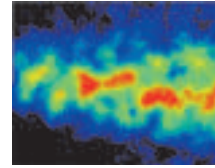


Chapter 8



The Somatic Sensory System

Overview

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

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

Cutaneous and Subcutaneous Somatic Sensory Receptors

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

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

TABLE 8.1
The Major Classes of Somatic Sensory Receptors

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

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

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

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

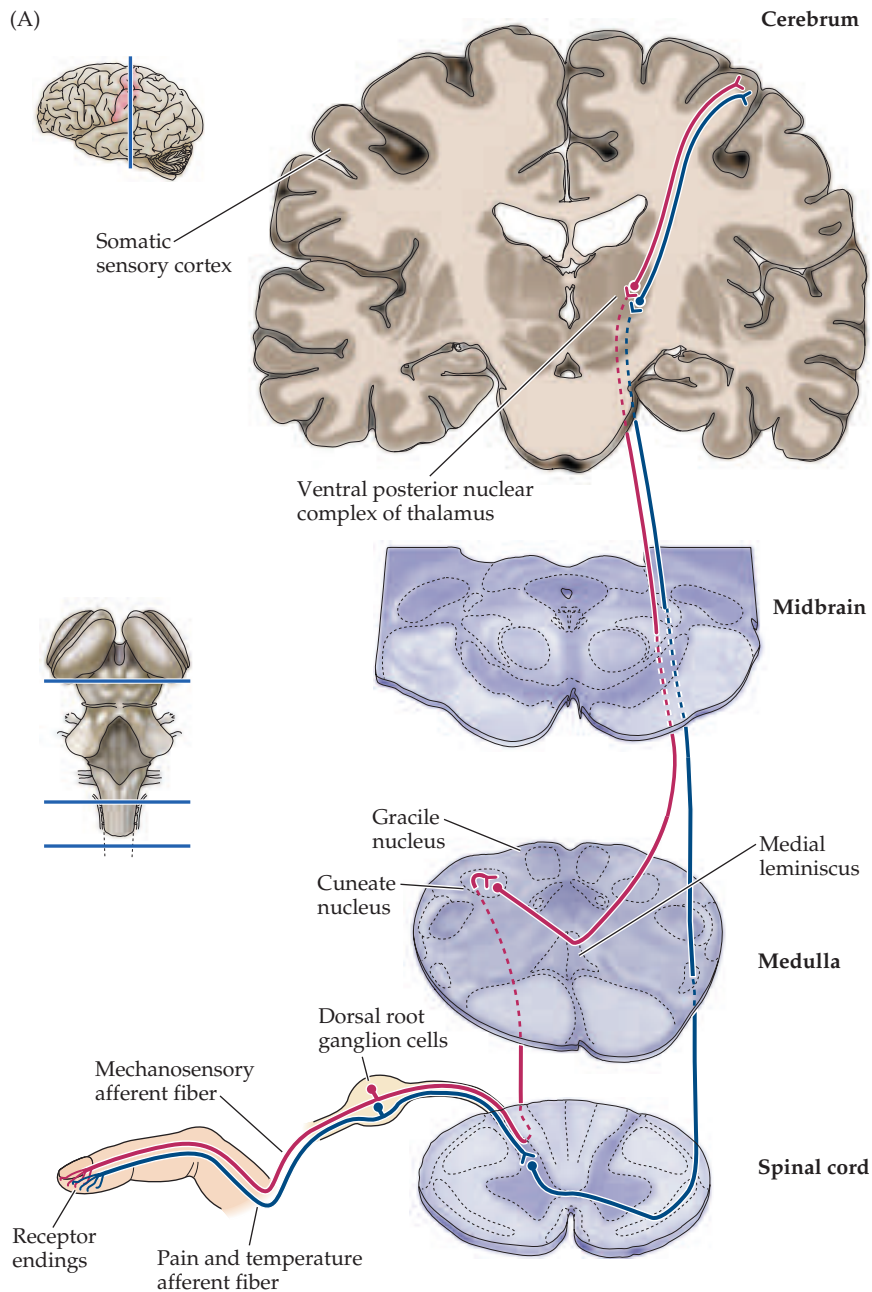
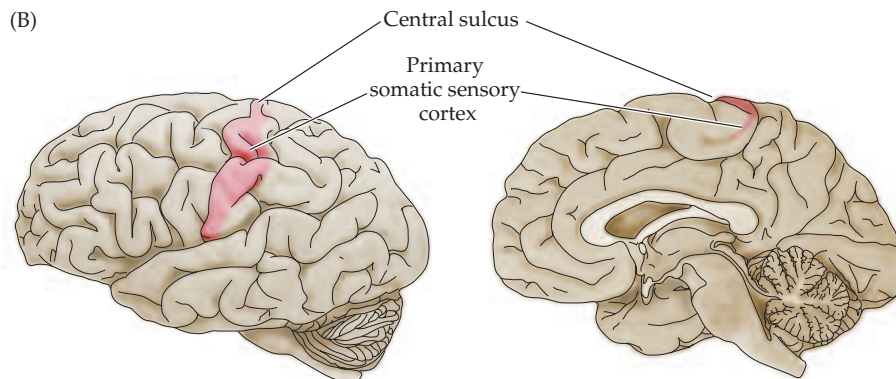


