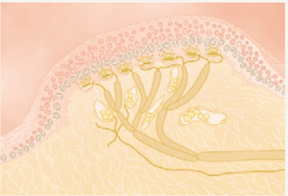
## CHAPTER 47

# Somatic Sensations: I. General Organization, the Tactile and Position Senses



The *somatic senses* are the nervous mechanisms that collect sensory information from all over the body. These senses are in contradistinction to the *special senses*, which mean specifically vision, hearing, smell, taste, and equilibrium.

## CLASSIFICATION OF SOMATIC SENSES

The somatic senses can be classified into three physiologic types: (1) the *mechanoreceptive somatic senses*, which include both *tactile* and *position* sensations that are stimulated by mechanical displacement of some tissue of the body; (2) the *thermoreceptive senses*, which detect heat and cold; and (3) the *pain sense*, which is activated by any factor that damages the tissues.

This chapter deals with the mechanoreceptive tactile and position senses. Chapter 48 discusses the thermoreceptive and pain senses. The tactile senses include *touch*, *pressure*, *vibration*, and *tickle* senses, and the position senses include *static position* and *rate of movement* senses.

**Other Classifications of Somatic Sensations.** Somatic sensations are also often grouped together in other classes, as follows.

*Exteroreceptive sensations* are those from the surface of the body. *Proprioceptive sensations* are those having to do with the physical state of the body, including position sensations, tendon and muscle sensations, pressure sensations from the bottom of the feet, and even the sensation of equilibrium (which is often considered a "special" sensation rather than a somatic sensation).

*Visceral sensations* are those from the viscera of the body; in using this term, one usually refers specifically to sensations from the internal organs.

*Deep sensations* are those that come from deep tissues, such as from fasciae, muscles, and bone. These include mainly "deep" pressure, pain, and vibration.

## Detection and Transmission of Tactile Sensations

**Interrelations Among the Tactile Sensations of Touch, Pressure, and Vibration.** Although touch, pressure, and vibration are frequently classified as separate sensations, they are all detected by the same types of receptors. There are three principal differences among them: (1) touch sensation generally results from stimulation of tactile receptors in the skin or in tissues immediately beneath the skin; (2) pressure sensation generally results from deformation of deeper tissues; and (3) vibration sensation results from rapidly repetitive sensory signals, but some of the same types of receptors as those for touch and pressure are used.

**Tactile Receptors.** There are at least six entirely different types of tactile receptors, but many more similar to these also exist. Some were shown in Figure 46–1 of the previous chapter; their special characteristics are the following.

First, some *free nerve endings*, which are found everywhere in the skin and in many other tissues, can detect touch and pressure. For instance, even light contact with the cornea of the eye, which contains no other type of nerve ending besides free nerve endings, can nevertheless elicit touch and pressure sensations.

Second, a touch receptor with great sensitivity is the *Meissner's corpuscle* (illustrated in Figure 46–1), an elongated encapsulated nerve ending of a large (type Aβ) myelinated sensory nerve fiber. Inside the capsulation are many branching terminal nerve filaments. These corpuscles are present in the nonhairy parts of the skin and are particularly abundant in the fingertips, lips, and other areas of the skin where one's ability to discern spatial locations of touch sensations is highly developed. Meissner's corpuscles adapt in a fraction of a second after they are stimulated, which means that they are particularly sensitive to movement of objects over the surface of the skin as well as to low-frequency vibration.

Third, the fingertips and other areas that contain large numbers of Meissner's corpuscles usually also contain large numbers of *expanded tip tactile receptors*, one type of which is *Merkel's discs,* shown in Figure 47–1. The hairy parts of the skin also contain moderate numbers of expanded tip receptors, even though they have almost no Meissner's corpuscles. These receptors differ from Meissner's corpuscles in that they transmit an initially strong but partially adapting signal and then a continuing weaker signal that adapts only slowly. Therefore, they are responsible for giving steady-state signals that allow one to determine continuous touch of objects against the skin.

Merkel's discs are often grouped together in a receptor organ called the *Iggo dome receptor*, which projects upward against the underside of the epithelium of the skin, as also shown in Figure 47–1. This causes the epithelium at this point to protrude outward, thus creating a dome and constituting an extremely sensitive receptor. Also note that the entire group of Merkel's discs is innervated by a single large myelinated nerve fiber (type Aβ). These receptors, along with the Meissner's corpuscles discussed earlier, play extremely important roles in localizing touch sensations to specific surface areas of the body and in determining the texture of what is felt.

Fourth, slight movement of any hair on the body stimulates a nerve fiber entwining its base. Thus, each hair and its basal nerve fiber, called the *hair end-organ*, are also a touch receptor. This receptor adapts readily and, like Meissner's corpuscles, detects mainly (a) movement of objects on the surface of the body or (b) initial contact with the body.

Fifth, located in the deeper layers of the skin and also in still deeper internal tissues are many *Ruffini's end-organs*, which are multibranched, encapsulated endings, as shown in Figure 46–1. These endings adapt very slowly and, therefore, are important for signaling continuous states of deformation of the tissues, such as heavy prolonged touch and pressure signals. They are also found in joint capsules and help to signal the degree of joint rotation.

Sixth, pacinian corpuscles, which were discussed in detail in Chapter 46, lie both immediately beneath the skin and deep in the fascial tissues of the body. They are stimulated only by rapid local compression of the tissues because they adapt in a few hundredths of a second. Therefore, they are particularly important for detecting tissue vibration or other rapid changes in the mechanical state of the tissues.

**Transmission of Tactile Signals in Peripheral Nerve Fibers.** Almost all specialized sensory receptors, such as Meissner's corpuscles, Iggo dome receptors, hair

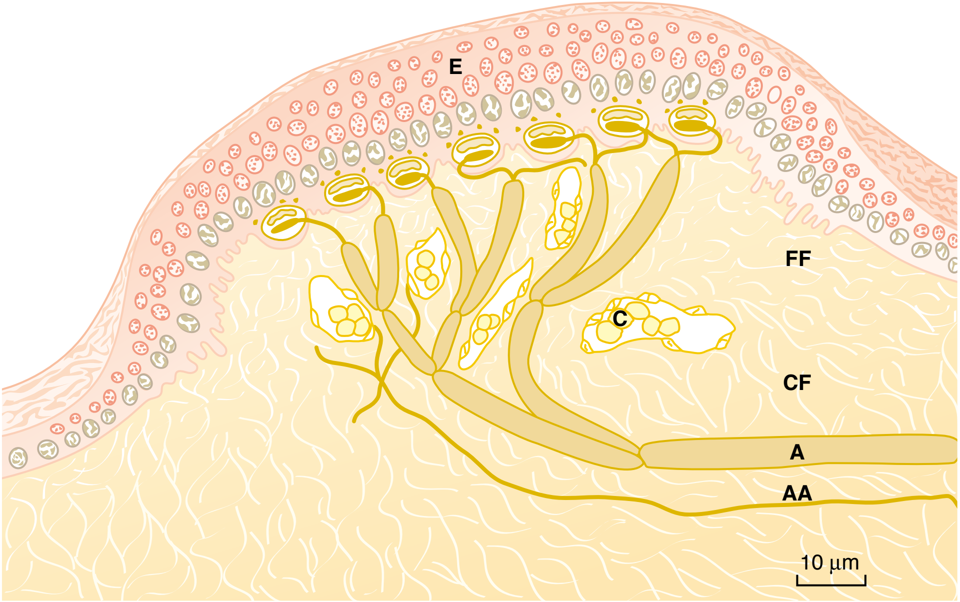


**Figure 47–1**

Iggo dome receptor. Note the multiple numbers of Merkel's discs connecting to a single large myelinated fiber and abutting tightly the undersurface of the epithelium. (From Iggo A, Muir AR: The structure and function of a slowly adapting touch corpuscle in hairy skin. J Physiol 200: 763, 1969.)

receptors, pacinian corpuscles, and Ruffini's endings, transmit their signals in type A$\beta$ nerve fibers that have transmission velocities ranging from 30 to 70 m/sec. Conversely, free nerve ending tactile receptors transmit signals mainly by way of the small type A$\delta$ myelinated fibers that conduct at velocities of only 5 to 30 m/sec.

