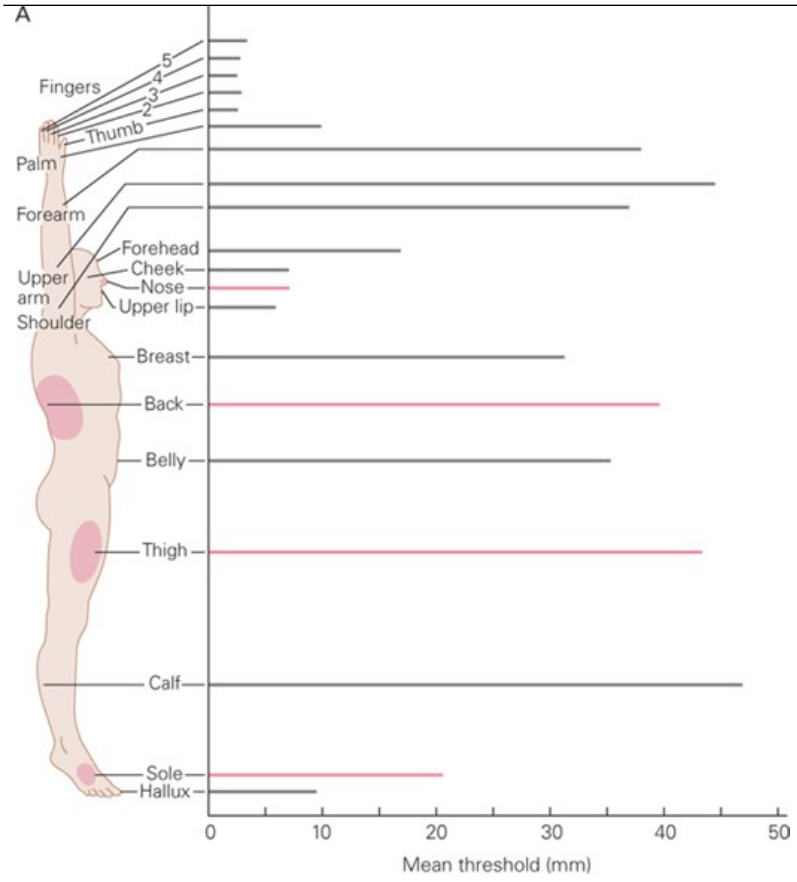
The threshold for *tactile acuity*—the separation that defines performance midway between chance and perfect discrimination—is approximately 1 mm on the fingertips of young adults, but declines in the elderly to about 2 mm. Tactile acuity is highest on the fingertips and the lips, where receptive fields are smallest. Tactile acuity on proximal parts of the body decreases in parallel with the size of receptive fields of SA1 and RA1 fibers (Figure 19–6A).

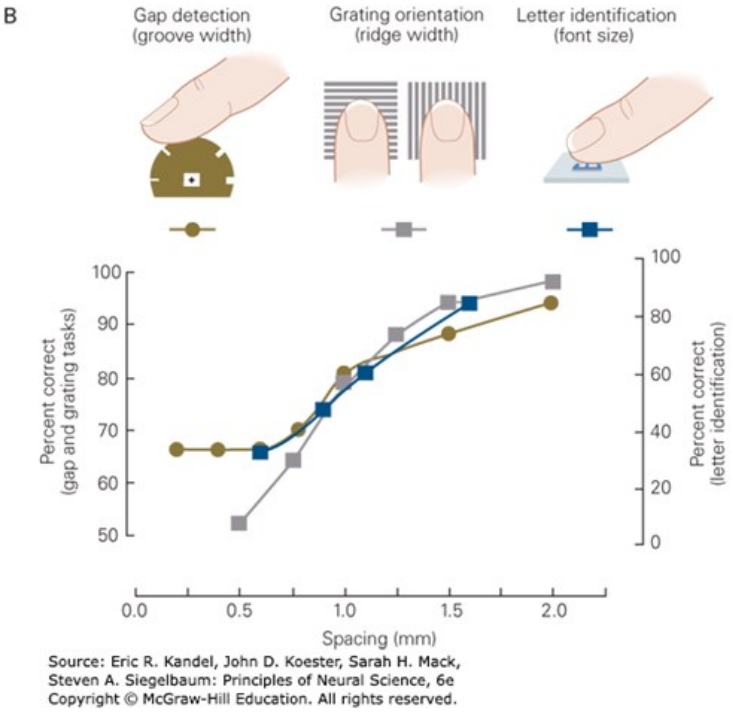
Figure 19–6

Tactile acuity in the human hand is highest on the fingertip.

A. The two-point threshold measures the minimum distance at which two stimuli are resolved as distinct. This distance varies for different body regions; it is approximately 2 mm on the fingers, but as much as 10 mm on the palm and 40 mm on the arm, thigh, and back. The mean two-point perceptual thresholds of different body parts, indicated by **pink** lines in the bar graph, match the mean receptive field diameters of the corresponding pink zones on the body. The greatest discriminative capacity is afforded in the fingertips, lips, and tongue, which have the smallest receptive fields. (Adapted, with permission, from Weinstein 1968. © Charles C. Thomas Publisher, Ltd.)

B. Spatial acuity is measured in psychophysical experiments by having a blindfolded subject touch a variety of textured surfaces. As shown here, the subject is asked to determine whether the surface of a wheel is smooth or contains a gap, whether the ridges of a grating are oriented across the finger or parallel to its long axis, or which letters appear on raised type used in letterpress printing. The tactile acuity threshold is defined as the groove width, ridge width, or font size that yields 75% correct performance (detectable midway between chance and perfect accuracy). The threshold spacing on the human fingertip is 1.0 mm in each of these tests. (Adapted, with permission, from Johnson and Phillips 1981.)





When we grasp or touch an object, we can discriminate features of its surface separated by as little as 0.5 mm. Humans are able to distinguish horizontal and vertical orientations of gratings with remarkably narrow spacing of the ridges (Figure 19–6B). Long edges, such as the ridges of a grating, evoke stronger responses from RA1 and SA1 afferents when they stimulate multiple sensory endings in the receptive field simultaneously,

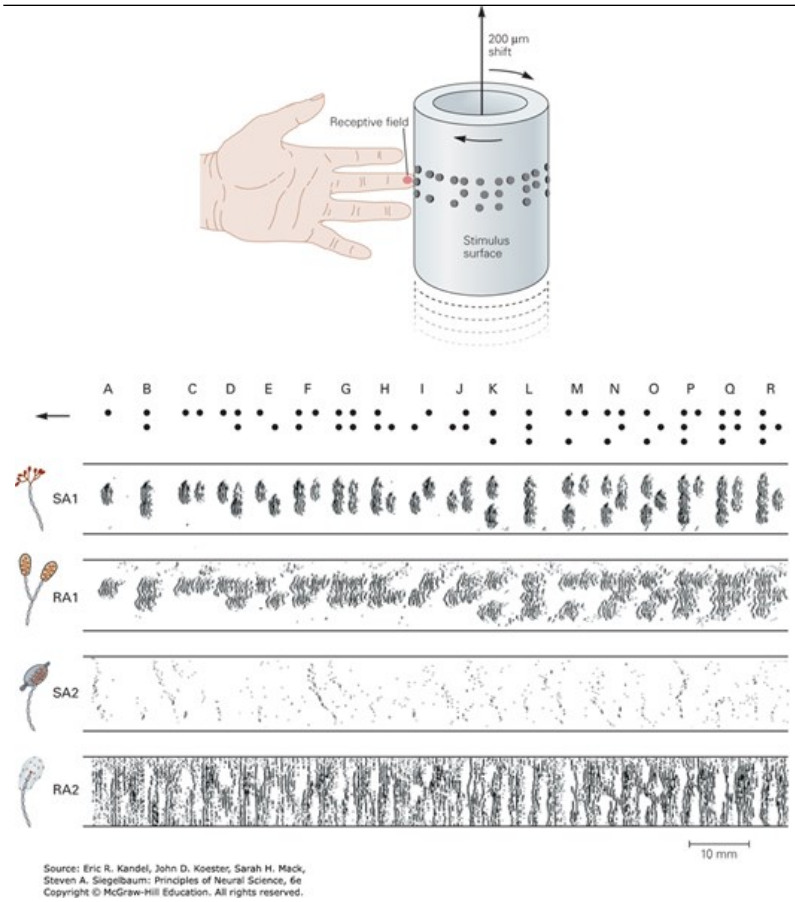
stressing the importance of multisensor receptive fields for tactile information processing. Roland Johansson and Andrew Pruszynski recently found that RA1 and SA1 fibers respond more intensely to edges that contact multiple sensory endings, allowing these afferents to distinguish vertical, horizontal, or oblique orientations.

Tactile acuity is slightly greater in women than in men and varies between fingers but not between hands; the gender difference is related primarily to the smaller papillary ridge diameter in women, and the resultant higher density of SA1 fibers per cm^2 of skin. The distal pad of the index finger has the keenest sensitivity; spatial acuity declines progressively from the index to the little finger and falls rapidly at locations proximal to the distal finger pads. Tactile spatial resolution is 50% poorer at the distal pad of the little finger and six to eight times coarser on the palm.

Blind individuals use the fine spatial sensitivity of SA1 and RA1 fibers to read Braille. The Braille alphabet represents letters as simple dot patterns that are easy to distinguish by touch. A blind person reads Braille by moving the fingers over the dot patterns. This hand 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.

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.)



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 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.

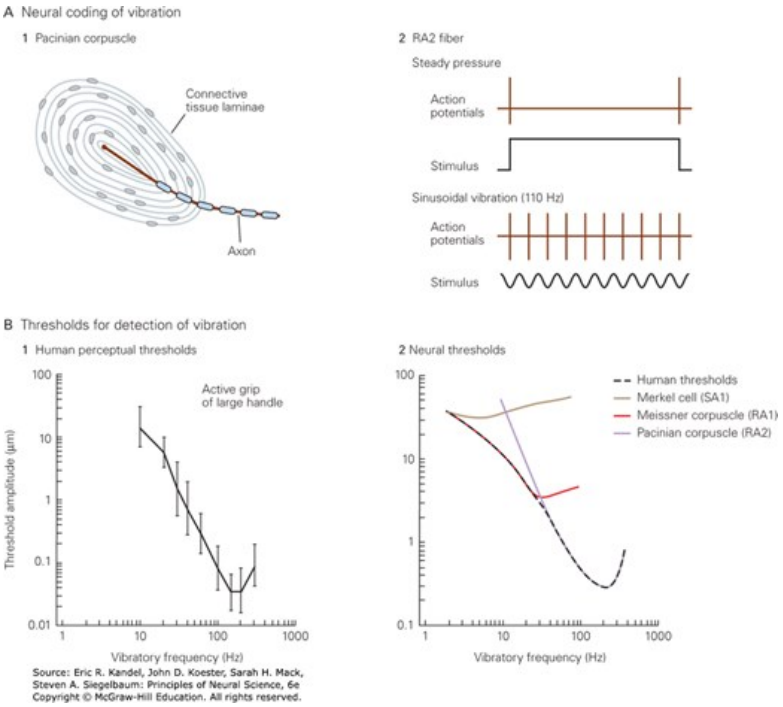
The RA2 receptor, the Pacinian corpuscle, is the most sensitive mechanoreceptor in the somatosensory system. It is exquisitely responsive to high-frequency (30–500 Hz) vibratory stimuli and can detect vibration of 250 Hz in the nanometer range (Figure 19–8B2). The ability of Pacinian corpuscles to filter 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.

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.)



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.

