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.

Touch receptors in the hand are further subdivided into two types based on size and location in the skin.

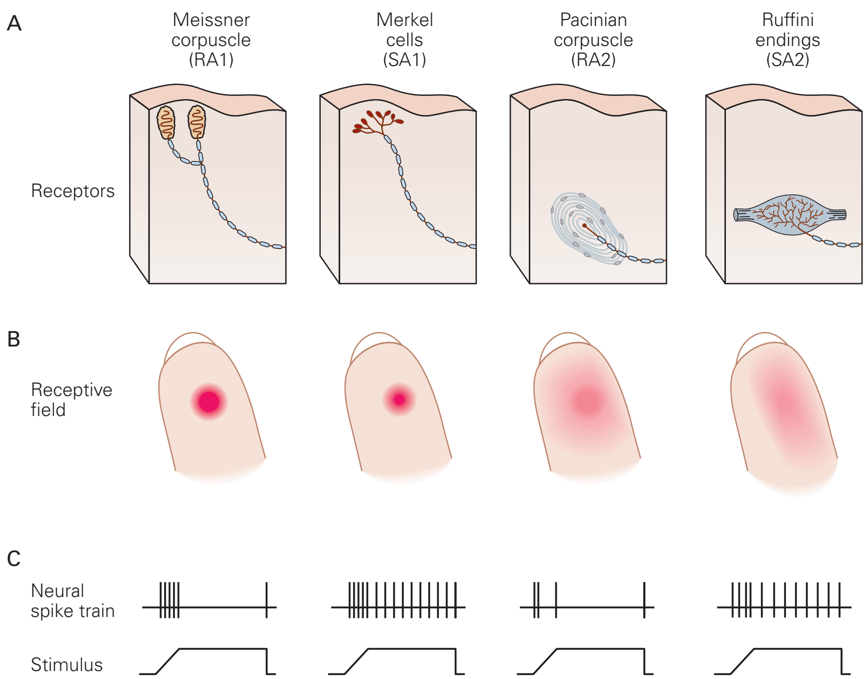

Figure 19–1 Four types of mechanoreceptors are responsible for the sense of touch in the human hand. The terminals of myelinated sensory nerves innervating the hand are surrounded by specialized structures that detect contact on the skin. The receptors differ in morphology, innervation patterns, location 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.

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.

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.

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

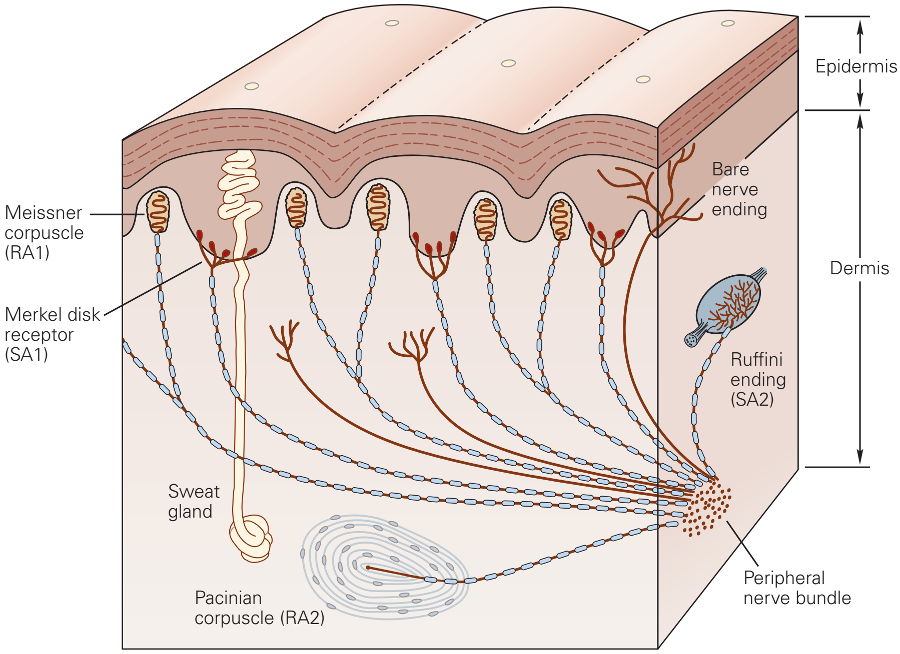

Figure 19–2 Tactile innervation of the glabrous skin in humans. A cross section of the glabrous skin shows the principal receptors for touch in the human hand. All of these receptors are innervated by large-diameter Aβ myelinated fibers. The Meissner corpuscles and Merkel cells lie in the superficial 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.)

