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Coding of Sensory Information

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SENSATION AND PERCEPTION provided the starting points for modern research into our mental processes. In the early nineteenth century the French philosopher Auguste Comte argued that the study of behavior should become a branch of the biological sciences and that the laws governing the mind should be derived from objective observation. Comte's new philosophy, which he called *positivism*, was influenced by the British empiricists John Locke, George Berkeley, and David Hume, who maintained that all knowledge is obtained through sensory experience—from what we see, hear, feel, taste, and smell. At birth, Locke proposed, the human mind is a *tabula rasa*, a blank slate upon which experience leaves its mark.

Let us then suppose the Mind to be, as we say, white Paper void of all Characters without any Ideas: How comes it to be furnished? Whence comes it by that vast store, which the busie and boundless Fancy of Man has painted on it with an almost endless variety? Whence has it all the materials of Reason and Knowledge? To this I answer, in one word, From *Experience.* In that all of our Knowledge is founded; and from that it ultimately derives itself.

It was this empiricist view that led to the emergence of psychology as a separate discipline apart from philosophy, which had long monopolized the study of the human mind. Thus, in its early days, psychology came to focus on the experimental study of mental processes by emphasizing sensation as the key to the mind. How does a stimulus lead to subjective experience? By what sequence of physiological events? For the fathers of experimental psychology—Ernst Weber, Gustav Fechner, Hermann Helmholtz, and Wilhelm Wundt—those were the central questions.

These researchers soon found that while the senses]

differed in their modes of reception, all the senses shared three common steps: (1) a physical stimulus, (2) a set of events transforming the stimulus into nerve impulses, and (3) a response to this signal in the form of a perception or conscious experience of sensation. Their findings gave rise to the fields of psychophysics and sensory physiology. Psychophysics focused on the relationship between the physical characteristics of a stimulus and the attributes of the sensory experience. Sensory physiology examined the neural consequences of a stimulus—how the stimulus is transduced by sensory receptors and processed in the brain. Some of the most exciting advances in our understanding of perception have come from merging these two approaches in, for example, recent human experiments that use positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) to scan brain function.

Early findings in psychophysics and sensory physiology, however, exposed one weakness in the empiricist argument: A newborn's mind is not blank, nor is our perceptual world formed simply from passive encounters with the physical properties of objects and stimuli. In fact, our perceptions differ qualitatively from the physical properties of stimuli because the nervous system extracts only *certain* pieces of information from each stimulus, while ignoring others, and then interprets this information in the context of the brain's intrinsic structure and previous experience. Thus we *receive* electromagnetic waves of different frequencies, but we *perceive* them as the colors red, blue, and green. We receive pressure waves from objects vibrating at different frequencies, but we hear sounds, words, and music. We encounter chemical compounds floating in the air or water, but we experience them as smells and tastes.

Colors, tones, smells, and tastes are mental creations constructed by the brain out of sensory experience. They do not exist, as such, outside the brain. Thus we can now answer the old riddle: Does a falling tree make a sound if no one is near enough to hear it? Sound, as we know it, occurs only when pressure waves from the falling tree are perceived by the brain of a living being.

Although our perceptions of the size, shape, and color of objects are derived entirely from patterns of light that strike our retinas, our perceptions nevertheless appear to correspond to the physical properties of objects. In most instances we can use our perceptions to manipulate an object and to predict aspects of its behavior. Perception, we can show, organizes an object's essential properties well enough to let us handle the object appropriately.

In short, our perceptions are not direct records of the world around us. Rather, they are constructed internally according to constraints imposed by the architecture of the nervous system and its functional abilities. The philosopher Immanuel Kant referred to these inherent brain properties as *a priori* knowledge. In Kant's view the mind was not the passive receiver of sense impressions envisaged by empiricists. Rather the human mind was built to conform with certain preexisting conditions, such as space, time, and causality. The existence of these ideals was *independent* of any physical stimuli coming from beyond the body. So knowledge, according to Kant, was based not simply on sensory experience but on the brain's properties that organize sensory experience

As we shall see later, the dialectical tension between Kant's idealism and Comte's empirical positivism continues to reverberate in studies of perception. Kant's concept of a priori knowledge left its mark on *Gestalt psychology*, which holds that aspects of perception are the product of the brain's inborn capacity to order simple sensations in characteristic ways. Positivism, meanwhile, influenced *behaviorist psychology*, with its focus on the observable components of behavior—a person's motor response to the physical properties of a stimulus.

In this chapter we consider, in general, how a stimulus impinges on the body and how sensation leads to conscious awareness of events in our world. Specifically we shall consider how stimuli are transduced by sensory receptors and encoded into neural signals. While succeeding chapters will explore in detail the individual coding mechanisms for touch, pain, vision, hearing, balance, smell, and taste, here we shall emphasize the organizational principles that are universal to all sensory systems. Indeed, it is striking how sensory systems—not just in humans but in animals—rely on the same basic principles of information processing. The extent to which these features have been conserved in the course of evolution seems nothing short of astonishing.

Sensory Systems Mediate Four Attributes of a Stimulus That Can Be Correlated Quantitatively With a Sensation

The modern study of sensation began in the nineteenth century with the pioneering work of Weber and Fechner in sensory psychophysics. They discovered that despite the diversity of sensations we experience, all sensory systems convey four basic types of information when stimulated—modality, location, intensity, and timing. Together, these four elementary attributes of a stimulus yield sensation. The fact that all sensory systems convey the same type of information may be one reason why they have such similar organization.

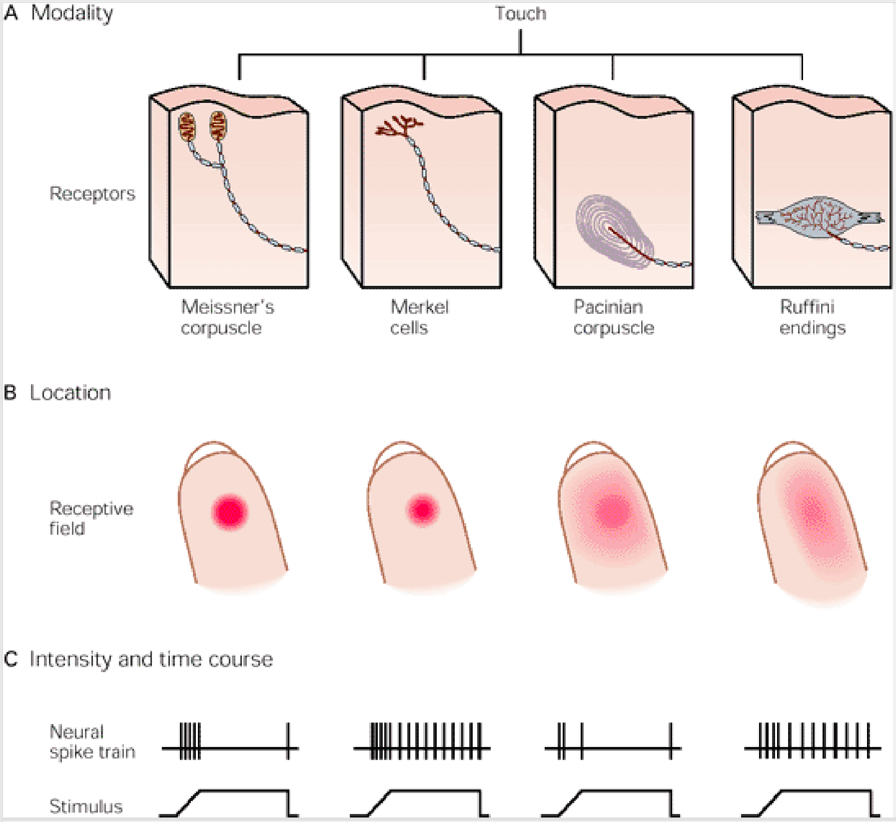

Figure 21-1 The sensory systems encode four elementary attributes of stimuli—modality, location, intensity, and timing—which are manifested in sensation. The four attributes of sensation are illustrated in this figure for the somatosensory modality of touch.

A. In the human hand the submodalities of touch are sensed by four types of mechanoreceptors. Specific tactile sensations occur when distinct types of receptors are activated. Firing of all four receptors produces the sensation of contact with an object. Selective activation of Merkel cells and Ruffini endings produces sensations of steady pressure on the skin above the receptor. When the same patterns of firing occur only in Meissner's and Pacinian corpuscles, the tingling sensation of vibration is perceived.

B. Location and other spatial properties of a stimulus are encoded by the spatial distribution of the population of activated receptors. Each receptor fires action potentials only when the skin close to its sensory terminals is touched, ie, when a stimulus impinges on the receptor's *receptive field* (see Figure 21-5). The receptive fields of mechanoreceptors—shown as **red** areas on the finger tip—differ in size and response to touch. Merkel cells and Meissner's corpuscles provide the most precise localization of touch, as they have the smallest receptive fields and are also more sensitive to pressure applied by a small probe.

C. The intensity of stimulation is signaled by the firing rates of individual receptors, and the duration of stimulation is signaled by the time course of firing. The spike trains below each finger indicate the action potentials evoked by pressure from a small probe at the center of the receptive field. Two of these receptors (Meissner's and Pacinian corpuscles) adapt rapidly to constant stimulation, while the other two adapt slowly (see Figure 21-8).

The four fundamental attributes of sensory experience are encoded within the nervous system by specialized subgroups of neurons. *Modality* defines a general class of stimulus, determined by the type of energy transmitted by the stimulus and the receptors specialized to sense that energy (Figure 21-1). Receptors, together with their central pathways and target areas in the brain, comprise a sensory system, and activity within a system gives rise to specific types of sensations such as touch, taste, vision, or hearing.

The *location* of the stimulus is represented by the set of sensory receptors within the sensory system that are active. Receptors are distributed topographically in a sense organ so that their activity signals not only the modality of the stimulus but also its position in space and its size. As a stimulus activates many receptors simultaneously,

the distribution of the active population provides important information to the brain about sensation

Table 21-1 Sensory Systems and Modalities

Sensory system	Modality	Stimulus energy	Receptor class[1]	Receptor cell types[2]
Visual	Vision	Light	Photoreceptor	Rods, cones
Auditory	Hearing	Sound	Mechanoreceptor	Hair cells (cochlea)
Vestibular	Balance	Gravity	Mechanoreceptor	Hair cells (vestibular labyrinth)
Somatosensory	Somatic senses:			Dorsal root ganglion neurons
	Touch	Pressure	Mechanoreceptor	Cutaneous mechanoreceptors
	Proprioception	Displacement	Mechanoreceptor	Muscle and joint receptors
	Temperature sense	Thermal	Thermoreceptor	Cold and warm receptors
	Pain	Chemical, thermal, or mechanical	Chemoreceptor, thermoreceptor, or mechanoreceptor	Polymodal, thermal, and mechanical nociceptors
	Itch	Chemical	Chemoreceptor	Chemical nociceptor
Gustatory	Taste	Chemical	Chemoreceptor	Taste buds
Olfactory	Smell	Chemical	Chemoreceptor	Olfactory sensory neurons

[1] See Figures 21-2 and 21-3.

[2] Receptor cell types are further specialized, forming the cellular basis for submodalities. These cell types are described in the chapters on individual sensory systems.

The *intensity* of the stimulus is signaled by the response amplitude of each receptor, which reflects the total amount of stimulus energy delivered to the receptor. The *timing* of stimulation is defined by when the response in the receptor starts and stops and is determined by how quickly the energy is received or lost by the receptor. Therefore, both the intensity and time course of stimulation are represented by the firing patterns of active sensory neurons.

Sensory Modality Is Determined by the Stimulus Energy

Since ancient times five major sensory modalities have been recognized: vision, hearing, touch, taste, and smell. In addition to these classical senses we also consider the somatic senses of pain, temperature, itch, and proprioception (posture and the movement of parts of the body) and the vestibular sense of balance (the position of the body in the gravitational field).

An early insight into the neuronal basis of sensation came in 1826, when Johannes Müller advanced his "laws of specific sense energies." Müller proposed that modality is a property of the sensory nerve fiber. Each nerve fiber is activated primarily by a certain type of stimulus and each makes specific connections to structures in the central nervous system whose activity gives rise to specific sensations. Thus Müller's laws of specific sense energies identified the most important mechanism for neural coding of stimulus modality.

Modality Is Encoded by a Labeled Line Code

In each sensory system the initial contact with the external world occurs through specialized neural structures called *sensory receptors.* The sensory receptor is the first cell in each sensory pathway and transforms stimulus energy into electrical energy, thus establishing a common signaling mechanism in all sensory systems. The electrical signal produced by the receptor is termed the *receptor potential.* The amplitude and duration of the receptor potential are related to the intensity and time course of stimulation of the particular receptor. The process by which specific stimulus energy is converted into an electrical signal is called *stimulus transduction.*

Receptors are morphologically specialized to transduce specific forms of energy. Each receptor has a specialized anatomical region where stimulus transduction occurs. Most sensory receptors are optimally selective for a single stimulus energy, a property termed *receptor specificity.* The unique stimulus that activates a specific receptor at a low energy level was called an *adequate stimulus* by Charles Sherrington.

The specificity of response in receptors underlies the *labeled line code*, the most important coding mechanism for stimulus modality. The fact that the receptor is selective for a particular type of stimulus energy means that the axon of the receptor functions as a modality-specific line of communication; activity in the axon necessarily conveys information about a particular type of stimulus. Excitation of a particular sensory neuron, whether naturally or artificially by direct electrical stimulation, elicits the same sensation. For example, electrical stimulation of the auditory nerve can be used to signal tones of different frequencies in patients with deafness caused by damage to receptors in the inner ear.

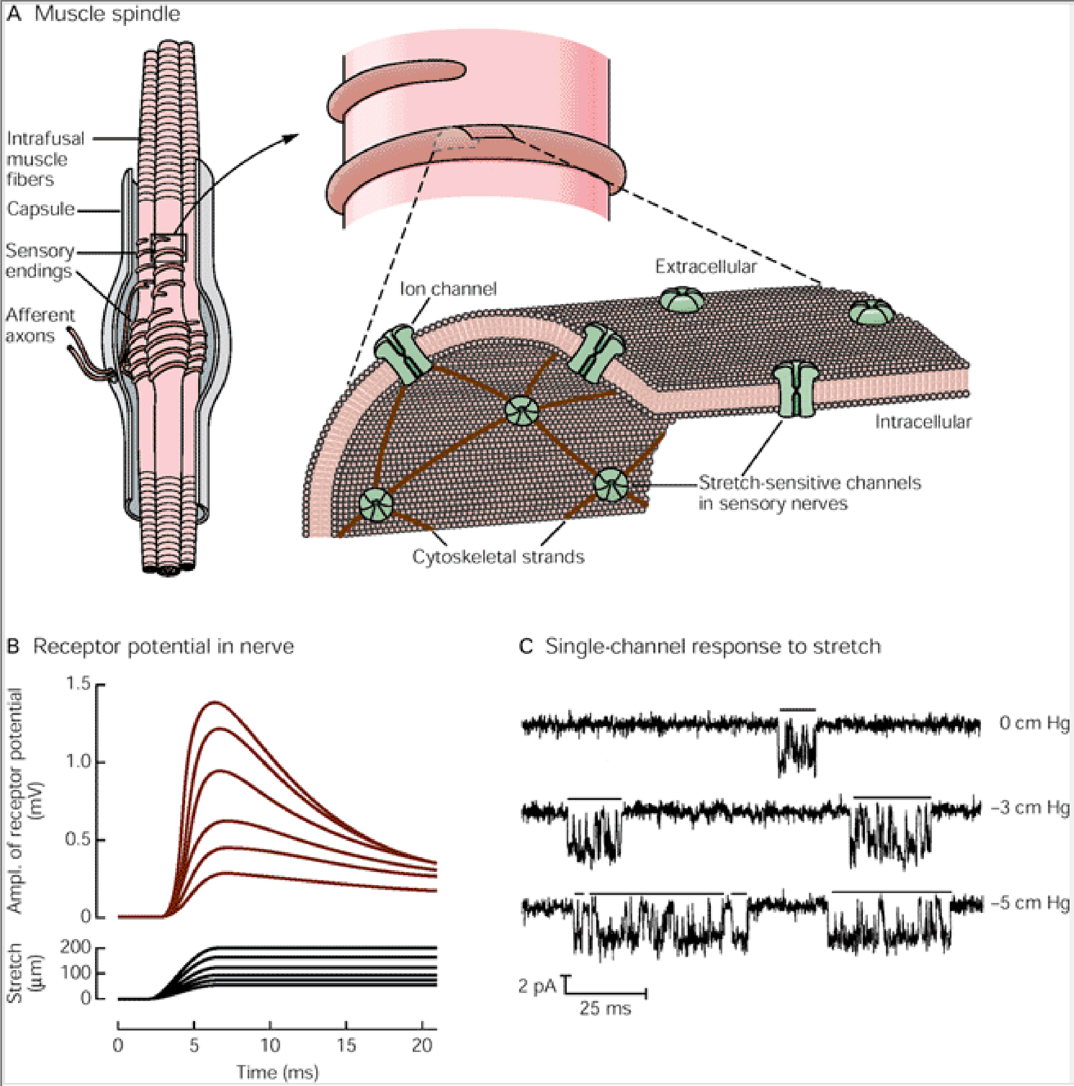

Figure 21-2 Mechanoreceptors are depolarized by stretch of the cell membrane and the depolarization is proportional to the stimulus amplitude.

A. The spindle organ in skeletal muscle mediates limb proprioception. These receptors signal muscle length and the speed at which the muscle is stretched. The receptor consists of a bundle of specialized (intrafusal) muscle fibers enclosed by a capsule. The sensory nerve endings respond to stretch of the muscle fibers. Stretch-sensitive ion channels in the nerve membrane are linked to the cytoskeleton by the protein spectrin. Mechanical deformation of the membrane opens these cation-selective channels. The influx of Na^+ and possibly Ca^{2+} depolarizes the nerve ending, producing the receptor potential. (Adapted from Sachs 1990.)

B. Response of an isolated muscle spindle to stretch. **Upper records** show the depolarizing receptor potentials recorded from the sensory axon when the muscle spindle is stretched to different lengths. **Lower records** show the amplitude and rate of stretch. Action potentials in this nerve have been blocked with tetrodotoxin to allow analysis of the receptor potentials. The initial depolarization of the muscle spindle in response to change in muscle length (dynamic response) is proportional to both the rate and amplitude of stretch. When stretch is maintained at a fixed length, the receptor potential decays to a lower value proportional only to the amount of stretch (static response). (Adapted from Ottoson and Shepherd 1971.)

C. Patch clamp records of a single stretch-sensitive channel recorded from skeletal myocytes. Pressure is applied to the receptor cell membrane by suction. At rest (**top record**) the stretch-sensitive channel opens sporadically for short time intervals, producing a transient depolarizing current. As the pressure on the membrane is increased (**lower records**), the channel opens more often and remains in the open state for longer time intervals (indicated by the bar above the channel openings). Each channel opening increases the membrane conductance to cations. The increase in the probability of opening and open time produces longer and larger depolarizations. (Adapted from Sachs 1990.)

Each class of sensory receptors makes connections with distinctive structures in the central nervous system, at least in the early stages of information processing. Thus, sight or touch is experienced because a particular central nervous structure is activated. Modality is therefore represented by the ensemble of neurons connected to a specific class of receptors. Such ensembles of neurons are referred to as *sensory systems* and comprise the somatosensory system, visual system, auditory system, vestibular system, olfactory system, and gustatory system.

Receptors Transduce Specific Types of Energy Into an Electrical Signal

Humans have four classes of receptors, each of which is sensitive primarily to one form of physical energy— mechanical, chemical, thermal, or electromagnetic (Table 21-1). The mechanoreceptors of the somatosensory system mediate the sense of touch, proprioceptive sensations (muscle stretch or contraction), and the sense of joint position, whereas the mechanoreceptors of the inner ear mediate hearing and the sense of balance. Chemoreceptors are involved in the senses of pain, itch, taste, and smell. Thermoreceptors in the skin sense the body temperature and also the temperature of the ambient air and the objects that we touch. Humans possess only one type of receptor for electromagnetic energy: the photoreceptors in the retina.

The mechanisms for transducing stimulus energy into the receptor potential vary with the types of physical stimuli. Mechanoreceptors sense physical deformation of the tissue in which they reside. Mechanical pressure, such as pressure on the skin or stretch of muscles, is transduced into electrical energy by the physical impact of the stimulus on cation channels in the membrane that are linked to the cytoskeleton (Figure 21-2A). Mechanical stimulation deforms the receptor membrane, thus opening the stretch-sensitive channels and increasing ion conductances that depolarize the receptor (Figure 21-2B). The depolarizing receptor potential is therefore similar in mechanism to the excitatory postsynaptic potential (see Chapter 10). The amplitude of the receptor potential is proportional to the stimulus intensity; by opening more ion channels for a longer time, strong pressure produces a greater depolarization than does weak pressure. Removal of the stimulus relieves mechanical stress on the receptor membrane and causes stretch-sensitive channels to close.

The mechanoreceptors of the inner ear demonstrate directional responses to mechanical stimulation. These receptors respond to bending of sensory cilia on their apical membrane. When the sensory hairs are deflected in one direction by a sound of the appropriate frequency, the receptor cell depolarizes, whereas deflection of the hairs in the opposite direction hyperpolarizes the receptor cell (Chapter 31).

Receptor potentials in chemoreceptors and photo-receptors are generated by intracellular second messengers activated when the stimulus agent binds to membrane receptors coupled to G proteins (Figure 21-3). The second messengers produce conductance changes locally or at remote sites. Chemoreceptors normally respond to the appropriate ligand with a depolarizing potential. Photoreceptors, by contrast, respond to light with hyperpolarization. As we have seen in Chapter 13, the great advantage of the second-messenger mechanism is that the sensory signal becomes amplified. A few quanta of light-activating photopigments, or a few odorant molecules binding to the receptor sites on olfactory neurons, can affect the conductance of many ionic channels in the receptor cell.

Each Receptor Responds to a Narrow Range of Stimulus Energy

Each of the major modalities has several constituent qualities or *submodalities.* For example, taste can be sweet, sour, salty, or bitter; objects that we see differ in color, shape, and movement; and touch has qualities of temperature, texture, and rigidity. Submodalities exist because each class of receptors—chemoreceptors, mechanoreceptors, thermoreceptors, and photoreceptors—is not homogenous. Instead, each class contains a variety of specialized receptors that respond to a limited range of stimulus energies.

The receptor behaves as a filter for a narrow range, or *bandwidth*, of energy. For example, individual photoreceptors are not sensitive to all wavelengths of light but to only a small part of the spectrum. We say that receptors are *tuned* to an adequate stimulus, the unique stimulus that activates a receptor at low energy. As a result, we can plot a tuning curve for each receptor based on physiological experiments. The tuning curve shows the receptor's range of sensitivity, including the preferred

stimulus energy band at which it is activated by the smallest amplitude stimulus. At greater or lesser values, the stimulus intensity must be substantially increased to excite the receptor (Figure 21-4).

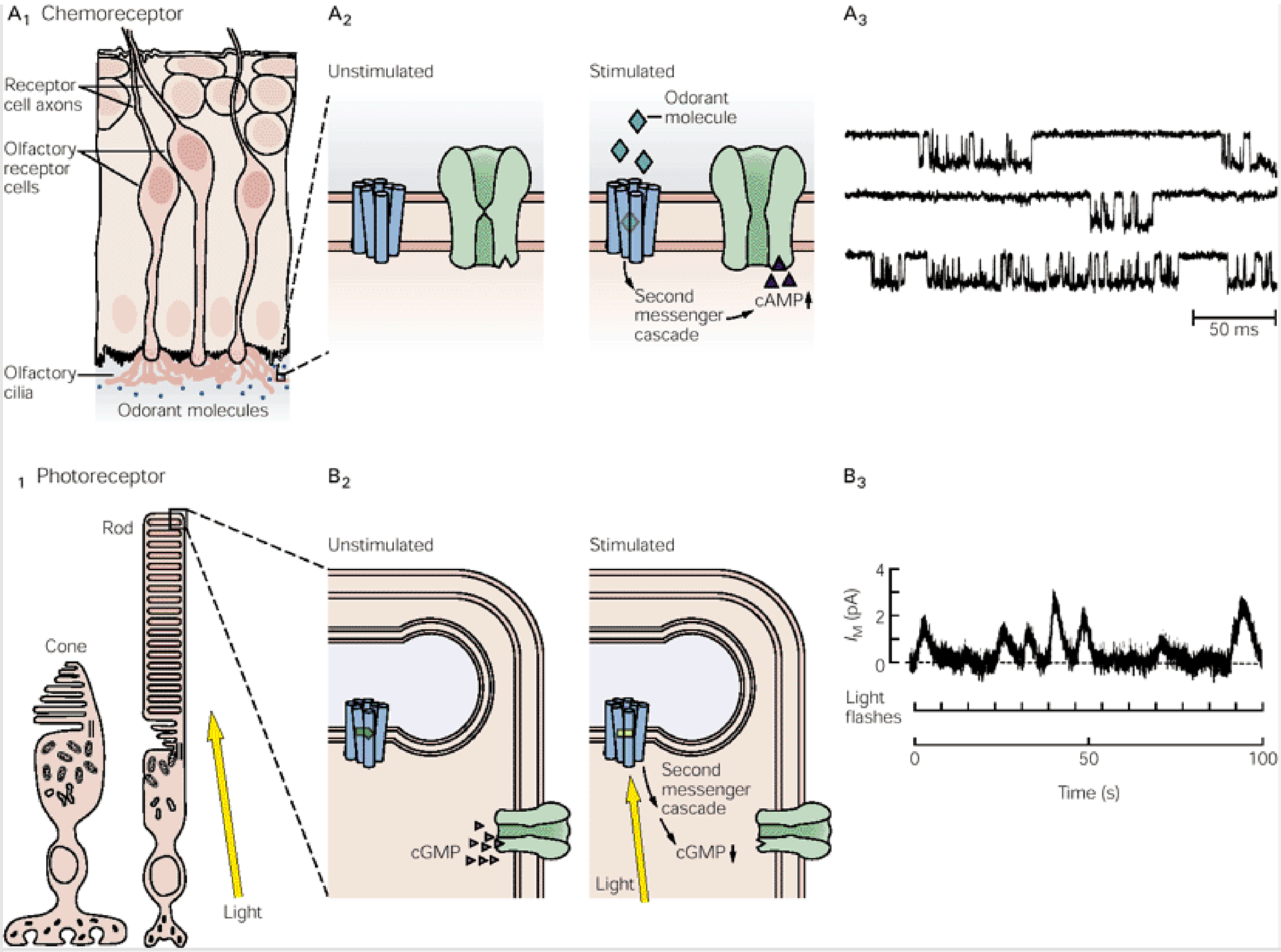

Figure 21-3 Transduction of stimulus energy into neural activity by chemoreceptors and photoreceptors requires intracellular second messengers. (Adapted from Shepherd 1994.)