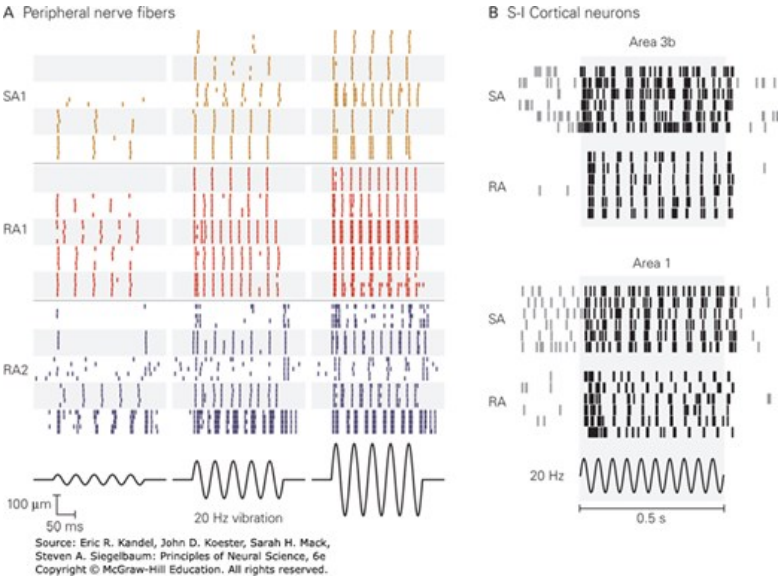
Figure 19–9

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.)



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 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.

Figure 19–10

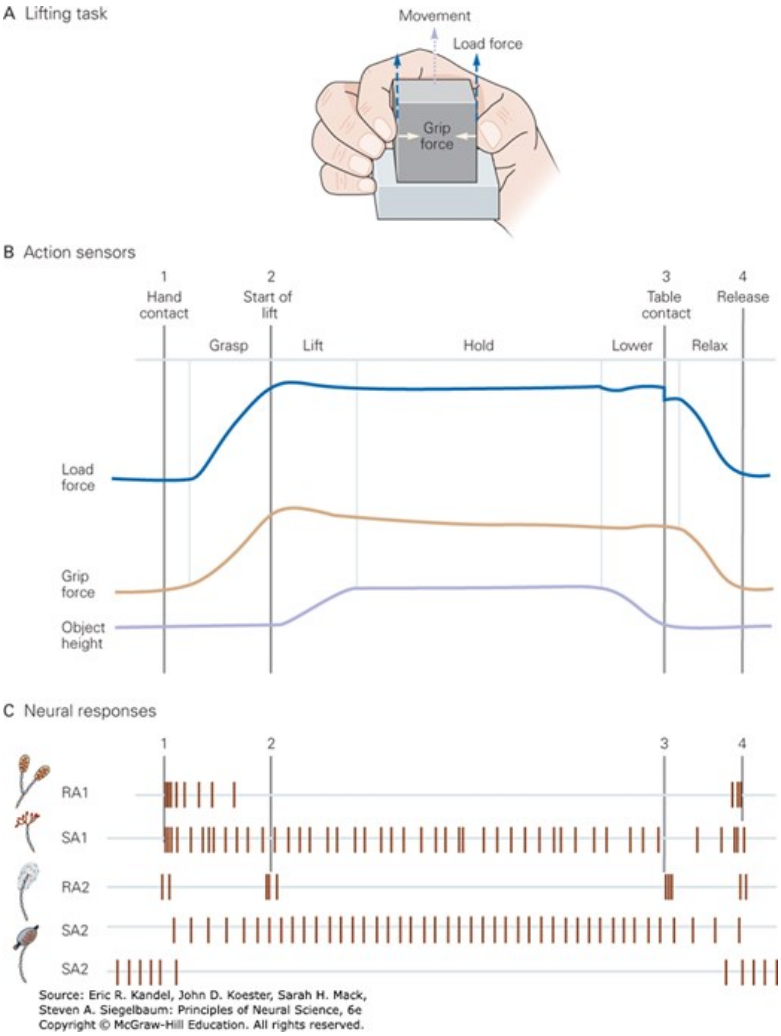
Sensory information from the hand during grasping and lifting. (Adapted, with permission, from Johansson 1996.)

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.)



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, 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

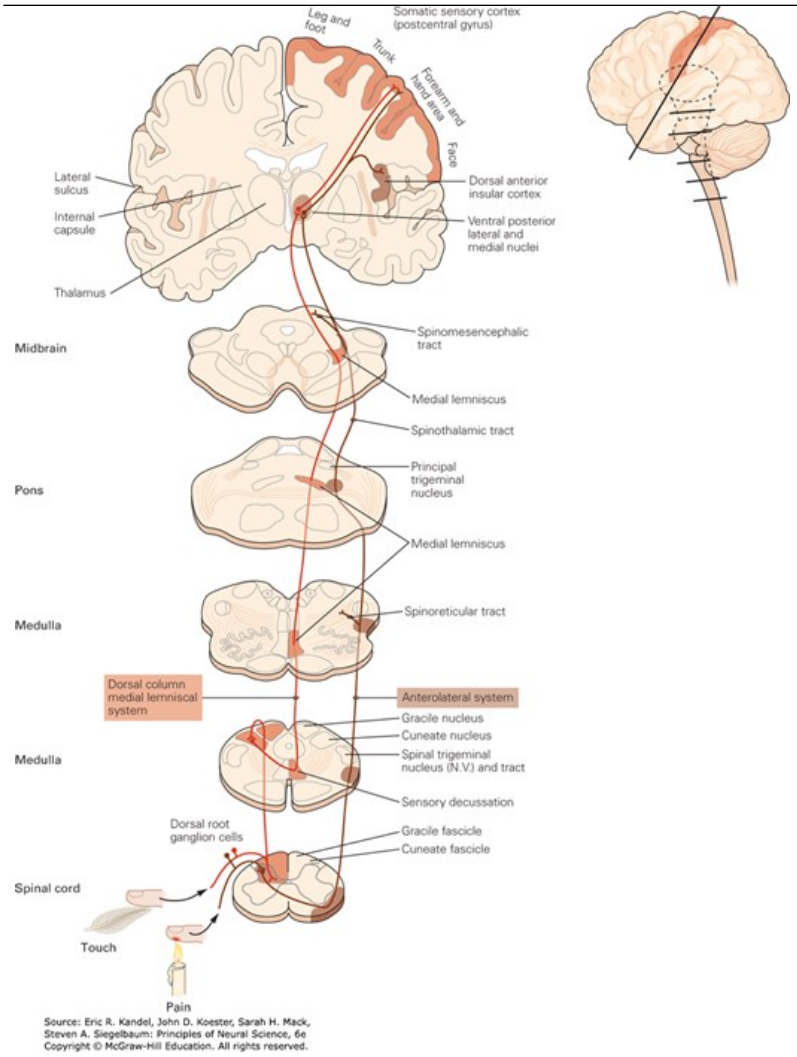
Sensory afferent fibers innervating the hand transmit tactile and other somatosensory information to the central nervous system through the median, ulnar, and superficial radial nerves. These nerves terminate ipsilaterally in spinal segments C6 to T1; other branches of these fibers project through the 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).

Figure 19–11

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.



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 cortex (S-I), whereas the VPS

nucleus conveys proprioceptive information principally to area 3a.

The Somatosensory Cortex Is Organized Into Functionally Specialized Columns

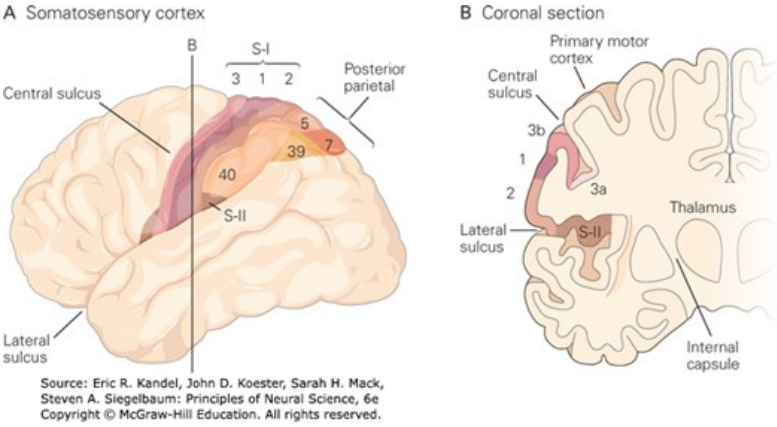
Conscious awareness of touch is believed to originate in the cerebral cortex. Tactile information enters the cerebral cortex through the primary somatosensory cortex (S-I) in the postcentral gyrus of the parietal lobe. The primary somatic sensory cortex comprises four cytoarchitectural areas: Brodmann's 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.

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.

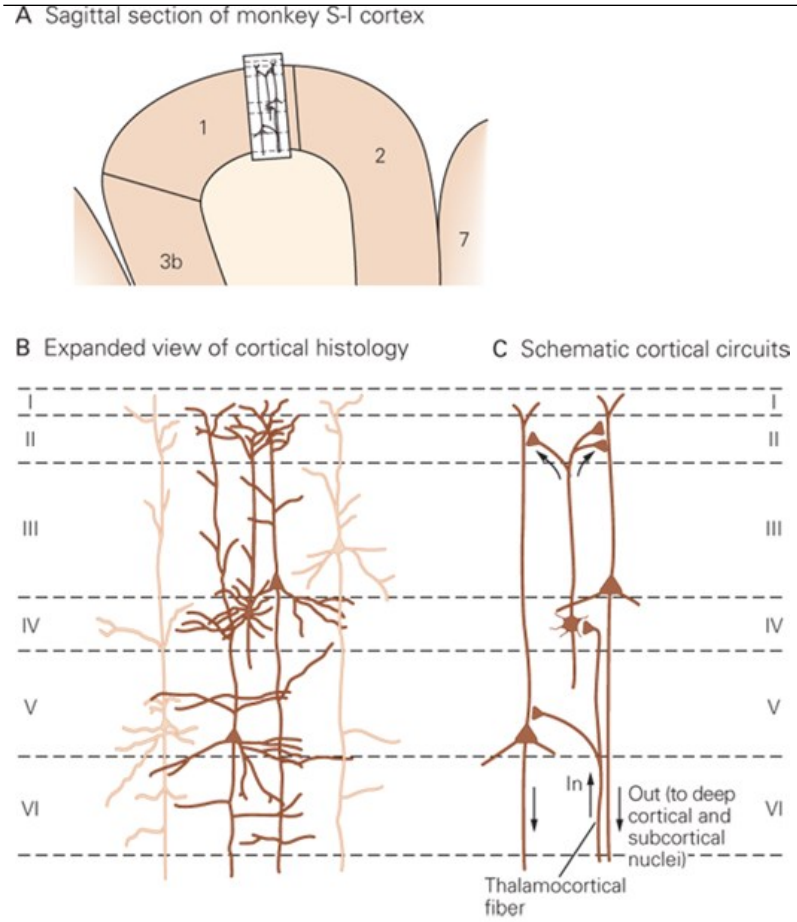
B. A coronal section through the postcentral gyrus illustrates the anatomical relationship of S-I, S-II, and the primary motor cortex (area 4). S-II lies adjacent to area 2 in S-I and extends medially along the upper bank of the lateral sulcus to the insular cortex. The primary motor cortex lies rostral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



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 µm 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.

Figure 19–13

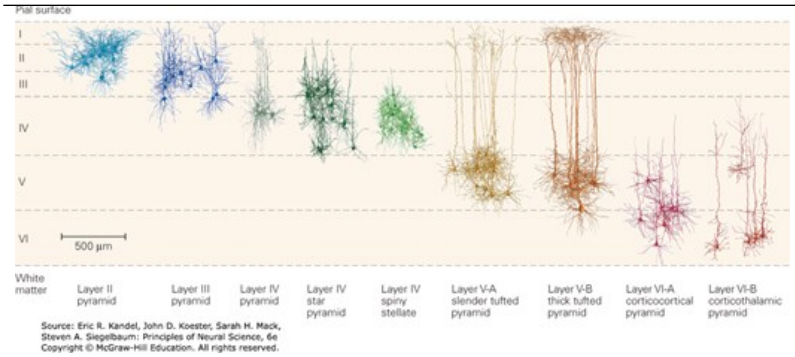
Organization of neuronal circuits within a column of somatosensory cortex. Sensory inputs from the skin or deep tissue are organized in columns of neurons that run from the surface of the brain to the white matter. Each column receives thalamic input primarily in layer IV from one part of the body. Excitatory neurons in layer IV send their axons vertically toward the surface of the cortex, contacting the dendrites of pyramidal neurons in layers II and III (supragranular layers) as well as the apical dendrites of pyramidal cells in the infragranular layers (layers V and VI). In this manner, tactile information from a body part such as a finger is distributed vertically within a column of neurons.