Some tactile free nerve endings transmit by way of type C unmyelinated fibers at velocities from a fraction of a meter up to 2 m/sec; these send signals into the spinal cord and lower brain stem, probably subserving mainly the sensation of tickle.

Thus, the more critical types of sensory signals—those that help to determine precise localization on the skin, minute gradations of intensity, or rapid changes in sensory signal intensity—are all transmitted in more rapidly conducting types of sensory nerve fibers. Conversely, the cruder types of signals, such as crude pressure, poorly localized touch, and especially tickle, are transmitted by way of much slower, very small nerve fibers that require much less space in the nerve bundle than the fast fibers.

### Detection of Vibration

All tactile receptors are involved in detection of vibration, although different receptors detect different frequencies of vibration. Pacinian corpuscles can detect signal vibrations from 30 to 800 cycles per second because they respond extremely rapidly to minute and rapid deformations of the tissues, and they also transmit their signals over type A$\beta$ nerve fibers, which can transmit as many as 1000 impulses per second. Low-frequency vibrations from 2 up to 80 cycles per second, in contrast, stimulate other tactile receptors, especially Meissner's corpuscles, which are less rapidly adapting than pacinian corpuscles.

## TICKLE AND ITCH

Neurophysiologic studies have demonstrated the existence of very sensitive, rapidly adapting mechanoreceptive free nerve endings that elicit only the tickle and itch sensations. Furthermore, these endings are found almost exclusively in superficial layers of the skin, which is also the only tissue from which the tickle and itch sensations usually can be elicited. These sensations are transmitted by very small type C, unmyelinated fibers similar to those that transmit the aching, slow type of pain.

The purpose of the itch sensation is presumably to call attention to mild surface stimuli such as a flea crawling on the skin or a fly about to bite, and the elicited signals then activate the scratch reflex or other maneuvers that rid the host of the irritant. Itch can be relieved by scratching if this removes the irritant or if the scratch is strong enough to elicit pain. The pain signals are believed to suppress the itch signals in the cord by lateral inhibition, as described in Chapter 48.

# Sensory Pathways for Transmitting Somatic Signals into the Central Nervous System

Almost all sensory information from the somatic segments of the body enters the spinal cord through the dorsal roots of the spinal nerves. However, from the entry point into the cord and then to the brain, the sensory signals are carried through one of two alternative sensory pathways: (1) the *dorsal column*–medial lemniscal system or (2) the *anterolateral system*. These two systems come back together partially at the level of the thalamus.

The dorsal column–medial lemniscal system, as its name implies, carries signals upward to the medulla of the brain mainly in the *dorsal columns* of the cord. Then, after the signals synapse and cross to the opposite side in the medulla, they continue upward through the brain stem to the thalamus by way of the *medial lemniscus*.

Conversely, signals in the anterolateral system, immediately after entering the spinal cord from the dorsal spinal nerve roots, synapse in the dorsal horns of the spinal gray matter, then cross to the opposite side of the cord and ascend through the anterior and lateral white columns of the cord. They terminate at all levels of the lower brain stem and in the thalamus.

The dorsal column–medial lemniscal system is composed of large, myelinated nerve fibers that transmit signals to the brain at velocities of 30 to 110 m/sec, whereas the anterolateral system is composed of smaller myelinated fibers that transmit signals at velocities ranging from a few meters per second up to 40 m/sec.

Another difference between the two systems is that the dorsal column–medial lemniscal system has a high degree of spatial orientation of the nerve fibers with respect to their origin, while the anterolateral system has much less spatial orientation. These differences immediately characterize the types of sensory information that can be transmitted by the two systems. That is, sensory information that must be transmitted rapidly and with temporal and spatial fidelity is transmitted mainly in the dorsal column–medial lemniscal system; that which does not need to be transmitted rapidly or with great spatial fidelity is transmitted mainly in the anterolateral system.

The anterolateral system has a special capability that the dorsal system does not have: the ability to transmit a broad spectrum of sensory modalities—pain, warmth, cold, and crude tactile sensations; most of these are discussed in detail in Chapter 48. The dorsal system is limited to discrete types of mechanoreceptive sensations.

With this differentiation in mind, we can now list the types of sensations transmitted in the two systems.

### Dorsal Column–Medial Lemniscal System

1. Touch sensations requiring a high degree of localization of the stimulus
2. Touch sensations requiring transmission of fine gradations of intensity
3. Phasic sensations, such as vibratory sensations
4. Sensations that signal movement against the skin
5. Position sensations from the joints
6. Pressure sensations having to do with fine degrees of judgment of pressure intensity

### Anterolateral System

1. Pain
2. Thermal sensations, including both warmth and cold sensations
3. Crude touch and pressure sensations capable only of crude localizing ability on the surface of the body
4. Tickle and itch sensations
5. Sexual sensations

## Transmission in the Dorsal Column–Medial Lemniscal System

### Anatomy of the Dorsal Column–Medial Lemniscal System

On entering the spinal cord through the spinal nerve dorsal roots, the large myelinated fibers from the specialized mechanoreceptors divide almost immediately to form a *medial branch* and a *lateral branch*, shown by the right-hand fiber entering through the spinal root in Figure 47–2. The medial branch turns medially first and then upward in the dorsal column, proceeding by way of the dorsal column pathway all the way to the brain.

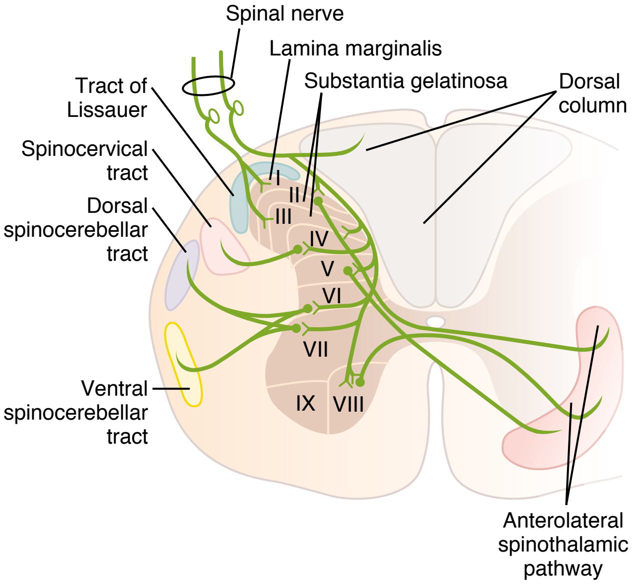


**Figure 47–2**

Cross section of the spinal cord, showing the anatomy of the cord gray matter and of ascending sensory tracts in the white columns of the spinal cord.

The lateral branch enters the dorsal horn of the cord gray matter, then divides many times to provide terminals that synapse with local neurons in the intermediate and anterior portions of the cord gray matter. These local neurons in turn serve three functions: (1) A major share of them give off fibers that enter the dorsal columns of the cord and then travel upward to the brain. (2) Many of the fibers are very short and terminate locally in the spinal cord gray matter to elicit local spinal cord reflexes, which are discussed in Chapter 54. (3) Others give rise to the spinocerebellar tracts, which we will discuss in Chapter 56 in relation to the function of the cerebellum.