A.1. The olfactory hair cell is a chemoreceptor that mediates the sense of smell. The olfactory cilia on the mucosal surface bind specific odorant molecules and depolarize the sensory nerve via a second-messenger system. The firing rate signals the concentration of odorant in the inspired air. **2.** Chemoelectric transduction is produced when the appropriate odorant binds to a receptor protein on the cell membrane, which activates G proteins linked to the receptor. Channel opening and depolarization in olfactory receptors and certain gustatory receptors are mediated by a second messenger (cAMP) stimulated by G protein activation. **3.** Receptor currents evoked by the appropriate odorant. (Reproduced with permission from Maue and Dionne 1987).

B.1. Rod and cone photoreceptors are the sensory receptors of the retina. The outer segment of both receptors contains the photopigment rhodopsin, which changes configuration when it absorbs light. **2.** Stimulation of the chromophore by light reduces the concentration of cGMP in the cytoplasm. This hyperpolarizes the photoreceptor by closing cation channels, decreasing the transmitter released by the photoreceptor terminals in the inner segment. **3.** Receptor currents evoked by light flashes. (Reproduced with permission from Baylor et al. 1979.)

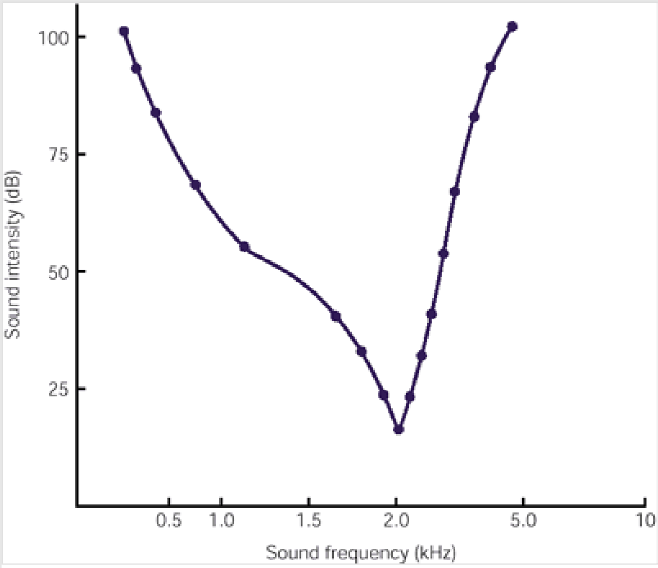

Figure 21-4 Tuning curves of sensory receptors measure the minimum amplitude of stimulation needed to activate a sensory receptor over a range of stimulus energies. Each sensory receptor responds optimally to a narrow range of intensities of a single type of energy. The tuning curve shown here is for an auditory receptor most sensitive to sound at 2.0 kHz. Higher and lower frequencies require stronger amplitude stimuli to evoke a response from the receptor. The tuning curve also illustrates the range of stimulus energies that can excite the receptor when presented at a given intensity. In this example, as the loudness of the tone rises, the receptor responds to a greater range of auditory frequencies. However, the receptor provides a stronger response at the preferred frequency than at other frequencies. Graded responses over the energy bandwidth provide a mechanism for sensory neurons to signal the particular type of stimulus energy that is presented. The auditory system tunes receptors in distinct parts of the sensory epithelium to different frequencies of sound. The relative response amplitude of these receptors to tones signals the sound frequency.

Under normal circumstances each sensory neuron is sensitive primarily to one type of stimulus. However, the sensitivity of a sensory nerve fiber to a particular type of stimulus is not absolute; if a stimulus is strong enough, it can activate several kinds of nerve fibers. For example, the retina is relatively insensitive to mechanical stimulation but very sensitive to light. Nevertheless, photoreceptors will respond to a blow to the eye, producing a perceptible flash of light (termed a phosphene). The mechanical stimulus produces a visual image because the receptor is connected to the visual centers of the central nervous system—an illustration of the principle that each sensory pathway conveys a specific modality.

The Spatial Distribution of Sensory Neurons Activated by a Stimulus Conveys Information About the Stimulus Location

The spatial arrangement of activated receptors within a sense organ conveys important information concerning the stimulus. In the modalities of somatic sensation and vision the spatial distribution of receptors conveys information about the location of the stimulus on the body or in the external world. In these modalities spatial awareness involves three distinct perceptual abilities: (1) locating the site of stimulation on the body or the stimulus source in space, (2) discriminating the size and shape of objects, and (3) resolving the fine detail of the stimulus or environment. These spacial abilities are linked to the structure of the *receptive field* of each sensory neuron—that area within the receptive sheet where stimulation excites the cell. The position of the receptive field is an important factor in the perception of the location of a stimulus on the body.

The Receptive Fields of Sensory Neurons in the Somatosensory and Visual Systems Define the Spatial Resolution of a Stimulus

The receptive field of a sensory neuron in somatic sensation and vision assigns a specific topographic location to the sensory information. For example, the receptive field of a mechanoreceptor for touch is the region of skin directly innervated by the terminals of the receptor neuron and thus includes the entire area of skin through which a tactile stimulus can be conducted to reach the nerve terminals (Figure 21-5). The receptive field of a photoreceptor in the retina is the region of the visual field projected by the lens of the eye onto the portion of the retina in which the photoreceptor is located.

Each receptor responds only to stimulation within its receptive field. A stimulus that affects an area larger than the receptive field of one receptor will activate adjacent receptors. The size of a stimulus therefore influences the total number of receptors that are stimulated. A large object, such as a basketball, held between both hands will contact and activate more touch receptors than a pencil grasped between the thumb and index finger.

The density of receptors in a given part of the body determines how well the sensory system can resolve the detail of stimuli in that area. A dense population of receptors leads to finer resolution of spatial detail because the receptors have smaller receptive fields (Figure 21-6). The spatial resolution of a sensory system is not uniform throughout the receptor sheet, however. For example, spatial discrimination is very acute in the finger tips and the central retina (or *fovea*), where sensory receptors are plentiful and the receptive fields are small. In other regions, such as the trunk or the outer margins of the retina, the spatial information signaled by individual nerves is less precise because receptors in those areas are fewer and thus have larger receptive fields. These differences in receptor density are reflected in the central nervous system in the maps of the body created by the topographic arrangement of afferent inputs. In each map the most densely innervated regions of the body occupy the largest areas while sparsely innervated regions occupy smaller areas because of the smaller number of inputs.

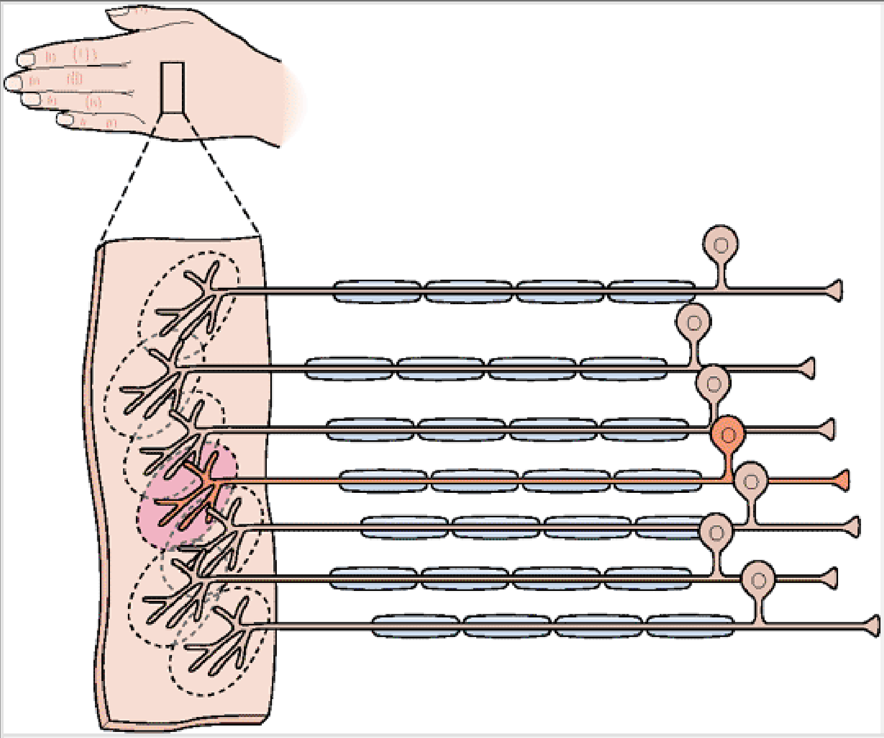

Figure 21-5 Structural basis of the receptive field of receptors for the sense of touch. The receptive field of a touch-sensitive neuron in the skin includes the sensory transduction apparatus in the nerve terminals and the surrounding skin in which the terminals are located. A patch of skin contains many overlapping receptive fields innervated by individual sensory nerve fibers. When this region is touched, spikes are initiated at the node of Ranvier closest to the nerve terminals in the skin. They are conducted past the cell body, located in the dorsal root ganglion, to the synaptic terminals in the spinal cord or medulla.

The Sensory Neurons for Hearing, Taste, and Smell Are Spatially Organized According to Sensitivity

For hearing and the chemical senses (taste and smell), the receptors are spatially distributed following the energy spectrum for these modalities. For example, auditory receptors are arranged according to the sound frequencies to which they respond. Receptors at a specific location vibrate most strongly when stimulated by a particular range of sounds, with high frequencies located at the base of the cochlea and low frequencies at the apex. Thus the organization of the inner ear's receptor sheet represents the spectrum of sound, not the location of the sounds in space.

For taste and smell, receptors that have particular chemical sensitivities are located in different parts of the receptive surface of the tongue and inside the nose. For example, specific regions of the tongue contain receptors sensitive to salts, sugars, acids, bases, or proteins. Different foods will excite specific combinations of these receptors to evoke their characteristic tastes. The spatial distribution of activity in the chemoreceptor population allows the brain to differentiate salty from sweet or bitter tastes.

Intensity of Sensation Is Determined by the Stimulus Amplitude

Historically, the early scientific studies of the mind focused not on subjective perceptions of qualities such as color or taste but on phenomena that could be *measured* precisely: the size, shape, amplitude, velocity, and timing of stimuli. Psychophysics had its beginnings in the systematic study of the intensity of sensations produced by stimuli of defined magnitude.

Natural stimuli vary greatly in intensity. For example, we experience a range of sounds, from a whisper to a

shout. The intensity or amount of a sensation depends on the strength of the stimulus. The capacity of sensory systems to extract information about the magnitude of the stimulus is important for two aspects of sensory discrimination: (1) distinguishing among stimuli that differ only in strength (as opposed to those that differ in modality or location) and (2) evaluating stimulus amplitude.

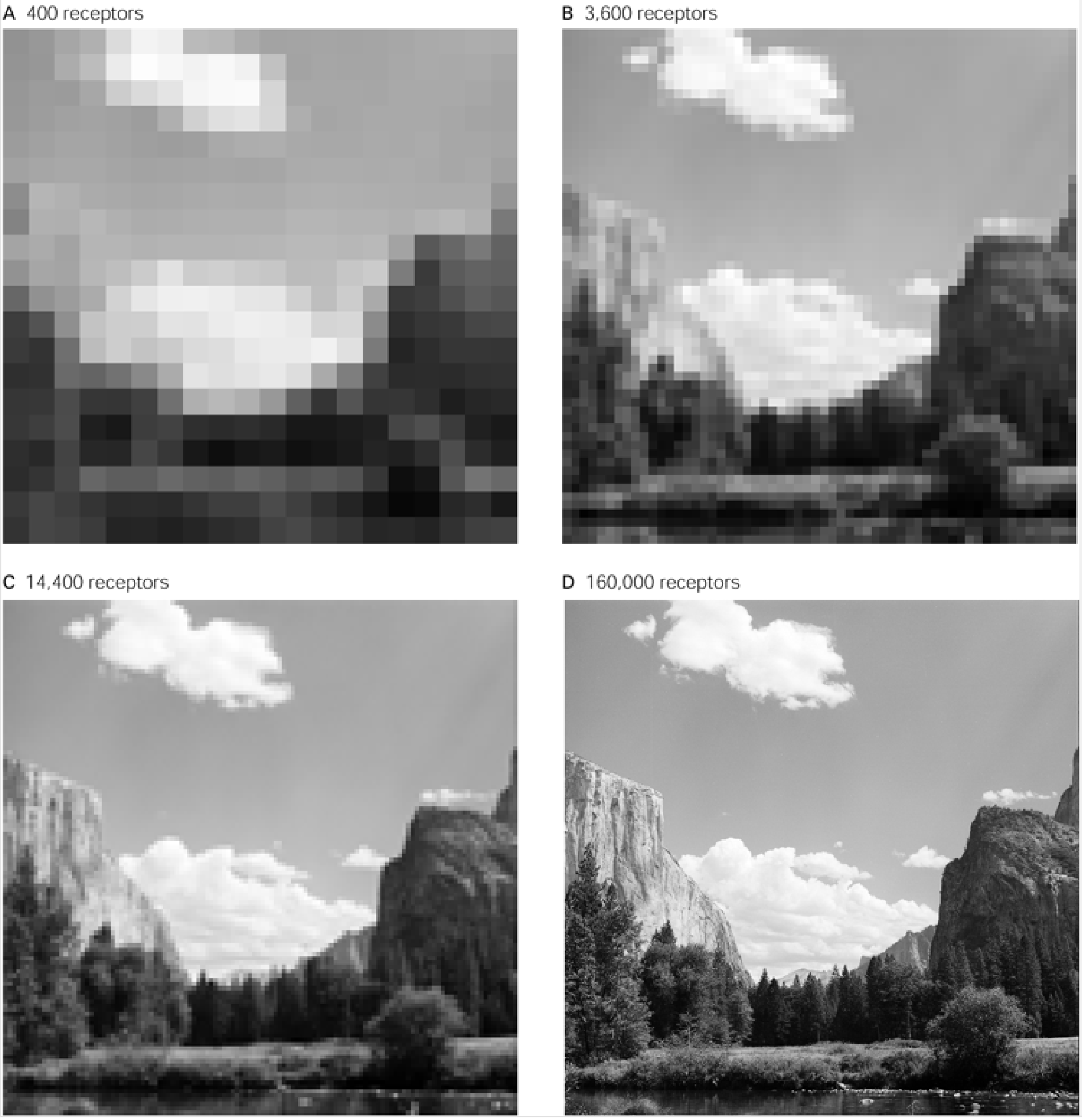

Figure 21-6 The density of sensory receptors in the retina and the size of the receptive field for each receptor determine the resolution of a visual image. Each square or pixel in these images represents a receptive field. The gray scale is proportional to the average light intensity in that region of the image. White pixels represent receptors with the highest firing rate, while black pixels represent receptors with the lowest firing rate. If there are a small number of receptors and each spans a large area of the scene, the result is a fuzzy, very schematic representation of the scene (**A**). There is no cue from this representation what the picture actually shows. As the density of receptors increases, and the size of the receptive field of each receptor decreases, the spatial detail becomes clearer (**B-D**). Clouds, mountains, trees, grasslands, and water emerge, until the scenery is identifiable as Yosemite valley. However, the increased resolution comes at the cost of enlarging the total size of the receptor population.

The brain resolves the conflict between information overload from a huge number of receptors and the need for resolution of spatial detail by having a higher density of receptors in regions of the body where high resolution of detail is behaviorally important and using progressively lower numbers of receptors in surrounding regions. Spatial resolution for vision and touch parallels the density of receptors in the retina and skin. Spatial resolution on the fingertips approaches that of the image in **D.** Receptor density and tactile sensitivity on the palm is similar to the resolution in **C.** Resolution of spatial detail on the forearm approaches that in image **B**, while on the trunk it is similar to that in image **A.** (Photographs courtesy of Daniel Gardner.)

Psychophysical Laws Govern the Perception of Stimulus Intensity

The first psychophysicists—Weber, Fechner, Helmholz, and von Frey—developed simple experimental paradigms to compare how two stimuli of different amplitudes are distinguished. They quantitated the intensity of sensations in the form of mathematical laws that allowed them to predict the relationship between stimulus magnitude and sensory discrimination. For example, in 1834 Weber demonstrated that the sensitivity of the sensory system to differences depends on the absolute strength of the stimuli. We easily perceive that 1 kg is different from 2 kg, but it is difficult to distinguish 50 kg from 51 kg. Yet both sets differ by 1 kg! This relationship is expressed in the equation now known as Weber's law:

$$\Delta S = K \times S,$$

where δS is the minimal difference in strength between a reference stimulus S and a second stimulus that can be discriminated, and K is a constant. This is termed the *just noticeable difference* or difference limen. It follows that the difference in magnitude necessary to discriminate between a reference stimulus and a second stimulus increases with the strength of the reference stimulus.

Fechner extended Weber's law in 1860 to describe the relationship between the stimulus strength (S) and the intensity of the sensation (I) experienced by a subject:

$$I = K \log S/S_0,$$

where S_0 is the threshold amplitude of the stimulus and K is a constant. In 1953 Stanley Stevens noted that, over an extended range of stimulation, the intensity of a sensation is best described by a power function rather than by a logarithmic relationship.

$$I = K(S - S_0)^n.$$

For some sensory experiences, such as the sense of pressure on the hand, there is a linear relationship between the stimulus magnitude and the perceived intensity. This represents an example of a power function with a unity exponent (ie, $n = 1$).

The lowest stimulus strength a subject can detect is termed the *sensory threshold.* Thresholds are normally determined statistically by presenting a subject with a series of stimuli of random amplitude. The percentage of times the subject reports detecting the stimulus is plotted as a function of stimulus amplitude, forming a relation called the *psychometric function* (Box 21-1). By convention, threshold is defined as the stimulus amplitude detected in half of the trials. Thresholds can also be determined by the method of limits, in which the subject reports the intensity at which a progressively decreasing stimulus is no longer detectible or an increasing stimulus is detectible.

The measurement of sensory thresholds is a useful diagnostic technique for determining sensory function in individual modalities. Elevation of threshold may signal an abnormality in sensory receptors (such as loss of hair cells in the inner ear caused by aging or exposure to very loud noise), deficits in nerve conduction properties (as in multiple sclerosis), or a lesion in sensory processing areas of the brain. Sensory thresholds may also be altered as a result of emotional or psychological factors related to the conditions in which stimulus detection is measured (Box 21-1).

The sensory threshold for a modality is limited by the sensitivity of receptors. The threshold energy is related to the minimum stimulus amplitude that generates action potentials in a sensory nerve. We define thresholds in terms of action potentials because receptor potentials are local signals; they are propagated passively, as are synaptic potentials, and therefore are not transmitted over distances greater than 1 mm. To convey a sensory message to the brain, the stimulus information must be represented as a series of action potentials.

Stimulus Intensity Is Encoded by the Frequency of Action Potentials in Sensory Nerves

The quantitative features of sensory stimuli measured in psychophysical studies are signaled by the firing patterns of the activated population of sensory neurons. The details of neuronal activity—how long a neuron fires, how fast, and how many neurons are firing— encode the intensity and time course of sensory experience. In the 1920s Edgar Adrian and Yngve Zotterman first noted that the discharge frequency of an afferent fiber increases with increasing stimulus intensity. This is because the activity of sensory receptors changes in relation to the stimulus amplitude. The change in membrane potential produced by the sensory stimulus is transformed into a digital pulse code, in which the frequency of action potentials reflects the amplitude of the receptor potential. Strong stimuli evoke larger receptor potentials, which generate a greater number and a higher frequency of action potentials (Figure 21-8A).

Box 21-1 Sensory Thresholds Are Modified by Psychological and Pharmacological Factors

Sensory thresholds depend upon psychological factors and the context in which the stimulus occurs. The threshold for pain is often heightened during competitive sports or in childbirth, as reflected in a shift in the psychometric function to higher stimulus intensities (Figure 21-7B, curve c). Similarly, sensory thresholds can be lowered. Consider a runner at the starting line prepared to respond to the starter's shot. It is advantageous to respond as rapidly as possible, and the slightest noise resembling the start gun may trigger a leap to action. The runner's response to a lower stimulus intensity is represented as a shift in the psychometric function to lower stimulus intensities (Figure 21-7B, curve a).

The modifiability of sensory thresholds can be understood by considering two aspects of sensation: (1) the absolute detectability of the stimulus and (2) the criterion the subject uses to evaluate whether a stimulus is present. Detectability measures the capacity of a sensory system to process a stimulus, whereas the response criterion reflects an attitude or bias of the subject toward the sensory experience.

In the 1950s Wilson Tanner and John Swets developed the signal detection theory to explain the observation that subjects often report a sensory experience (ie, detection of a stimulus) when no stimulus is actually presented. A consequence of this decrease in response criterion (or bias) is that a subject is more likely to make mistakes. For example, the runner at the starting block is likely to make a false start in a crucial race. Similarly, elderly patients with sensory loss may falsely report feeling stimuli tested in a neurological examination as a denial of aging. The opposite condition—ignoring the occurrence of a stimulus such as pain—is also common.

The separate measures of stimulus detectability and response criterion can be combined with the concept of threshold to explain the mechanisms of drug action. For example, morphine, a potent analgesic, elevates the pain threshold both by reducing the detectability of a painful stimulus and by elevating the criterion the subject uses to determine whether a stimulus is painful or not. Marijuana also increases pain thresholds, but does so by increasing the response criterion rather than decreasing stimulus detectability—the stimulus is just as painful but the subject is more tolerant.

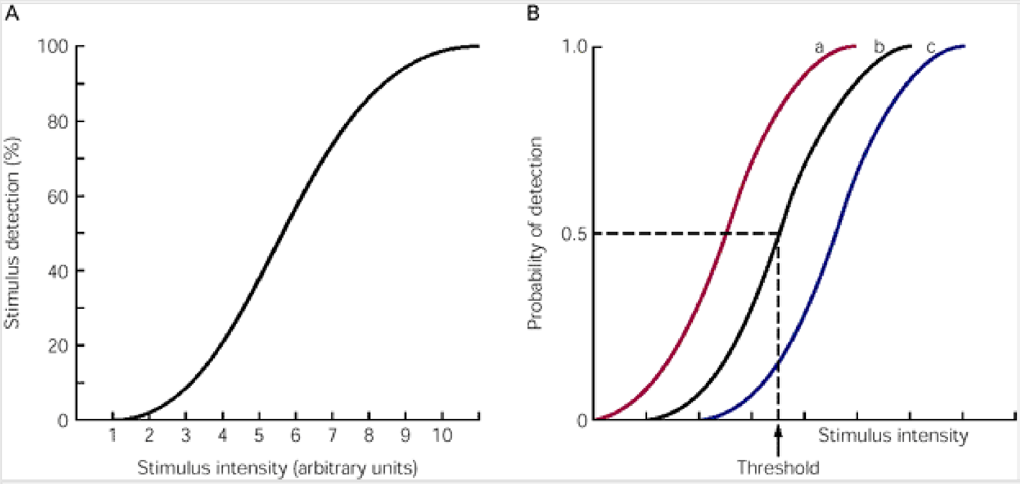

Figure 21-7 Sensory thresholds and the just noticeable difference (JND) between stimuli that differ in intensity, frequency, or other parametric features are quantifiable.

A. The psychometric function plots the percentage of stimuli detected by a human observer as a function of stimulus intensity. Threshold is defined as the stimulus intensity detected on 50% of the trials.