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.

Figure 19–14

Columnar organization of the somatosensory cortex. Cortical excitatory neurons in the six layers have distinctive pyramidal-type shapes with large cell bodies, a single apical dendrite that projects vertically toward the cortical surface and arborizes in more superficial layers, and multiple basal dendrites that arborize close to the cell body. Pyramidal neurons differ in size, gene expression patterns, the length and thickness of their apical dendrite, and the projection targets of their axons. All of these neurons synapse on targets within the cerebral cortex. Additionally, the pyramidal neurons in layer V project subcortically to the spinal cord, brain stem, midbrain, and basal ganglia. Corticothalamic neurons in layer VI project back to the afferent thalamic nucleus providing sensory input to that column. Spiny stellate neurons in layer IV are the only excitatory cells shown that are not pyramidal neurons. (Adapted, with permission, from Oberlaender et al. 2012.)



Pyramidal neurons form the principal excitatory class of somatosensory cortex; they compose approximately 80% of S-I neurons. Pyramidal neurons in each of the six cortical layers project to specific targets (Figure 19–14). Recurrent horizontal connections link pyramidal neurons in the same or neighboring columns, allowing them to share information when activated simultaneously by the same stimulus. Neurons in layers II and III also project to layer V in the same column, to higher cortical areas in the same hemisphere, and to mirror-image locations in the opposite hemisphere. These feedforward connections to higher cortical areas allow complex signal integration, as described later in this chapter.

Pyramidal neurons in layer V provide the principal output from each column. They receive excitatory inputs from neurons in layers II and III in the same and adjacent columns as well as sparse thalamocortical inputs. Neurons in the superficial portion of layer V (layer V-A) send feedforward outputs bilaterally to layer IV of higher-order cortical areas (see Figure 19–17C) as well as to the striatum. Neurons deeper in layer V (layer V-B) project to subcortical structures, including the basal ganglia, superior colliculus, pontine and other brain stem nuclei, the spinal cord, and dorsal column nuclei. Layer VI neurons project to local cortical neurons, and back to the thalamus, particularly to regions of the ventral posterior nuclei providing inputs to that column.

In addition to feedforward signals of information from touch receptors, feedback signals from layers II and III of higher somatosensory cortical areas are provided to layer I in lower cortical areas, regulating their excitability. Such feedback signals originate not only in somatosensory cortical areas but also in sensorimotor areas of the posterior parietal cortex, frontal motor areas, limbic areas, and regions of the medial temporal lobe involved in memory formation and storage. These feedback signals are thought to play a role in the selection of sensory information for cognitive processing (by the mechanisms of attention) and in short-term memory tasks. Feedback pathways may also gate sensory signals during motor activity. Various local inhibitory interneurons within each column serve to focus columnar output.

Cortical Columns Are Organized Somatotopically

The columns within the primary somatic sensory cortex are arranged topographically such that there is a complete somatotopic representation of the body in each of the four areas of S-I (Figure 19–15). The cortical map of the body corresponds roughly to the spinal dermatomes (see Figure 18–13). Sacral segments are represented medially, lumbar and thoracic segments centrally, cervical segments more laterally, and the trigeminal representation of the face at the most lateral portion of S-I cortex. Knowledge of the neural map of the body in the brain is important for localizing damage to the cortex from stroke or head trauma.

Figure 19–15

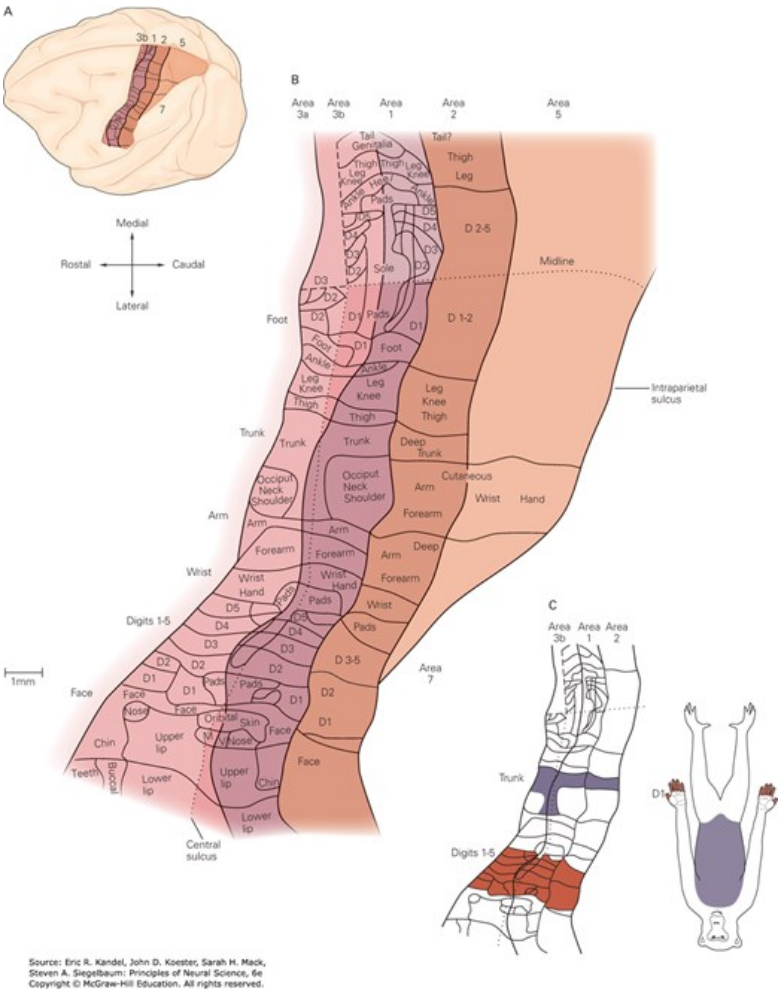
Each region of the primary somatosensory cortex contains a topographic neural map of the entire body surface. (Adapted, with permission, from Nelson et al. 1980. Copyright © 1980 Alan R. Liss, Inc.)

A. The primary somatosensory cortex in the macaque monkey lies caudal to the central sulcus as in the human brain. The colored areas on the macaque cortex correspond to the homologous Brodmann's areas of the human brain in Figure 19–12. Area 5 in the macaque monkey is homologous to areas 5 and 7 in humans. Area 7 in macaques is homologous to areas 39 and 40 in humans.

B. The flat map diagram on the right shows the somatosensory cortex of the macaque monkey unfolded along the central sulcus (**dotted line** that parallels the border between areas 3b and 1). The upper part of the diagram includes cortex unfolded from the medial wall of the hemisphere. Body maps were obtained from microelectrode recordings in the postcentral gyrus. The body surface is mapped to columns within rostrocaudal bands arranged in the order of the spinal dermatomes. The body maps in areas 3b and 1 form mirror images of the distal-proximal or dorsal-ventral axes of

each dermatome. Each finger (D5–D1) has its own representation along the medial-lateral axis of the cortex in areas 3b and 1, but inputs from several adjacent fingers converge in the receptive fields of neurons in areas 2 and 5.

C. Cortical magnification of highly innervated skin areas. Although the trunk (**violet**) is covered by a greater area of skin than the fingers (**red**), the number of cortical columns responding to touch on the fingers is nearly three times the number activated by touching the trunk because of the higher innervation density of the fingers.



The body surface is represented in at least 10 distinct neural maps in the parietal lobe: four in S-I, four in S-II, and at least two in the posterior parietal cortex. As a result, these regions mediate different aspects of tactile sensation. Neurons in areas 3b and 1 of S-I process details of surface texture, whereas those in area 2 represent the size and shape of objects. These attributes of somatic sensation are further elaborated in S-II and the posterior parietal cortex, where neurons are engaged in object discrimination and manipulation, respectively.

Another important feature of somatotopic maps is the amount of cerebral cortex devoted to each body part. The neural map of the body in the human brain, termed the *homunculus*, does not duplicate exactly the spatial topography of the skin. Rather, each part of the body is represented in proportion to its importance to the sense of touch. Disproportionately large areas are devoted to certain body regions, particularly the hand, foot, and mouth, and relatively smaller areas to more proximal body parts. In humans and monkeys, more cortical columns are devoted to the fingers than to the entire trunk (Figure 19–15C).

The amount of cortical area devoted to a unit area of skin—called the *cortical magnification*—varies by more than a hundredfold across different body surfaces. It is closely correlated with the innervation density and thus the spatial acuity of the touch receptors in an area of skin. The areas with greatest magnification in the human brain—the lips, tongue, fingers, and toes—have tactile acuity thresholds of 0.5, 0.6, 1.0, and 4.5 mm, respectively.

Rodents and other mammals that probe the environment with their whiskers have a large number of columns in S-I, named *barrels*, that receive inputs

from individual vibrissae on the face (Box 19–2). Barrel cortex provides a widely used experimental preparation for studying cortical circuitry.

Box 19–2 The Rodent Whisker-Barrel System

The rodent whisker-barrel system is a widely used animal model in modern neuroscience. Most mammals and all primates except man possess specialized tactile hairs on their face called *vibrissae*. Distinct from other hairs on the skin, vibrissae grow from a follicle that is densely innervated by the trigeminal cranial nerve and surrounded by a blood-filled sinus.

Many mammalian species actively move these large facial whiskers using specialized muscles that wrap like slings around each individual follicle. Mice and rats, two of the most commonly used vertebrate model organisms, rely more heavily on their sense of whisker-mediated touch than on their other senses during exploration.

Rodents rhythmically sweep their whiskers across objects in much the same way that humans palpate objects with their fingertips. Despite their structural differences, vibrissae and fingertips afford similar psychophysical thresholds and discriminative sensitivities. Whiskers mediate diverse abilities, including localizing objects in space, discriminating textures and shapes, navigating the environment, interacting socially, and capturing prey.

The rodent somatosensory cortex has evolved proportional to this system's high ethological relevance. For instance, the rat somatosensory cortex is thicker than the primary visual cortex of the cat, a highly visual animal.

The representation of the largest whiskers (macrovibrissae) in rodent S-I is enlarged relative to that of other parts of the body (Figure 19–16). In contrast to the continuous representations of the skin or retina, the cortical networks dedicated to processing information from individual whiskers are discrete and anatomically identifiable. Each whisker maps one-to-one onto a distinct cluster of excitatory neurons visible in cortical layer IV called a *barrel*.

Barrels are densely interconnected networks that are established during development by the interaction of thalamocortical axons with cortical neurons. This unique correspondence facilitates diverse studies of cortical microcircuits, development, experience-dependent plasticity, sensorimotor integration, tactile behavior, and disease.

Randy M. Bruno

Figure 19–16

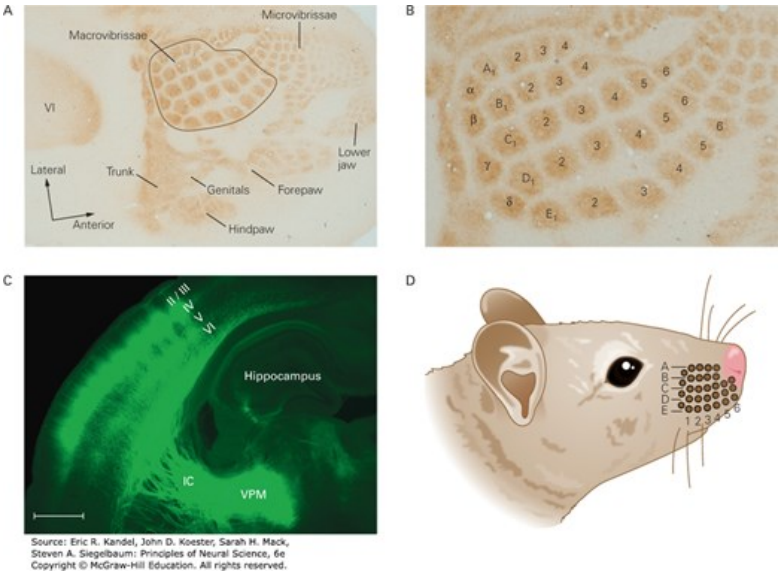
The "barrel cortex" of rodents represents the vibrissae in topographic patterns. The barrel cortex, a subregion of the rodent primary somatosensory (**S-I**) cortex that represents the facial vibrissae, is a widely studied structure used to decipher cortical circuits. (Adapted from Bennett-Clarke et al. 1997 and Wimmer et al. 2010.)