"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

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

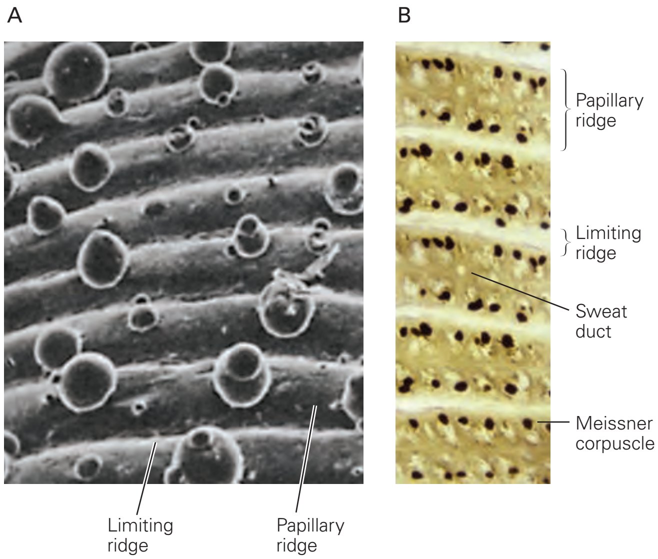

Figure 19–3 The skin of the human fingertip.

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.)

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.

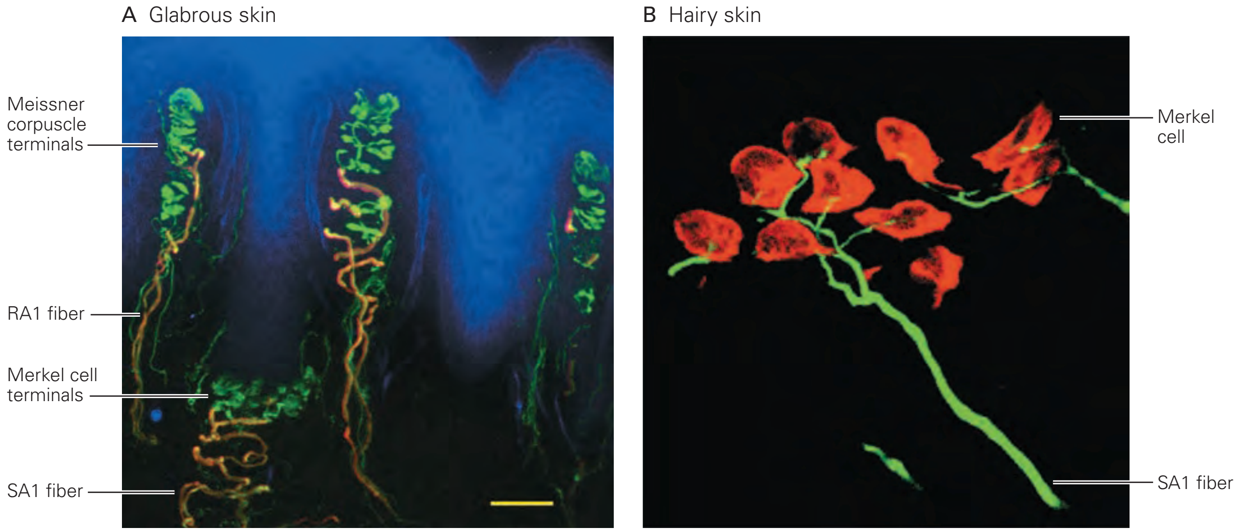

Figure 19–4 **Innervation pattern of Meissner corpuscles and Merkel cells in glabrous and hairy skin.**

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.)

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.

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).