B. The absolute sensory threshold (curve **b**) is an idealized relationship between stimulus intensity and the probability of stimulus detection. If the sensory system's ability to detect the stimulus is increased or the subject's response criterion is decreased, curve **a** would be observed; curve **c** illustrates the converse.

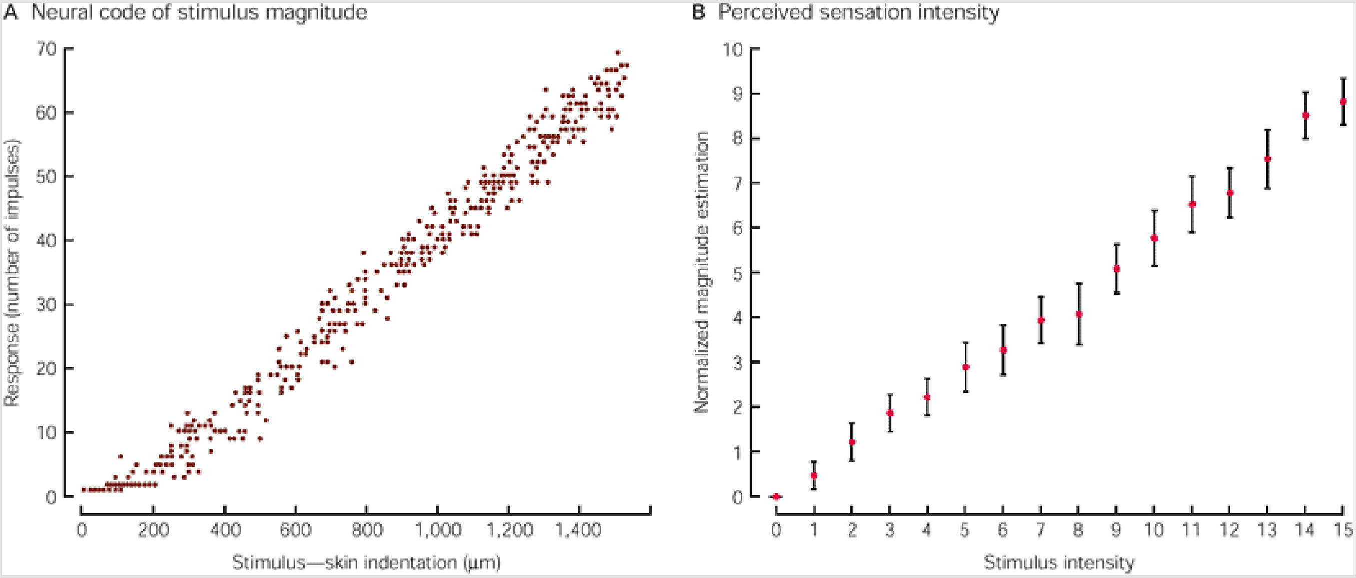

Figure 21-8 The firing rates of sensory nerves encode the stimulus magnitude. (Adapted from Mountcastle et al. 1966.)

A. The number of action potentials per second in a slowly adapting mechanoreceptor action the amount of skin indentation. This receptor required a minimum indentation of 80 µm to respond. The relationship between increases in frequency of firing and pressure on the skin is linear.

B. Estimates made by a human subject of the magnitude of sensation produced by pressure on the hand increase linearly as a function of skin indentation. The relation between a subject's estimate of the intensity of the stimulus and its strength resembles the relation between the discharge frequency of a sensory neuron and the stimulus strength. These data suggest that the neural coding of stimulus intensity is faithfully transmitted from the peripheral receptors to the cortical centers that mediate sensation.

The translation of the receptor potential amplitude into a frequency code is similar to the process governing repetitive firing of neurons in response to synaptic potentials. The timing of action potentials following depolarization of a neuron depends on the neuron's threshold for firing, which in turn varies depending on the neuron's previous firing. Immediately after the action potential there is an absolute refractory period, lasting 0.8-1.0 ms, during which action potentials cannot be generated because Na^+ channels are inactivated. The upper limit on neuronal firing is about 1000-1200 spikes per second.

The nerve fires a second impulse when the amplitude of the receptor potential exceeds the neuronal threshold. Receptor potentials of small amplitude are only slightly larger than the resting threshold. Therefore, the second impulse is generated late in the refractory period or at its end, resulting in a long interval between the first and second spikes fired by the receptor's axon. However, a large-amplitude receptor potential produced by a strong stimulus allows the threshold to be reached earlier in the refractory period, reducing the time between impulses. Thus, a large depolarization produces a short interspike interval and high firing rates, whereas a small depolarization results in long interspike intervals and low firing rates.

In addition to increasing the frequency of firing of individual sensory neurons, stronger stimuli also activate a greater number of receptors. Therefore, the intensity of a stimulus is also encoded in the size of the responding receptor population. These *population codes* depend on the fact that individual receptors in a sensory system differ in their sensory thresholds. Most sensory systems have at least two kinds of receptors: low- and high-threshold receptors. When the stimulus intensity is increasing from weak to strong, low-threshold receptors are first recruited, followed by high-threshold receptors.

The Duration of a Sensation Is Determined in Part by the Adaptation Rates of Receptors

The temporal properties of a stimulus are encoded as changes in the frequency of sensory neuron activity. Stimuli appear, rise in intensity, fluctuate or remain steady, and eventually disappear. Many receptors signal the rate at which the stimulus increases or decreases in intensity by rapidly changing their firing rate. For example, when a probe touches the skin, the initial spike discharge is proportional to both the speed at which the skin is indented and the total amount of pressure (Figure 21-9A). During steady pressure the firing rate slows to a level proportional to skin indentation. Firing stops when the probe is retracted. Thus, neurons signal important properties of stimuli not only when they fire but also when they stop firing.

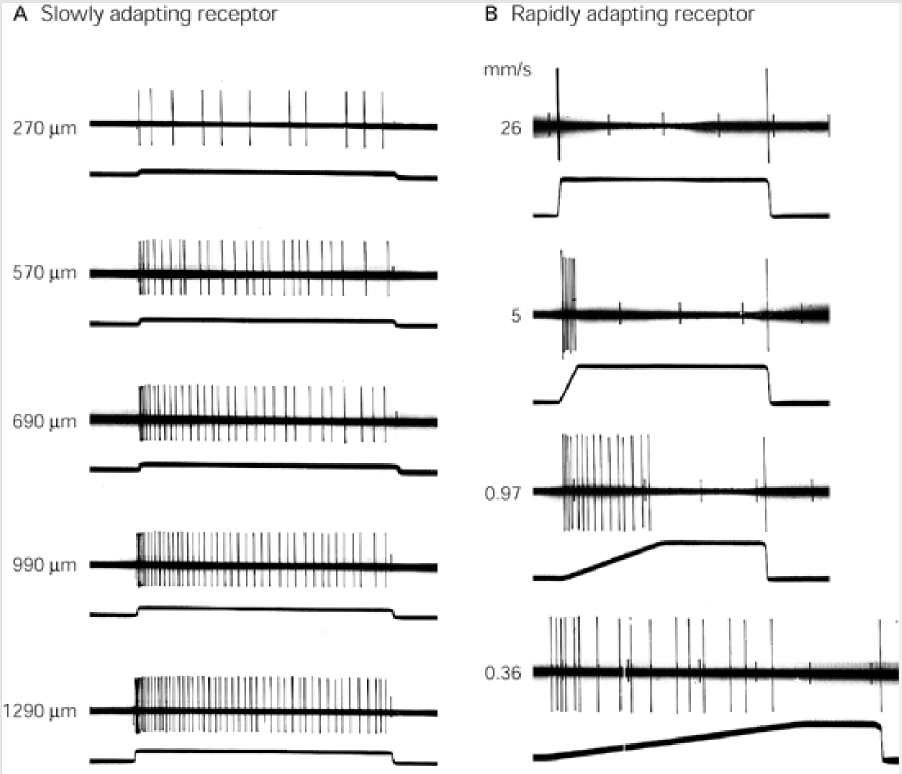

Figure 21-9 Measurements of firing rates quantify how sensory neurons represent the intensity of stimulation over time.

A. Slowly adapting mechanoreceptors respond throughout a continuous stimulus. Each successive trace illustrates the response to increases in the pressure applied to the skin; the trace below each spike record illustrates the amplitude and time course of the stimulus. As the pressure increases, the total number of action potentials discharged rises, leading to higher firing rates. The firing rate is higher at the beginning of skin contact than during steady pressure, as these receptors also sense how rapidly pressure is applied to the skin. When the probe is removed from the skin, the spike activity ceases. (Adapted from Mountcastle et al. 1966.)

B. Rapidly adapting mechanoreceptors respond only at the beginning and end of the stimulus, signaling the rate at which the stimulus is applied or removed. The slope of the pressure pulse indicates the speed of skin indentation in millimeters per second; all the stimuli have the same final amplitude. Slowly applied pressure evokes a long-lasting burst of low frequency firing; rapid indentation produces a very brief burst of high frequency firing. Motion of the probe against the skin is signaled by both the rate and duration of firing of this receptor. The receptor is silent when the indentation is maintained at a fixed amplitude and fires again when the probe is removed from the skin. (Adapted from Talbot et al. 1968.)

Although the continuous firing of a sensory neuron encodes the intensity of the stimulus, if the stimulus persists for several minutes without a change in position or amplitude, its intensity diminishes and sensation is lost. This decrease is called *adaptation.* All sensory receptors adapt to constant stimulation. Receptor adaptation is thought to be an important neural basis of perceptual adaptation in which a constant stimulus fades from consciousness.

Receptors can adapt slowly or rapidly. Receptors that respond to prolonged and constant stimulation are designated *slowly adapting receptors.* These receptors are able to signal stimulus magnitude for several minutes. The stimulus duration is signaled by persistent depolarization and generation of action potentials throughout the period of stimulation (Figure 21-9A). These receptors adapt gradually to a stimulus as a result of slow inactivation of Na^+ or Ca^{2+} channels by the depolarizing receptor potential, or as a result of activation of calcium-dependent K^+ channels.

Some receptors *cease* firing in response to constant-amplitude stimulation and are active only when the stimulus intensity increases or decreases. These *rapidly adapting receptors* respond only at the beginning and end of a stimulus, signaling the rate or velocity of stimulation (Figure 21-9B). Adaptation of rapidly adapting receptors depends on two factors. First, in many of these receptors the prolonged depolarization of the receptor potential inactivates the spike generation mechanism in the axon. Second, the receptor structure filters the steady components of the stimulus by changing shape, thus decreasing the electrical signal generated by the receptor (Figure 21-10)

The existence of two kinds of receptors—rapidly and slowly adapting sensors—shows another important principle of sensory coding. Sensory systems detect *contrasts* in discrete stimuli, ie, changes in the pattern of stimulation in time and space. Rapidly adapting receptors sense the time derivatives of stimuli (velocity and acceleration) that signal motion. The firing rates of these receptors are proportional to the speed of motion; they stop firing when the stimulus comes to rest. Activation of rapidly adapting receptors at the beginning and end of stimulation conveys information about the changing sensory environment to the brain.

Many sensory receptors also sense spatial contrasts. In Chapters 22 and 25 we will learn that certain neurons mediating touch and vision are particularly sensitive to edges. These neurons fire much faster if the spatial properties of a stimulus in their receptive field change abruptly than if the stimulus has uniform spatial properties.

Sensory Systems Have a Common Plan

We have learned that the various sensory systems use similar neural codes for the properties of modality, location, intensity, and timing of physical stimuli. When a sensory neuron fires, it communicates to the brain that a certain form of energy has been received at a specific location in the sense organ. The details of the action potential code tell the brain how much energy was received at that place, when it began, when it stopped, and how quickly the energy changed in intensity. All sensory systems also have similar central processing mechanisms, which are briefly reviewed in this section and more fully described in later chapters.

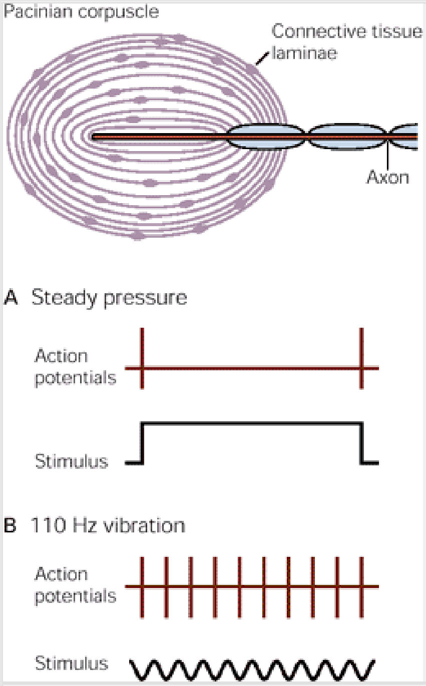

Figure 21-10 Receptor morphology influences adaptation in rapidly adapting mechanoreceptors. The Pacinian corpuscle is a rapidly adapting mechanoreceptor located in the skin, in joint capsules, and in the mesentary of the abdominal wall. The receptor consists of concentrically arranged, fluid-filled lamellae of connective tissue that form a capsule surrounding the sensory nerve terminal. Because of this capsule, the sensory endings specialize in the detection of motion.

A. The capsule of the Pacinian corpuscle deflects steady pressure. The receptor responds with one or two action potentials at the beginning and end of a pressure stimulus but is silent when the stimulus is constant in intensity. When a stimulus first impinges on the skin, the capsule is deformed, compressing the nerve terminal. The pressure pulse activates stretch-sensitive channels in the nerve terminal, producing the response to stimulus onset. During steady pressure the capsule changes shape, reducing stretch of the nerve membrane. The outer lamellae of the capsule are compressed, absorbing the static load and preventing the deformation from being transmitted to the inner core of the capsule and the nerve terminal. When the pressure is removed, the capsule resumes its initial shape, and the resultant tissue movement stimulates the nerve terminal again, producing an "off" response.

B. Pacinian corpuscles are sensitive to vibration. Rapid movements are transmitted through the lamellae to the nerve terminal, generating a receptor potential and action potential for each vibratory cycle.

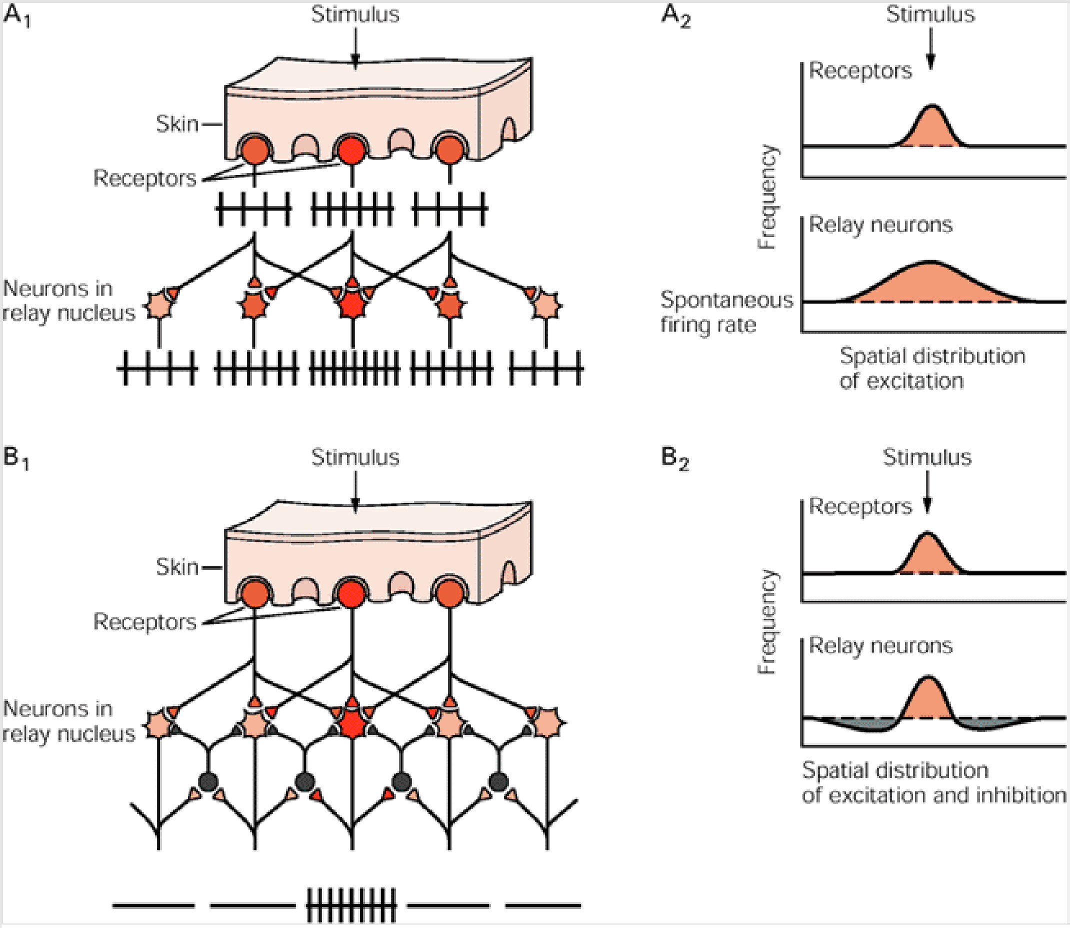

Figure 21-11 The functional and anatomical organization of sensory processing networks is hierarchical. Stimulation of a population of receptors initiates signals that are transmitted through a series of relay nuclei to higher centers in the brain (only one relay is shown). At each processing stage the signals are integrated into more complex sensory information. (Adapted from Dudel 1983.)

A. In the somatosensory system excitatory synaptic connections from each receptor in the skin are widely distributed to a large group of postsynaptic neurons at each relay nucleus. **1.** Each relay neuron receives sensory input from a large group of receptors and therefore has a bigger receptive field than any of the input neurons. **2.** Receptors closest to the stimulus respond more vigorously than distant receptors.

B.1. The addition of inhibitory interneurons (**gray**) narrows the discharge zone. **2.** On either side of the excitatory region the discharge rate is driven below the resting level by feedback inhibition.

Sensory Information Is Conveyed by Populations of Sensory Neurons Acting Together

The richness of sensory experience—the complexity of sounds in a Mahler symphony, the subtle layering of color and texture in views of the Grand Canyon, or the multiple flavors of a salsa—is obviously conveyed not by a single receptor or sensory axon but by populations of nerve fibers. The activity of whole populations of sensory neurons is orchestrated by the myriad of stimuli that typically impinge on receptors at once. The messages of individual sensors are integrated, not merely added up, as the signals converge on processing centers in the central nervous system. Understanding how sensory information conveyed by simultaneously activated receptors is processed in parallel pathways before it is combined in the highest centers of the cerebral cortex is key to understanding sensory perception.

Parallel processing is of particular importance in vision, where nearly all of the photoreceptors of the retina simultaneously receive light of varying hue and brightness. To make sense of a scene, the visual system needs to group the signals produced by individual objects, separate them, and distinguish objects of interest from the background. Thus in humans, of all sensory modalities, vision is the most highly developed; over half of the cortex processes visual information.

Specific submodalities, such as the color turquoise or the taste of a nectarine, depend upon the combined activity of populations of receptors sensitive to overlapping energy ranges rather than the unique firing of a single type of receptor. The subjective experience of a particular color or taste is constructed by the brain by integrating the inputs from these diverse receptors.

Sensory Systems Process Information in a Series of Relay Nuclei

The constituent pathways of sensory systems have a serial organization. Receptors project to first-order neurons in the central nervous system, which in turn project to second- and higher-order neurons. This sequence of connections gives rise to a distinct functional hierarchy. In the somatic sensory system, for example, primary afferent fibers converge onto second-order neurons, usually located in the central nervous system, and then onto third- and higher-order neurons (Figure 21-11).

The relay nuclei serve to preprocess sensory information and determine whether it is transmitted to the cortex. They filter out noise or sporadic activity in single fibers by transmitting only strong sequences of repetitive activity from individual sensory fibers or activity transmitted simultaneously by multiple receptors. The convergent connections from sensory receptors within the relay nucleus allow each of the higher-order neurons to interpret the sensory message in the context of activity in neighboring input channels.

Like receptor neurons, neurons in each sensory relay nucleus have a receptive field. The receptive field of each relay neuron is defined by the population of presynaptic cells that converge on it. The receptive fields of second-order and higher-order sensory neurons are larger and more complex than those of receptor neurons. They are larger because they receive convergent input from many hundreds of receptors, each with a slightly different but overlapping receptive field. They are more complex because they are sensitive to specific stimulus features, such as movement in a particular direction in the visual field.

Inhibitory Interneurons Within Each Relay Nucleus Help Sharpen Contrast Between Stimuli

Unlike the uniformly excitatory receptive field of the sensory receptor, the receptive field of higher-order sensory neurons in the visual and somatosensory systems usually has both excitatory and inhibitory regions. Inhibition is produced by inhibitory interneurons in the relay nuclei. The inhibitory region in a receptive field is an important way of enhancing the contrast between stimuli and thus gives the sensory systems additional power to resolve spatial detail.

Inhibitory interneurons are activated by three distinct pathways (Figure 21-12). The most important is the one in which the afferent fibers of receptors or lower-order relay neurons make connections with inhibitory interneurons which have connections with nearby projection neurons in the nucleus. This *feed-forward inhibition* by afferent fibers allows the most active afferents to reduce the output of adjacent, less active projection neurons. It permits what Sherrington called a singleness of action, a winner-take-all strategy, which ensures that only one of two or more competing responses is expressed.

The inhibitory interneurons can also be activated by the projection neurons in the relay nucleus through recurrent axon collaterals from the projection neurons. This *feedback inhibition* allows the most active output neurons to limit the activity of less active neurons. Such inhibitory networks create zones of contrasting activity within the central nervous system: a central zone of active neurons surrounded by a ring of less active neurons (Figure 21-11B). As we shall see, in the visual system these cellular interactions contribute to selective attention, by which we attend to one stimulus and not to another

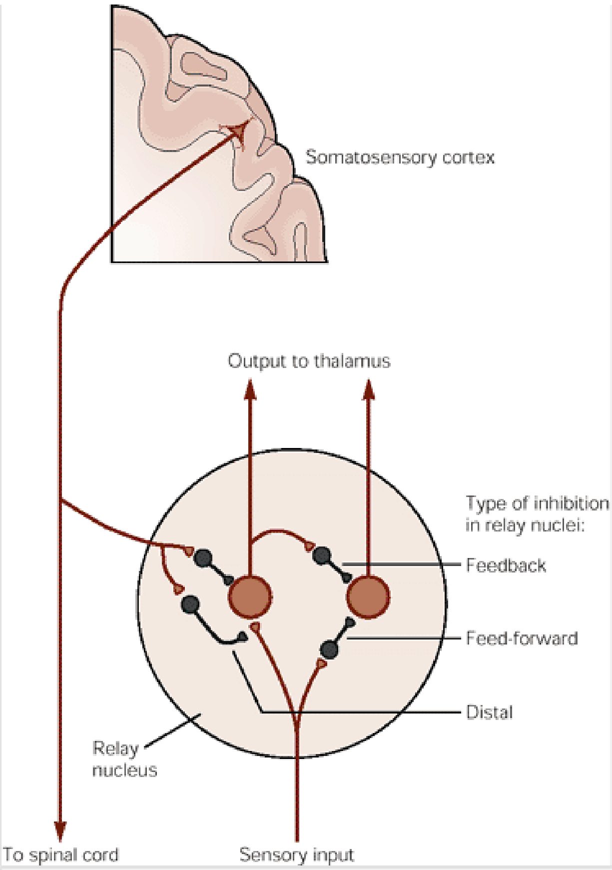

Figure 21-12 Inhibition of selected projection neurons in a sensory relay nucleus enhances the contrast between stimuli. The illustration shows three inhibitory pathways in the circuitry of the dorsal column nuclei, the first relay in the system for touch. The projection (or relay) cells (**brown**) send their axons to the thalamus. They receive excitatory input from touch receptor axons traveling in the dorsal columns. These afferent fibers also excite inhibitory interneurons (**gray**) that make *feed-forward* inhibitory connections onto adjacent projection cells. In addition, activity in the projection cells can inhibit surrounding cells by means of *feedback* connections. Finally, neurons in the cerebral cortex can modulate the firing of projection cells by *distal* inhibition of either the terminals of primary sensory neurons or the cell bodies of projection neurons.

In addition to the local feed-forward and feedback circuits for inhibition in a relay nucleus, the inhibitory interneurons can be activated by neurons in more distant sites, such as the cerebral cortex. In this way higher brain centers can control the flow of information through relay nuclei. Unlike the local feed-forward and feedback mechanisms, inhibition from distant regions of the brain is not necessarily related to the intensity of the sensory-evoked responses.