A. Tangential histological section through layer IV of the somatosensory cortex of a juvenile rat stained for serotonin. The darker immunoreactive patches correspond to cortical representations of specific body parts. The largest part of the rodent somatosensory cortical map is devoted to the vibrissae.

B. Enlarged view of the macrovibrissae representation in S-I. The spatial pattern of the whiskers on the face is stereotyped from animal to animal, allowing each cortical "barrel" to be identified by row with the letter, and by arc (column) with the number of the corresponding whisker. Neurons in each barrel are most responsive to motion of this principal whisker.

C. A rat brain section cut obliquely along the path axons travel from the ventroposterior medial (**VPM**) thalamic nucleus to S-I. Green fluorescent protein–labeled VPM axons project through the internal capsule (**IC**) to the subcortical white matter and travel parallel to the pial surface before entering the cortex. The axons densely innervate layer IV where they form discrete barrels and more sparsely and diffusely innervate the border of layers V and VI. Scale bar = 1 mm.

D. The topographic arrangement of the barrels in the cortex matches the spatial arrangement of vibrissae on the face in rows (letters) and arcs (numbers).



The Receptive Fields of Cortical Neurons Integrate Information From Neighboring Receptors

The neurons in S-I are at least three synapses beyond touch receptors in the skin. Their inputs represent information processed in the dorsal column nuclei, the thalamus, and the cortex itself. Each cortical neuron receives inputs arising from receptors in a specific area of the skin, and these inputs together are its receptive field. We perceive that a particular location on the skin is touched because specific populations of neurons in the cortex are activated. This experience can be induced experimentally by electrical or optogenetic stimulation of the same cortical neurons.

The receptive fields of cortical neurons are much larger than those of somatosensory fibers in peripheral nerves. For example, the receptive fields of SA1 and RA1 fibers innervating the fingertip are tiny spots on the skin (Figure 19–5), whereas those of the cortical neurons receiving these inputs cover an entire fingertip or several adjacent fingers (Figure 19–17B). The receptive field of a neuron in area 3b represents a composite of inputs from 300 to 400 nerve fibers, and typically covers a single phalanx or palm pad. Inputs from SA1 and RA1 touch receptors in the same skin region converge on common neurons in area 3b.

Figure 19–17

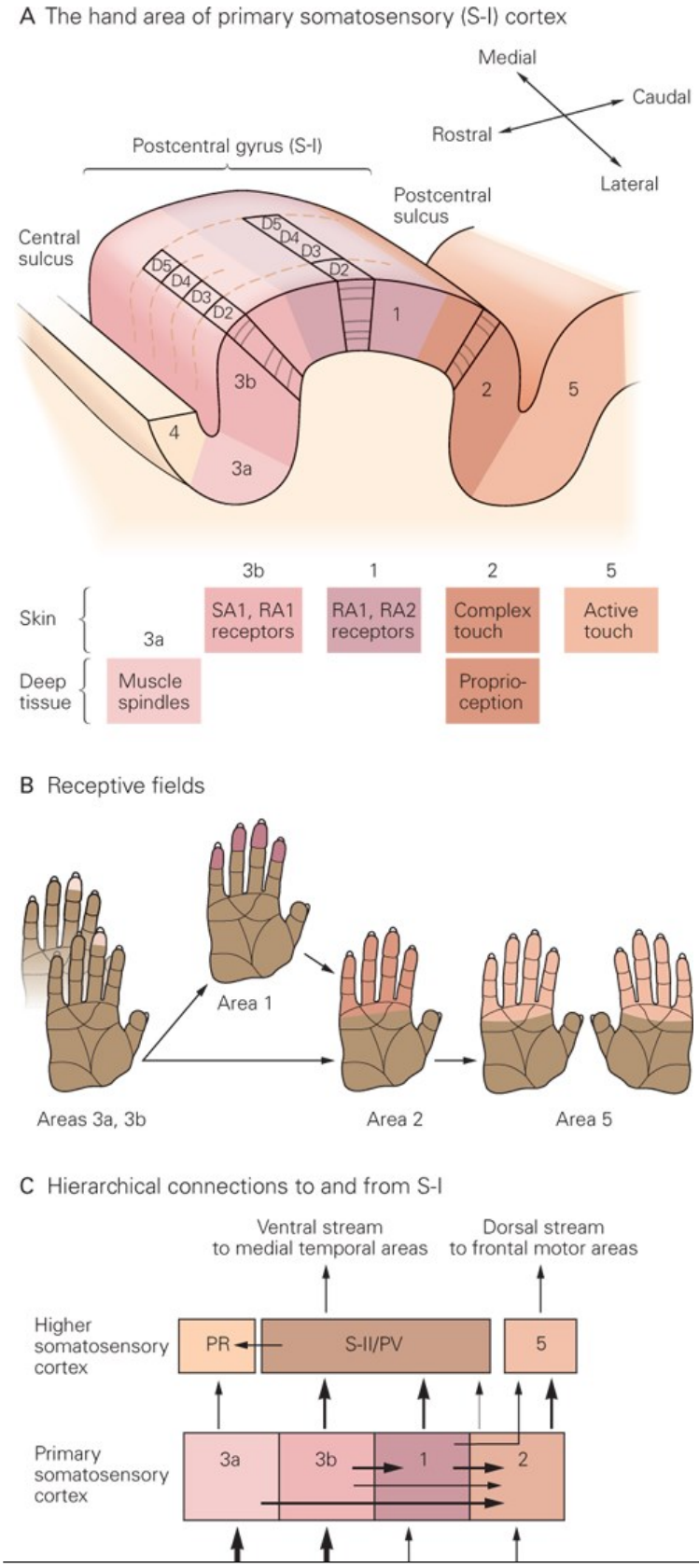
The hand area of S-I cortex.

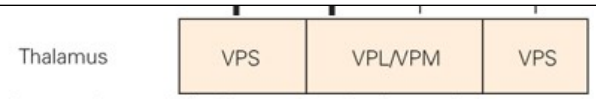
A. This sagittal section through the hand representation illustrates the rostrocaudal anatomy of the four subregions of S-I (areas 3a, 3b, 1, and 2) in the human brain and the adjacent primary motor cortex (area 4) and posterior parietal cortex (area 5). Labels on the cortical surface indicate columns representing individual fingers (D2–D5); arrows to the right denote the section orientation in the brain. The four S-I regions process different types of somatosensory information indicated by color-matched rectangles below the cortical section. Neurons in area 5 respond mainly to goal-directed active hand movements. (Abbreviations: **RA1**, rapidly adapting type 1; **RA2**, rapidly adapting type 2; **SA1**, slowly adapting type 1.)

B. Typical receptive fields of neurons in each area of S-I of macaque monkeys are shown as colored patches on the hand icons. The fields are outlined by applying light touch to the skin or moving individual joints. Receptive fields are smallest in areas 3a and 3b, where tactile information first enters the cortex, and are progressively larger in areas 1, 2, and 5, reflecting convergent inputs from neurons in area 3b that are stimulated together when the hand is used. Neurons in area 5 and in S-II cortex often have bilateral receptive fields because they respond to touch at mirror-image locations on both hands. (Adapted from Gardner 1988; Iwamura et al. 1993; Iwamura, Iriki, and Tanaka 1994.)

C. Feedforward hierarchical connections between somatosensory cortical areas. The strength of thalamocortical and corticocortical connections is indicated by the thickness of arrows interconnecting these areas. Neurons in the thalamus send their axons mainly to areas 3a and 3b, but some also project to areas 1 and 2. In turn, neurons in cortical areas 3a and 3b project to areas 1 and 2. Information from the four areas of S-I is conveyed to neurons in the posterior parietal cortex (area 5) and in S-II. Many of these connections are bidirectional; neurons in higher order cortical areas project back to lower order regions, particularly to layer I. (**PR**, parietal rostroventral cortex; **PV**, parietal ventral cortex; **VPL**, ventral posterior lateral nuclei;

VPM, ventral posterior medial nuclei; **VPS**, ventral posterior superior nuclei). (Adapted, with permission, from Felleman and Van Essen 1991. Copyright © 1991, Oxford University Press.)





Receptive fields in higher cortical areas are even larger, spanning functional regions of skin that are activated simultaneously during motor activity. These include the tips of several adjacent fingers, or an entire finger, or both the fingers and the palm. Neurons in areas 1 and 2 of S-I are concerned with information more abstract than just their innervation sites on the body. Neurons whose receptive fields include more than one finger fire at higher rates when several fingers are touched simultaneously and, in this way, signal the size and shape of objects held in the hand. These large receptive fields allow cortical neurons to integrate the fragmented information from individual touch receptors, enabling us to recognize the overall shape of an object. For example, such neurons may distinguish the handle of a screwdriver from its blade.

Convergent inputs from different sensory receptors in S-I may also allow individual neurons to detect the size and shape of objects. Whereas neurons in areas 3b and 1 respond only to touch and neurons in area 3a respond to muscle stretch, many of the neurons in area 2 receive both inputs. Thus, neurons in area 2 can integrate information about the hand shape used to grasp an object, the grip force applied by the hand, and the tactile stimulation produced by the object; this integrated information may be sufficient to recognize the object.

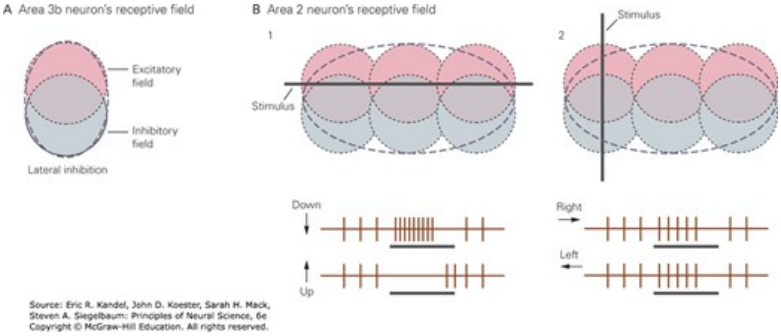
The receptive fields of cortical neurons usually have an excitatory zone surrounded by or superimposed upon inhibitory zones (Figure 19–18A). Stimulation of regions of skin outside the excitatory zone may reduce the neuron's responses to tactile stimulation within the receptive field. Similarly, repeated stimulation within the receptive field may also decrease neuronal responsiveness because the excitability of the pathway is diminished by longer lasting inhibition mediated by local interneurons.

Figure 19–18

The spatial arrangement of excitatory and inhibitory inputs to a cortical neuron determines which stimulus features are encoded by the neuron.

A. A neuron in area 3b of the primary somatosensory cortex has overlapping excitatory and inhibitory zones within its receptive field. (Adapted, with permission, from DiCarlo et al. 1998; Sripati et al. 2006. Copyright © Society for Neuroscience.)

B. Convergence of three presynaptic neurons with the same arrangement of excitatory and inhibitory zones allows direction and orientation selectivity in a neuron in area 2. **1.** Downward motion of a horizontal bar across the receptive field of the postsynaptic cell produces a strong excitatory response because the excitatory fields of all three presynaptic neurons are contacted 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 receptive field evokes a weak response because it simultaneously crosses the excitatory and inhibitory receptive fields of the input neurons. Motion to the left or right cannot be distinguished in this example.