**The Dorsal Column–Medial Lemniscal Pathway.** Note in Figure 47–3 that nerve fibers entering the dorsal columns pass uninterrupted up to the dorsal medulla, where they synapse in the *dorsal column nuclei* (the *cuneate* and *gracile nuclei*). From there, *second-order neurons*

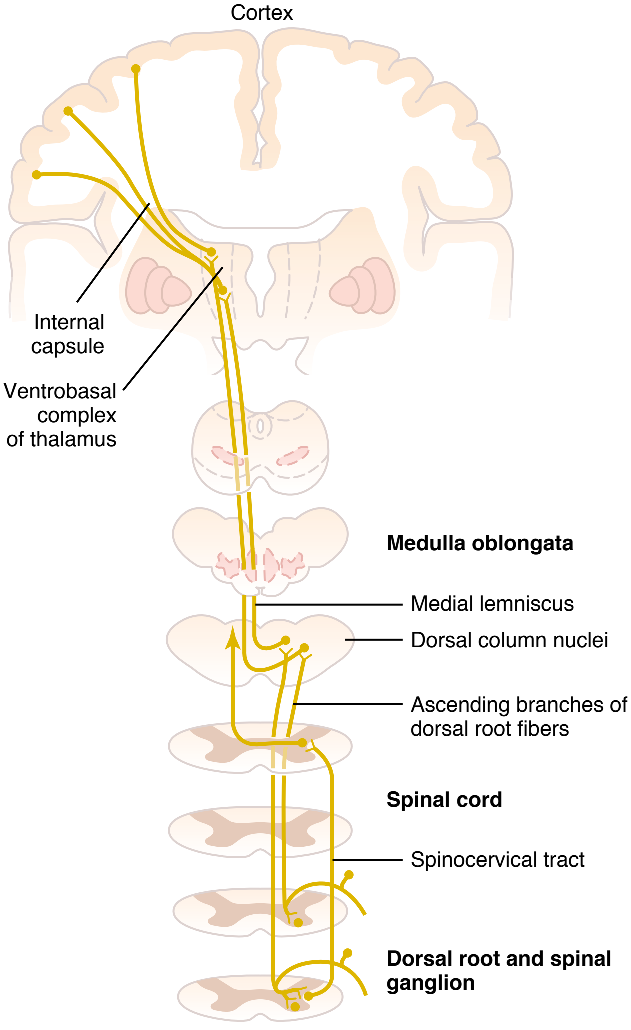


**Figure 47–3**

The dorsal column–medial lemniscal pathway for transmitting critical types of tactile signals. (Modified from Ranson SW, Clark SL: Anatomy of the Nervous System. Philadelphia: WB Saunders Co, 1959.)

decussate immediately to the opposite side of the brain stem and continue upward through the *medial lemnisci* to the thalamus. In this pathway through the brain stem, each medial lemniscus is joined by additional fibers from the *sensory nuclei of the trigeminal nerve*; these fibers subserve the same sensory functions for the head that the dorsal column fibers subserve for the body.

In the thalamus, the medial lemniscal fibers terminate in the thalamic sensory relay area, called the *ventrobasal complex*. From the ventrobasal complex, *third-order nerve fibers* project, as shown in Figure 47–4, mainly to the *postcentral gyrus* of the *cerebral cortex*, which is called *somatic sensory area I* (as shown in Figure 47–6, these fibers also project to a smaller area in the lateral parietal cortex called *somatic sensory area II*).

### Spatial Orientation of the Nerve Fibers in the Dorsal Column-Medial Lemniscal System

One of the distinguishing features of the dorsal column–medial lemniscal system is a distinct spatial orientation of nerve fibers from the individual parts of the body that is maintained throughout. For instance, in the dorsal columns of the spinal cord, the fibers from the lower parts of the body lie toward the center of the cord, whereas those that enter the cord at progressively higher segmental levels form successive layers laterally.

In the thalamus, distinct spatial orientation is still maintained, with the tail end of the body represented by the most lateral portions of the ventrobasal complex and the head and face represented by the medial areas of the complex. Because of the crossing of the medial lemnisci in the medulla, the left side of the body is represented in the right side of the thalamus, and the right side of the body in the left side of the thalamus.

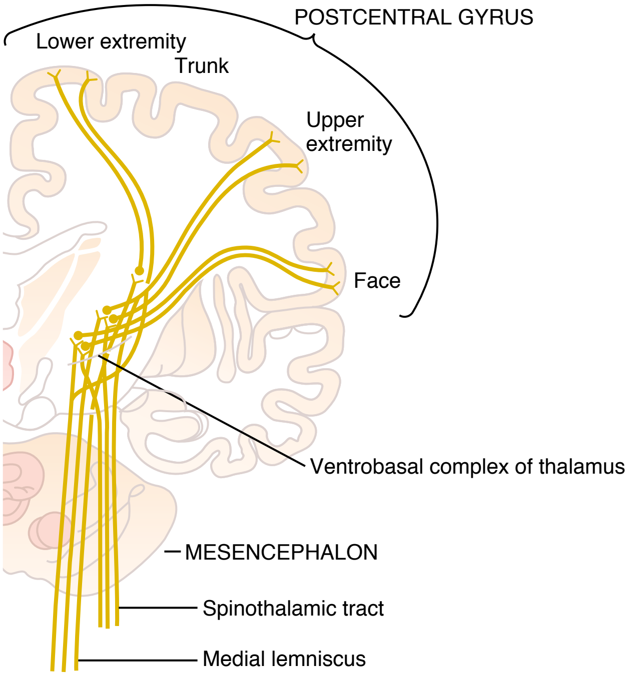


**Figure 47–4**

Projection of the dorsal column–medial lemniscal system through the thalamus to the somatosensory cortex. (Modified from Brodal A: Neurological Anatomy in Relation to Clinical Medicine. New York: Oxford University Press, 1969, by permission of Oxford University Press.)

## Somatosensory Cortex

Before discussing the role of the cerebral cortex in somatic sensation, we need to give an orientation to the various areas of the cortex. Figure 47–5 is a map of the human cerebral cortex, showing that it is divided into about 50 distinct areas called *Brodmann's areas* based on histological structural differences. This map is important because virtually all neurophysiologists and neurologists use it to refer by number to many of the different functional areas of the human cortex.

Note in the figure the large *central fissure* (also called *central sulcus*) that extends horizontally across the brain. In general, sensory signals from all modalities of sensation terminate in the cerebral cortex immediately posterior to the central fissure. And, generally, the anterior half of the parietal lobe is concerned almost entirely with reception and interpretation of *somatosensory signals*. But the posterior half of the parietal lobe provides still higher levels of interpretation.

*Visual signals* terminate in the occipital lobe, and *auditory signals* in the temporal lobe.

Conversely, that portion of the cerebral cortex anterior to the central fissure and constituting the posterior half of the frontal lobe is called the *motor cortex* and is devoted almost entirely to control of muscle contractions and body movements. A major share of this motor control is in response to somatosensory

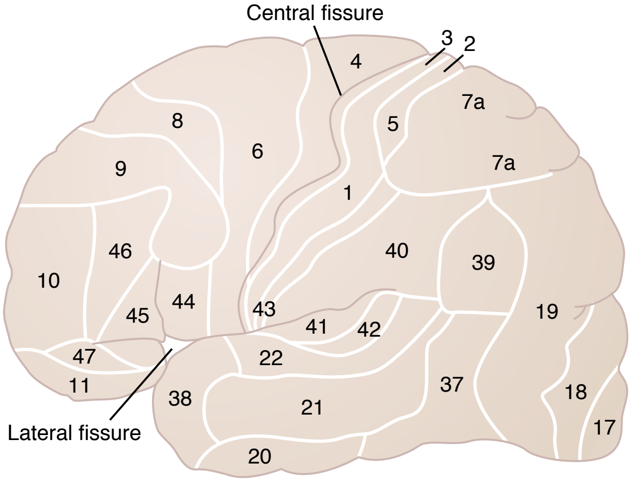


**Figure 47–5**

Structurally distinct areas, called Brodmann's areas, of the human cerebral cortex. Note specifically areas 1, 2, and 3, which constitute *primary somatosensory area I*, and areas 5 and 7, which constitute the *somatosensory association area*.