An Overall View

Our sensory systems are the way in which we perceive the external world, remain alert, form a body image, and regulate our movements. Sensations occur when external stimuli interact with receptors. Sensory information is conveyed to the brain as trains of action potentials traveling along individual sensory neurons and by populations of such neurons acting together. All sensory systems respond to four elementary features of stimuli—modality, location, intensity, and duration. The diverse sensations we experience, the sensory modalities, reflect different forms of energy that are transduced by receptors into depolarizing or hyperpolarizing electrical signals called receptor potentials. Receptors specialized for particular forms of energy, and sensitive to particular ranges of the energy bandwidth, allow humans to sense many kinds of mechanical, thermal, chemical, and electromagnetic events. To maintain the specificity of each modality within the nervous system, receptor axons are segregated into discrete anatomical pathways and processing areas.

The location and spatial dimensions of a stimulus are conveyed topographically, through each activated receptor's position in the sensory epithelium, called its receptive field. The identity of the active sensory neurons therefore signals not only the modality of a stimulus, but also the place where it occurs. The intensity and duration of stimulation, meanwhile, are reflected by the amplitude and time course of the receptor potential and by the total number of receptors activated. In the brain, intensity is conveyed by an action potential code in which the frequency of firing is proportional to the strength of the stimulus. The temporal features of a stimulus, such as duration and changes in magnitude, are signaled by the dynamics of the spike train.

The complex qualities of sounds, visual images, shapes, textures, tastes, and odors require the activation of large ensembles of receptors acting in parallel, each one signaling a particular stimulus attribute. For us to savor the richness and diversity of perception, the central nervous system must integrate the activity of an entire sensory population.

Sensory information in the central nervous system is processed in stages, in the sequential relay nuclei of the spinal cord, brain stem, thalamus, and cerebral cortex. Each of these processing stations brings together sensory inputs from adjacent receptors and—using networks of inhibitory neurons—transforms the information to emphasize the strongest signals.

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Back

22

The Bodily Senses

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Thomas M. Jessell

STUDY OF THE NEUROPHYSIOLOGICAL mechanisms of sensation began in 1925, when Edgar Adrian and Yngve Zotterman first recorded action potentials in a sensory nerve innervating the muscle spindle receptor. They discovered that the nerve transmits information from the receptor by modulation of the frequency of electrical impulses. Subsequently, Zotterman and other investigators clearly established the notion of specific nerve energies articulated by Johannes Müller in the early nineteenth century. This concept, as we have seen, states that morphologically distinct receptors transduce particular forms of energy and transmit this information to the brain through nerve fibers dedicated to that modality. Zotterman's studies demonstrated, for example, that pain is not the result of overstimulation of a generalized cutaneous receptor but results from electrical activity transmitted by specific sensory receptors called *nociceptors.*

We begin the study of the individual sensory systems with somatic sensation, the modality that was the subject of the first electrophysiological studies of sensation. Somatic sensibility arises from information provided by a variety of receptors distributed throughout the body. Somatic sensibility has four major modalities: *discriminative touch* (required to recognize the size, shape, and texture of objects and their movement across the skin), *proprioception* (the sense of static position and movement of the limbs and body), *nociception* (the signaling of tissue damage or chemical irritation, typically perceived as pain or itch), and *temperature sense* (warmth and cold).

Each of these modalities is mediated by a distinct system of receptors and pathways to the brain. However all share a common class of sensory neurons: the dorsal root ganglion neurons. Individual dorsal root ganglion neurons respond selectively to specific types of stimuli because of morphological and molecular specialization of their peripheral terminals.

In this chapter we describe in general the sensory response properties of dorsal root ganglion neurons that innervate the skin and mediate the senses of touch, temperature, pain, and itch. We consider how specialization of the nerve terminals allows these receptors to sense specific forms of energy. We will learn why some receptors sense light touch and others pressure, and why a painful stimulus, such as burning the skin, activates small-diameter sensory nerve fibers but not those neurons with thicker myelinated fibers that respond to light touch. In addition, we briefly consider nociceptors, proprioceptors, and visceral receptors, which are discussed in detail in later chapters when we consider, respectively, pain perception, voluntary movement, and the autonomic nervous system. Finally, we review the two major anatomical pathways that convey somatosensory information to the forebrain. Understanding the anatomy of these pathways is necessary to appreciate why certain lesions of the spinal cord may interrupt ipsilateral sensations of touch but not pain or temperature, while contralaterally producing the opposite deficits. In the next chapter, where we concentrate on touch, we will see how these afferent pathways convey somato-sensory information to the cerebral cortex and how the cortex processes and integrates this information.

The Dorsal Root Ganglion Neuron Is the Sensory Receptor in the Somatic Sensory System

Irrespective of modality, all somatosensory information from the limbs and trunk is conveyed by dorsal root ganglion neurons. Somatosensory information from cranial structures (the face, lips, oral cavity, conjunctiva, and dura mater) is transmitted by the trigeminal sensory neurons, which are functionally and morphologically homologous to dorsal root ganglion neurons. As we have seen in Chapter 5, the dorsal root ganglion neuron is well suited to its two principal functions: (1) stimulus transduction and (2) transmission of encoded stimulus information to the central nervous system. The cell body lies in a ganglion on the dorsal root of a spinal nerve. The axon has two branches, one projecting to the periphery and one projecting to the central nervous system (Figure 22-1). The terminal of the peripheral branch of the axon is the only portion of the dorsal root ganglion cell that is sensitive to natural stimuli. The properties of the nerve terminal determine the sensory function of each dorsal root ganglion neuron. The remainder of the peripheral branch, together with the central branch, is called the *primary afferent fiber;* it transmits the encoded stimulus information to the spinal cord or brain stem.

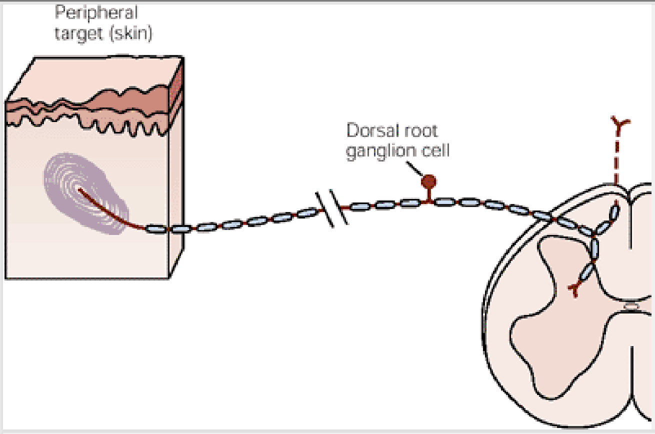


Figure 22-1 The morphology of a dorsal root ganglion cell. The cell body lies in a ganglion on the dorsal root of a spinal nerve. The axon has two branches, one projecting to the periphery, where its specialized terminal is sensitive to a particular form of stimulus energy, and one projecting to the central nervous system.

The peripheral terminals of dorsal root ganglion neurons are of two types. The terminal may be a bare nerve ending or the nerve ending may be encapsulated by a nonneural structure (Figure 22-2). Dorsal root ganglion neurons with encapsulated terminals mediate the somatic modalities of touch and proprioception (Table 22-1). They sense stimuli that indent or otherwise physically deform the receptive surface. In contrast, dorsal root ganglion neurons with bare nerve endings mediate painful or thermal sensations. Mechanoreceptors and proprioceptors are innervated by dorsal root ganglion neurons with large-diameter, myelinated axons that conduct action potentials rapidly. Thermal receptors and nociceptors have small-diameter axons that are either unmyelinated or thinly myelinated; these nerves conduct impulses more slowly.

Neurologists distinguish between two classes of somatic sensation: epicritic and protopathic. *Epicritic sensations* involve fine aspects of touch and are mediated by encapsulated receptors. These sensations include the ability to (1) detect gentle contact of the skin and localize the position that is touched (*topognosis*); (2) discern vibration and determine its frequency and amplitude; (3) resolve by touch spatial detail, such as the texture of surfaces, and the spacing of two points touched simultaneously (two-point discrimination); and (4) recognize the shape of objects grasped in the hand (*stereognosis*). *Protopathic sensations* involve pain and temperature senses (as well as itch and tickle) and are mediated by receptors with bare nerve endings. Distinguishing between epicritic and protopathic sensation helps explain changes in sensation that take place following peripheral nerve damage. Protopathic sensations are considered to be cruder than epicritic sensations, in part because, more intense stimuli are needed to evoke pain. Nevertheless, the coding mechanisms for pain are very sensitive to the noxious or tissue-damaging aspects of the stimulus.

Table 22-1 Receptor Types Active in Somatic Sensation

Receptor type	Fiber groups[1]	Fiber name[1]	Modality
Cutaneous and subcutaneous mechanoreceptors			Touch
Meissner's corpuscle	Aα,β	RA	Stroking, fluttering
Merkel disk receptor	Aα,β	SAI	Pressure, texture
Pacinian corpuscle[2]	Aα,β	PC	Vibration
Ruffini ending	Aα,β	SAII	Skin stretch
Hair-tylotrich, hair-guard	Aα,β	G1, G2	Stroking, fluttering
Hair-down	Aδ	D	Light stroking
Field	Aα,β	F	Skin stretch
Thermal receptors			Temperature
Cool receptors	Aδ	III	Skin cooling (25°C)
Warm receptors	C	IV	Skin warming (41°C)
Heat nociceptors	Aδ	III	Hot temperatures (>45°C)
Cold nociceptors	C	IV	Cold temperatures (<5°C)
Nociceptors			Pain
Mechanical	Aδ	III	Sharp, pricking pain
Thermal-mechanical	Aδ	III	Burning pain
Thermal-mechanical	C	IV	Freezing pain
Polymodal	C	IV	Slow, burning pain
Muscle and skeletal mechanoreceptors			Limb proprioception
Muscle spindle primary	Aα	Ia	Muscle length and speed
Muscle spindle secondary	Aβ	II	Muscle stretch
Golgi tendon organ	Aα	Ib	Muscle contraction
Joint capsule mechanoreceptors	Aβ	II	Joint angle
Stretch-sensitive free endings	Aδ	III	Excess stretch or force

[1] See Table 22-2.

[2] Pacinian corpuscles are also located in the mesentery, between layers of muscle, and on interosseous membranes.

Touch Is Mediated by Mechanoreceptors in the Skin

Tactile sensitivity is greatest on the hairless (*glabrous*) skin on the fingers, the palmar surface of the hand, the sole of the foot, and the lips. Glabrous skin is characterized by a regular array of ridges formed by folds of the epidermis. The ridges are arranged in circular patterns called *fingerprints* and contain a dense matrix of mechanoreceptors. These receptors mediate the sense of touch; they are excited by indentation of the skin or by motion across its surface. When an object presses against the hand, the skin conforms to its contours. The depth of indentation depends on the force exerted by the object on the skin as well as its geometry. All mechanoreceptors sense these changes in skin contour but differ morphologically in important ways that affect their physiological function (Figure 22-2).

Mechanoreceptors Differ in Morphology and Skin Location

Virtually all mechanoreceptors have specialized end organs surrounding the nerve terminal. Although the sensitivity of these receptors to mechanical displacement is a property of the nerve terminal membrane, their dynamic response to stimulation is shaped by the specialized capsule. These nonneural structures must be deformed in particular ways in order to excite the sensory nerve. Histological and physiological studies have identified four major types of mechanoreceptors in glabrous skin. Two of these receptors are located in the superficial layers of the skin, and two are situated in the subcutaneous tissue (see Figure 22-2). The small superficial receptors sense deformation of the papillary ridges in which they reside. The larger subcutaneous receptors sense deformation of a wider area of skin that extends beyond the overlying ridges.

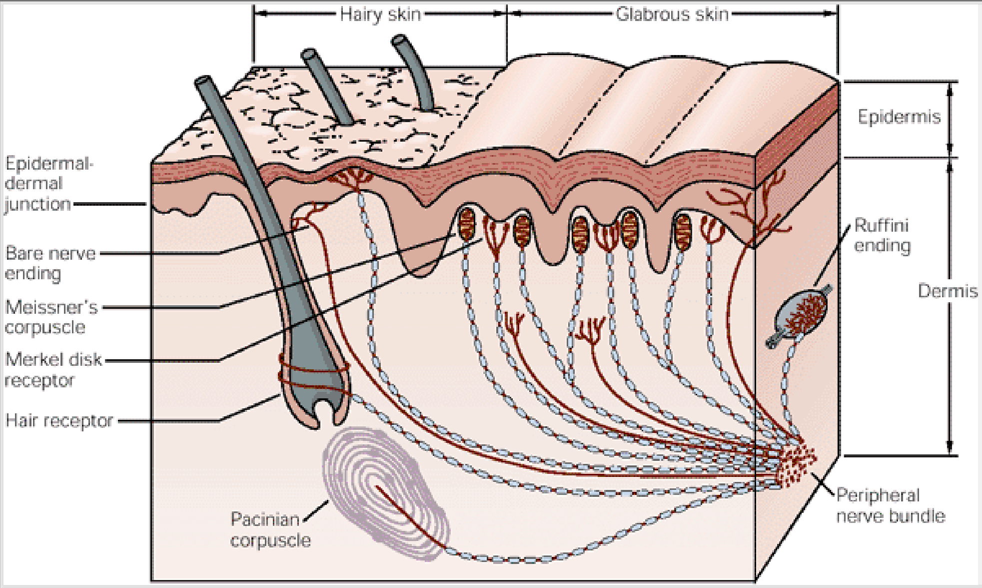


Figure 22-2 The location and morphology of mechanoreceptors in hairy and hairless (glabrous) skin of the human hand. Receptors are located in the superficial skin, at the junction of the dermis and epidermis, and more deeply in the dermis and subcutaneous tissue. The receptors of the glabrous skin are Meissner's corpuscles, located in the dermal papillae; Merkel disk receptors, located between the dermal papillae; and bare nerve endings. The receptors of the hairy skin are hair receptors, Merkel's receptors (having a slightly different organization than their counterparts in the glabrous skin), and bare nerve endings. Subcutaneous receptors, beneath both glabrous and hairy skin, include Pacinian corpuscles and Ruffini endings. Nerve fibers that terminate in the superficial layers of the skin are branched at their distal terminals, innervating several nearby receptor organs; nerve fibers in the subcutaneous layer innervate only a single receptor organ. The structure of the receptor organ determines its physiological function.

The two principal mechanoreceptors in the superficial layers of the skin are the Meissner's corpuscle and the Merkel disk receptor. The *Meissner's corpuscle*, a rapidly adapting receptor, is coupled mechanically to the edge of the papillary ridge, a relationship that confers fine mechanical sensitivity. The receptor is a globular, fluid-filled structure that encloses a stack of flattened epithelial cells; the sensory nerve terminal is entwined between the various layers of the corpuscle. The *Merkel disk* receptor, a slowly adapting receptor, is a small epithelial cell that surrounds the nerve terminal. The Merkel cell encloses a semirigid structure that transmits compressing strain from the skin to the sensory nerve ending, evoking sustained, slowly adapting responses. Merkel disk receptors are normally found in clusters at the center of the papillary ridge.

The two mechanoreceptors found in the deep subcutaneous tissue are the Pacinian corpuscle and the Ruffini ending. These receptors are much larger than the Merkel cells and Meissner's corpuscles, and less numerous. The *Pacinian corpuscle* is physiologically similar to the Meissner's corpuscle. It responds to rapid indentation of the skin but not to steady pressure because of the connective tissue lamellae that surround the nerve ending (see Figure 21-10). The large capsule of this receptor is flexibly attached to the skin, allowing the receptor to sense vibration occurring several centimeters away. These receptors are activated selectively by the common neurological test of touching a tuning fork (oscillating at 200-300 Hz) to the skin or bony prominence. *Ruffini endings* are slowly adapting receptors that link the subcutaneous tissue to folds in the skin at the joints and in the palm or to the fingernails. These receptors sense stretch of the skin or bending of the fingernails as these stimuli compress the nerve endings. Mechanical information sensed by Ruffini endings contributes to our perception of the shape of grasped objects. The anatomical arrangement of mechanoreceptors in glabrous skin is shown in Figure 22-2.

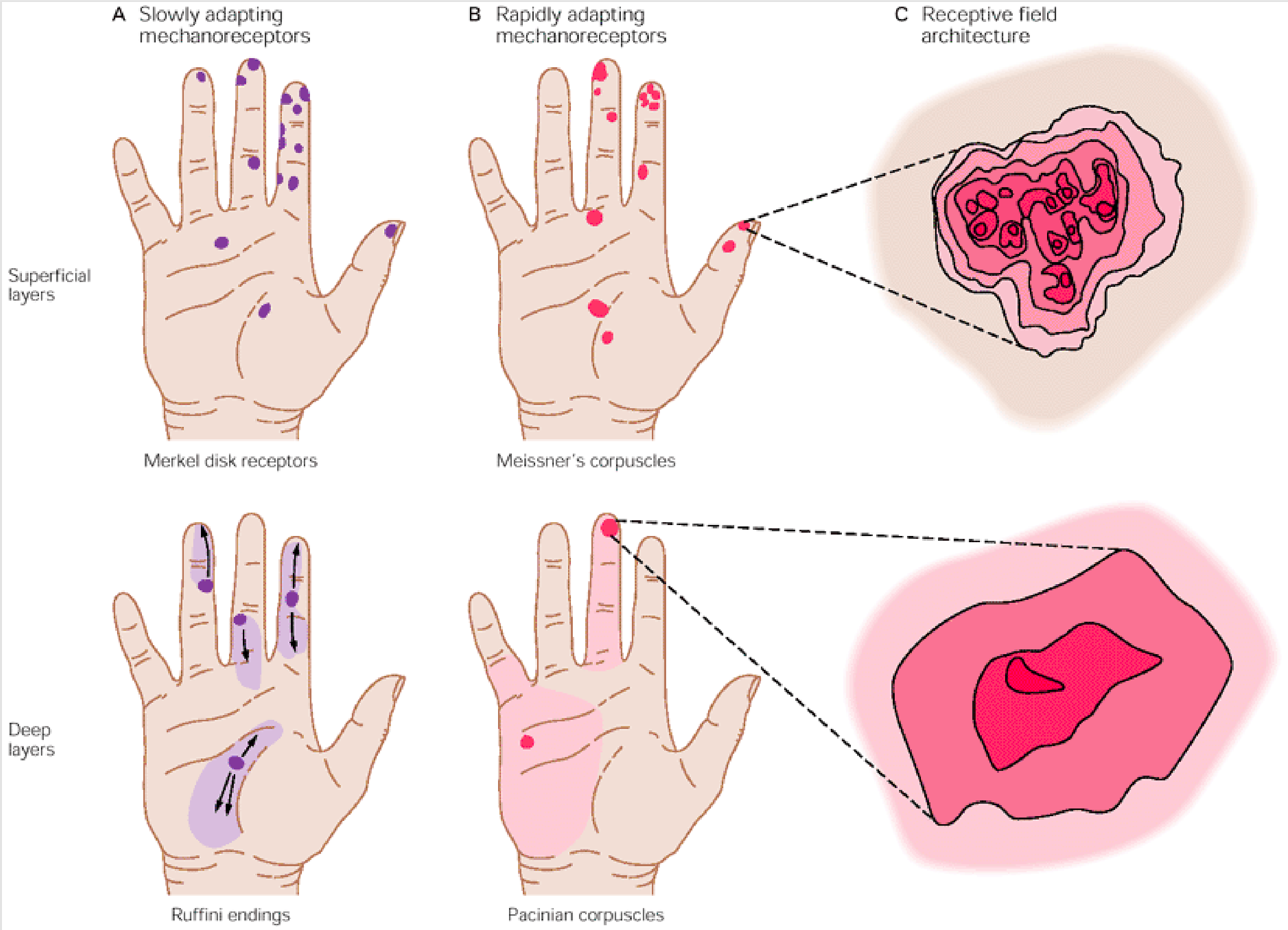


Figure 22-3 Mechanoreceptors in glabrous skin vary in the size and structure of their receptive fields. Each colored area on the hands indicates the receptive field of a different sensory nerve fiber in the human median nerve. (Adapted from Johansson and Vallbo 1983.)

A. The Merkel disk receptor in the superficial skin and the subcutaneous Ruffini ending are slowly adapting receptors (see Figure 21-9A). The Merkel disk receptor has a small, highly localized receptive field, whereas the Ruffini ending has a large field (**light purple**) with a central zone of maximal sensitivity (**dark purple**). Depending on their location, individual Ruffini endings are excited by stretch of the skin in specific directions as indicated by arrows.

B. The Meissner's corpuscle in the superficial skin and the subcutaneous Pacinian corpuscle are rapidly adapting receptors (see Figure 21-9B). Meissner's corpuscles on the fingertips have receptive fields averaging 2-3 mm in diameter, while receptive fields on the palm average 10 mm in diameter. The receptive fields of Pacinian corpuscles cover larger continuous surfaces on the fingers or palm (**light pink**) but have a central zone of maximal sensitivity located directly above the receptor (**red**).

C. Expanded view of the receptive fields of mechanoreceptors in the superficial and deep layers of glabrous skin. The relative sensitivity to pressure is shown as a contour map in which the most sensitive regions are indicated in **red** and the least sensitive areas in **pale pink.** Receptive fields in the superficial layers of the skin have many points of high sensitivity, marking the positions of the Meissner's corpuscles or Merkel disk receptors. Receptive fields in the deep layers have a single point of maximal sensitivity overlying the Pacinian or Ruffini receptor.

Similar mechanoreceptors are found in the hairy skin that covers most of the body surface. The principal rapidly adapting mechanoreceptors of the hairy skin are the hair follicle receptor and the field receptor. Hair follicle receptors respond to hair displacement. The three separate classes of these receptors (down, guard, and tylotrich hairs) differ in sensitivity to hair movement and conduction velocity (see Table 22-1). Field receptors are located primarily over the joints of the fingers, wrist, and elbow. They sense skin stretch when the joint is flexed or when the skin is rubbed.

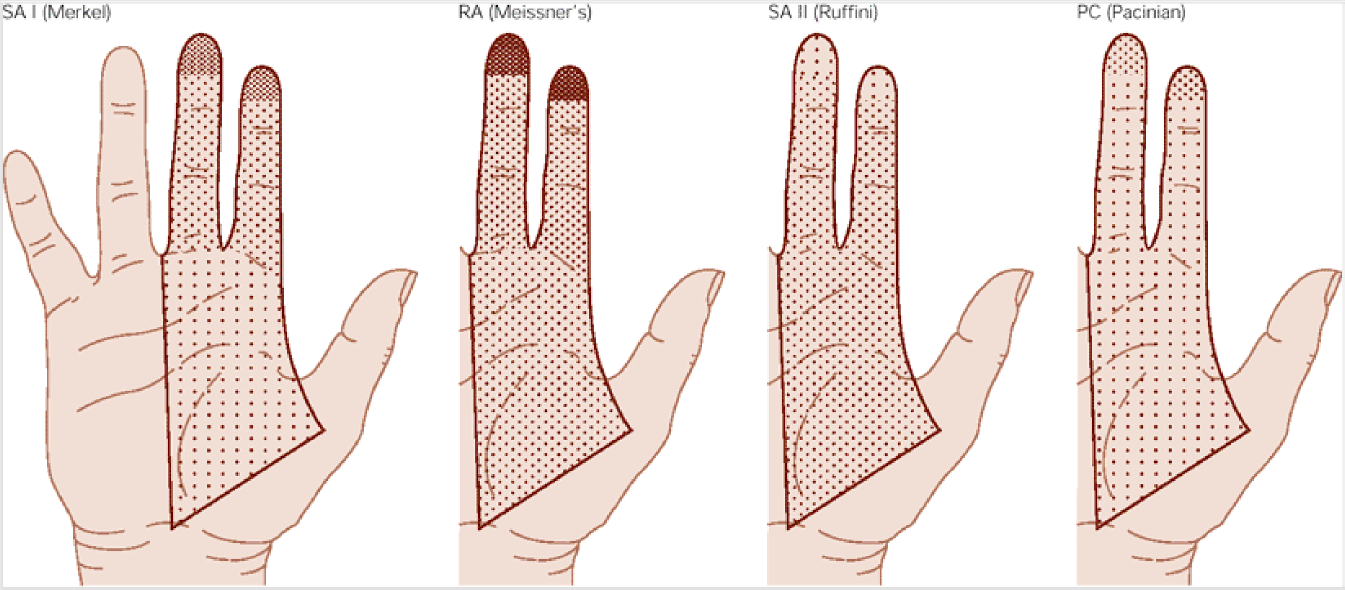


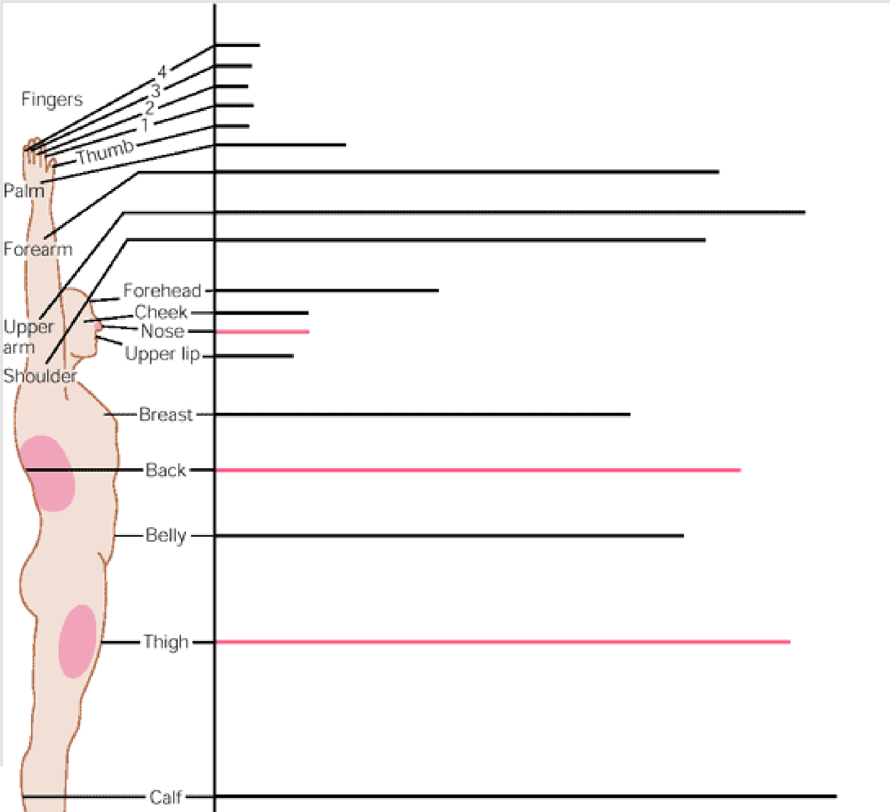
Figure 22-4 The distribution of receptor types in the human hand varies. The number of sensory nerve fibers innervating an area is indicated by the stippling density, with the highest density of receptors shown by the heaviest stippling. (**RA** = 5 rapidly adapting, **SA** = 5 slowly adapting.) Meissner's corpuscles (RA) and Merkel disk receptors (SA I) are the most numerous receptors; they are distributed preferentially on the distal half of the fingertip. Pacinian corpuscles (PC) and Ruffini endings (SA II) are much less common; they are distributed more uniformly on the hand, showing little differentiation of the distal and proximal regions. The fingertips are the most densely innervated region of skin in the human body, receiving approximately 300 mechanoreceptive nerve fibers per square centimeter. The number of mechanoreceptive fibers is reduced to 120/cm^2 in the proximal phalanges, and to 50/cm^2 in the palm. (Adapted from Vallbo and Johansson 1978.)