Inhibitory receptive fields result from feedforward and feedback connections through interneurons in the dorsal column nuclei, the thalamus, and the cortex itself that limit the spread of excitation. Inhibition generated by strong activity in one circuit reduces the output of nearby neurons that are only weakly excited. The inhibitory networks ensure that the strongest of several competing responses is transmitted, permitting a winner-take-all strategy. These circuits prevent blurring of tactile details such as texture when large populations of touch neurons are stimulated. In addition, higher centers in the brain use inhibitory circuits to focus attention on relevant information from the hand when it is used in skilled tasks, by suppressing unwanted, distracting inputs.

The size and position of receptive fields on the skin are not fixed permanently but can be modified by experience or injury to sensory nerves (Chapter 53). Cortical receptive fields appear to be formed during development and maintained by simultaneous activation of the input pathways. If a peripheral nerve is injured or transected, its cortical projection targets acquire new receptive fields from less effective sensory inputs that are normally suppressed by inhibitory networks, or from newly developed connections from neighboring skin areas that retain innervation. Likewise, extensive stimulation of afferent pathways through repeated practice may strengthen synaptic inputs, improving perception and thereby performance.

Touch Information Becomes Increasingly Abstract in Successive Central Synapses

Somatosensory information is conveyed in parallel from the four areas of S-I to higher centers in the cortex, such as the secondary somatosensory cortex (S-II), the posterior parietal cortex, and the primary motor cortex (Figure 19–17C). As information flows toward higher-order cortical areas, specific combinations of stimulus patterns are needed to excite individual neurons.

Signals from neighboring neurons are combined in higher cortical areas to discern global properties of objects such as their orientation on the hand, or the direction of motion (Figure 19–19). In general, cortical neurons in higher cortical areas are concerned with sensory features that are independent of the stimulus position in their receptive field, abstracting object properties common to a particular class of stimuli.

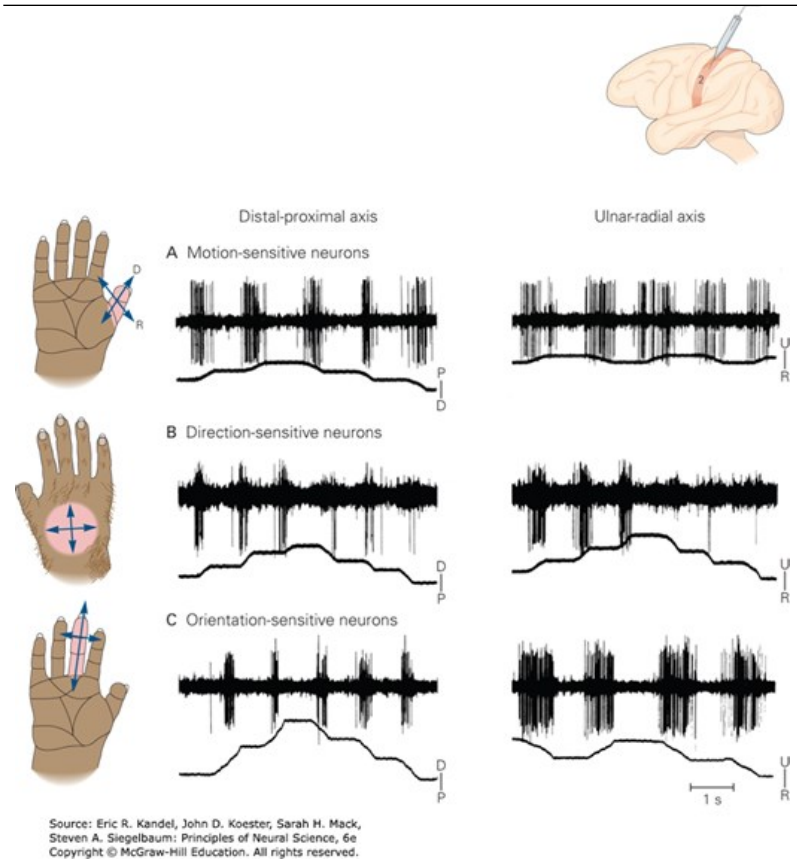
Figure 19–19

Neurons in area 2 encode complex tactile information. These neurons respond to motion of a probe across the receptive field but not to touch at a single point. The lower trace indicates the direction of motion by upward and downward deflections. (Adapted, with permission, from Warren, Hämäläinen, and Gardner 1986.)

A. A motion-sensitive neuron responds to stroking the skin in all directions.

B. A direction-sensitive neuron responds strongly to motion toward the ulnar side of the palm but fails to respond to motion in the opposite direction. Responses to distal or proximal movements are weaker.

C. An orientation-sensitive neuron responds better to motion across a finger (ulnar-radial) than to motion along the finger (distal-proximal), but does not distinguish ulnar from radial or proximal from distal directions.



A cortical neuron is able to detect the orientation of an edge or the direction of motion because of the spatial arrangement of the presynaptic receptive fields. The receptive fields of the excitatory presynaptic neurons are typically aligned along a common axis that generates the preferred orientation of the postsynaptic neuron. In addition, the receptive fields of inhibitory presynaptic neurons at one side of the excitatory fields reinforce the orientation and direction selectivity of postsynaptic neurons (Figure 19–18B).

Cognitive Touch Is Mediated by Neurons in the Secondary Somatosensory Cortex

An S-I neuron's response to touch depends primarily on input from within the neuron's receptive field. This feedforward pathway is often described as a *bottom-up* process because the receptors in the periphery are the principal source of excitation of S-I cortical neurons.

Higher-order somatosensory areas not only receive information from peripheral receptors but are also strongly influenced by top-down cognitive processes, such as goal-setting and attentional modulation. Data obtained from a variety of studies—single-neuron studies in monkeys, neuroimaging studies in humans, and clinical observations of patients with lesions in higher-order somatosensory areas—suggest that the ventral and dorsal regions of the parietal lobe serve complementary functions in the touch system similar to the "what" and "where" pathways of the visual system (see Figure 17–13).

S-II is located on the upper bank and adjacent parietal operculum of the lateral sulcus in both humans and monkeys (Figures 19–12B and 19–20B). Like S-I, the S-II cortex contains four distinct anatomical subregions with separate maps of the body. The central zone—consisting of S-II proper and the adjacent parietal ventral area—receives its major input from areas 3b and 1, largely tactile information from the hand and face. A more rostral region, the parietal rostroventral area, receives information from area 3a about active hand movements as well as tactile information from areas 3b and 1 (Figure 19–20). The most caudal somatosensory region of the lateral sulcus extends onto the parietal operculum (Figure 19–12A). This region abuts the posterior parietal cortex and plays a role in integrating somatosensory and visual properties of objects.

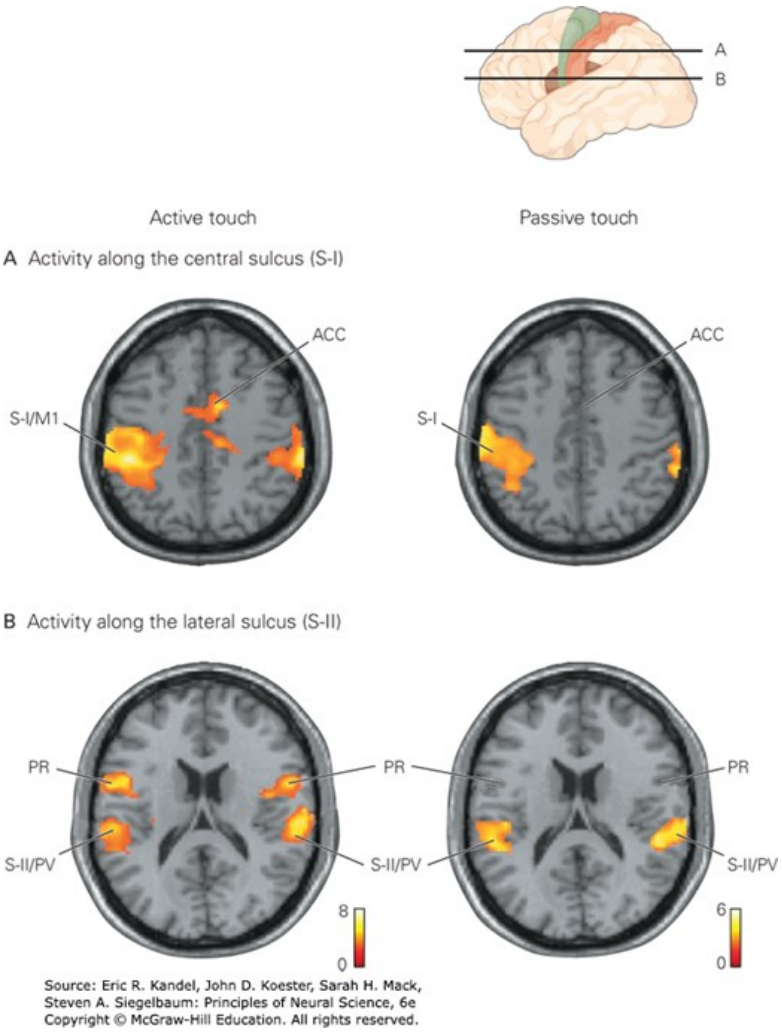
Figure 19–20

Responses in S-I and S-II to active touch are more complex than those evoked by passive touch. Cortical regions in the human brain stimulated by passive and active touch are localized using functional magnetic resonance imaging (**fMRI**). (Adapted, with permission, from Hinkley et

al. 2007.)

A. Axial views of activity along the central sulcus during passive stroking of the right hand with a sponge (*right panel*) and during active touching of the sponge (*left panel*). Areas 3b and 1 are activated in the left hemisphere in both conditions. Active touch also engages the primary motor cortex (**M1**) in the left hemisphere, the anterior cingulate cortex (**ACC**), and evokes weak activity in the ipsilateral S-I (right hemisphere). These sites were confirmed independently using magnetoencephalography in the same subjects.

B. Axial views of activity along the Sylvian fissure in the same experiment. Bilateral activity occurs in S-II and the parietal ventral (**PV**) area during passive stroking and is stronger when the subject actively moves the hand. The parietal rostroventral area (**PR**) is active only during active touch. Magnetoencephalographic responses in S-II/PV and PR occur later than in S-I, reflecting serial processing of touch from S-I to S-II/PV and from S-II/PV to PR.



Source: Eric R. Kandel, John D. Koester, Sarah H. Mack, Steven A. Siegelbaum: Principles of Neural Science, 6e

Physiological studies indicate that S-II plays key roles in tactile recognition of objects placed in the hand (stereognosis), distinguishing spatial features, such as shape and texture, and temporal properties, such as vibratory frequency. The receptive fields of neurons in S-II are larger than those in S-I, covering the entire surface of the hand, and are often bilateral, representing symmetric, mirror-image locations on the contralateral and ipsilateral hands. Such large receptive fields enable us to sense the shape of an entire large object grasped in one hand, allowing us to integrate the overall contours of a tool as it contacts the palm and different fingers. Bilateral receptive fields enable us to perceive still larger objects with two hands, such as a watermelon or basketball, sharing the load between them.

The large receptive fields of S-II neurons also influence their physiological responses to motion and vibration. S-II neurons do not represent vibration as periodic spike trains linked to the oscillatory frequency, as do the sensory fibers from the skin or S-I neurons (Figure 19–9). Instead, S-II neurons abstract temporal or intensive properties of the vibratory stimulus, firing at different mean rates for different frequencies. A similar frequency-

dependent transition from temporal- to rate-coding neurons underlies sound processing in primary auditory cortex (Chapter 28), a brain region juxtaposed to S-II cortex in the parietal operculum.

Importantly, the firing rates of S-II neurons depend on the behavioral context or motivational state of the subject. In elegant recent studies, Ranulfo Romo and his colleagues compared responses to vibratory stimuli of neurons in S-I, S-II, and various regions of the frontal lobe of monkeys while the animals performed a two-alternative forced-choice task. The animals were rewarded if they correctly recognized which of two vibratory stimuli was higher in frequency.