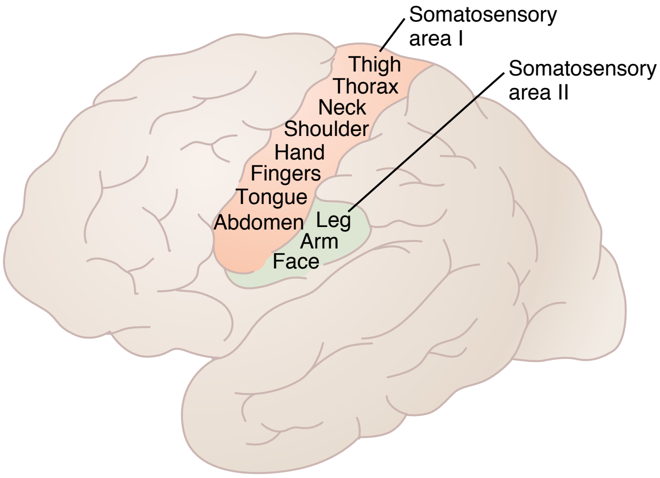


**Figure 47–6**

Two somatosensory cortical areas, somatosensory areas I and II.

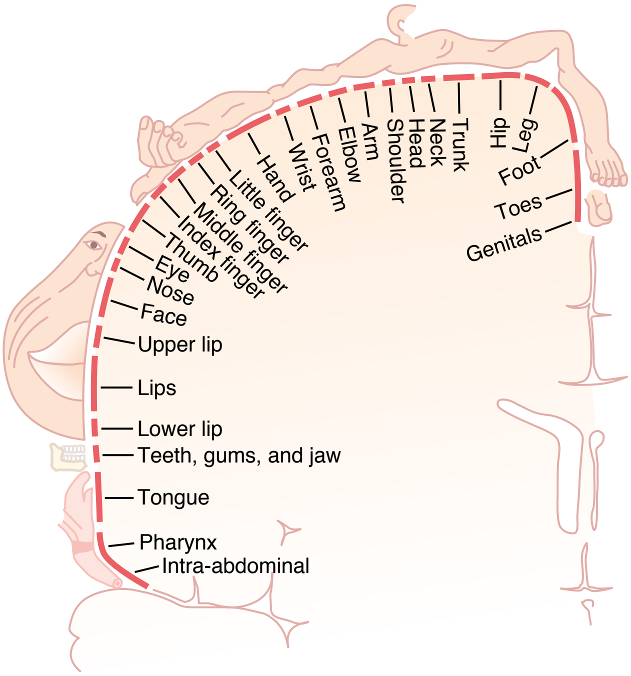


**Figure 47–7**

Representation of the different areas of the body in somatosensory area I of the cortex. (From Penfield W, Rasmussen T: Cerebral Cortex of Man: A Clinical Study of Localization of Function. New York: Hafner, 1968.)

signals received from the sensory portions of the cortex, which keep the motor cortex informed at each instant about the positions and motions of the different body parts.

**Somatosensory Areas I and II.** Figure 47–6 shows two separate sensory areas in the anterior parietal lobe called *somatosensory area I* and *somatosensory area II*. The reason for this division into two areas is that a distinct and separate spatial orientation of the different parts of the body is found in each of these two areas. However, somatosensory area I is so much more extensive and so much more important than somatosensory area II that in popular usage, the term "somatosensory cortex" almost always means area I.

Somatosensory area I has a high degree of localization of the different parts of the body, as shown by the names of virtually all parts of the body in Figure 47–6. By contrast, localization is poor in somatosensory area II, although roughly, the face is represented anteriorly, the arms centrally, and the legs posteriorly.

Little is known about the function of somatosensory area II. It is known that signals enter this area from the brain stem, transmitted upward from both sides of the body. In addition, many signals come secondarily from somatosensory area I as well as from other sensory areas of the brain, even from the visual and auditory areas. Projections from somatosensory area I are required for function of somatosensory area II. However, removal of parts of somatosensory area II has no apparent effect on the response of neurons in somatosensory area I. Thus, much of what we know about somatic sensation appears to be explained by the functions of somatosensory area I.

**Spatial Orientation of Signals from Different Parts of the Body in Somatosensory Area I.** Somatosensory area I lies immediately behind the central fissure, located in the postcentral gyrus of the human cerebral cortex (in Brodmann's areas 3, 1, and 2).

Figure 47–7 shows a cross section through the brain at the level of the postcentral gyrus, demonstrating representations of the different parts of the body in separate regions of somatosensory area I. Note, however, that each lateral side of the cortex receives sensory information almost exclusively from the opposite side of the body.

Some areas of the body are represented by large areas in the somatic cortex—the lips the greatest of all, followed by the face and thumb—whereas the trunk and lower part of the body are represented by relatively small areas. The sizes of these areas are directly proportional to the number of specialized sensory receptors in each respective peripheral area of the body. For instance, a great number of specialized nerve endings are found in the lips and thumb, whereas only a few are present in the skin of the body trunk.

Note also that the head is represented in the most lateral portion of somatosensory area I, and the lower part of the body is represented medially.

### Layers of the Somatosensory Cortex and Their Function

The cerebral cortex contains *six* layers of neurons, beginning with layer I next to the brain surface and extending progressively deeper to layer VI, shown in Figure 47–8. As would be expected, the neurons in each layer perform functions different from those in other layers. Some of these functions are:

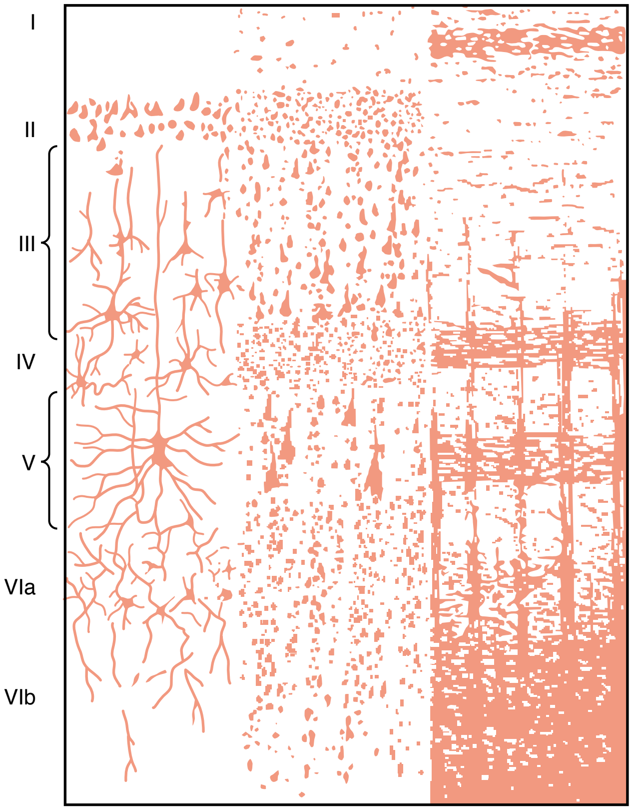


**Figure 47–8**

Structure of the cerebral cortex, showing I, molecular layer; II, external granular layer; III, layer of small pyramidal cells; IV, internal granular layer; V, large pyramidal cell layer; and VI, layer of fusiform or polymorphic cells. (From Ranson SW, Clark SL [after Brodmann]: Anatomy of the Nervous System. Philadelphia: WB Saunders, 1959.)