Mechanoreceptors in the Superficial and Deep Layers of Skin Have Different Receptive Fields

Each individual dorsal root ganglion neuron conveys sensory information from a limited area of skin determined by the location of its receptive endings. As we saw in Chapter 21, the region of skin from which a sensory neuron is excited is called its receptive field.

The size and structure of receptive fields differ for receptors in the superficial and deep layers of the skin. A single dorsal root ganglion cell innervating the superficial layers receives input from a cluster of 10-25 Meissner's corpuscles or Merkel disk receptors. The afferent fiber has a receptive field that spans a small circular area with a diameter ranging from 2 to 10 mm (Figure 22-3). These receptive fields are at least an order of magnitude greater in diameter than that of an individual receptor. Therefore, nerve fibers innervating the superficial layers of the skin sample the activity of many different sensory receptors of one particular sort. In contrast, each nerve fiber innervating the deep layers of skin innervates a single Pacinian corpuscle or Ruffini ending. Consequently, the receptive fields of these receptors cover large areas of skin, and their borders are indistinct (Figure 22-3). Usually, these receptive fields have a single "hot spot" where sensitivity to touch is greatest; this point is located directly above the receptor. The large receptive fields result from the ability of these receptors to sense mechanical displacement at some distance from the end organ.

The difference in size of the receptive fields of receptors in the superficial and deep layers of the skin plays an important role in the functions of the receptors. Meissner's corpuscle and Merkel disk receptors in the superficial layers resolve fine spatial differences because they transmit information from a restricted area of skin. As these receptors are smaller in diameter than the fingerprint ridges of glabrous skin, individual receptors can be stimulated by very small bumps on a surface. This very fine spatial resolution allows humans to perform fine tactile discrimination of surface texture and to read Braille. Pacinian corpuscles and Ruffini endings in the deep layers resolve only coarse spatial differences. They are poorly suited for accurate spatial localization or for resolution of fine spatial detail. Mechanoreceptors in the deep layers of the skin sense more global properties of objects and detect displacements from a wide area of skin.



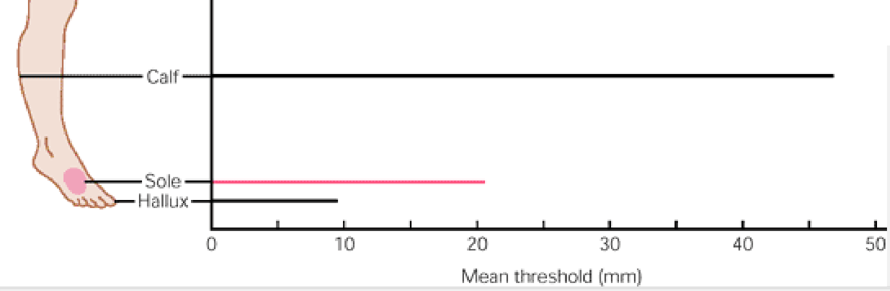


Figure 22-5 Two-point discrimination varies throughout the body surface. The two-point threshold measures the minimum distance at which two stimuli are resolved as distinct. At smaller separations the stimuli are blurred into a single continuous sensation spanning the distance between the points. Two-point thresholds are measured clinically using a calibrated compass in which the separation of the tips is accurately scaled. Two-point thresholds can also be determined from measurements of the ability of subjects to discriminate the orientation of grating ridges as a function of their spacing. This method measures spatial acuity more accurately. The two-point threshold varies for different body regions; it is about 2 mm on the finger tip but increases to 10 mm on the palm and 40 mm on the arm. The two-point thresholds highlighted in **pink** match the diameter of the corresponding receptive fields shown in pink on the body. The greatest discriminative capacity is afforded in the finger tips, lips, and tongue, which have the smallest receptive fields. (Adapted from Weinstein 1968.)

The Spatial Resolution of Stimuli on the Skin Varies Throughout the Body Because the Density of Mechanoreceptors Varies

In addition to the differences in spatial resolution between receptor classes due to differences in receptive field size, the skin area enclosed within receptive fields varies throughout the body. The smallest receptive fields are found on the tips of the fingers. Receptive fields are slightly larger on the proximal phalanges and even bigger on the palm. The receptive fields on hairy skin also increase in area as stimuli are moved proximally from the wrist to the trunk. These variations in receptive field size reflect the density of mechanoreceptors in the different regions of skin. Although individual dorsal root ganglion neurons innervate approximately the same number of sensory receptors

in the skin, there are far more Meissner's corpuscles and Merkel disk receptors in the fingertip skin than on the palm. The spacing of mechanoreceptors is therefore smallest on the fingertips and widens proximally on the palm, where receptors are less densely packed (Figure 22-4).

Box 22-1 Vibration Sense Is Coded by Spike Trains in Mechanoreceptors in the Skin

Vibration is the sensation produced by sinusoidal oscillation of objects placed against the skin. Vibration may be produced by the hum of an electric motor, the strings of a musical instrument, or a tuning fork used in the neurological examination. Mechanoreceptors in the skin respond to these oscillations by a pulse code in which each action potential signals one cycle of the sinusoidal wave (Figure 22-6A). The vibratory frequency is signaled by the frequency of action potentials fired by the sensory nerves.

Individual mechanoreceptors differ in their threshold sensitivity to vibration (Figure 22-6B). Merkel disk receptors are most responsive to extremely low frequencies (5-15 Hz); Meissner's corpuscles are most sensitive to midrange stimuli (20-50 Hz). The Pacinian corpuscles have the lowest thresholds for high frequencies (60-400 Hz); at 250 Hz they detect vibrations as small as 1 = μm but at 30 Hz require stimuli with much larger amplitudes.

The receptor tuning thresholds determine the ability to sense vibration. Humans are most sensitive to vibration at frequencies of 200-250 Hz. To be felt, lower and higher frequencies must have proportionately larger amplitude vibrations.

The perception of vibration as a series of repeating events results from the fact that the receptors under the probe are activated synchronously and therefore fire action potentials simultaneously. The intensity of vibration is signaled by the total number of sensory nerve fibers that are active rather than the frequency of firing, which codes the vibratory frequency. If a patient is tested with a 250 Hz vibration near sensory threshold, only Pacinian corpuscles right under the contact point in the skin are activated. As the vibratory amplitude is increased, more distant Pacinian corpuscles as well as Meissner's corpuscles under the vibrator become activated. The total number of active sensory nerves is linearly related to the amplitude of vibration.

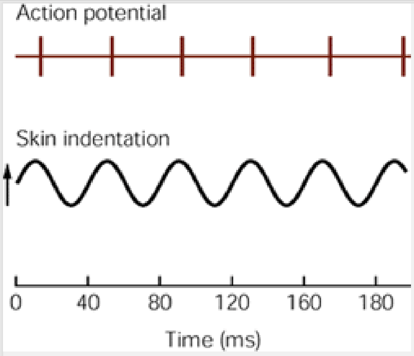


Figure 22-6A A rapidly adapting mechanoreceptor responds to sinusoidal mechanical stimuli with a single action potential for each cycle. The record here is for a receptor stimulated with a 25 Hz vibratory stimulus; the firing frequency of the receptor is 25 action potentials per second. The lowest stimulus intensity that evokes one action potential per cycle of the sinusoidal stimulus is called the receptor's "tuning threshold." (Adapted from Talbot et al. 1968.)

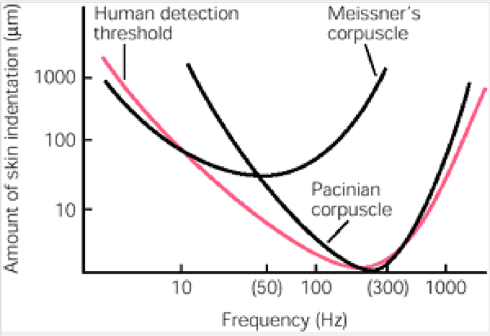


Figure 22-6B The threshold for detecting vibration corresponds to the tuning threshold of the mechanoreceptor. The sensitivity threshold for Meissner's corpuscles is lowest for frequencies of 20-50 Hz. Pacinian corpuscles sense higher frequencies. (Adapted from Mountcastle et al. 1972.)

The size of the receptive fields in a particular region of skin delimits the capacity to determine whether one or more points are stimulated. A sensory neuron innervating Meissner's corpuscles and Merkel disk receptors transmits information about the *largest* skin indentation within its receptive field. If two points within the same receptive field are stimulated, the neuron will signal only the larger indentation. But if the points are located in the receptive fields of two different nerve fibers, then information about both points of stimulation will be signaled. The farther apart the points lie on the surface, the greater the likelihood that the two active nerves will be separated by silent nerve fibers. The contrast between active and inactive nerve fibers seems to be necessary for resolving spatial detail.

Spatial resolution of stimuli on various regions of the skin can be quantified in humans by measuring their ability to perceive a pair of nearby stimuli as two distinct entities. The minimum distance between two detectable stimuli is called the *two-point threshold.* The two-point threshold varies for different body regions (Figure 22-5). These variations are correlated with the size of sensory receptive fields and the innervation density of mechanoreceptors in the superficial layers of the skin. Thus, measurements of sensory function of the human hand reveal important information concerning the organization of peripheral sense organs.

Mechanoreceptors Differ in Adaptation Properties and Sensory Thresholds

Why is each layer of the skin endowed with two different sets of mechanoreceptors with similar receptive fields? The answer lies in their physiological function. Although all four types of mechanoreceptor are excited by indentation of the skin, they signal different information. As we learned in Chapter 21, mechanoreceptors respond to touch with sustained slowly adapting responses or with rapidly adapting bursts at the beginning and end of contact. The slowly adapting receptors signal the pressure and shape of objects by their average firing rate (see Figure 21-9A). The total number of action potentials evoked per second is proportional to the indentation force applied to the receptor. Rapidly adapting receptors sense motion of objects on the skin (see Figure 21-9B). These receptors respond during the period when the position of a stimulus changes, and they stop firing when it comes to rest. Their firing rates are proportional to the speed of motion, and the duration of activity signals the duration of the motion. They sense vertical impact such as the pressure wave produced when the hand contacts an object and vibration when the object oscillates (see Box 22-1). Rapidly adapting receptors are also stimulated by lateral motion such as stroking, rubbing, or palpation.

Mechanoreceptors also differ in sensory thresholds, the minimum intensity of stimulation required to generate an action potential in the nerve. Rapidly adapting receptors have lower touch thresholds than slowly adapting receptors. The Pacinian corpuscle is the most sensitive mechanoreceptor (Figure 22-6A,22-6B). These receptors are able to detect the minute vibrations produced by impacts on a surface on which the hand rests or caused by the hum of an electric motor. Pacinian corpuscles also sense the frictional displacement of the skin when the hand moves across an object, regardless of whether the surface is smooth or rough. The Meissner's corpuscle is particularly sensitive to abrupt changes in the shape of objects that occur at the edges or corners and to small irregularities on the surface sensed during palpation by the hand. Meissner's corpuscles are used to detect and localize small bumps or ridges on an otherwise smooth surface.

More salient bumps or edges are required to activate the slowly adapting Merkel disk receptors. However, once stimulated, the Merkel receptors provide a clearer image of contours by changes in the frequency of firing. If the surface is flat, these receptors fire continuously at relatively low rates. Convexities that indent the skin increase firing rates, whereas concavities silence these receptors. Responses are proportional to the surface curvature; large-diameter, gently curved objects evoke weaker responses than small-diameter objects (Figure 22-7). The strongest responses occur when sharp edges or punctate probes, such as a pencil point, contact the receptive field. These changes in receptor activity are reflected in the corresponding perceptions of object shape experienced when we grasp spheres of different diameters between the thumb and index finger. A tiny sphere, such as a ball bearing, feels relatively sharp, whereas a ping-pong ball feels blunt.

The Spatial Characteristics of Objects Are Signaled by Populations of Mechanoreceptors

If the firing rate of slowly adapting receptors signals both pressure and shape, how does the brain decipher which parameter is signaled by an individual receptor? In fact, one receptor cannot signal both of these properties unambiguously. Information about size and shape is signaled by populations of receptors that are stimulated by different portions of the object. A small-diameter object, which indents the skin at a small localized spot, produces a sharply peaked response in which a small number of adjacent receptors fire at high rates. A gently rounded object, which contacts a large region of skin, evokes weak responses in a large population of receptors, forming a broad, low-amplitude profile (Figure 22-7A).

Information about texture is also mediated by populations of mechanoreceptors. Humans are able to sense the roughness of surfaces as well as the spacing and orientation of texture patterns, such as gratings or arrays of Braille dots. When the hand is rubbed over a set of Braille dots, the Merkel disk receptors and Meissner's corpuscles fire bursts of action potentials as each dot in the pattern crosses their receptive fields and are silent as the smooth regions between dots pass. The periodic firing of these receptors signals the spatial arrangement of the texture pattern (Figure 22-8).

However, each receptor axon is stimulated by only a small portion of the pattern. The overall picture is not contained in the firing patterns of any one individual

nerve fiber but in the total ensemble of inputs provided by the active and inactive sensory nerves. The distribution of active and inactive nerve fibers represents the spacing and arrangement of the dots in the texture pattern. Therefore, a representation of the texture pattern is transmitted by a group of activated receptor axons in the peripheral nerve innervating the finger. We will learn in Chapter 23 how the central nervous system uses convergent connections to compare activity among members of the population to abstract the arrangement of dots comprising the textured surface.

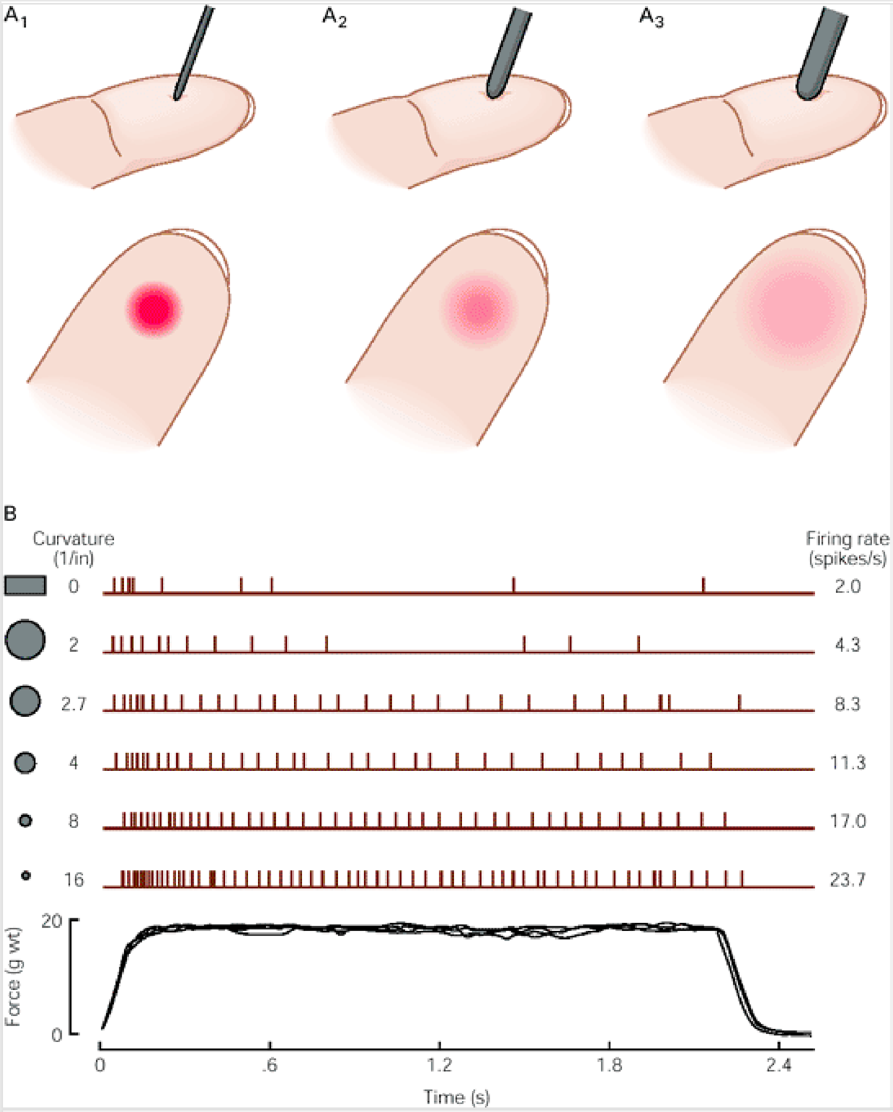


Figure 22-7 The shape and size of objects touching the hand are encoded by populations of Merkel disk receptors.

A. The area of contact on the skin determines the total number of stimulated Merkel disk receptors in the population. The **pink region** on the fingertip shows the spread of excitation when probes of different diameters are pressed upon the skin with constant force. The intensity of color is proportional to the firing rates of the stimulated receptors. **1.** A small-diameter, sharp probe activates a small population of Merkel receptors. However, the active receptors fire intensely because all of the force is concentrated at the small probe tip. **2.** An intermediate-size probe excites more receptors but the peak firing rate in the population is reduced. The probe does not feel as sharp as the small-diameter probe. **3.** A gently rounded, large-diameter probe stimulates a large population of receptors spread across the width of the finger. These receptors fire at low rates because the force is spread over a larger area of skin. (Adapted from Goodwin et al. 1995.)

B. The firing rate of individual Merkel disk receptors signals the probe diameter. These recordings of action potentials fired by a Merkel disk receptor illustrate the responses evoked when probes of decreasing size are pressed on the center of the receptive field. All of the probes evoke a strong initial response as contact is made with the skin. The firing rate of the neuron during steady pressure is proportional to the curvature of each probe. The weakest responses are evoked by flat surfaces and gently rounded (large diameter) probes. The firing rate increases as the probe diameter becomes smaller. (Adapted from Srinivasan and LaMotte 1991.)

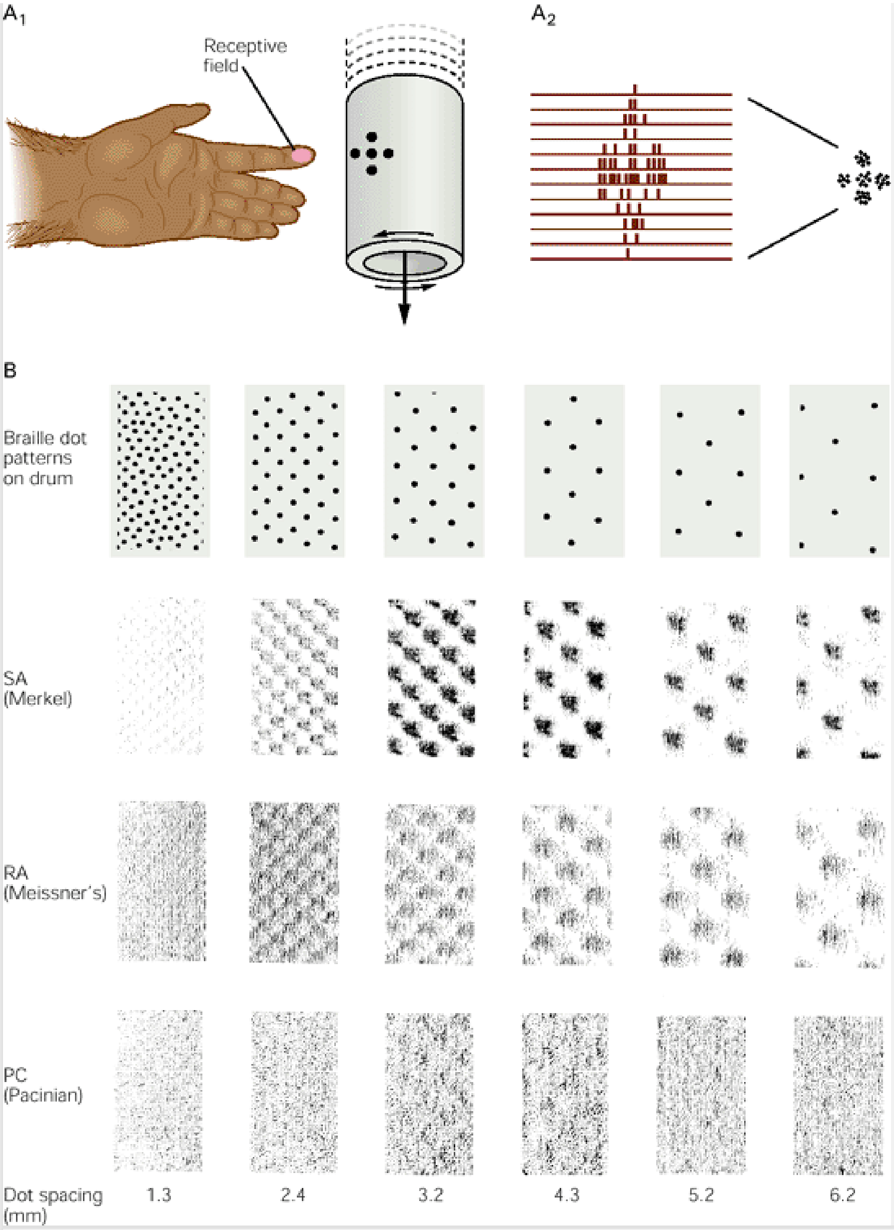


Figure 22-8 The firing patterns of mechanoreceptors in the superficial layers of the skin encode the texture of objects rubbed across the skin.

A. 1. The nerve responses to textures are measured with the hand immobilized. The receptive field of a single receptor on a monkey's finger is stimulated with an embossed array of raised dots on a rotating drum. The pattern moves horizontally over the receptive field as the drum rotates. The experimenter thus controls the speed of movement and the location of the dot pattern in the receptive field. The pattern is moved laterally on successive rotations to allow the dots to cross the medial, central, and lateral portions of the receptive field on successive rotations. The composite response of an individual nerve fiber to successive views of the raised dots simulates the distribution of active and inactive nerve fibers in the population. **2.** Sequential action potentials discharged by individual receptors during each revolution of the drum are represented in spatial event plots in which each action potential is a small dot, and each horizontal row of dots represents a scan with the pattern shifted laterally on the finger.

B. Spatial event plots of three types of mechanoreceptors to dot patterns with different spacing. Slowly adapting Merkel disk receptors and rapidly adapting Meissner's corpuscles differentiate between dots and blank space when the spacing of the dots exceeds the receptive field diameter. A receptor fires bursts of action potentials for each dot, spaced by silent intervals. As the dots are brought closer together, the resolution of individual dots blurs. Pacinian corpuscles do not distinguish texture patterns because their receptive fields are larger than the dot spacing. (Reproduced from Connor et al. 1990.)