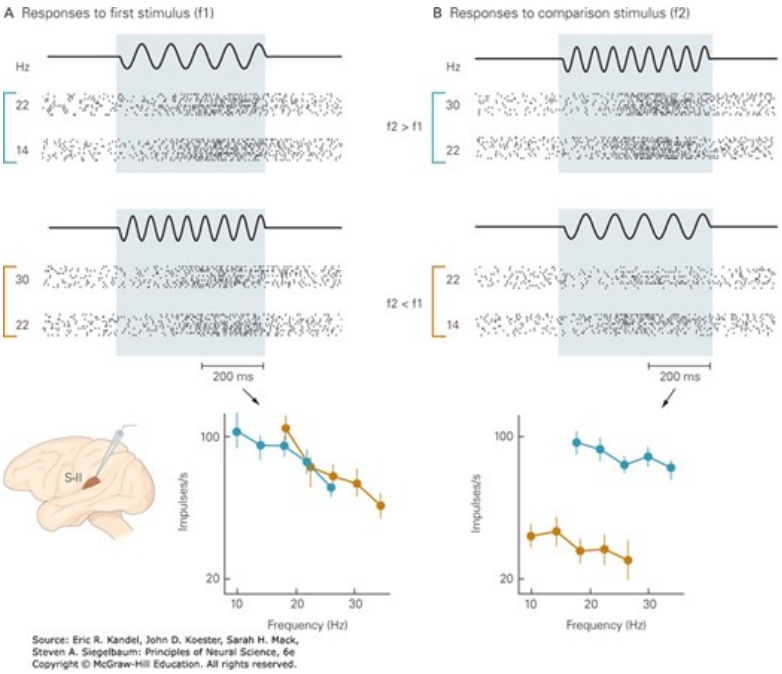
Neurons in S-I faithfully represent the vibratory cycles of each stimulus using a temporal code: they fire brief spike bursts in phase with each cycle (Figure 19–9B). In contrast, S-II neurons respond to the first stimulus with nonperiodic spike trains in which their mean firing rates are directly or inversely correlated with the vibratory frequency (Figure 19–21A). Their responses to the second stimulus are even more abstract. S-II spike trains combine the frequencies of both stimuli (Figure 19–21B). In other words, S-II responses to vibration depend on the stimulus context: the same vibratory stimulus can evoke different firing rates depending on whether the preceding stimulus is higher or lower in frequency.

Figure 19–21

The sensitivity of an S-II neuron to vibratory stimuli is modulated by attention and behavioral conditions. A monkey was trained to compare two vibratory stimuli applied at a 3-second interval to the fingertips (**f1** and **f2**) and to indicate which had the higher frequency. The plots show the mean firing rates of the neuron during each of the two stimuli. The animal's decision about which frequency is higher can be predicted from the neural data during each type of trial. The mean firing rates of this neuron are significantly higher at each stimulation frequency when f2 is greater than f1 than when f2 is less than f1. (Adapted, with permission, from Romo et al. 2002. Copyright © 2002 Springer Nature.)

A. Raster plots show the responses of an S-II neuron to various sample stimuli (f1). The vertical tick marks in each row denote action potentials, and individual rows are separate trials of the stimulus pairs. Trials are grouped according to the frequencies tested. The firing rate of the neuron encodes the vibratory frequency of the sample stimulus; it is higher for low-frequency vibration regardless of the subsequent events. Note that the firing patterns recorded in S-II are not phase-locked to the vibratory cycle as in S-I (see Figure 19–9B).

B. Each row in the raster plots illustrates responses to the comparison stimulus (f2) during the same trials shown in A. The neuron's response to f2 reflects the frequency of both f2 and f1. When f2 > f1, the neuron fires at high rates during f2 and the animal reports that f2 is the higher frequency. When f2 < f1, the neuron fires at low rates during f2 and the animal reports that f1 is the higher frequency. In this manner, the responses of S-II neurons reflect the animal's memory of an earlier event.



Even more interesting, Romo's group found that neurons in S-II send copies of the spike trains evoked by the first stimulus to the prefrontal and

premotor cortex in order to preserve a memory of that response. Neurons in these frontal cortical areas continue to fire during the delay period after the first stimulus ends. Romo and colleagues proposed that these regions in the frontal lobe send the memory signal back to S-II when the second stimulus occurs, thereby modifying the response of S-II neurons to the direct tactile signals from the hand. In this manner, sensorimotor memories of previous stimuli influence sensory processing in the brain, allowing subjects to make cognitive judgments about newly arriving tactile stimuli.

S-II is the gateway to the temporal lobe via the insular cortex. Regions of the medial temporal lobe, particularly the hippocampus, are vital to the storage of explicit memory (Chapter 53). We do not store in memory every scintilla of tactile information that enters the nervous system, only that which has some behavioral significance. In light of the demonstration that the firing patterns of S-II neurons are modified by selective attention, S-II could make the decision whether a particular bit of tactile information is remembered.

Active Touch Engages Sensorimotor Circuits in the Posterior Parietal Cortex

Studies in the mid-1970s by Vernon Mountcastle, Juhani Hyvärinen, and others demonstrated that regions of the posterior parietal cortex surrounding the intraparietal sulcus play an important role in the sensory guidance of movement rather than in discriminative touch. These regions include areas 5 and 7 in monkeys and the superior parietal lobule (Brodmann's areas 5 and 7) and inferior parietal cortex (areas 39 and 40) in humans. These and subsequent studies demonstrated that neural activity in the posterior parietal cortex during reaching and grasping coincides with activation of neurons in motor and premotor areas of the frontal cortex and precedes activity in S-I. Areas 5 and 7 are postulated to be engaged in the planning of hand actions, because the posterior parietal cortex receives convergent central and peripheral signals that allow it to compare central motor commands with somatosensory feedback during reaching and grasping behaviors. Sensory feedback from S-I to the posterior parietal cortex is used to confirm the goal of the planned action, thereby reinforcing previously learned skills or correcting those plans when errors occur.

Predicting the sensory consequences of hand actions is an important component of active touch. For example, when we view an object and reach for it, we predict how heavy it should be and how it should feel in the hand; we use such predictions to initiate grasping. Daniel Wolpert and Randy Flanagan have proposed that during active touch the motor system controls the afferent flow of somatosensory information to the brain so that subjects can predict when tactile information should arrive in S-I and reach consciousness. Convergence of central and peripheral signals allows neurons to compare planned and actual movements. Corollary discharge from motor areas to somatosensory regions of the cortex may play a key role in active touch. It provides posterior parietal cortex neurons with information on intended actions, allowing them to learn new skills and perform them smoothly.

Lesions in Somatosensory Areas of the Brain Produce Specific Tactile Deficits

Patients with lesions in S-I cortex have difficulty responding to simple tactile tests: touch thresholds, vibration and joint position sense, and two-point discrimination (Figure 19–22A). These patients also perform poorly on more complex tasks, such as texture discrimination, stereognosis, and visual–tactile matching tests.

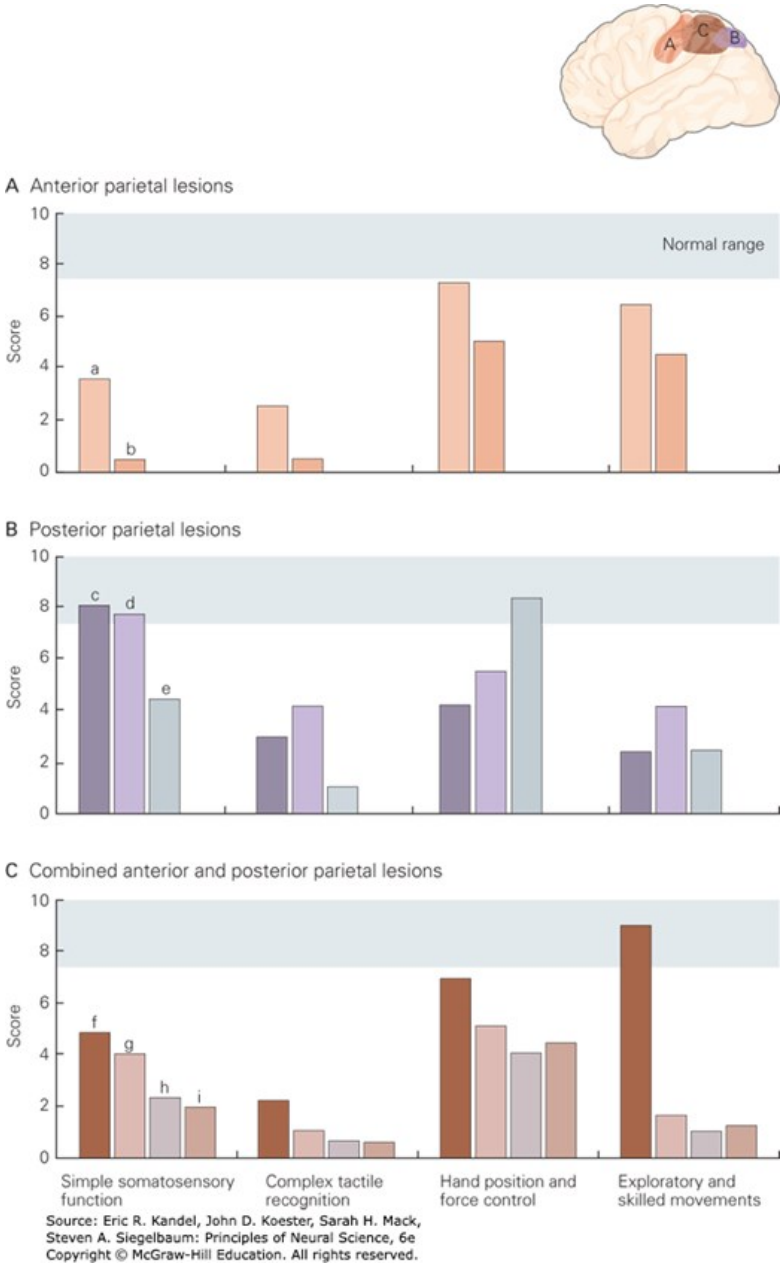
Figure 19–22

Lesions of anterior and posterior regions of the parietal lobe produce characteristic sensory and motor deficits of the hand. Bar graphs rank the performance of nine patients (a–i) with unilateral parietal cortex brain lesions on four sets of standardized tests of sensory and motor function of the contralateral hand. The behavioral scores are ranked from normal (10) to maximal deficit (0). The normal range shown is the performance score of these patients for the ipsilateral hand. Tests of *simple somatosensory function* include light touch from a 1-g force-calibrated probe, two-point discrimination on the finger and palm, vibration sense, and position sense of the index finger metacarpophalangeal joint. Tests of *complex tactile recognition* assess texture discrimination, form recognition, and size discrimination. Tests of *hand position and force control* measure grip force, tapping, and reaching to a target. Tests of *exploratory and skilled movements* evaluate insertion of pegs in slots, pincer grip of small objects, and exploratory movements when palpating objects. (Adapted, with permission, from Pause et al. 1989. Copyright © 1989, Oxford University Press.)

A. Two patients with lesions to the anterior parietal lobe show severe impairment in both sets of tactile tests but only moderate impairment in the motor tasks.

B. Three patients with posterior parietal lesions show only minor deficits in simple somatosensory tests but severe impairment in complex tests of stereognosis and form. Motor deficits are greater in skilled tasks.

C. Four patients with combined lesions to anterior and posterior parietal cortex show severe impairment in all tests. Interestingly, the patient who showed the least impairment in this group (patient f) suffered brain damage at birth; the developing brain was able to compensate for the loss of major somatosensory areas. Lesions in the other patients resulted from strokes later in life.



Loss of tactile sensation in the hand produces significant motor as well as sensory deficits. Motor deficits are less pronounced than sensory losses, particularly during tests of force and position control. Exploratory movements and skilled tasks such as catching a ball or pinching small objects between the fingertips are also abnormal.

Local anesthesia of sensory nerve fibers in the hand provides a direct way to appreciate the sensorimotor role of touch. Under local anesthesia of the median and ulnar nerves, hand movements are clumsy and poorly coordinated, and force generation during grasping is abnormally slow. With the loss of tactile sensibility, one is completely reliant on vision for directing the hand. Loss of touch does not cause paralysis or weakness because much of skilled movement is predictive, relying on sensory feedback for adjustment if necessary. The motor system in these subjects compensates for the absence of tactile information by generating more force than necessary.