1. The incoming sensory signal excites neuronal layer IV first; then the signal spreads toward the surface of the cortex and also toward deeper layers.
2. Layers I and II receive diffuse, nonspecific input signals from lower brain centers that facilitate specific regions of the cortex; this system is described in Chapter 57. This input mainly controls the overall level of excitability of the respective regions stimulated.
3. The neurons in layers II and III send axons to related portions of the cerebral cortex on the opposite side of the brain through the *corpus callosum*.
4. The neurons in layers V and VI send axons to the deeper parts of the nervous system. Those in layer V are generally larger and project to more distant areas, such as to the basal ganglia, brain stem, and spinal cord where they control signal transmission. From layer VI, especially large numbers of axons extend to the thalamus, providing signals from the cerebral cortex that interact with and help to control the excitatory levels of incoming sensory signals entering the thalamus.

### The Sensory Cortex Is Organized in Vertical Columns of Neurons; Each Column Detects a Different Sensory Spot on the Body with a Specific Sensory Modality

Functionally, the neurons of the somatosensory cortex are arranged in vertical columns extending all the way through the six layers of the cortex, each column having a diameter of 0.3 to 0.5 millimeter and containing perhaps 10,000 neuronal cell bodies. Each of these columns serves a single specific sensory modality, some columns responding to stretch receptors around joints, some to stimulation of tactile hairs, others to discrete localized pressure points on the skin, and so forth. At layer IV, where the input sensory signals first enter the cortex, the columns of neurons function almost entirely separately from one another. At other levels of the columns, interactions occur that initiate analysis of the meanings of the sensory signals.

In the most anterior 5 to 10 millimeters of the postcentral gyrus, located deep in the central fissure in Brodmann's area 3a, an especially large share of the vertical columns respond to muscle, tendon, and joint stretch receptors. Many of the signals from these sensory columns then spread anteriorly, directly to the motor cortex located immediately forward of the central fissure. These signals play a major role in controlling the effluent motor signals that activate sequences of muscle contraction.

As one moves posteriorly in somatosensory area I, more and more of the vertical columns respond to slowly adapting cutaneous receptors, and then still farther posteriorly, greater numbers of the columns are sensitive to deep pressure.

In the most posterior portion of somatosensory area I, about 6 per cent of the vertical columns respond only when a stimulus moves across the skin in a particular direction. Thus, this is a still higher order of interpretation of sensory signals; the process becomes even more complex as the signals spread farther backward from somatosensory area I into the parietal cortex, an area called the *somatosensory association area*, as we discuss subsequently.

### Functions of Somatosensory Area I

Widespread bilateral excision of somatosensory area I causes loss of the following types of sensory judgment:

1. The person is unable to localize discretely the different sensations in the different parts of the body. However, he or she can localize these sensations crudely, such as to a particular hand, to a major level of the body trunk, or to one of the legs. Thus, it is clear that the brain stem, thalamus, or parts of the cerebral cortex not normally considered to be concerned with somatic sensations can perform some degree of localization.
2. The person is unable to judge critical degrees of pressure against the body.
3. The person is unable to judge the weights of objects.
4. The person is unable to judge shapes or forms of objects. This is called *astereognosis*.

5. The person is unable to judge texture of materials because this type of judgment depends on highly critical sensations caused by movement of the fingers over the surface to be judged.

Note that in the list nothing has been said about loss of pain and temperature sense. In specific absence of only somatosensory area I, appreciation of these sensory modalities is still preserved both in quality and intensity. But the sensations are poorly localized, indicating that pain and temperature *localization* depend greatly on the topographical map of the body in somatosensory area I to localize the source.

## Somatosensory Association Areas

Brodmann's areas 5 and 7 of the cerebral cortex, located in the parietal cortex behind somatosensory area I (see Figure 47–5), play important roles in deciphering deeper meanings of the sensory information in the somatosensory areas. Therefore, these areas are called *somatosensory association areas*.

Electrical stimulation in a somatosensory association area can occasionally cause an awake person to experience a complex body sensation, sometimes even the "feeling" of an object such as a knife or a ball. Therefore, it seems clear that the somatosensory association area combines information arriving from multiple points in the primary somatosensory area to decipher its meaning. This also fits with the anatomical arrangement of the neuronal tracts that enter the somatosensory association area because it receives signals from (1) somatosensory area I, (2) the ventrobasal nuclei of the thalamus, (3) other areas of the thalamus, (4) the visual cortex, and (5) the auditory cortex.

**Effect of Removing the Somatosensory Association Area—Amorphosynthesis.** When the somatosensory association area is removed on one side of the brain, the person loses ability to recognize complex objects and complex forms felt on the opposite side of the body. In addition, he or she loses most of the sense of form of his or her own body or body parts on the opposite side. In fact, the person is mainly oblivious to the opposite side of the body—that is, forgets that it is there. Therefore, he or she also often forgets to use the other side for motor functions as well. Likewise, when feeling objects, the person tends to recognize only one side of the object and forgets that the other side even exists. This complex sensory deficit is called *amorphosynthesis*.

## Overall Characteristics of Signal Transmission and Analysis in the Dorsal Column–Medial Lemniscal System

**Basic Neuronal Circuit in the Dorsal Column–Medial Lemniscal System.** The lower part of Figure 47–9 shows the basic organization of the neuronal circuit of the spinal cord dorsal column pathway, demonstrating that at each synaptic stage, divergence occurs. The upper curves of the figure show that the cortical neurons that discharge to the greatest extent are those in a central part of the cortical "field" for each respective receptor. Thus, a weak stimulus causes only the centralmost neurons to fire. A stronger stimulus causes still more neurons to fire, but those in the center discharge at a considerably more rapid rate than do those farther away from the center.

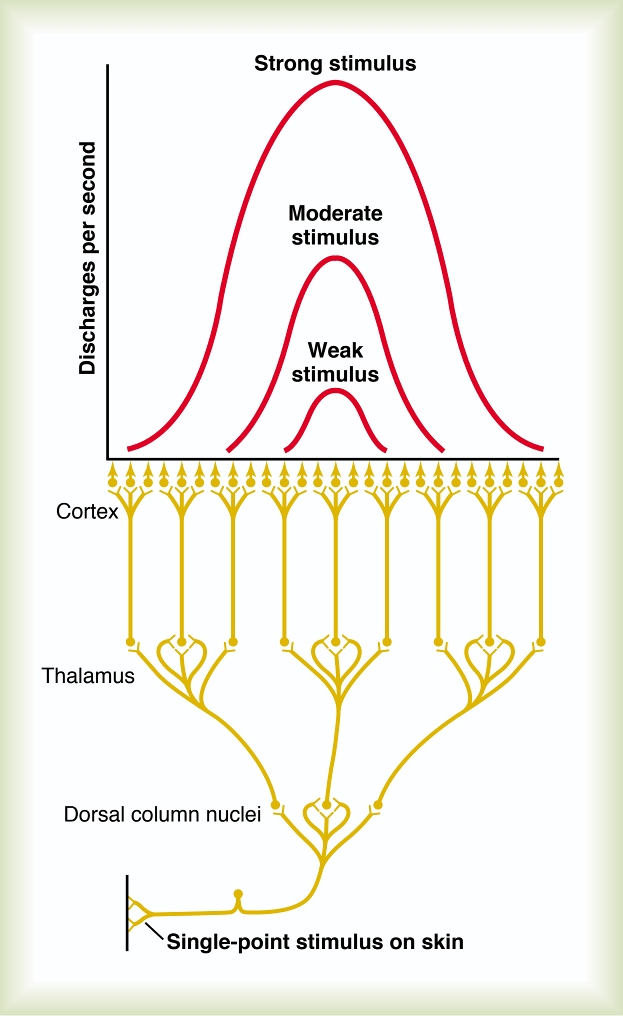


**Figure 47–9**

Transmission of a pinpoint stimulus signal to the cerebral cortex.