The spatial resolution of detail within a pattern depends on the total area of skin innervated by each sensory nerve (see Figure 21-6). The Merkel disk receptors provide the sharpest resolution of spatial pattern, as each receptor axon monitors a single dot. Meissner's corpuscles also resolve individual dots but the image of the pattern that they provide is not as sharp because they have slightly larger receptive fields. Pacinian corpuscles do not signal changes in surface contour because their large receptive fields encompass several dots in the textured surface. Instead they fire continuously, measuring the speed at which the hand moves across the surface. The

activity of Pacinian corpuscles provides timing information that allows the brain to convert the number of bursts per second fired by Meissner's corpuscles and Merkel disk receptors into spatial information about the number of dots per centimeter on the textured surface.

The pure sensory experiences evoked by the stimuli used in the neurological examination—a light tap, pressure from a pin, or a sinusoidal vibratory stimulus—are quite different from the tactile sensations evoked by the complex natural stimuli that we usually encounter. Natural stimuli rarely activate a single type of receptor; rather they activate different combinations of mechanoreceptors that act synergistically. For example, when we grasp, lift, and replace an object on a surface, the four classes of receptors signal important phases of the movement. Meissner's corpuscles are highly active during the initial period of contact as grasp force increases; these receptors also fire a second burst when the grip is released. Merkel disk receptors are also stimulated during the initial grip, but they continue to fire as the object is lifted, signaling grip force; they cease firing when the grip is released. Pacinian corpuscles are most sensitive to transient mechanical pressures at the start and stop of motion, when the object is lifted off and replaced on the surface. The vertical gravitational forces applied to the skin as the object is lifted are signaled by Ruffini endings. The coordinated sensory information from these receptors provides important signals to the motor system controlling the hand, which we shall study in Chapter 38.

Other Somatic Sensations Are Mediated by a Variety of Specialized Receptors

Warmth and Cold Are Mediated by Thermal Receptors

Although the size, shape, and texture of objects are also sensed by vision, the thermal qualities of objects are uniquely somatosensory. Humans recognize four distinct types of thermal sensation: cold, cool, warm, and hot. These thermal sensations result from differences between the external temperature of the air or of objects contacting the body and the normal skin temperature of 34°C.

Thermal receptors modulate their firing as a function of temperature. At constant temperatures they have tonic discharges, firing action potentials at a steady rate governed by the actual temperature sensed. Unlike mechanoreceptors, which are silent in the absence of tactile stimuli, cold receptors and warmth receptors fire action potentials continuously at low rates (2-5 spikes per second) when the skin temperature is set at its normal value of 34°C (Figure 22-9A). The steady-state firing rate

does not increase or decrease monotonically if the skin is slowly warmed or cooled. Instead, each class of thermal receptor shows peak firing at a preferred skin temperature. Cold receptors fire most vigorously at skin temperatures of 25°C, whereas warmth receptors are most active at 45°C. Temperatures above or below these values evoke progressively weaker responses. Therefore, individual cold and warmth receptors do not give a precise reading of the skin temperature, as the same firing rate can be evoked by stimuli greater than or less than the preferred value. Rather, the code for skin temperature involves comparing the relative activity of the different populations of thermal receptors and nociceptors.

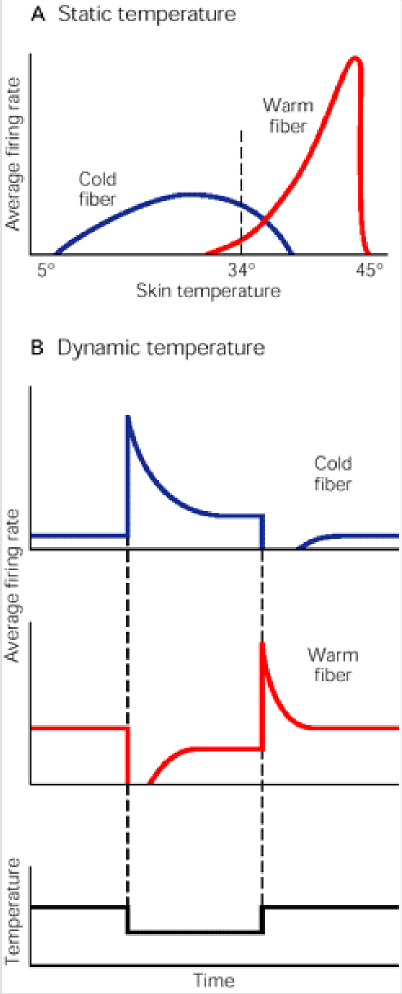


Figure 22-9 Skin temperature is coded by warmth receptors and cold receptors.

A. Static temperatures. Cold receptors and warmth receptors differ in the range of steady-state temperatures to which they respond and in their peak temperature sensitivities. Cold receptors respond to steady-state temperatures of 5-40°C. Warmth receptors are tonically active at steady temperatures of 29-45°C. Cold receptors fire at highest rates at a skin temperature of 25°C, while warmth receptors are most active at 45°C. At the normal skin temperature of 34°C, cold receptors are more active than warmth receptors. (Adapted from Darian-Smith 1973.)

B. Dynamic temperatures. Both receptors are more sensitive to changes in skin temperature than to constant temperatures. Cooling the skin below the resting level evokes a sharp rise in the firing rate of cold receptors and silences warmth receptors. If the cold temperature is maintained, the firing rates of the cold receptors adapt. When the skin temperature is rewarmed to the resting level, cold receptors are briefly silenced, whereas warmth receptors fire a burst of impulses. Warming the skin produces the opposite firing patterns in warmth and cold receptors. (Adapted from Hensel 1973.)

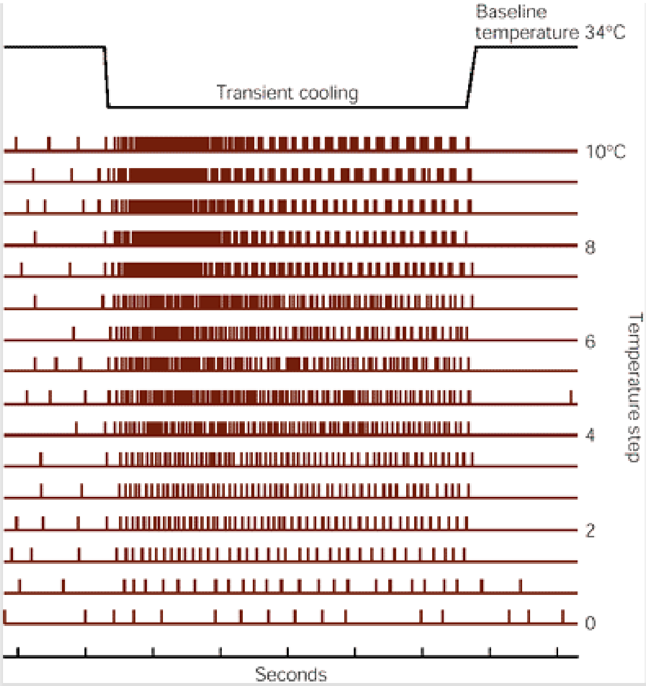


Figure 22-10 The rate and amplitude of cooling the skin is coded by the firing rates of cold receptors. Action potentials were recorded from a cold fiber when the skin was cooled rapidly. Each successive trace shows a smaller cooling pulse. The cold fiber shows a sharp rise in firing rate when the skin is cooled by 10° from 34°C to 24°C. Smaller cooling steps (eg, from 34°C to 30°C) evoke a smaller rise in the firing rate of the cold fiber. The frequency of discharge of cold fibers is linearly related to the size of the cooling step. Warming the skin at the end of the stimulus silences the cold fiber. (Reproduced from Darian-Smith et al. 1973.)

The coding of object temperature is analogous to the representation of color in the visual system. In each of these modalities there are populations of receptors sensitive to limited ranges of the energy bandwidth. Each population has a peak sensitivity in a specific position of the energy band. The perceived temperature or color is determined by the relative activity of each of the responding populations of receptors.

Thermal receptors are very sensitive to differences between the temperature of the skin and the temperature of objects that are touched. Rapid changes in skin temperature evoke dynamic responses, with increases in temperature signaled by warmth receptors and decreases by cold receptors (Figure 22-9B). If contact with the object is maintained for several seconds, the firing rate of the receptor drops to a lower rate (Figure 22-10). The adaptation of the spike discharge corresponds to the phenomenon of sensory adaptation.

Warmth receptors respond proportionally to increases in skin temperature above the resting value of 34°C. However, if the stimulus temperature exceeds 45°C, warmth fibers fire an intense burst of impulses and then cease firing even if the heat stimulus is maintained. Warmth receptors are unresponsive to hot temperatures, as stimuli above 50°C fail to excite them. At these high temperatures humans perceive heat pain rather than sensations of warmth.

Pain Is Mediated by Nociceptors

The receptors that respond selectively to stimuli that can damage tissue are called *nociceptors* (Latin *nocere*, to injure). They respond directly to some noxious stimuli and indirectly to others by means of one or more chemicals released from cells in the traumatized tissue. A variety of substances have been proposed to act as the chemical intermediary for pain in humans: histamine, K^+ released from injured cells, bradykinin, substance P and other related peptides, acidity (ie, decreases in the local pH around the nerve terminals), ATP, serotonin, and acetylcholine. Humans experience burning pain when these substances stimulate nociceptors. Therefore, it is likely that most nociceptors are really chemoreceptors sensitive to the concentration of irritant chemicals released in the surrounding tissue by noxious thermal or mechanical stimuli, or to exogenous chemicals that may penetrate the skin and bind to their sensory endings. Some nociceptors respond to chemicals such as histamine, yielding itching sensations. These fibers become tonically active in inflamed tissue owing to the release of histamine, peptides, or certain exogenous chemicals such as allergens.

Three classes of nociceptors can be distinguished on the basis of the type of stimulus: mechanical and thermal nociceptors are activated by particular forms of noxious stimuli, whereas polymodal nociceptors, the largest class, are sensitive to the destructive effects of a stimulus rather than to its physical properties.

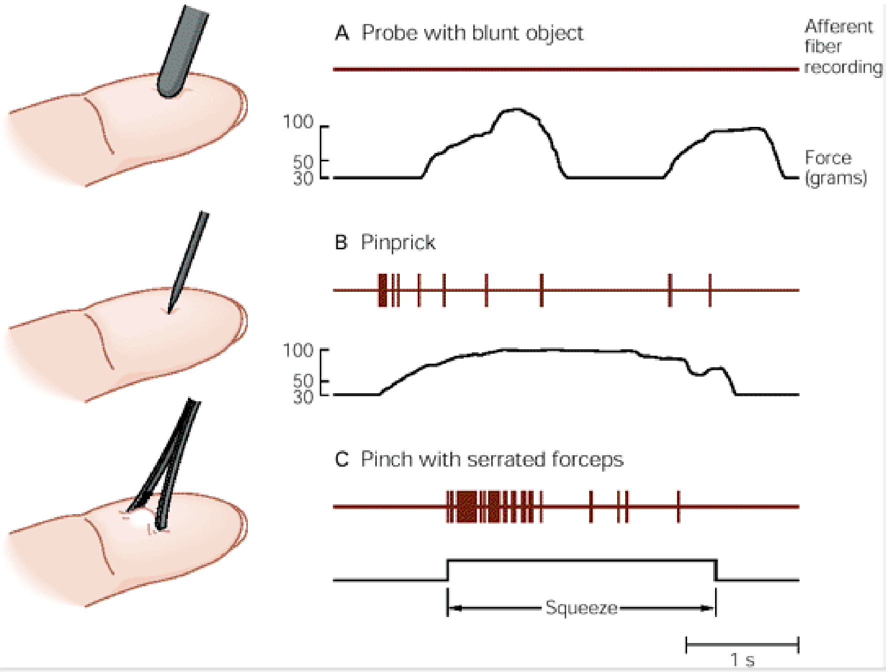


Figure 22-11 Mechanical nociceptors are activated by strong stimuli and mediate sharp, pricking sensations. Pressure on the cell's receptive field with a blunt-tipped probe elicits no response even if the skin is indented by 2 mm (**A**), but the tip of a needle that punctures the skin produces a clear response (**B**). The bottom traces in parts A and B are the output of a force transducer coupled to the stimulator. Pinching the skin with serrated forceps (**C**), which is more traumatic than a pin prick, produces the strongest response. (Adapted from Perl 1968.)

Mechanical nociceptors require strong, often painful tactile stimuli, such as a pinch, in order to respond. They are also excited by sharp objects that penetrate, squeeze, or pinch the skin (Figure 22-11), and therefore mediate sensations of sharp or pricking pain. Their firing rates increase with the destructiveness of mechanical stimuli, from near-damaging to overtly destructive of the skin. The afferent fibers for mechanical nociceptors have bare nerve endings and, because they are myelinated, are the fastest-conducting nociceptive afferents.

Thermal nociceptors are excited by extremes of temperature as well as by strong mechanical stimuli. One group of thermal nociceptors is excited by noxious heat (temperatures above 45°C). A second group responds to noxious cold (cooling the skin below 5°C).

Polymodal nociceptors respond to a variety of destructive mechanical, thermal, and chemical stimuli. They are activated by noxious mechanical stimuli, such as pinch or puncture, by noxious heat and noxious cold, and by irritant chemicals applied to the skin. These receptors are insensitive to gentle mechanical stimuli, such as stroking the skin or light pressure. Stimulation of these receptors in humans evokes sensations of slow, burning pain. Polymodal nociceptors provide the major sensory innervation of the tooth pulp.

Proprioception Is Mediated by Mechanoreceptors in Skeletal Muscle and Joint Capsules

Proprioception (Latin *proprius*, belonging to one's own self) is the sense of position and movement of one's own limbs and body without using vision. There are two submodalities of proprioception: the sense of stationary position of the limbs (limb-position sense) and the sense of limb movement (kinesthesia). These sensations are important for controlling limb movements, manipulating objects that differ in shape and mass, and maintaining an upright posture.

Three types of mechanoreceptors in muscle and joints signal the stationary position of the limb and the speed and direction of limb movement: (1) specialized stretch receptors in muscle termed *muscle spindle receptors;* (2) Golgi tendon organs, receptors in the tendon that sense contractile force or effort exerted by a group of muscle fibers; and (3) receptors located in joint capsules that sense flexion or extension of the joint. The morphology and physiology of these proprioceptors will be discussed in detail in conjunction with their role in spinal reflex pathways (Chapter 36).

In addition, stretch-sensitive receptors in the skin (Ruffini endings, Merkel cells in hairy skin, and field receptors) also signal postural information. Cutaneous proprioception is particularly important for control of lip movements in speech and facial expression.

The Viscera Have Mechanosensory and Chemosensory Receptors

Although humans normally do not experience conscious sensations from the viscera, sensory innervation plays an important role in the neural control of visceral function. (Gastrointestinal discomfort is mediated by receptors in the peritoneal lining of the gut.) The viscera are innervated by dorsal root ganglion neurons with free nerve endings. The morphology of mechanosensory visceral afferents is similar to that of mechanical nociceptors in the skin. They are activated by distention and stretching of visceral muscle, which may evoke sensations of pain. Chemosensory nerve endings in the viscera play important roles in monitoring visceral function and provide the afferent limb for many autonomic reflexes. These sensory functions are described in more detail in our discussion of the autonomic nervous system (Chapter 49).

Table 22-2 Afferent Fiber Groups in Peripheral Nerves

		Muscle nerve☆	Cutaneous nerve☆	Fiber diameter (μm)	Conduction velocity (m/s)
Myelinated					
Large		I	Aα	12-20	72-120
Medium		II	Aβ	6-12	36-72
Small		III	Aδ	1-6	4-36
Unmyelinated		IV	C	0.2-1.5	0.4-2.0

☆ Sensory nerves in muscle are classified according to their fiber diameters. Sensory afferents in cutaneous nerves are classified by conduction velocities. The types of receptors innervated by each type of afferent are listed in Table 22-1.

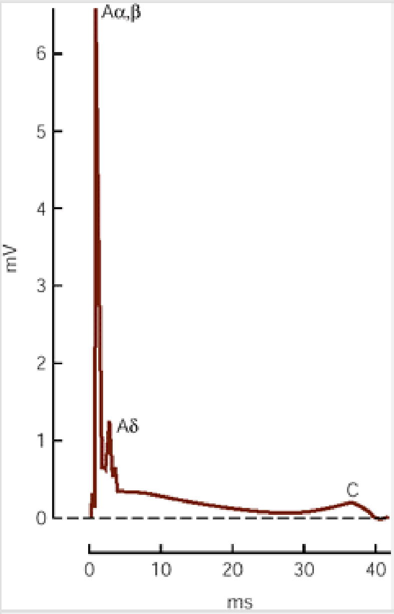


Figure 22-12 Conduction velocities of peripheral nerves are measured clinically from compound action potentials. By electrically stimulating a peripheral nerve at varying intensities different populations of nerve fibers are activated. The action potentials of all the nerves activated by a particular level of current are summed to create the compound action potential. The example in this figure has two major deflections corresponding to action potentials conducted by large and small myelinated fibers (Aα, β, and Aδ fibers). The conduction velocity of each fiber group is computed by dividing the latency of the peaks (the time between the electric shock and the appearance of the neural response) by the distance along the nerve between the stimulating and recording electrodes. Although there are approximately equal numbers of large- and small-diameter myelinated fibers in this nerve, the Aδ peak of the compound action potential is smaller because the spike amplitude of each nerve fiber is proportional to the fiber diameter. Action potentials in unmyelinated nerves (C fibers) are conducted slowly and produce a small late peak. (Reproduced from Gasser 1941).

The Afferent Fibers of Different Receptors Conduct Action Potentials at Different Rates

The diverse modalities of somatic sensation—touch, proprioception, pain, and temperature sense—are mediated by the terminals of dorsal root ganglion cells that differ in the morphology of their terminals and stimulus selectivity. They also differ in the size and conduction velocity of their axons. Mechanoreceptors and proprioceptors are innervated by large-diameter myelinated axons, whereas thermal receptors and nociceptors have small myelinated or unmyelinated axons. These differences in fiber size are important physiologically, because they affect the speed at which action potentials are conducted to the brain (Table 22-2).

Large fibers conduct action potentials more rapidly because the internal resistance to current flow along the axon is low and the nodes of Ranvier are more widely spaced along its length (see Chapter 8). The conduction velocity of large myelinated fibers is approximately six times the axon diameter, while that of thinly myelinated fibers is five times the axon diameter. The factor for converting axon diameter to conduction velocity is much smaller for unmyelinated fibers (1.5-2.5).

Box 22-2 Mapping the Innervation of the Dorsal Roots

The area of skin innervated by a single dorsal root, known as a dermatome, can be identified in experimental animals by probing the skin with different stimuli and observing the response of the fibers within the root. The dermatomes follow a highly regular pattern on the body (Figure 22-13).

Dermatomal maps are an important diagnostic tool for locating the site of injury to the spinal cord and dorsal roots. For example, on the basis of the dermatomal map for the human forearm, we can predict that sensory changes limited to the distal forearm and the fourth and fifth fingers are the result of injury to the C8 and T1 dorsal roots.

In actuality, the boundaries of the dermatomes are less distinct than shown here because the axons making up a dorsal root originate from several different peripheral nerves. Similarly, individual peripheral nerves contribute axons to several adjacent dorsal roots, leading to overlap in the area innervated by each segment. Pain dermatomes mapped with a pinprick overlap less than tactile dermatomes mapped with light mechanical stimuli.

The merging of axons from several peripheral nerves has important clinical consequences. Damage to a dorsal root often results in a small sensory deficit throughout the broad area innervated by that root. In contrast, cutting the distal portion of a peripheral cutaneous nerve results in a complete loss of sensory receptors in the circumscribed area innervated by the nerve.

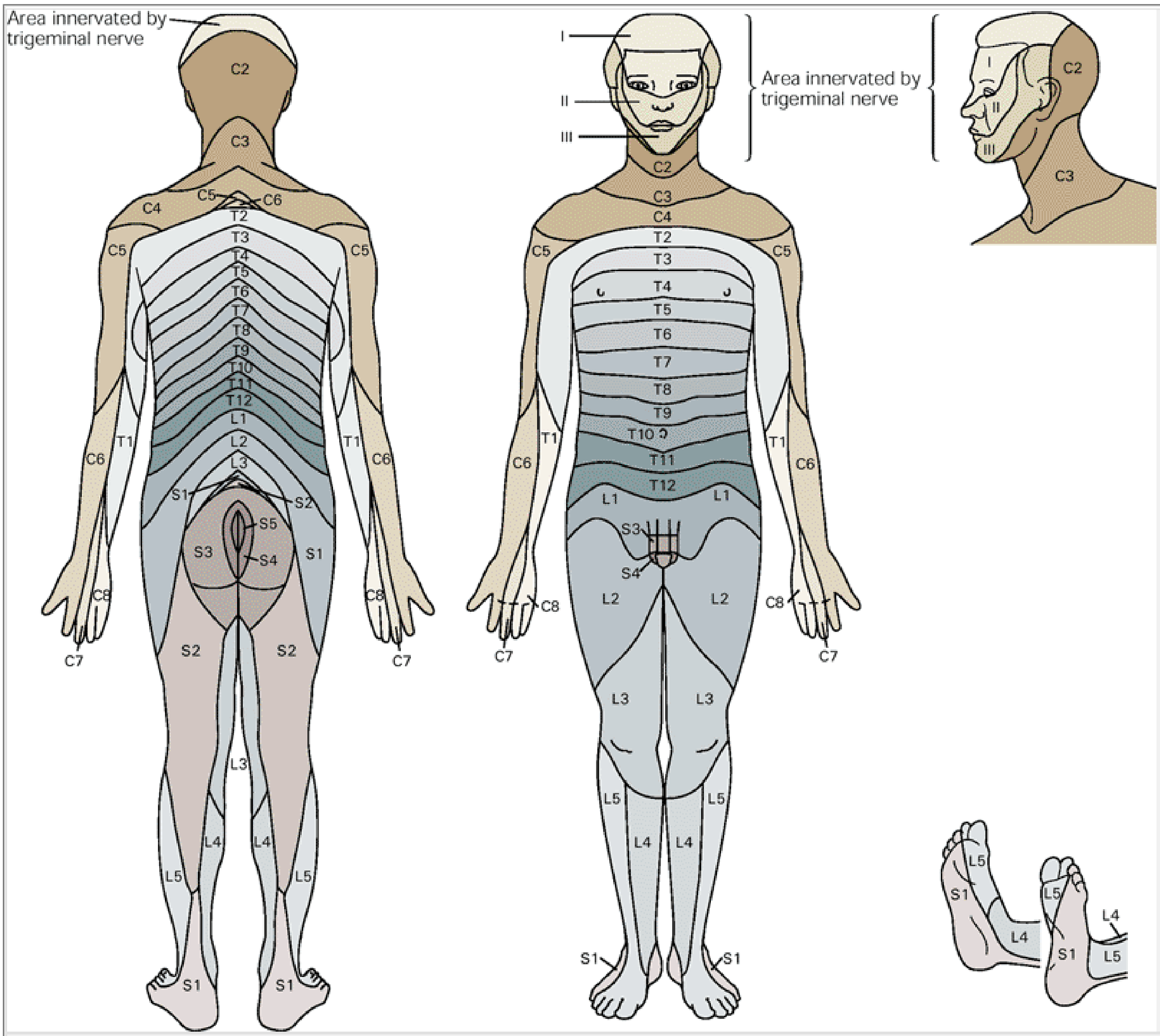


Figure 22-13 The distribution of dermatomes. The 31 pairs of dorsal roots are labeled by the corresponding vertebral foramen through which the root enters the spinal cord. There are 7 cervical (C), 12 thoracic (T), 5 lumbar (L), and 5 sacral (S) roots, which are numbered rostrally to caudally for each division of the vertebral column. Note that there is no dorsal root at C1, only a ventral (or motor) root, and that the S5 dermatome located in the perianal region is not shown. The facial skin is innervated by the three branches of the trigeminal nerve: the ophthalmic (I), maxillary (II), and mandibular (III) branches.

The clinician takes advantage of the known distribution of conduction velocities of afferent fibers in peripheral nerves to diagnose diseases that result in degeneration of the fibers. In certain conditions there is a selective loss of axons; in diabetes, for example, large sensory fibers degenerate (large-fiber neuropathy). This selective loss is reflected in a reduction in the peak of the compound action potential (Figure 22-12), a slowing of nerve conduction, and a corresponding diminution of sensory capacity. Similarly, in multiple sclerosis the myelin sheath of large-diameter fibers degenerates, producing slowing of nerve conduction or failure of impulse transmission.

Afferent Fibers Conveying Different Somatic Sensory Modalities Have Distinct Terminal Patterns in the Spinal Cord and Medulla

The topographic arrangement of receptors in the skin is preserved as the central processes of the dorsal root ganglion neurons enter the spinal cord through the dorsal roots. The area of skin innervated by the nerve fibers comprising a dorsal root is called a *dermatome.* The distribution of dermatomes for all spinal segments has been mapped by studying sensation and reflex responsiveness that remain after injury to dorsal roots (Box 22-2). Dermatomes are arranged in a caudal-rostral sequence, with the anus and genitalia most caudally and the shoulder, neck, and dorsum of the head rostrally. The three branches of the trigeminal nerve also preserve the topographic arrangements of receptors in the face through their projections to the trigeminal nuclei of the brain stem.