Figure 8.1 General organization of the somatic sensory system. (A) Mechanosensory information about the body reaches the brain by way of a three-neuron relay (shown in red). The first synapse is made by the terminals of the centrally projecting axons of dorsal root ganglion cells onto neurons in the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



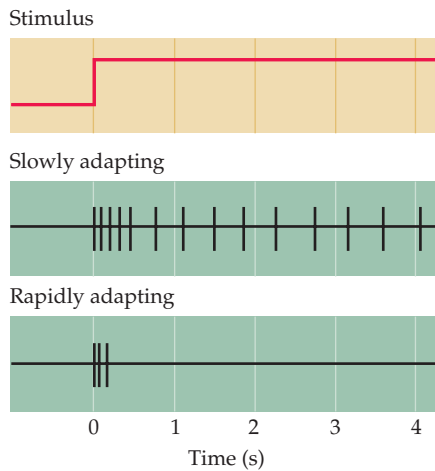


Figure 8.2 Slowly adapting mechanoreceptors continue responding to a stimulus, whereas rapidly adapting receptors respond only at the onset (and often the offset) of stimulation. These functional differences allow the mechanoreceptors to provide information about both the static (via slowly adapting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

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

Mechanoreceptors Specialized to Receive Tactile Information

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

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

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

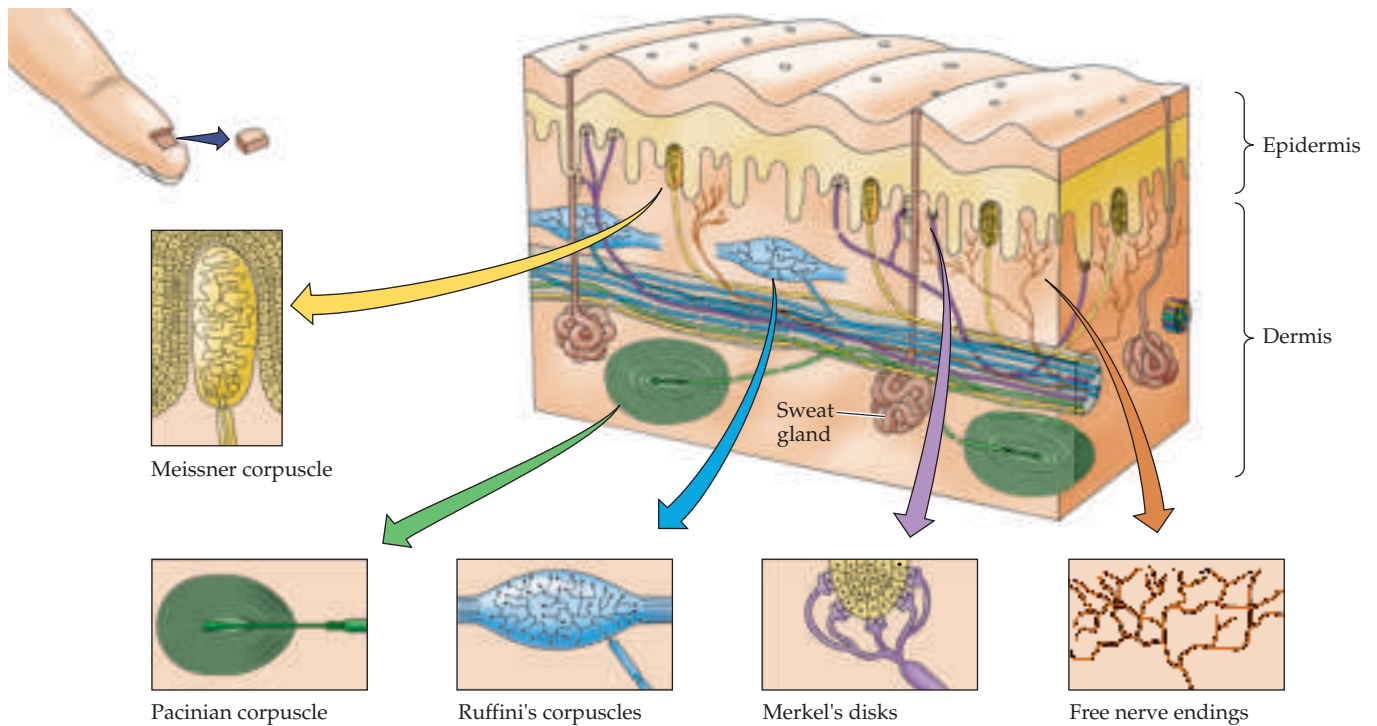


Figure 8.3 The skin harbors a variety of morphologically distinct mechanoreceptors. This diagram represents the smooth, hairless (also called glabrous) skin of the fingertip. The major characteristics of the various receptor types are summarized in Table 8.1. (After Darian-Smith, 1984.)

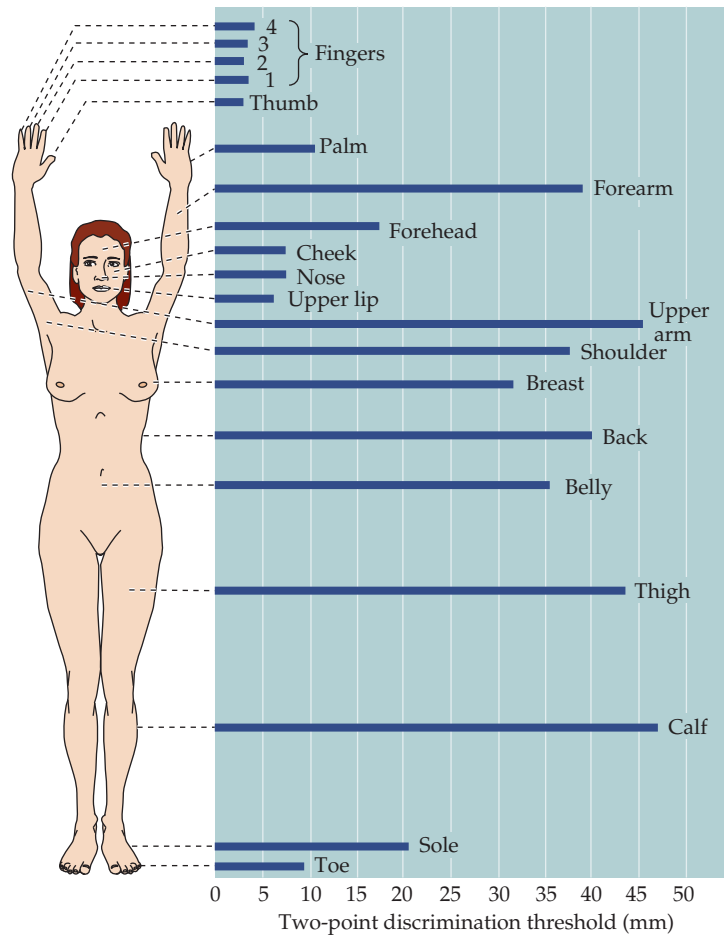
Slowly adapting cutaneous mechanoreceptors include **Merkel's disks** and **Ruffini's corpuscles** (see Figure 8.3 and Table 8.1). Merkel's disks are located in the epidermis, where they are precisely aligned with the papillae that lie beneath the dermal ridges. They account for about 25% of the mechanoreceptors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

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

Differences in Mechanosensory Discrimination across the Body Surface

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

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



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