**Two-Point Discrimination.** A method frequently used to test tactile discrimination is to determine a person's so-called "two-point" discriminatory ability. In this test, two needles are pressed lightly against the skin at the same time, and the person determines whether two points of stimulus are felt or one point. On the tips of the fingers, a person can distinguish two separate points even when the needles are as close together as 1 to 2 millimeters. However, on the person's back, the needles must usually be as far apart as 30 to 70

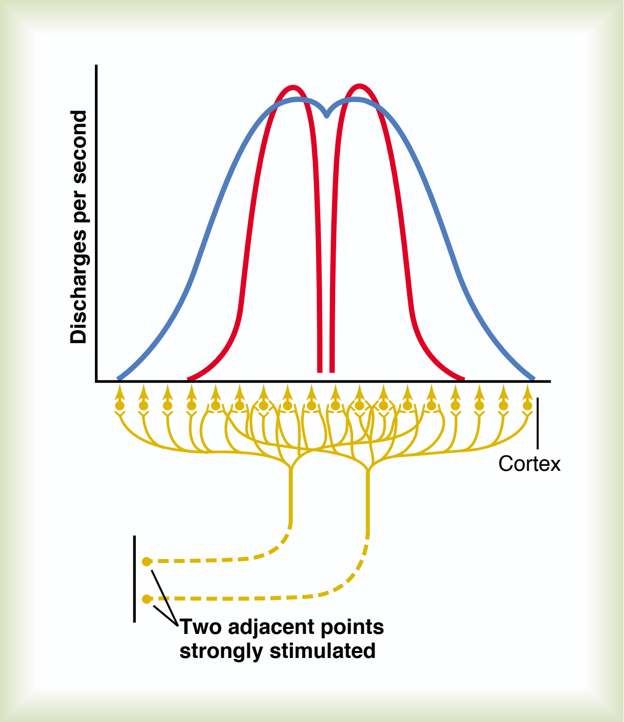


**Figure 47–10**

Transmission of signals to the cortex from two adjacent pinpoint stimuli. The blue curve represents the pattern of cortical stimulation without "surround" inhibition, and the two red curves represent the pattern when "surround" inhibition does occur.

millimeters before two separate points can be detected. The reason for this difference is the different numbers of specialized tactile receptors in the two areas.

Figure 47–10 shows the mechanism by which the dorsal column pathway (as well as all other sensory pathways) transmits two-point discriminatory information. This figure shows two adjacent points on the skin that are strongly stimulated as well as the areas of the somatosensory cortex (greatly enlarged) that are excited by signals from the two stimulated points. The blue curve shows the spatial pattern of cortical excitation when both skin points are stimulated simultaneously. Note that the resultant zone of excitation has two separate peaks. These two peaks, separated by a valley, allow the sensory cortex to detect the presence of two stimulatory points, rather than a single point. The capability of the sensorium to distinguish this presence of two points of stimulation is strongly influenced by another mechanism, *lateral inhibition*, as explained in the next section.

**Effect of Lateral Inhibition (Also Called *Surround Inhibition*) to Increase the Degree of Contrast in the Perceived Spatial Pattern.** As pointed out in Chapter 46, virtually every sensory pathway, when excited, gives rise simultaneously to lateral *inhibitory* signals; these spread to the sides of the excitatory signal and inhibit adjacent neurons. For instance, consider an excited neuron in a dorsal column nucleus. Aside from the central excitatory signal, short lateral pathways transmit inhibitory signals to the surrounding neurons. That is, these signals pass through additional interneurons that secrete an inhibitory transmitter.

The importance of *lateral inhibition* is that it blocks lateral spread of the excitatory signals and, therefore, increases the degree of contrast in the sensory pattern perceived in the cerebral cortex.

In the case of the dorsal column system, lateral inhibitory signals occur at each synaptic level—for instance, in (1) the dorsal column nuclei of the medulla, (2) the ventrobasal nuclei of the thalamus, and (3) the cortex itself. At each of these levels, the lateral inhibition helps to block lateral spread of the excitatory signal. As a result, the peaks of excitation stand out, and much of the surrounding diffuse stimulation is blocked. This effect is demonstrated by the two red curves in Figure 47–10, showing complete separation of the peaks when the intensity of lateral inhibition is great.

**Transmission of Rapidly Changing and Repetitive Sensations.** The dorsal column system also is of particular importance in apprising the sensorium of rapidly changing peripheral conditions. Based on recorded action potentials, this system can recognize changing stimuli that occur in as little as 1/400 of a second.

**Vibratory Sensation.** Vibratory signals are rapidly repetitive and can be detected as vibration up to 700 cycles per second. The higher-frequency vibratory signals originate from the pacinian corpuscles in the skin and deeper tissues, but lower-frequency signals (below about 200 per second) can originate from Meissner's corpuscles as well. These signals are transmitted only in the dorsal column pathway. For this reason, application of vibration (e.g., from a "tuning fork") to different peripheral parts of the body is an important tool used by neurologists for testing functional integrity of the dorsal columns.

## Interpretation of Sensory Stimulus Intensity

The ultimate goal of most sensory stimulation is to apprise the psyche of the state of the body and its surroundings. Therefore, it is important that we discuss briefly some of the principles related to transmission of sensory *stimulus intensity* to the higher levels of the nervous system.

The first question that comes to mind is, how is it possible for the sensory system to transmit sensory experiences of tremendously varying intensities? For instance, the auditory system can detect the weakest possible whisper but can also discern the meanings of an explosive sound, even though the sound intensities of these two experiences can vary more than 10 billion times; the eyes can see visual images with light intensities that vary as much as a half million times; and the skin can detect pressure differences of 10,000 to 100,000 times.

As a partial explanation of these effects, Figure 46–4 in the previous chapter shows the relation of the receptor potential produced by the pacinian corpuscle to the intensity of the sensory stimulus. At low stimulus intensity, slight changes in intensity increase the potential markedly, whereas at high levels of stimulus intensity, further increases in receptor potential are slight. Thus, the pacinian corpuscle is capable of accurately measuring extremely minute *changes* in stimulus at low-intensity levels, but at high-intensity levels, the change in stimulus must be much greater to cause the same amount of *change* in receptor potential.

The transduction mechanism for detecting sound by the cochlea of the ear demonstrates still another method for separating gradations of stimulus intensity. When sound stimulates a specific point on the basilar membrane, weak sound stimulates only those hair cells at the point of maximum sound vibration. But as the sound intensity increases, many more hair cells in each direction farther away from the maximum vibratory point also become stimulated. Thus, signals are transmitted over progressively increasing numbers of nerve fibers, which is another mechanism by which stimulus intensity is transmitted to the central nervous system. This mechanism, plus the direct effect of stimulus intensity on impulse rate in each nerve fiber, as well as several other mechanisms, makes it possible for some sensory systems to operate reasonably faithfully at stimulus intensity levels changing as much as millions of times.

**Importance of the Tremendous Intensity Range of Sensory Reception.** Were it not for the tremendous intensity range of sensory reception that we can experience, the various sensory systems would more often than not be operating in the wrong range. This is demonstrated by the attempts of most people, when taking photographs with a camera, to adjust the light exposure without using a light meter. Left to intuitive judgment of light intensity, a person almost always overexposes the film on bright days and greatly underexposes the film at twilight. Yet, that person's own eyes are capable of discriminating with great detail visual objects in bright sunlight or at twilight; the camera cannot do this without very special manipulation because of the narrow critical range of light intensity required for proper exposure of film.

## Judgment of Stimulus Intensity

**Weber-Fechner Principle—Detection of "Ratio" of Stimulus Strength.** In the mid-1800s, Weber first and Fechner later proposed the principle that *gradations of stimulus strength are discriminated approximately in proportion to the logarithm of stimulus strength.* That is, a person already holding 30 grams weight in his or her hand can barely detect an additional 1-gram increase in weight. And, when already holding 300 grams, he or she can barely detect a 10-gram increase in weight. Thus, in this instance, the *ratio* of the change in stimulus strength required for detection remains essentially constant, about 1 to 30, which is what the logarithmic principle means. To express this mathematically.

$$\text{Interpreted signal strength} = \text{Log (Stimulus)} + \text{Constant}$$

More recently, it has become evident that the Weber-Fechner principle is quantitatively accurate only for higher intensities of visual, auditory, and cutaneous sensory experience and applies only poorly to most other types of sensory experience. Yet the Weber-Fechner principle is still a good one to remember, because it emphasizes that the greater the background sensory intensity, the greater an additional change must be for the psyche to detect the change.