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

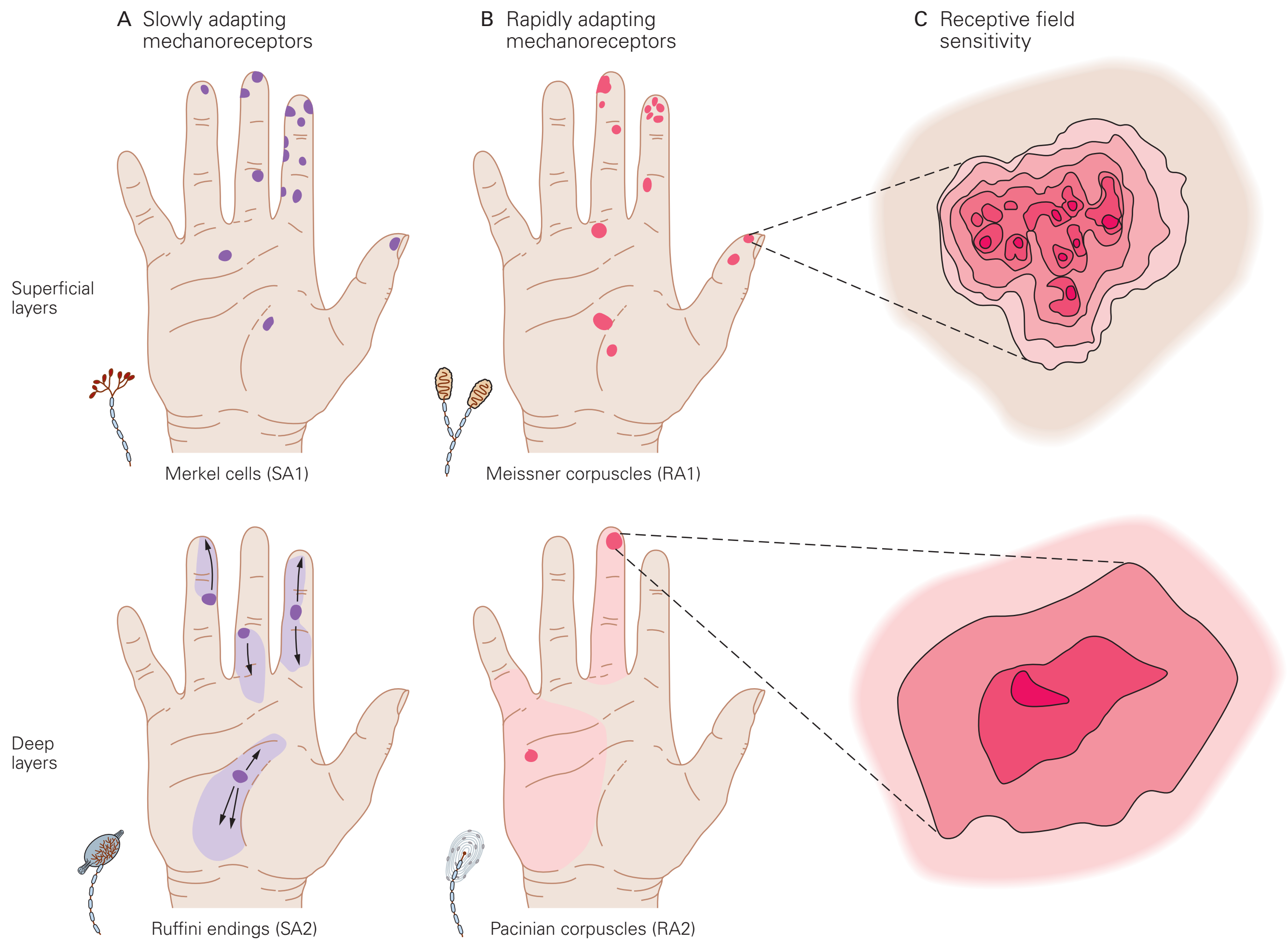

Figure 19–5 Receptive fields in the human hand are smallest at the fingertips. Each colored area on the hands indicates the receptive field of an individual sensory nerve fiber. (Adapted, with permission, from Johansson and Vallbo 1983.)

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.