Upon entry to the spinal cord the central axons of dorsal root ganglion neurons branch extensively and project to nuclei in the spinal gray matter and brain stem. The spinal gray matter is divided into three functionally distinct regions: the dorsal horn, the intermediate zone, and the ventral horn. Based on its cytoarchitecture, the spinal gray matter is also divided into 10 layers (laminae). Each layer contains functionally distinct nuclei that have different patterns of projections. Laminae I-VI correspond to the dorsal horn, lamina VII is roughly equivalent to the intermediate zone, and laminae VIII and IX comprise the ventral horn. Lamina X consists of the gray matter surrounding the central canal.

The sensory specialization of dorsal root ganglion neurons is preserved in the central nervous system through distinct ascending pathways for the various somatic modalities. The modalities of touch and proprioception are transmitted directly to the medulla through the ipsilateral dorsal columns. Pain and temperature sense are relayed through synapses in the spinal cord to the contralateral anterolateral quadrant, where axons of dorsal horn neurons ascend to the brain stem and thalamus.

The Dorsal Column-Medial Lemniscal System Is the Principal Pathway for Perception of Touch and Proprioception

The principal central branch of the axon of neurons mediating tactile sensation and proprioception from the limbs and trunk ascends in the spinal cord in the ipsilateral dorsal columns to the medulla. Secondary branches terminate in the dorsal horn. Axons that enter the cord in the sacral region are found near the midline of the dorsal columns; axons that enter the cord at successively higher levels are added in progressively more lateral positions.

At upper spinal levels the dorsal columns are divided into two bundles (fascicles) of axons: the *gracile fascicle* and the *cuneate fascicle.* The gracile fascicle is located medially and contains fibers that ascend from the

ipsilateral sacral, lumbar, and lower thoracic segments. The cuneate fascicle is located laterally and contains fibers from the upper thoracic and cervical segments. Axons in the two bundles terminate in the lower medulla in the gracile nucleus and cuneate nucleus, respectively (Figure 22-14A). Mechanosensory information from the face and scalp is transmitted to the principal trigeminal nucleus (Figure 22-14), which is in the pons rostral to the dorsal column nuclei.

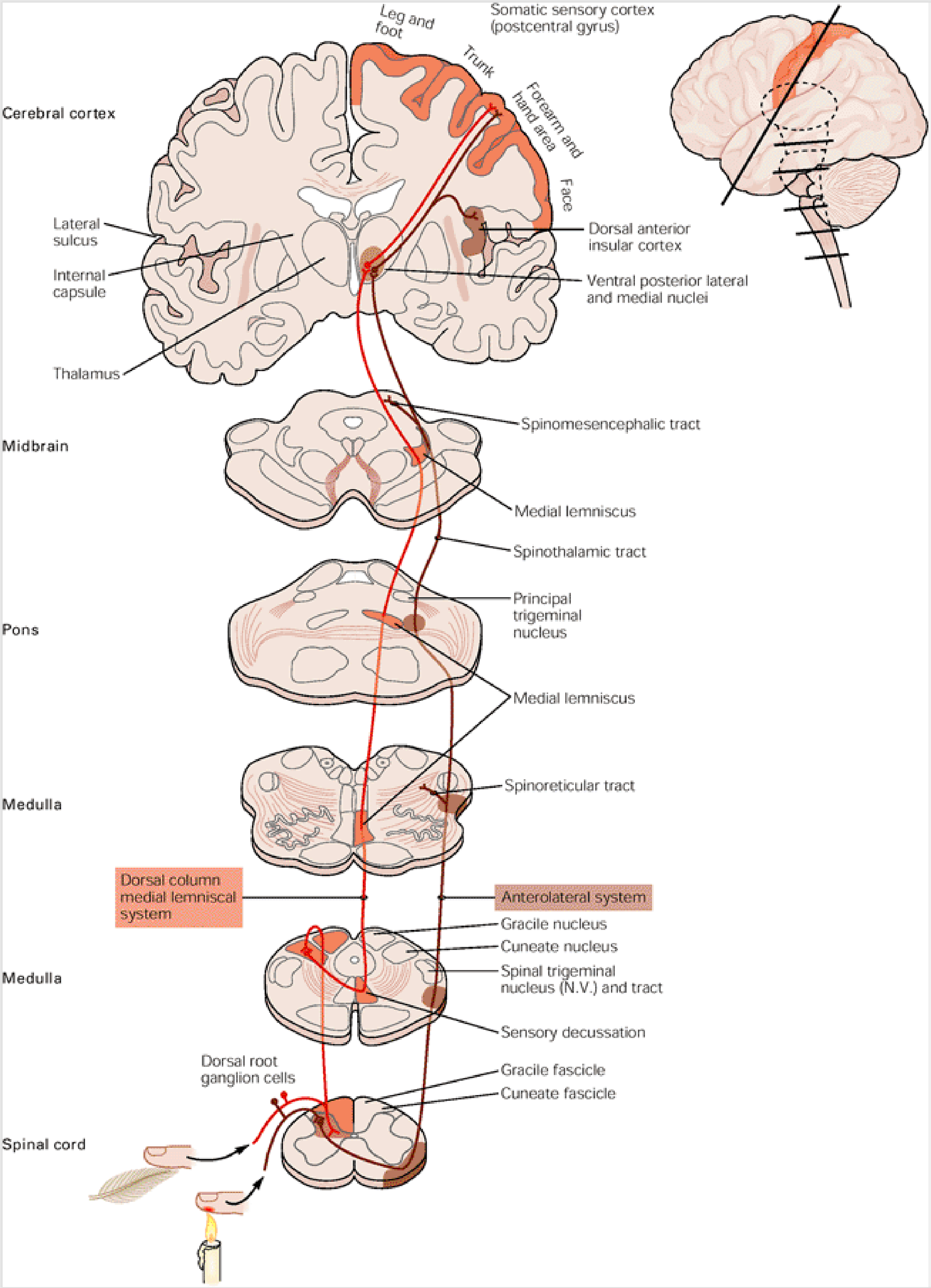


Figure 22-14 (Opposite) Sensory information from the limbs and trunk is conveyed to the thalamus and cerebral cortex by two ascending pathways. The anatomy of the pathways is shown on a series of brain slices. The top slice is a schematic oblique section through the postcentral gyrus, which is the location of the primary somatic sensory cortex. The bottom five slices are schematic transverse sections through the brain stem and spinal cord at levels marked on the neuraxis.

Tactile sensation and limb proprioception are transmitted to the thalamus by the dorsal column-medial lemniscal system (**orange**). Painful and thermal sensations are transmitted to the thalamus by the anterolateral system (**brown**).

In the spinal cord the large-diameter dorsal root ganglion axons mediating touch and proprioception diverge from the smaller sensory afferents for pain and temperature sense. The large fibers ascend in ipsilateral dorsal columns to the brain stem where they terminate in the cuneate nucleus. The small fibers terminate on second-order neurons in the dorsal horn of the spinal cord, and the axons of these neurons cross the midline of the spinal cord to form the anterolateral tract. Thus touch and proprioception ascend *ipsilaterally* in the spinal cord, whereas pain and temperature sense ascend *contralaterally.*

The second-order neurons in the dorsal column nuclei send axons across the midline in the medulla, where they form the medial lemniscus. As these axons ascend through the brain stem they shift laterally, joining fibers of the spinothalamic tract in the midbrain, before terminating in the ventral posterior lateral nucleus of the thalamus. Spinothalamic fibers terminate in other thalamic nuclei that are not illustrated in this brain slice. Thalamic neurons mediating touch and proprioception send their axons to the primary somatic sensory cortex in the postcentral gyrus. Thalamic neurons sensitive to painful or thermal stimuli project to the primary somatic sensory cortex, to the dorsal anterior insular cortex, and to the anterior cingulate gyrus rostral to this section. (Adapted from Carpenter and Sutin 1983.)

The somatotopic organization of the axons relaying input from receptors in the skin and joints is maintained throughout the entire ascending somatosensory pathway, through the thalamus, to the somatosensory areas in the postcentral gyrus of the cerebral cortex. In Chapter 23 we will see how the topographic arrangement of sensory nerve fibers creates sensory maps of the body at each sensory relay nucleus. These maps are the basis for integrating information from receptors in adjoining areas of the skin, or from agonist or antagonist muscle pairs.

Sensory information from the cuneate, gracile, and principal trigeminal nuclei is transmitted directly to the thalamus. The axons of the neurons in the cuneate and gracile nuclei cross to the other side of the brain stem and ascend to the ventral posterior lateral nucleus of the thalamus in a fiber bundle called the *medial lemniscus* (Figure 22-14). As the medial lemniscal fibers cross, the body map becomes reversed: The sacral segments are located most laterally and the cervical segments medially. An adjacent parallel pathway from the principal trigeminal nucleus, the *trigeminal lemniscus*, conveys tactile and proprioceptive information from the face and terminates in the ventral posterior medial nucleus. The trigeminal lemniscus later joins axons from the arm and back of the head in the medial lemniscus.

Because of the crossing of the fibers in the medulla, and pons, the right side of the brain receives sensory input from the limbs and trunk on the left side of the body, and vice versa. As sensory information ascends in the brain stem, the topographic arrangement of the axons changes, so that when the axons enter the thalamus they have the same mediolateral organization as the ventral posterior nuclei. Inputs from the legs are located most laterally, while those from the arm are located more medially. Inputs from the face are most medial.

Although the dorsal columns contain both tactile and proprioceptive axons, these two submodalities remain segregated anatomically. The axons from proprioceptors are positioned more ventrally in the dorsal columns than those of tactile receptors, which are located dorsally. Furthermore, proprioceptors terminate more rostrally in the gracile and cuneate nuclei. A similar segregation of cutaneous and proprioceptive axons exists in the spinal cord. Neurons mediating the sense of touch terminate in the nucleus proprius (laminae III and IV) of the dorsal horn, whereas proprioceptive afferents terminate more ventrally in the nucleus of Clarke's column (located in lamina VII), on interneurons in laminae V and VI, and on motor neurons in lamina IX.

The Anterolateral System Mediates Sensations of Pain and Temperature

Neurons mediating sensations of pain or temperature from the limbs and trunk terminate in the ipsilateral dorsal horn of the spinal cord. These dorsal root ganglion neurons have much smaller axons and cell bodies than the neurons transmitting sensations of touch or proprioception, and most are unmyelinated. These small fibers branch extensively in the white matter, forming the *tract of Lissauer*, and terminate in the most superficial regions of the dorsal horn. Thus neurons in the marginal zone and substantia gelatinosa (laminae I and II) respond almost exclusively to painful or thermal stimuli. Trigeminal sensory afferents that carry sensations of pain and temperature from the head and face form the descending *spinal* trigeminal tract that terminates in the spinal trigeminal nucleus (a portion of which is also called the medullary dorsal horn). The spinal trigeminal nucleus contains a marginal zone and substantia gelatinosa that receive nociceptive information and a magnocellular division that is innervated by mechanoreceptors and corresponds to the nucleus proprius.

Like the information on touch and proprioception conveyed in the dorsal column-medial lemniscal system, pain and temperature information also ascends to the thalamus, in an anatomical pathway located in the anterolateral quadrant of the contralateral spinal cord (Figure 22-14). The anterolateral pathway originates from neurons in the marginal zone (lamina I), the nucleus proprius (lamina IV), the deep layers of the dorsal horn (laminae V and VI), and the intermediate zone (lamina VII). These spinal neurons send their axons across the midline of the spinal cord and ascend in the anterolateral column of the opposite side of the body. The axons of trigeminal neurons also decussate in the brain stem and join ascending fibers from the most rostral spinal segments.

Like axons in the dorsal columns, the axons of the anterolateral tract are also arranged somatotopically. At each successive spinal segment entering axons lie adjacent to those ascending from lower portions of the spinal cord. Thus, anterolateral fibers from sacral segments are located most laterally, with lumbar fibers slightly more medially, and cervical segments occupying the most medial locations. This somatotopic

arrangement of ascending fibers is important clinically for diagnosing and treating pain disorders.

Unlike the medial lemniscus, which transmits sensory information directly to the thalamus, the anterolateral system has both direct and indirect paths to the thalamus. The anterolateral tract consists of three ascending pathways: the spinothalamic, spinoreticular, and spinomesencephalic. The spinothalamic tract conveys information about painful and thermal stimuli directly to the ventral posterior lateral nucleus of the thalamus. Axons in the spinoreticular tract synapse on neurons in the reticular formation of the medulla and pons, which then relay information to the intralaminar and posterior nuclei of the thalamus and to other structures in the diencephalon, such as the hypothalamus.

An Overall View

The somatic sensory system transmits information about four major modalities: touch, proprioception, pain, and temperature sense. Although the four modalities share the same type of sensory neuron—the dorsal root ganglion cell—the receptors for each modality have distinct morphological and molecular specializations that allow them to sense specific types of stimuli.

Discriminative touch and limb proprioception depend on encapsulated mechanoreceptors sensitive to physical deformation produced by indentation or lateral motion across the skin, stretch or contraction of muscles, or the angle of individual joints. Mechano-receptors in the skin are further specialized to transduce pressure or motion, allowing them to sense the shape and surface texture of objects. Spatial resolution depends on the receptive fields of these receptors and is greatest on the finger tips and lips, where the receptors are most abundant.

The sense of temperature is mediated by the bare endings of thinly myelinated or unmyelinated nerves sensitive to specific ranges of thermal energy. Separate classes of thermal receptors sense temperatures that are perceived as cold, cool, warm, and hot, as they differ in their peak sensitivities and temperature ranges. Painful sensations are mediated by free nerve endings, called nociceptors, that sense destructive mechanical stimuli that squeeze, pinch, or puncture the skin; extremely hot or cold temperatures that might burn or freeze the skin; or chemical substances released from cells as a result of tissue damage.

The four modalities are conveyed in separate ascending pathways to the thalamus and cerebral cortex. Touch and proprioception are transmitted by large-diameter axons with fast conduction velocities to the dorsal horn of the spinal cord and then to the brain stem and thalamus through the dorsal column-medial lemniscal system. Pain and temperature sense are conveyed by thinly myelinated and unmyelinated nerves that terminate in the most superficial layers of the spinal or trigeminal dorsal horn. These modalities are conveyed directly, and through multisynaptic networks, to the thalamus through the contralateral anterolateral pathway

The somatic sensory stimuli we encounter in everyday life are complex, cover large areas of skin, and have many characteristics. Each type of receptor is selectively activated by distinct spatial and qualitative properties of a stimulus. Different types of information about an object are transmitted by populations of different types of sensory neurons, and conveyed in parallel pathways to the primary somatosensory cortex, where all the information is combined into a unified somatic percept. How this occurs is the subject of the next chapter.

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Back

23

Touch

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INFORMATION TRANSMITTED to the brain from mech-anoreceptors in the fingers enables us to feel the shape and texture of objects and permits us to read braille, play musical instruments, type on computer keyboards, or perform fine surgical dissections. In this chapter we shall examine how neuronal activity of mechanoreceptors in the skin gives rise to perception of discriminative touch and why the fingertips are best suited to this task.

Since this chapter is the first in which we discuss, in cell-physiological detail, the central projections of a sensory system to the cerebral cortex, we also address two key questions about the cerebral cortex. How does it work on the cellular level? How does it integrate and transform sensory information coming from the periphery? Thus, we describe how the cortex constructs an image of objects we touch from the fragmented information provided by the receptors of the skin. Moreover, in this chapter we use the sense of touch as a model for deriving principles of cortical organization that give rise to conscious perception. Specifically, we examine the degree to which the various somatic modalities are functionally segregated in the central nervous system and how they are recombined for coherent perception of tactile information. We have chosen the modality of touch to introduce the principles of cortical function because these principles were first established for the somatosensory cortex and later extended to other sensory and motor cortical areas, as we shall see in subsequent chapters.

Tactile Information About an Object is Fragmented by Peripheral Sensors and Must Be Integrated by the Brain

The ability to recognize objects placed in the hand on the basis of touch alone is one of the most important and complex functions of the somatosensory system. By holding an object in the hand we can perceive its size, shape, texture, mass, and temperature. These properties together give rise to the percept of a coherent object. Neurologists call the ability to perceive form through touch *stereognosis.* Stereognosis not only tests the ability of the dorsal column-medial lemniscal system to transmit sensations from the hand but also measures the ability of cognitive processes in the brain to integrate that information.

Many familiar objects such as an apple, a screwdriver, or a set of keys are much larger than the receptive field of any one receptor in the hand. These objects stimulate a large population of sensory nerve fibers, each of which scans a small portion of the object. The peripheral sensory apparatus deconstructs the object into tiny segments because, as we saw in Chapter 22, a sensory nerve fiber conveys information from only a small area of the receptor sheet. When a particular nerve fiber fires an action potential, it signals that its territory has been contacted at an intensity sufficient to cause it to fire. By analyzing which nerve fibers have been excited, the brain reconstructs the pattern made by the object.

In addition, objects excite more than one kind of receptor. For example, a textured surface such as an array of Braille dots stimulates Merkel disk receptors, Meissner's corpuscles, and Pacinian corpuscles but evokes a different discharge pattern in each type of receptor because each signals a special feature of the stimulus. Similarly, the shape of an object is signaled by the firing patterns of Merkel disk receptors, which sense the curvature of the object's surface; by Meissner's corpuscles, which signal edges (where the curvature changes abruptly); and by the postural information provided by receptors in the muscles and joints of the hand.

Thus, no single sensory axon, or even class of sensory axons, signals all of the relevant information. Spatial properties are processed by populations of receptors that form many parallel pathways to the brain. It is the job of the central nervous system to construct a coherent image of an object from fragmented information conveyed in multiple pathways. In this chapter we shall examine how neural circuits in the dorsal column-medial lemniscal system and the somatosensory areas of the cerebral cortex integrate information from neighboring areas of skin and different populations of receptors in order to form a *percept.*

The Primary Somatic Sensory Cortex Integrates Information About Touch

The anatomical plan of the somatic sensory system reflects an organizational principle common to all sensory systems: Sensory information is processed in a series of relay regions within the brain. We learned in Chapter 22 that there are only three synaptic relay sites between sensory receptors in the skin and the cerebral cortex (see Figure 22-14). Mechanoreceptors in the skin send their axons to the caudal medulla, where they terminate in the gracile or cuneate nuclei. These second-order neurons project directly to the contralateral thalamus, terminating in the ventral posterior lateral nucleus. A parallel pathway from the principal trigeminal nucleus, which represents the face, ascends to the ventral posterior medial nucleus. The third-order neurons in the thalamus send axons to the primary somatic sensory cortex (S-I), located in the postcentral gyrus of the parietal lobe.

As we learned in Chapter 20, the primary somatic cortex S-I contains four cytoarchitectural areas: Brodmann's areas 3a, 3b, 1, and 2 (Figure 23-1). Most thalamic fibers terminate in areas 3a and 3b, and the cells in areas 3a and 3b project their axons to areas 1 and 2. Thalamic neurons also send a small projection directly to Brodmann's areas 1 and 2. These four regions of the cortex differ functionally. Areas 3b and 1 receive information from receptors in the skin, whereas areas 3a and 2 receive proprioceptive information from receptors in muscles and joints. However, the four areas of the cortex are extensively interconnected, so that both serial and parallel processing are involved in higher-order elaboration of sensory information.

The *secondary somatic sensory cortex* (S-II), located on the superior bank of the lateral fissure, is innervated by neurons from each of the four areas of S-I (Figure 23-1C). The projections from S-I are required for the function of S-II. For example, when the neural connections from the hand area of S-I are removed, stimuli applied to the skin of the hand do not activate neurons in S-II. In contrast, removal of parts of S-II has no effect on the response of neurons in S-I. The S-II cortex projects to the *insular cortex*, which in turn innervates regions of the temporal lobe believed to be important for tactile memory.

Finally, as we have seen in Chapters 19 and 20, other important somatosensory cortical areas are located in the *posterior parietal cortex* (Brodmann's areas 5 and 7). These areas receive input from S-I as well as input from the pulvinar and thus have an associational function. They are also connected bilaterally through the corpus callosum. Area 5 integrates tactile information from mechanoreceptors in the skin with proprioceptive

inputs from the underlying muscles and joints. This region also integrates information from the two hands. Area 7 receives visual as well as tactile and proprioceptive inputs, allowing integration of stereognostic and visual information. The posterior parietal cortex projects to the motor areas of the frontal lobe and plays an important role in sensory initiation and guidance of movement.

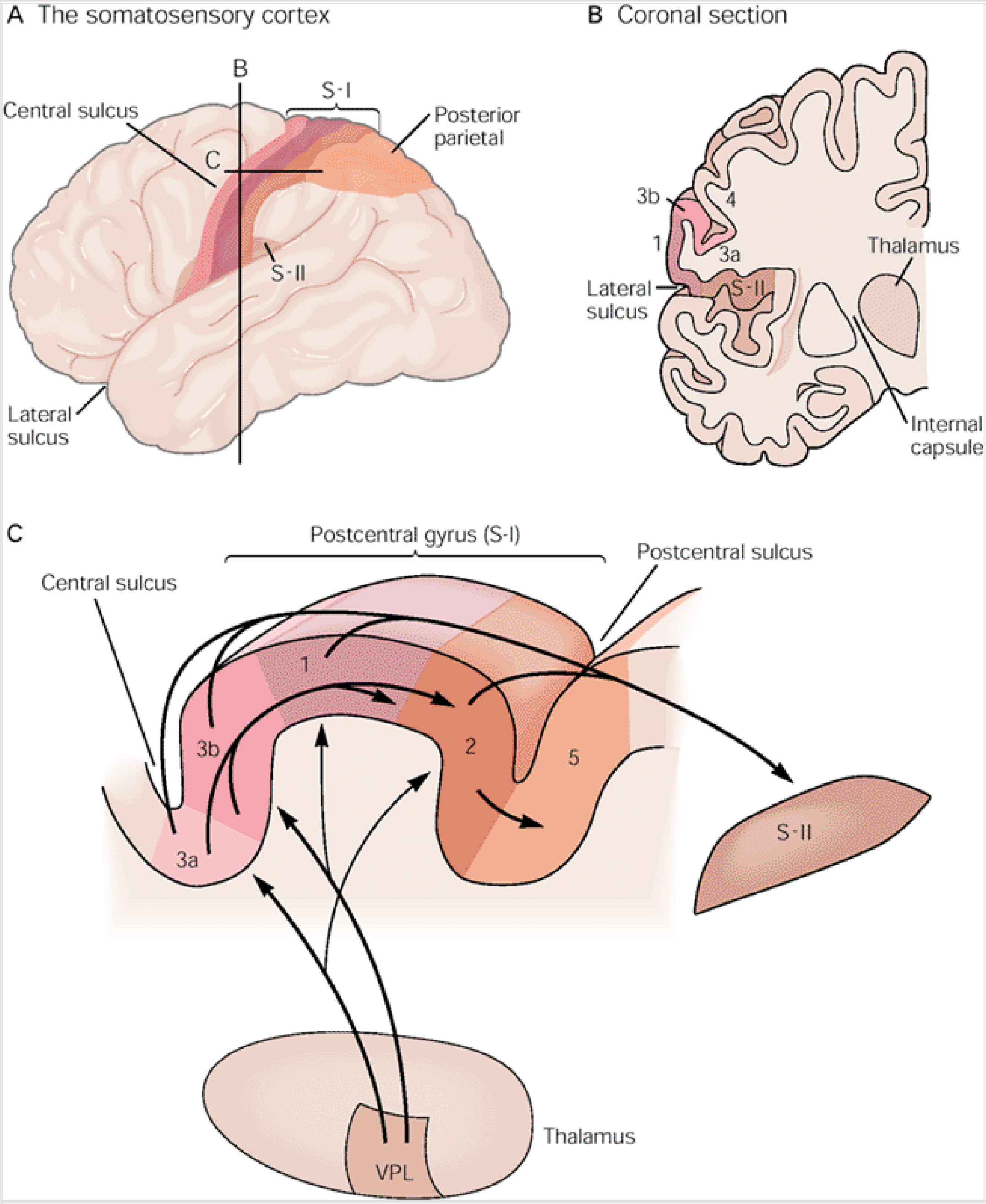

Figure 23-1 The somatic sensory cortex has three major divisions: the primary and secondary somatosensory cortices and the posterior parietal cortex.

A. The anatomical location of the three divisions of the somatic sensory cortex is seen best from a lateral perspective of the surface of the cerebral cortex. The *primary somatic sensory cortex* (S-I) forms the most rostral portion of the parietal lobe. It covers the postcentral gyrus, beginning at the bottom of the central sulcus and extending posteriorly to the postcentral and intraparietal sulci. The postcentral gyrus also extends into the medial wall of the hemisphere to the cingulate gyrus. The *posterior parietal cortex* (Brodmann's areas 5 and 7) lies immediately posterior to S-I. The *secondary somatic sensory cortex* (S-II) is located on the parietal operculum of the lateral sulcus (fissure of Sylvius).

B. The relationship of the S-I to the S-II cortex is illustrated in a coronal section through the cortex. The S-II cortex lies lateral to S-I, and extends laterally to the insular cortex, forming the superior bank of the lateral sulcus. The numbers on the section indicate Brodmann's cytoarchitectural areas.