**Power Law.** Another attempt by physiopsychologists to find a good mathematical relation is the following formula, known as the power law.

$$\text{Interpreted signal strength} = \text{K} \bullet (\text{Stimulus} - \text{k})^{y}$$

In this formula, the exponent $y$ and the constants K and k are different for each type of sensation.

When this power law relation is plotted on a graph using double logarithmic coordinates, as shown in Figure 47–11, and when appropriate quantitative values for the constants $y$, K, and k are found, a linear relation can be attained between interpreted stimulus strength and actual stimulus strength over a large range for almost any type of sensory perception.

## Position Senses

The *position senses* are frequently also called *proprioceptive senses*. They can be divided into two subtypes: (1) *static position sense*, which means conscious perception of the orientation of the different parts of the body with respect to one another, and (2) *rate of movement sense*, also called *kinesthesia* or *dynamic proprioception*.

**Position Sensory Receptors.** Knowledge of position, both static and dynamic, depends on knowing the degrees of angulation of all joints in all planes and their rates of change. Therefore, multiple different types of receptors help to determine joint angulation and are used

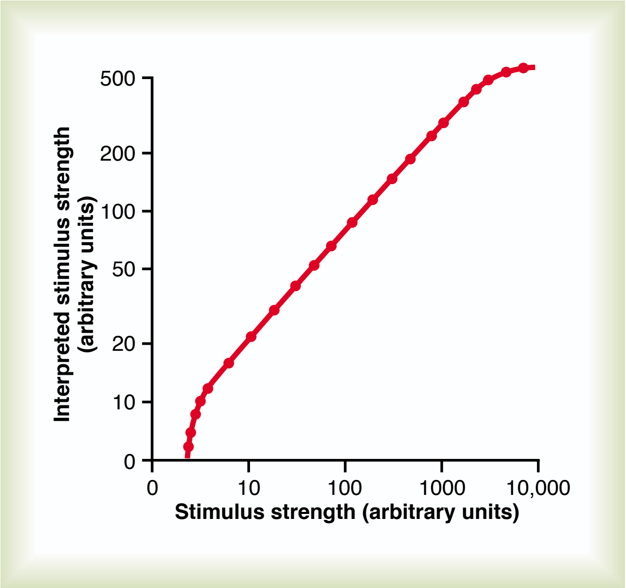


**Figure 47–11**

Graphical demonstration of the "power law" relation between actual stimulus strength and strength that the psyche interprets it to be. Note that the power law does not hold at either very weak or very strong stimulus strengths.

together for position sense. Both skin tactile receptors and deep receptors near the joints are used. In the case of the fingers, where skin receptors are in great abundance, as much as half of position recognition is believed to be detected through the skin receptors. Conversely, for most of the larger joints of the body, deep receptors are more important.

For determining joint angulation in mid ranges of motion, among the most important receptors are the *muscle spindles*. They are also exceedingly important in helping to control muscle movement, as we shall see in Chapter 54. When the angle of a joint is changing, some muscles are being stretched while others are loosened, and the net stretch information from the spindles is transmitted into the computational system of the spinal cord and higher regions of the dorsal column system for deciphering joint angulations.

At the extremes of joint angulation, stretch of the ligaments and deep tissues around the joints is an additional important factor in determining position. Types of sensory endings used for this are the pacinian corpuscles, Ruffini's endings, and receptors similar to the Golgi tendon receptors found in muscle tendons.

The pacinian corpuscles and muscle spindles are especially adapted for detecting rapid rates of change. It is likely that these are the receptors most responsible for detecting rate of movement.

**Processing of Position Sense Information in the Dorsal Column–Medial Lemniscal Pathway.** Referring to Figure 47–12, one sees that *thalamic neurons* responding to joint rotation are of two categories: (1) those maximally stimulated when the joint is at full rotation and (2) those maximally stimulated when the joint is at minimal rotation. Thus, the signals from the individual joint receptors are used to tell the psyche how much each joint is rotated.

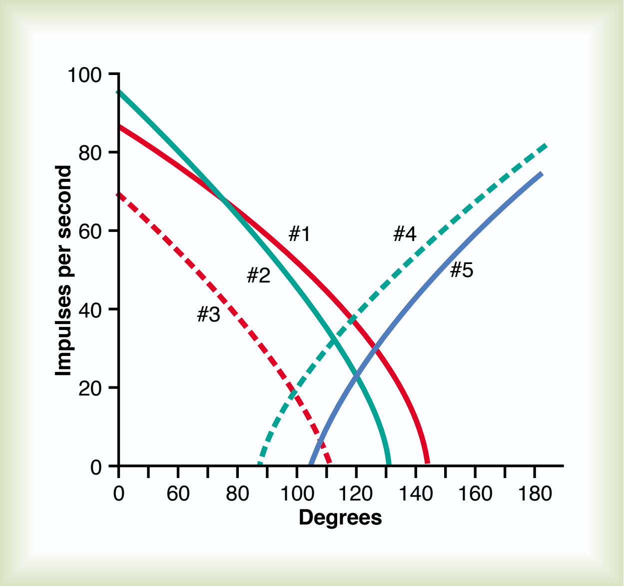


**Figure 47–12**

Typical responses of five different thalamic neurons in the thalamic ventrobasal complex when the knee joint is moved through its range of motion. (Data from Mountcastle VB, Poggie GF, Werner G: The relation of thalamic cell response to peripheral stimuli varied over an intensive continuum. J Neurophysiol 26:807, 1963.)

## Transmission of Less Critical Sensory Signals in the Anterolateral Pathway

The anterolateral pathway for transmitting sensory signals up the spinal cord and into the brain, in contrast to the dorsal column pathway, transmits sensory signals that do not require highly discrete localization of the signal source and do not require discrimination of fine gradations of intensity. These types of signals include pain, heat, cold, crude tactile, tickle, itch, and sexual sensations. In Chapter 48, pain and temperature sensations will be discussed specifically.

### Anatomy of the Anterolateral Pathway

The *spinal cord anterolateral fibers* originate mainly in dorsal horn laminae I, IV, V, and VI (see Figure 47–2). These laminae are where many of the dorsal root sensory nerve fibers terminate after entering the cord.

As shown in Figure 47–13, the anterolateral fibers cross immediately in the *anterior commissure* of the cord to the opposite *anterior* and *lateral white columns*, where they turn upward toward the brain by way of the *anterior spinothalamic* and *lateral spinothalamic tracts*.

The upper terminus of the two spinothalamic tracts is mainly twofold: (1) throughout the *reticular nuclei of the brain stem* and (2) in two different nuclear complexes of the thalamus, the *ventrobasal complex* and the *intralaminar nuclei*. In general, the tactile signals are transmitted mainly into the ventrobasal complex, terminating in some of the same thalamic nuclei where the dorsal column tactile signals terminate. From here, the signals are transmitted to the somatosensory cortex along with the signals from the dorsal columns.

Conversely, only a small fraction of the pain signals project directly to the ventrobasal complex of the thalamus. Instead, most pain signals terminate in the reticular nuclei of the brain stem and from there are relayed to the intralaminar nuclei of the thalamus where the pain signals are further processed, as discussed in greater detail in Chapter 48.