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

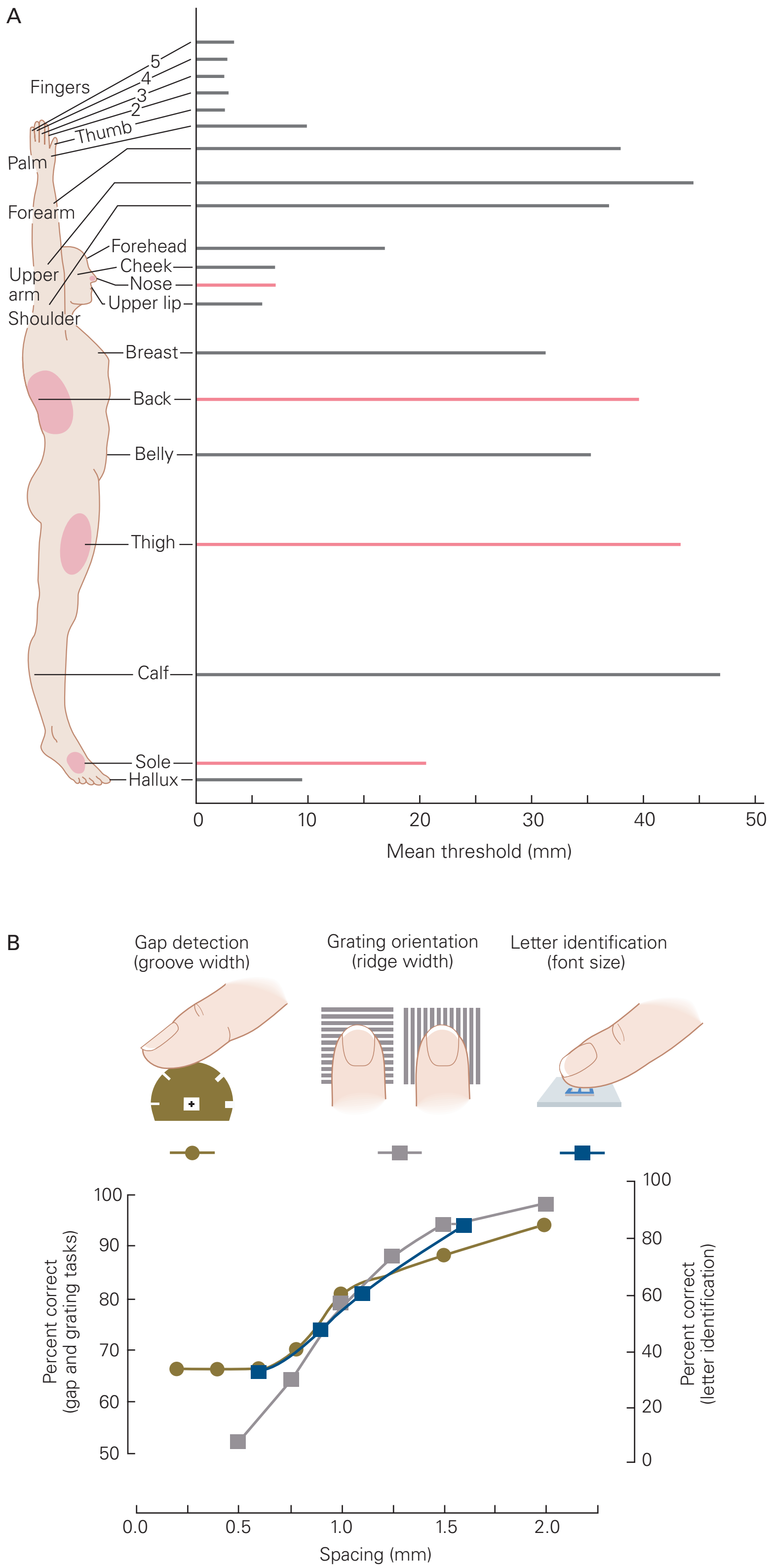

Figure 19–6 **Tactile acuity in the human hand is highest on the fingertip.**

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.)

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

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

Slowly Adapting Fibers Detect Object Pressure and Form

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

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

To understand why these objects evoke different sensations, we need to consider the physical events that occur when the skin is touched. When a pencil tip is pressed against the skin, it dimples the surface at the contact point and forms a shallow, sloped basin in the surrounding region (approximately 4 mm in radius). Although the indentation force is concentrated in the center, the surrounding region is also perturbed by local stretch, called tensile strain. SA1 receptors at both the center and the surrounding "hillsides" of skin are stimulated, firing spike trains proportional to the degree of local stretch.

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

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

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

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