These motor problems are exacerbated by long-term, chronic loss of tactile function because of injury to peripheral nerves or dorsal column lesions.

Deafferentation produces major changes in the afferent connections in the brain, as do certain diseases. Myelinated afferent fibers in the dorsal columns degenerate in patients with demyelinating diseases, such as multiple sclerosis. In late-stage syphilis, the large-diameter neurons in the dorsal root ganglia are destroyed (tabes dorsalis). These patients have severe chronic deficits in touch and proprioception but often little loss of temperature perception and nociception. The somatosensory losses are accompanied by motor deficits: clumsy and poorly coordinated movements and dystonia. Similar impairments occur in patients with damage to S-I caused by stroke or head trauma, or following surgical excision of the postcentral gyrus.

Patients with lesions in the posterior parietal cortex usually have only mild difficulty with simple tactile tests. However, they have profound difficulty with complex tactile recognition tasks and use few exploratory and skilled movements (Figure 19–22B). They display kinematic deficits when interacting with objects, failing to shape and orient the hand properly to grasp them and misdirecting the arm during reaching. They typically use too much grip force when an object is placed in their hand and are unable to direct the fingers properly when asked to evaluate its size and shape. These deficits are described clinically as the “useless hand” syndrome (tactile apraxia).

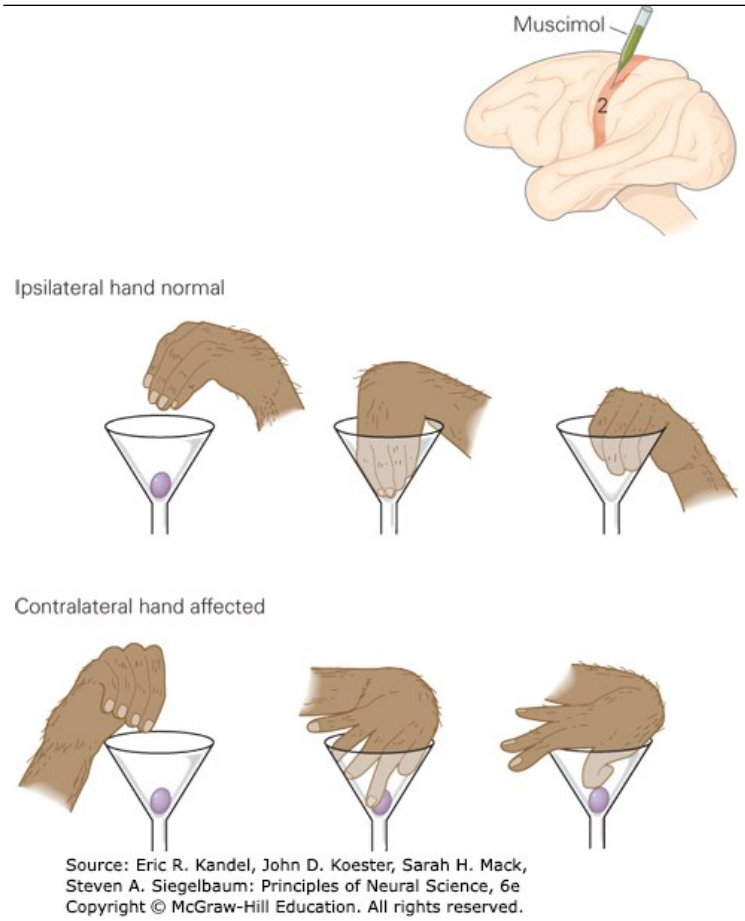
Studies of sensory deficits in human patients are complicated by the fact that disease states or trauma rarely produce damage confined to one localized brain area. For this reason, analyses of experimentally controlled lesions in animals have been useful for understanding the etiology of the sensory deficits observed in human patients. For example, macaque monkeys with a lesion of the cuneate fascicle show chronic losses in tactile discrimination, such as higher touch thresholds, impaired vibration sense, and poor two-point discrimination. They also display major deficits in the control of fine finger movements during grooming, scratching, and object manipulation. A similar deficit in skilled movements can be produced experimentally in monkeys by inhibiting the neurons in the hand-representation region of area 2.

Experimental ablation of somatosensory areas of the cortex in monkeys has provided valuable information about the function of these areas. Small lesions limited to area 3b produce major deficits in touch sensation from a particular part of the body. 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. The damage to tactile function is less severe when such lesions are made in infant animals, apparently because in the developing brain S-II cortex may take over functions normally assumed by S-I.

Removal of S-II cortex in monkeys causes severe impairment in the discrimination of both shape and texture and prevents the animals from learning new tactile discriminations. Ablation or inhibition of areas 2 or 5 produces deficits in roughness discrimination but few other alterations in passive touch. However, motor performance is impaired as these animals misdirect reaching toward objects, fail to preshape the hand to grasp objects skillfully, and have difficulty coordinating finger movements because tactile feedback is absent (Figure 19–23).

Figure 19–23

Finger coordination is disrupted when synaptic transmission in the somatic sensory cortex is inhibited in a monkey. Muscimol, a γ-aminobutyric acid (GABA) agonist that inhibits cortical cells, was injected into Brodmann’s area 2 on the left side of a monkey’s brain. Within minutes after injection, the finger coordination of the right hand (contralateral) was severely disrupted; the monkey was unable to pick up a grape from a funnel. The injection effects are shown to be specific to the injected hemisphere because the left hand (ipsilateral) continues to perform normally. (Adapted, with permission, from Hikosaka et al. 1985. Copyright © 1985 Elsevier B.V.)



Source: Eric R. Kandel, John D. Koester, Sarah H. Mack, Steven A. Siegelbaum: Principles of Neural Science, 6e

The similarity between impairments observed in humans and monkeys is an important basis for understanding clinical losses of somatosensory function. We shall learn in later chapters that lesioning studies of other cortical areas in monkeys have also provided insight into higher-order sensory and motor functions of the brain.

Highlights

1. When we explore an object with our hands, a large part of the brain may become engaged by the sensory experience, by the thoughts and emotions it evokes, and by motor responses to it. These sensations result from the parallel actions of multiple cortical areas engaged in feedforward and feedback networks.

2. At the first touch, the peripheral sensory apparatus deconstructs the object into tiny segments, distributed over a large population of approximately 20,000 sensory nerve fibers. The SA1 system provides high-fidelity information about the object's spatial structure that is the basis of form and texture perception. The SA2 system provides information about the hand conformation and posture during grasping and other hand movements. The RA1 system conveys information about motion of the object in the hand, which enables us to manipulate it skillfully. Together with RA2 receptors, they sense vibration of objects that allows us to use them as tools.

3. The information from touch receptors is conveyed to consciousness by the dorsal column fiber tracts of the spinal cord, relay nuclei in the brain stem and thalamus, and a hierarchy of intracortical pathways. By analyzing patterns of activity across the entire population, the brain constructs a neural representation of objects and actions of the hand.

4. Computations in central pathways are complex and accomplished serially, beginning in the dorsal column nuclei, progressing through the thalamus and several cortical stages, and terminating in regions of the medial temporal cortex concerned with memory and perception and in motor areas of the frontal lobe that mediate voluntary movements.

5. The brain's processing of touch is aided by the topographic, somatotopic organization of the neurons involved at each relay. Adjacent skin areas

that are stimulated together are linked anatomically and functionally in central relays. Body parts that are especially sensitive to touch—the hands, feet, and mouth—are represented in large areas of the brain, reflecting the importance of tactile information conveyed from these regions.

6. Another function of the central pathways is the transformation of the disaggregated representation of object properties among thousands of neurons to an integrated representation of complex object properties in a few neurons. Convergent excitatory connections between neurons representing neighboring skin areas and intracortical inhibitory circuits enable higher-order cortical cells to integrate global features of objects. In this manner, the somatosensory areas of the brain represent properties common to particular classes of objects.

7. A third function is regulating the afferent flow of somatosensory information. The peripheral fibers deliver much more information than can be handled at any one moment; the central neural pathways compensate by selecting information for delivery to the mechanisms of perception and memory. Recurrent pathways from higher brain areas modify the ascending information provided by touch receptors, thus fitting the stream of sensory information to previous experience and task goals.

8. Finally, the touch system provides information necessary for the control and guidance of movement. Interactions between sensory and motor areas of parietal and frontal cortex provide a neural mechanism for planning desired actions, for predicting the sensory consequences of motor behaviors, and for skill learning from repeated experience.

Esther P. Gardner

Selected Reading

Freund HJ. 2003. Somatosensory and motor disturbances in patients with parietal lobe lesions. Adv Neurol 93:179–193.

Harris KD, Shepherd GMG. 2015. The neocortical circuit: themes and variations. Nat Neurosci 18:170–181. [PubMed: 25622573]

Johnson KO. 2001. The roles and functions of cutaneous mechanoreceptors. Curr Opin Neurobiol 11:455–461. [PubMed: 11502392]

Jones EG. 2000. Cortical and subcortical contributions to activity-dependent plasticity in primate somatosensory cortex. Annu Rev Neurosci 23:1–37. [PubMed: 10845057]

Jones EG, Peters A (eds). 1986. *Cerebral Cortex.* Vol 5, *Sensory-Motor Areas and Aspects of Cortical Connectivity.* New York: Plenum Press.

Kaas JH, Gardner EP (eds). 2008. *The Senses: A Comprehensive Reference.* Vol 6, *Somatosensation.* Oxford: Elsevier.

Milner AD, Goodale MA. 1995. *The Visual Brain in Action*. Oxford: Oxford Univ. Press.

Mountcastle VB. 1995. The parietal system and some higher brain functions. Cerebral Cortex 5:377–390. [PubMed: 8547786]

Mountcastle VB. 2005. *The Sensory Hand: Neural Mechanisms of Somatic Sensation*. Cambridge, MA: Harvard Univ. Press.

Romo R, Salinas E. 2003. Flutter discrimination: neural codes, perception, memory and decision making. Nat Rev Neurosci 4:203–218. [PubMed: 12612633]

Wing AM, Haggard P, Flanagan JR (eds). 1996. *Hand and Brain.* San Diego, CA: Academic Press.

References

Bennett-Clarke CA, Chiaia NL, Rhodes RW. 1997. Contributions of raphe-cortical and thalamocortical axons to the transient somatotopic pattern of serotonin immunoreactivity in rat cortex. Somatosens Mot Res 14:27–33. [PubMed: 9241726]

Birznieks I, Macefield VG, Westling G, Johansson RS. 2009. Slowly adapting mechanoreceptors in the borders of the human fingernail encode fingertip forces. J Neurosci 29:9370–9379. [PubMed: 19625527]

Bolanowski SJ, Pawson L. 2003. Organization of Meissner corpuscles in the glabrous skin of monkey and cat. Somatosens Mot Res 20:223–231. [PubMed: 14675961]

Brisben AJ, Hsiao SS, Johnson KO. 1999. Detection of vibration transmitted through an object grasped in the hand. J Neurophysiol 81:1548–1558. [PubMed: 10200190]

Brochier T, Boudreau M-J, Paré M, Smith AM. 1999. The effects of muscimol inactivation of small regions of motor and somatosensory cortex on independent finger movements and force control in the precision grip. Exp Brain Res 128:31–40. [PubMed: 10473737]

Carlson M. 1981. Characteristics of sensory deficits following lesions of Brodmann's areas 1 and 2 in the postcentral gyrus of *Macaca mulatta*. Brain Res 204:424–430. [PubMed: 7459637]

Chapman CE, Meftah el-M. 2005. Independent controls of attentional influences in primary and secondary somatosensory cortex. J Neurophysiol 94:4094–4107. [PubMed: 16148278]

Connor C, Hsiao SS, Phillips J, Johnson KO. 1990. Tactile roughness: neural codes that account for psychophysical magnitude estimates. J Neurosci 10:3823–3836. [PubMed: 2269886]

Costanzo RM, Gardner EP. 1980. A quantitative analysis of responses of direction-sensitive neurons in somatosensory cortex of alert monkeys. J Neurophysiol 43:1319–1341. [PubMed: 6768849]

DiCarlo JJ, Johnson KO, Hsaio SS. 1998. Structure of receptive fields in area 3b of primary somatosensory cortex in the alert monkey. J Neurosci 18:2626–2645. [PubMed: 9502821]

Edin BB, Abbs JH. 1991. Finger movement responses of cutaneous mechanoreceptors in the dorsal skin of the human hand. J Neurophysiol 65:657–670. [PubMed: 2051199]

Felleman DJ, Van Essen DC. 1991. Distributed hierarchical processing in the primate cerebral cortex. Cereb Cortex 1:1–47. [PubMed: 1822724]

Fitzgerald PJ, Lane JW, Thakur PH, Hsiao SS. 2006. Receptive field properties of the macaque second somatosensory cortex: representation of orientation on different finger pads. J Neurosci 26:6473–6484. [PubMed: 16775135]

Flanagan JR, Vetter P, Johansson RS, Wolpert DM. 2003. Prediction precedes control in motor learning. Curr Biol 13:146–150. [PubMed: 12546789]

Fogassi L, Luppino G. 2005. Motor functions of the parietal lobe. Curr Opin Neurobiol 15:626–631. [PubMed: 16271458]

Gardner EP. 1988. Somatosensory cortical mechanisms of feature detection in tactile and kinesthetic discrimination. Can J Physiol Pharmacol 66:439–454. [PubMed: 3139269]

Gardner EP. 2008. Dorsal and ventral streams in the sense of touch. In: JH Kaas, EP Gardner (eds). *The Senses: A Comprehensive Reference.* Vol. 6, *Somatosensation*, pp. 233–258. Oxford: Elsevier.