**Characteristics of Transmission in the Anterolateral Pathway.** In general, the same principles apply to transmission in the anterolateral pathway as in the dorsal column–medial lemniscal system, except for the following differences: (1) the velocities of transmission are only one third to one half those in the dorsal column–medial lemniscal system, ranging between 8 and 40 m/sec; (2) the degree of spatial localization of signals is poor; (3) the gradations of intensities are also far less accurate, most of the sensations being recognized in 10 to 20 gradations of strength, rather than as many as 100 gradations for the dorsal column system;

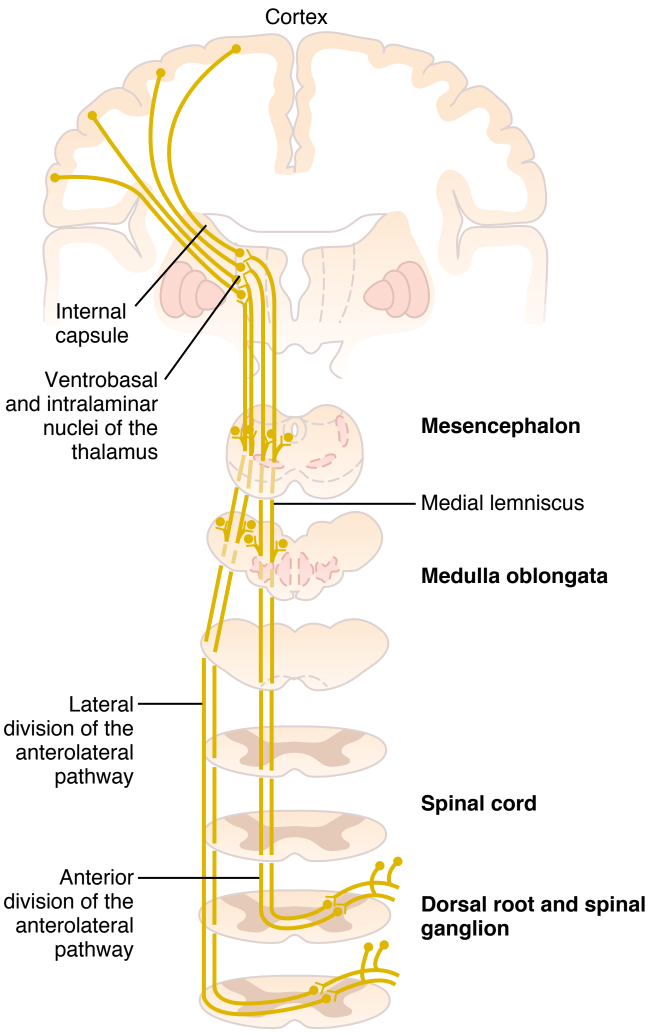


**Figure 47–13**

Anterior and lateral divisions of the anterolateral sensory pathway.

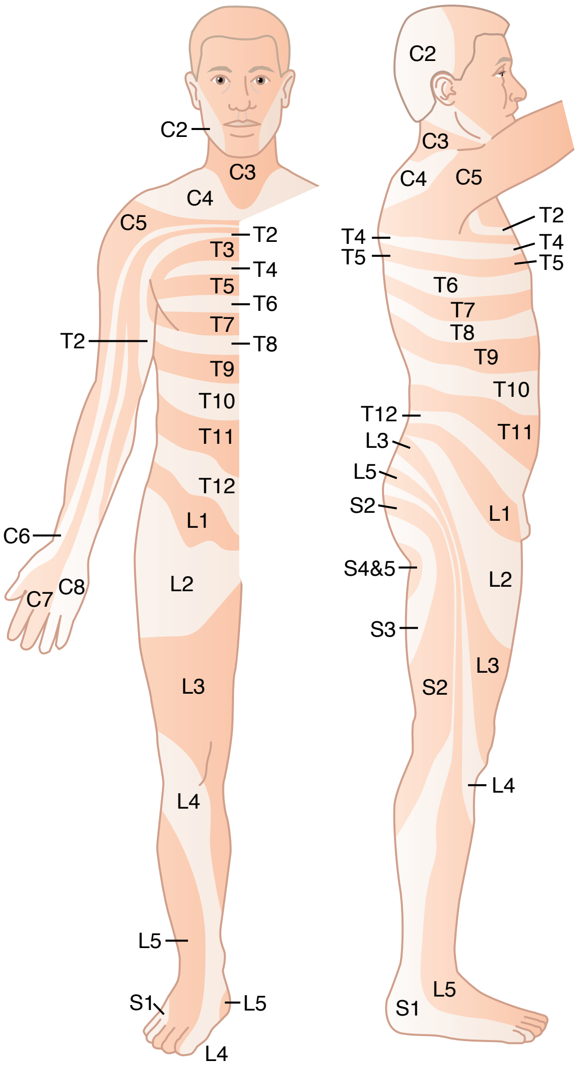


**Figure 47–14**

Dermatomes. (Modified from Grinker RR, Sahs AL: Neurology, 6th ed. Springfield, IL: Charles C Thomas, 1966. Courtesy of Charles C Thomas, Publisher, Ltd., Springfield, Illinois.)

and (4) the ability to transmit rapidly changing or rapidly repetitive signals is poor.

Thus, it is evident that the anterolateral system is a cruder type of transmission system than the dorsal column–medial lemniscal system. Even so, certain modalities of sensation are transmitted only in this system and not at all in the dorsal column–medial lemniscal system. They are pain, temperature, tickle, itch, and sexual sensations, in addition to crude touch and pressure.

## Some Special Aspects of Somatosensory Function

### Function of the Thalamus in Somatic Sensation

When the somatosensory cortex of a human being is destroyed, that person loses most critical tactile sensibilities, but a slight degree of crude tactile sensibility does return. Therefore, it must be assumed that the thalamus (as well as other lower centers) has a slight ability to discriminate tactile sensation, even though the thalamus normally functions mainly to relay this type of information to the cortex.

Conversely, loss of the somatosensory cortex has little effect on one's perception of pain sensation and only a moderate effect on the perception of temperature. Therefore, there is much reason to believe that the lower brain stem, the thalamus, and other associated basal regions of the brain play dominant roles in discrimination of these sensibilities. It is interesting that these sensibilities appeared very early in the phylogenetic development of animals, whereas the critical tactile sensibilities and the somatosensory cortex were late developments.

## Cortical Control of Sensory Sensitivity—"Corticofugal" Signals

In addition to somatosensory signals transmitted from the periphery to the brain, *corticofugal* signals are transmitted in the backward direction from the cerebral cortex to the lower sensory relay stations of the thalamus, medulla, and spinal cord; they control the intensity of sensitivity of the sensory input.

Corticofugal signals are almost entirely inhibitory, so that when sensory input intensity becomes too great, the corticofugal signals automatically decrease transmission in the relay nuclei. This does two things: First, it decreases lateral spread of the sensory signals into adjacent neurons and, therefore, increases the degree of sharpness in the signal pattern. Second, it keeps the sensory system operating in a range of sensitivity that is not so low that the signals are ineffectual nor so high that the system is swamped beyond its capacity to differentiate sensory patterns. This principle of corticofugal sensory control is used by all sensory systems, not only the somatic system, as explained in subsequent chapters.

## Segmental Fields of Sensation—The Dermatomes

Each spinal nerve innervates a "segmental field" of the skin called a *dermatome*. The different dermatomes are shown in Figure 47–14. They are shown in the figure as if there were distinct borders between the adjacent dermatomes, which is far from true because much overlap exists from segment to segment.

The figure shows that the anal region of the body lies in the dermatome of the most distal cord segment, dermatome S5. In the embryo, this is the tail region and the most distal portion of the body. The legs originate embryologically from the lumbar and upper sacral segments (L2 to S3), rather than from the distal sacral segments, which is evident from the dermatomal map. One can use a dermatomal map as shown in Figure 47–14 to determine the level in the spinal cord at which a cord injury has occurred when the peripheral sensations are disturbed by the injury.

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