Gardner EP, Babu KS, Ghosh S, Sherwood A, Chen J. 2007. Neurophysiology of prehension: III. Representation of object features in posterior parietal cortex of the macaque monkey. J Neurophysiol 98:3708–3730. [PubMed: 17942625]

Hikosaka O, Tanaka M, Sakamoto M, Iwamura Y. 1985. Deficits in manipulative behaviors induced by local injections of muscimol in the first somatosensory cortex of the conscious monkey. Brain Res 325:375–380. [PubMed: 3978429]

Hinkley LB, Krubitzer LA, Nagarajan SS, Disbrow EA. 2007. Sensorimotor integration in S2, PV, and parietal rostroventral areas of the human Sylvian fissure. J Neurophysiol 97:1288–1297. [PubMed: 17122318]

Hyvärinen J, Poranen A. 1978. Movement-sensitive and direction and orientation-selective cutaneous receptive fields in the hand area of the post-central gyrus in monkeys. J Physiol (Lond) 283:523–537.

Iwamura Y, Iriki A, Tanaka M. 1994. Bilateral hand representation in the postcentral somatosensory cortex. Nature 369:554–556. [PubMed: 8202155]

Iwamura Y, Tanaka M, Sakamoto M, Hikosaka O. 1993. Rostrocaudal gradients in neuronal receptive field complexity in the finger region of the alert monkey's postcentral gyrus. Exp Brain Res 92:360–368. [PubMed: 8454001]

Jenmalm P, Birznieks I, Goodwin AW, Johansson RS. 2003. Influence of object shape on responses of human tactile afferents under conditions characteristic of manipulation. Eur J Neurosci 18:164–176. [PubMed: 12859350]

Johansson RS. 1996. Sensory control of dexterous manipulation in humans. In: AM Wing, P Haggard, JR Flanagan (eds). *Hand and Brain,* pp. 381–414. San Diego, CA: Academic Press.

Johansson RS, Flanagan JR. 2009. Coding and use of tactile signals from the fingertips in object manipulation tasks. Nat Rev Neurosci 10:345–359. [PubMed: 19352402]

Johansson RS, Landström U, Lundström R. 1982. Responses of mechanoreceptive afferent units in the glabrous skin of the human hand to sinusoidal skin displacements. Brain Res 244:17–25. [PubMed: 6288178]

Johansson RS, Vallbo ÅB. 1983. Tactile sensory coding in the glabrous skin of the human hand. Trends Neurosci 6:27–32.

Johnson KO, Phillips JR. 1981. Tactile spatial resolution: I. Two-point discrimination, gap detection, grating resolution and letter recognition. J Neurophysiol 46:1177–1191. [PubMed: 7320742]

Jones EG, Powell TPS. 1969. Connexions of the somatic sensory cortex of the rhesus monkey. I. Ipsilateral cortical connexions. Brain 92:477–502. [PubMed: 4979846]

Klatzky RA, Lederman SJ, Metzger VA. 1985. Identifying objects by touch: an "expert system." Percept Psychophys 37:299–302. [PubMed: 4034346]

Koch KW, Fuster JM. 1989. Unit activity in monkey parietal cortex related to haptic perception and temporary memory. Exp Brain Res 76:292–306. [PubMed: 2767186]

LaMotte RH, Mountcastle VB. 1979. Disorders in somethesis following lesions of parietal lobe. J Neurophysiol 42:400–419. [PubMed: 106093]

Lederman SJ, Klatzky RL. 1987. Hand movements: a window into haptic object recognition. Cogn Psychol 19:342–368. [PubMed: 3608405]

Lieber JD, Xia X, Weber AI, Bensmaia SJ. 2017. The neural code for tactile roughness in the somatosensory nerves. J Neurophysiol 118:3107–3117. [PubMed: 28855289]

Manfredi LR, Saal, HP, Brown KJ, et al. 2014. Natural scenes in tactile texture. J Neurophysiol 111:1792–1802. [PubMed: 24523522]

Mountcastle VB. 1997. The columnar organization of the neocortex. Brain 120:701–722. [PubMed: 9153131]

Mountcastle VB, LaMotte RH, Carli G. 1972. Detection thresholds for stimuli in humans and monkeys: comparison with threshold events in mechanoreceptive afferent fibers innervating the monkey hand. J Neurophysiol 35:122–136.

Mountcastle VB, Lynch JC, Georgopoulos AP, Sakata H, Acuna C. 1975. Posterior parietal association cortex of the monkey: command functions for

operations within extrapersonal space. J Neurophysiol 38:871–908. [PubMed: 808592]

Muniak MA, Ray S, Hsiao SS, Dammann JF, Bensmaia SJ. 2007. The neural coding of stimulus intensity: linking the population response of mechanoreceptive afferents with psychophysical behavior. J Neurosci 27:11687–11699. [PubMed: 17959811]

Murray EA, Mishkin M. 1984. Relative contributions of SII and area 5 to tactile discrimination in monkeys. Behav Brain Res 11:67–83. [PubMed: 6696789]

Nelson RJ, Sur M, Felleman DJ, Kaas JH. 1980. Representations of the body surface in postcentral parietal cortex of *Macaca fascicularis.* J Comp Neurol 192:611–643. [PubMed: 7419747]

Nolano M, Provitera V, Crisci C, et al. 2003. Quantification of myelinated endings and mechanoreceptors in human digital skin. Ann Neurol 54:197–205. [PubMed: 12891672]

Oberlaender M, de Kock CP, Bruno RM, et al. 2012. Cell type-specific three-dimensional structure of thalamocortical circuits in a column of rat vibrissal cortex. Cereb Cortex 22:2375–2391. [PubMed: 22089425]

Pandya DN, Seltzer B. 1982. Intrinsic connections and architectonics of posterior parietal cortex in the rhesus monkey. J Comp Neurol 204:196–210. [PubMed: 6276450]

Pause M, Kunesch E, Binkofski F, Freund H-J. 1989. Sensorimotor disturbances in patients with lesions of the parietal cortex. Brain 112:1599–1625. [PubMed: 2598000]

Pei Y-C, Denchev P V, Hsiao SS, Craig JC, Bensmaia SJ. 2009. Convergence of submodality-specific input onto neurons in primary somatosensory cortex. J Neurophysiol 102:1843–1853. [PubMed: 19535484]

Peters RM, Hackeman E, Goldreich D. 2009. Diminutive digits discern delicate details: fingertip size and the sex difference in tactile spatial acuity. J Neurosci 29:15756–15761. [PubMed: 20016091]

Phillips JR, Johansson RS, Johnson KO. 1990. Representation of braille characters in human nerve fibres. Exp Brain Res 81:589–592. [PubMed: 2226691]

Pons TP, Garraghty PE, Mishkin M. 1992. Serial and parallel processing of tactual information in somatosensory cortex of rhesus monkeys. J Neurophysiol 68:518–527. [PubMed: 1527572]

Pons TP, Garraghty PE, Ommaya AK, Kaas JH, Taub E, Mishkin M. 1991. Massive cortical reorganization after sensory deafferentation in adult macaques. Science 252:1857–1860. [PubMed: 1843843]

Pruszynski JA, Johansson RS. 2014. Edge-orientation processing in first-order tactile neurons. Nat Neurosci 17:1404–1409. [PubMed: 25174006]

Quilliam TA. 1978. The structure of finger print skin. In: G Gordon (ed). *Active Touch*, pp. 1–18. Oxford: Pergamon Press.

Robinson CJ, Burton H. 1980. Somatic submodality distribution within the second somatosensory (SII), 7b, retro-insular, postauditory and granular insular cortical areas of *M. fascicularis*. J Comp Neurol 192:93–108. [PubMed: 7410615]

Romo R, Hernandez A, Zainos A, Lemus L, Brody CD. 2002. Neuronal correlates of decision-making in secondary somatosensory cortex. Nat Neurosci 5:1217–1235. [PubMed: 12368806]

Saal HP, Bensmaia SJ. 2014. Touch is a team effort: interplay of submodalities in cutaneous sensibility. Trends Neurosci 37:689–697. [PubMed: 25257208]

Salinas E, Hernandez A, Zainos A, Romo R. 2000. Periodicity and firing rate as candidate neural codes for the frequency of vibrotactile stimuli. J Neurosci 20:5503–5515. [PubMed: 10884334]

Snider WD. 1998. How do you feel? Neurotrophins and mechanotransduction. Nat Neurosci 1:5–6. [PubMed: 10195097]

Srinivasan MA, Whitehouse JM, LaMotte RH. 1990. Tactile detection of slip: surface microgeometry and peripheral neural codes. J Neurophysiol 63:1323–1332. [PubMed: 2358880]

Sripati AP, Yoshioka T, Denchev P, Hsiao SS, Johnson KO. 2006. Spatiotemporal receptive fields of peripheral afferents and cortical area 3b and 1 neurons in the primate somatosensory system. J Neurosci 26:2101–2114. [PubMed: 16481443]

Talbot WH, Darian-Smith I, Kornhuber HH, Mountcastle VB. 1968. The sense of flutter-vibration: comparison of the human capacity with response patterns of mechanoreceptive afferents from the monkey hand. J Neurophysiol 31:301–334. [PubMed: 4972033]

Vega-Bermudez F, Johnson KO. 1999. Surround suppression in the responses of primate SA1 and RA mechanoreceptive afferents mapped with a probe array. J Neurophysiol 81:2711–2719. [PubMed: 10368391]

Warren S, Hämäläinen HA, Gardner EP. 1986. Objective classification of motion- and direction-sensitive neurons in primary somatosensory cortex of awake monkeys. J Neurophysiol 56:598–622. [PubMed: 3783213]

Weber AI, Saal HP, Lieber JD, et al. 2013. Spatial and temporal codes mediate the tactile perception of natural textures. Proc Nat Acad Sci USA 110:17107–17112. [PubMed: 24082087]

Weinstein S. 1968. Intensive and extensive aspects of tactile sensitivity as a function of body part, sex, and laterality. In: DR Kenshalo (ed). *The Skin Senses*, pp. 195–222. Springfield, IL: Thomas.

Westling G, Johansson RS. 1987. Responses in glabrous skin mechanoreceptors during precision grip in humans. Exp Brain Res 66:128–140. [PubMed: 3582527]

Wimmer VC, Bruno RM, de Kock CP, Kuner T, Sakmann B. 2010. Dimensions of a projection column and architecture of VPM and POm axons in rat vibrissal cortex. Cereb Cortex 20:2265–2276. [PubMed: 20453248]