C. S-I is subdivided into four distinct cytoarchitectonic regions (Brodmann's areas). This sagittal section illustrates the spatial relationship of these four regions to area 5 of the posterior parietal cortex. Somatosensory input to the cortex originates from the ventral posterior lateral nucleus of the thalamus. Neurons in this nucleus project to all areas in S-I, mainly to Brodmann's areas 3a and 3b but also to areas 1 and 2. In turn, neurons in areas 3a and 3b project to areas 1 and 2, and all of these project to S-II and to posterior parietal cortex. These higher-order somatosensory areas also contain distinct cytoarchitectonic and functional subregions that are not illustrated here. (Modified from Jones and Friedman 1982.)

Box 23-1 Extracellular Recordings Are Used to Study Neurons in the Central Nervous System

Much of what we know about the processing of somatic sensory information in the brain, particularly in the cerebral cortex, has been learned from studies of monkeys. The monkey has proven so useful because primates have sensory receptors identical to those of humans. Furthermore, psychophysical measurements of somatosensory discriminative abilities indicate that humans and monkeys experience the same tactile sensations in their hands when they feel vibration, palpate objects, or touch a textured surface.

The techniques for studying the physiology of the cerebral cortex at the cellular level were developed by Vernon Mountcastle and his colleagues in the 1950s. Using extracellular microelectrodes (which had just become available) they recorded the electrical responses of individual neurons. Extracellular recordings reveal only the action potentials of the cell and thus, do not show synaptic activity except under certain circumstances. (Extracellular recording, however, is much simpler than intracellular recording in the intact brain because the brain pulsates, making it difficult to maintain intracellular penetrations.) Nevertheless, extracellular recording has been a useful tool in defining how sensory stimuli modulate the firing patterns of single cells.

Microelectrode recording allows the receptive fields of several neurons at adjacent locations in the brain to be examined in sequence (Figure 23-2). By systematically moving the electrode in steps of thousandths of a millimeter, one can reconstruct a three-dimensional map of the cerebral cortex. This technique, termed micromapping, forms the experimental foundation for what we know about the columnar and somatotopic organization of the cortex.

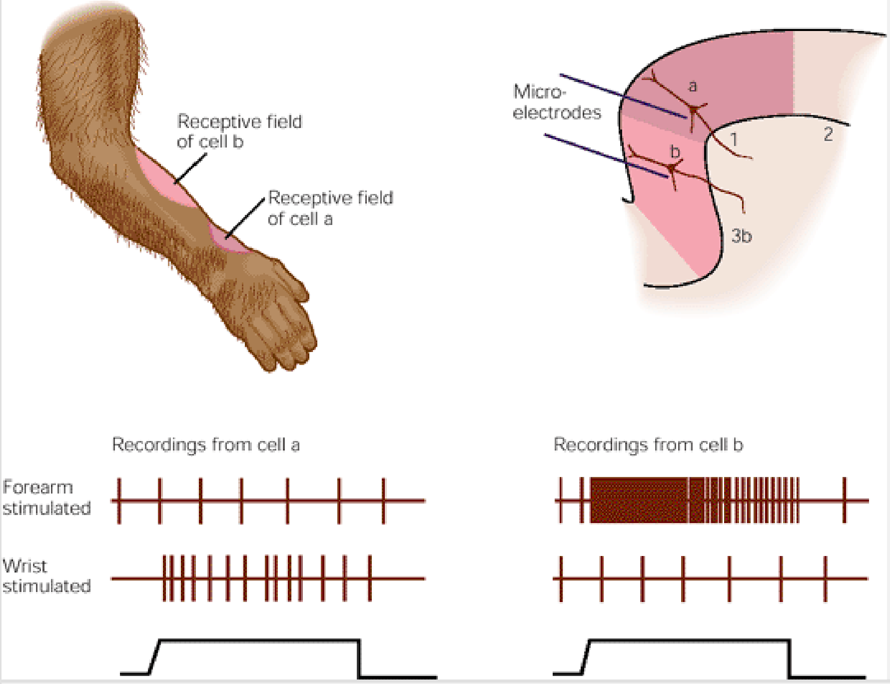

Figure 23-2 Three-dimensional functional maps of the cerebral cortex are created by examining the receptive fields of adjacent cortical neurons in sequence. In this example a pair of microelectrodes are advanced into the S-I cortex. The neuron recorded at location **a** in area 1 has a sustained, slowly adapting response to pressure applied to the wrist with a small blunt probe and ceases firing when the probe is removed from the skin. It does not respond to pressure on the forearm. The neuron recorded at location **b** in area 3b responds vigorously to pressure on the forearm but not on the wrist. Note that cortical neurons, unlike sensory afferents, fire action potentials at low rates in the absence of stimuli.

Cortical Neurons Are Defined by Their Receptive Fields As Well As by Modality

To understand the function of these different regions of the cortex, we begin by examining the properties of individual cortical neurons. The neurons in the primary somatic sensory cortex are at least three synapses beyond the peripheral receptors. Thus their response properties reflect information processing in the dorsal column nuclei, the thalamus, and in the cortex itself. Cortical neurons, like neurons elsewhere in the brain, are usually studied using the technique of extracellular recording (see Box 23-1). Microelectrodes are inserted into the cortex to record both the spike trains that occur spontaneously and those evoked by appropriate stimuli.

Like mechanoreceptors, the cortical neurons receiving sensory information from the skin are either slowly adapting or rapidly adapting neurons, signaling either the amplitude or rate of the peripheral skin indentation. Moreover, since each cortical neuron receives inputs from receptors in a specific area of the skin, central neurons also have receptive fields. Thus, each cortical neuron is defined by its receptive field as well as by its sensory modality. Any point on the skin is represented in the cortex by a population of cortical cells connected to the afferent fibers that innervate that point on the skin. When a point on the skin is touched, the population of cortical neurons connected to the receptors at that location is excited. Stimulation of another point on the skin activates another population of cortical neurons. We perceive contact at a particular location on the skin because a specific population of neurons in the brain is activated. Conversely, as we saw in Chapter 19, when a point on the cortex is stimulated electrically, we experience tactile sensations on a specific part of the skin. We shall show later in this chapter that cortical neurons are grouped by function and that their receptive fields are arranged in an orderly topographic sequence that forms a map of the body.

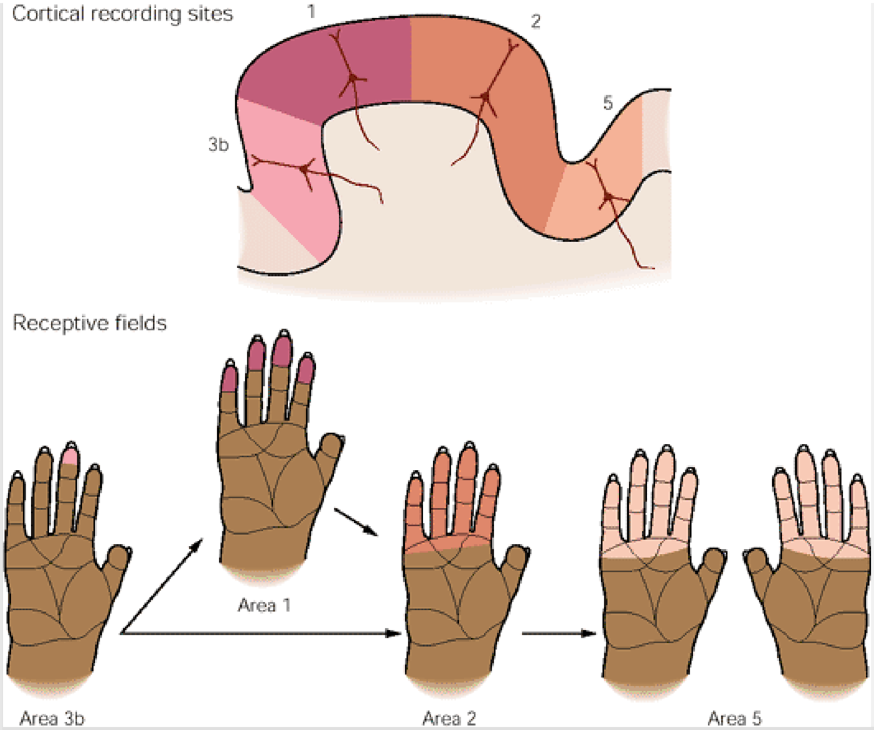

Figure 23-3 The receptive fields of neurons in the primary somatic sensory cortex are larger than those of the sensory afferents. Each of the hand figurines shows the receptive field of an individual neuron in areas 3b, 1, 2, and 5 of the primary somatic sensory cortex, based on recordings made in alert monkeys. The colored regions indicate the region of the hand where light touch elicits action potentials from the neuron. Neurons that participate in later stages of cortical processing (Brodmann's areas 1 and 2) have larger receptive fields and more specialized inputs than neurons in area 3b. The neuron illustrated from area 2 is directionally sensitive to motion toward the fingertips. Neurons in area 5 often have symmetric bilateral receptive fields at mirror image locations on the contralateral and ipsilateral hand. (Adapted from Gardner 1988, Iwamura et al. 1994.)

The receptive fields of cortical neurons are much larger than those of dorsal root ganglion neurons. For example, the receptive fields of sensory neurons innervating a finger cover tiny spots on the skin, while those of the cortical cells receiving these inputs are large areas covering an entire fingertip, or several adjacent fingers, or the palmar surface of the contralateral hand (Figure 23-3). The receptive field of a neuron in area 3b represents a composite of inputs from about 300-400 mechanoreceptive afferents. Receptive fields in higher cortical areas are even larger. In the posterior parietal cortex, receptive fields are often bilateral, located at symmetric positions on the contralateral and ipsilateral hands.

Cortical receptive fields encompass functional regions of skin that are activated simultaneously during motor activity. The size and position of cortical receptive fields on the skin are not fixed permanently but can be modified by experience or by injury to sensory nerves. Cortical receptive fields appear to be formed during development and maintained by simultaneous activation of the input pathways.

Although the receptive fields of cortical neurons cover a large area of skin, a cortical neuron is nevertheless able to discriminate fine detail because it responds best to excitation in the middle of its receptive field. As the stimulation site is moved toward the periphery of the field, responses become progressively weaker until eventually no spikes are recorded. Thus, a stimulus applied to the tip of the index finger strongly excites some neurons, while others fire weakly or not at all. If a more proximal spot on the finger is touched, many of the same cells are activated but in different proportions. Information

provided by the entire population of excited cells localizes a stimulus on the skin.

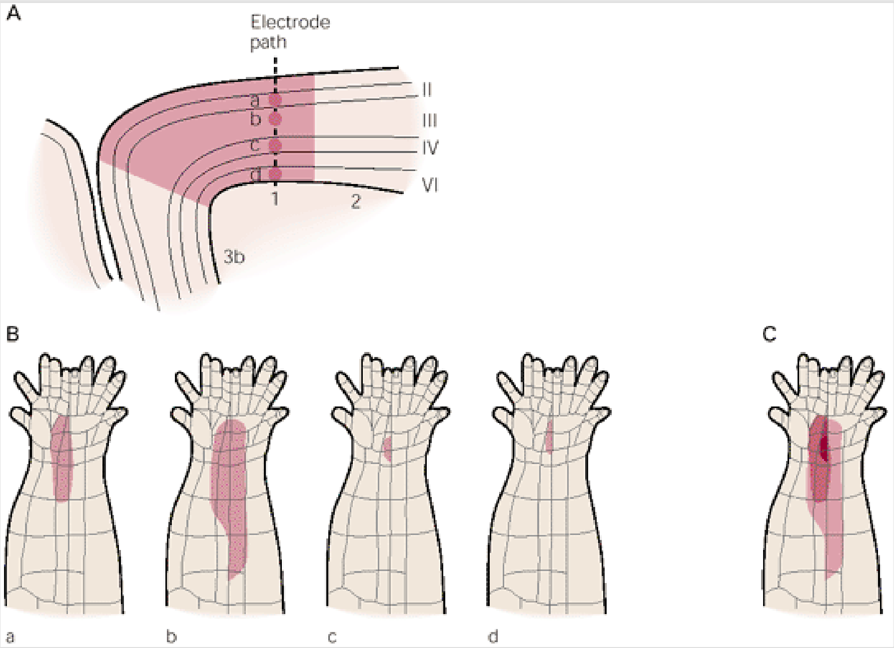

Figure 23-4 The receptive fields of cells in a column in Brodmann's area 1 share a common central location on the skin. The columns representing a given skin location are approximately 300-600 μm wide. (Adapted from Favorov and Whitsel 1988.)

A. Sagittal section through S-I cortex illustrating the recording sites of a group of neurons located in a single column. The most superficial neuron (**a**) is located in layer II, and the deepest neuron (**d**) is located in layer VI. Neuron **b** is located in layer III, and neuron **c** is situated in layer IV.

B. Receptive fields of the four neurons shown in A. The neurons in this column share receptive fields on the ulnar portion of the forearm, wrist, and hand. The dorsal and volar surfaces of the hand and arm have been juxtaposed to illustrate the continuity of receptive fields along the ulnar margin. The receptive fields are labeled according to depth in the cortex. Neuron **c** has the smallest receptive field, localized near the wrist; it is located in layer IV where the thalamic afferents terminate. Pyramidal neurons in layers II and III have larger receptive fields because their large basal dendritic fields extend into the neighboring columns.

C. Superimposition of the receptive fields illustrated in **B.** The darkest region in the center is shared by all receptive fields of the neurons in the column; this region is used to reconstruct the representation area of the column in the somatotopic map. The skin areas surrounding the central focus are shared by most, but not all, of the neurons in the column. The skin locations at the outer margins of the column's global receptive field are represented in only a few cells' receptive fields.

The Properties of Cortical Receptive Fields Are Due to Convergent and Divergent Connections in the Relay Nuclei

The increase in area of the receptive fields of cortical neurons reflects the anatomical circuitry within the relay nuclei. Relay nuclei, such as the dorsal column or thalamic nuclei, are composed of projection (or relay) neurons that send their axons to the next nucleus in the pathway and inhibitory interneurons that terminate upon relay neurons. Sensory inputs to the relay nucleus are characterized by extensive convergence and divergence. Each sensory afferent has a branched terminal that innervates several postsynaptic neurons, so that each projection neuron receives synaptic input from many sensory axons. This pattern of divergent presynaptic connections and convergent postsynaptic connections is repeated at each relay in the pathway.

Inputs to the Somatic Sensory Cortex Are Organized in Columns by Receptive Field and Modality

Although convergence of sensory afferents enlarges the receptive fields of projection neurons at successive relay nuclei, the topographic arrangement of the receptive fields is preserved. In a series of pioneering studies Mountcastle discovered that the cortex is organized into vertical columns or slabs, 300-600 μm wide, spanning all six layers from the cortical surface to the white matter. All of the neurons within a column receive inputs from the same local area of skin and respond to a single class of receptors. Although the receptive fields of the neurons comprising a column are not precisely congruent, they do share a common center, which is most clearly evident in layer IV (Figure 23-4). A column therefore provides an anatomical structure that preserves the properties of location and modality. Neurons lying within a column comprise an elementary functional module of the cortex (Figure 23-5). We shall see in later chapters that columnar organization is a basic organizational and structural principle of the cerebral cortex.

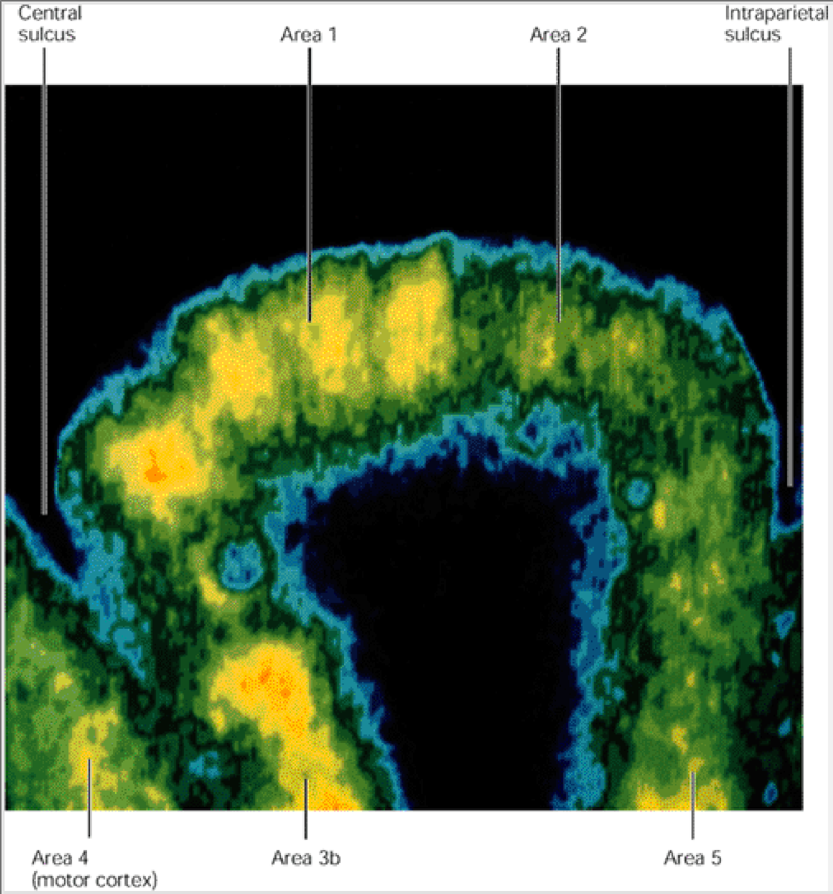

Figure 23-5 Columns of neurons in the primary somatic sensory cortex comprise the elementary functional modules of cortical processing of somatosensory information. This autoradiograph shows the pattern of ^{14}C 2-deoxyglucose (2-DG) labeling of neurons in a sagittal section through the hand area of the S-I cortex after 45 minutes of stroking the hand and wrist with a brush. Uptake of 2-DG in the brain is proportional to neuronal activity. Stimulation of the hand produces dense patches of labeled neurons in both area 3b and in area 1. Active neurons are found in vertical columns extending from layer II through layer V, with the strongest responses seen in layer IV (pale **red**). Columns are continuous in area 3b, but form distinct modules in area 1. Very little activity is seen in area 2, which receives input from deep receptors. (Photograph courtesy of S. Juliano, P. Hand, and B. Whitsel.)

The columnar organization of the cortex is a direct consequence of cortical circuitry. The pattern of intrinsic connections within the cerebral cortex is oriented vertically, perpendicular to the surface of the cortex (Figure 23-6). Thalamic afferents to the cortex terminate mainly on clusters of stellate cell neurons in layer IV. The axons of the stellate cells project vertically toward the surface of the cortex. Similarly, both the apical dendrites and axons of the pyramidal cells are oriented vertically, parallel to the stellate cell axons. The thalamocortical input is therefore relayed to a narrow vertical column of pyramidal cells whose apical dendrites are contacted by the stellate cell axons. This means that the same information is relayed up and down through the thickness of the cortex in columnar fashion.

In addition to sharing a common focal location on the skin, all of the neurons in a column usually respond to only one modality: touch, pressure, temperature, or pain. This is not surprising, as we have seen that the various somatosensory modalities are conveyed by anatomically separate pathways. The cells that make up these pathways have distinctive response properties inasmuch as each pathway conveys information from a different class of receptor. Sensory receptors and primary sensory neurons responsive to one submodality, such as pressure or vibration, are connected to clusters of cells in the dorsal column nuclei and thalamus that receive inputs only for that submodality. These relay neurons in turn project to modality-specific cells in the cortex.

Although each of the four areas of the primary somatic sensory cortex (3a, 3b, 1, and 2) receives input from all areas of the body surface, one modality tends to dominate in each area. In area 3a the dominant input is from proprioceptors signaling muscle stretch. Area 3b receives input primarily from cutaneous mechanoreceptors. Here the inputs from a discrete site on the skin are divided into two sets of columns, one each for inputs from rapidly adapting and slowly adapting receptors (Figure 23-7). In area 1 rapidly adapting cutaneous receptors predominate, and the receptive fields of these cells are considerably larger than those of cells in area 3b, often covering several adjacent fingers. In area 2 and higher cortical areas the modality segregation is much weaker. Columns of neurons in area 2 receive convergent input from slowly and rapidly adapting cutaneous receptors or from cutaneous receptors and proprioceptors in the underlying muscles and joints. Thus, the receptive fields and response properties of neurons in areas 1 and 2 represent convergent input from regions of the hand and fingers that are represented separately in areas 3a and 3b.

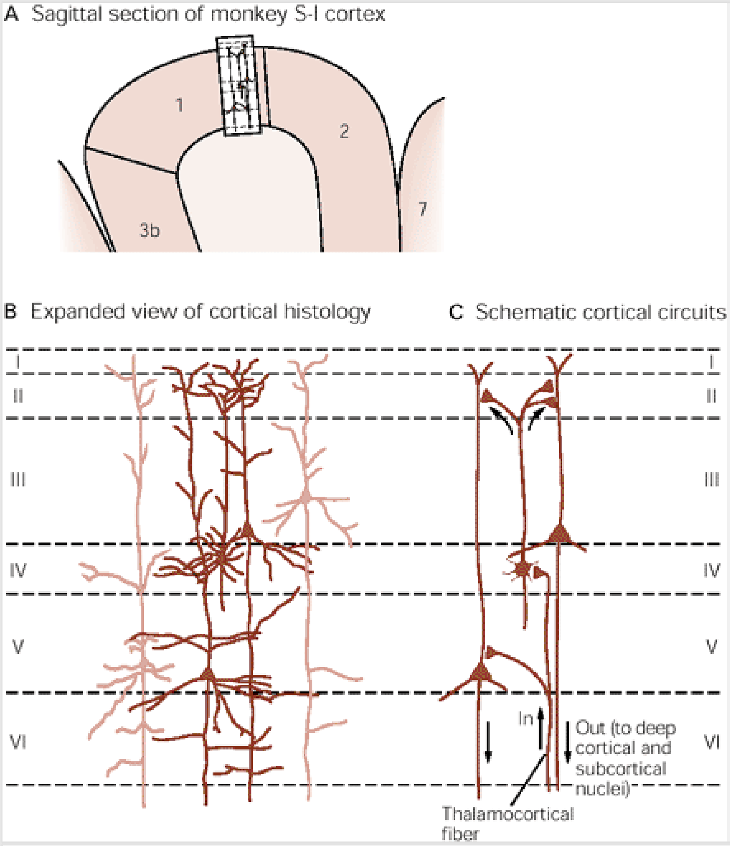

Figure 23-6 The columnar organization of cortical neurons is a consequence of the pattern of connections between neurons in different layers of cortex. (Modified from Jones 1981.)

A. The dendrites and axons of most cortical neurons extend vertically from the surface to white matter, forming the anatomical basis of the columnar structure of the cortex.

B. Morphology of the relay neurons of layers III-V. Stellate neurons (small spiny cell) are located in layer IV. These neurons are the principal target of thalamocortical axons. The axons of the stellate neurons project vertically toward the surface of the cortex, terminating on the apical dendrites of a narrow beam of pyramidal cells whose somas lie in layers II, III, and V above or below them. Stellate cell axons also terminate on the basal branches of pyramidal cells in layers II and III. The axons of pyramidal neurons project vertically to deeper layers of the cortex and to other cortical or subcortical regions; they also send horizontal branches within the same cortical region to activate columns of neurons sharing similar physiological properties.

C. Schematic diagram of intracortical excitatory circuits. The principal connections are made vertically between neurons in different layers.

How does the layering of the cortex contribute to the functional organization of the cortex? As described in Chapter 19, each layer of cells has connections with different parts of the brain: Layer IV receives input from the thalamus; layer VI projects back to the thalamus; layers II and III project to other cortical regions; and layer V projects to subcortical structures. As a result, the information on stimulus location and modality processed in each column is conveyed to different regions of the brain.

The Body Surface Is Represented in the Brain by the Somatotopic Arrangement of Sensory Inputs

The columns of neurons in the somatic sensory cortex are arranged such that there is a complete topographic representation of the body in each of the four areas (3a, 3b, 1, and 2). The cortical map of the body corresponds to the spinal dermatomes defined by the afferent fibers entering the spinal cord at successively rostral levels (see Box 22-2). Sacral segments are represented medially, lumbar and thoracic segments centrally, cervical segments more laterally, and the trigeminal representation at the most lateral portion of the S-I cortex (Figure 23-8). The maps in adjacent cytoarchitectonic areas are rough mirror images of the distal-proximal or dorsal-ventral axes of each dermatome.

Topographic maps of the human parietal cortex have been constructed from measurements of sensory-evoked potentials or by using electrical stimulation of the cortex. These techniques, together with more modern noninvasive diagnostic tools such as magnetoencephalography (MEG), functional magnetic resonance imaging (fMRI), and positron emission tomography

(PET scan), allow neurologists to image the somatotopic functioning of the cortex in individual patients. While these imaging methods are less precise than the microelectrode maps made in animals, they are useful diagnostic tools in clinical neurology.

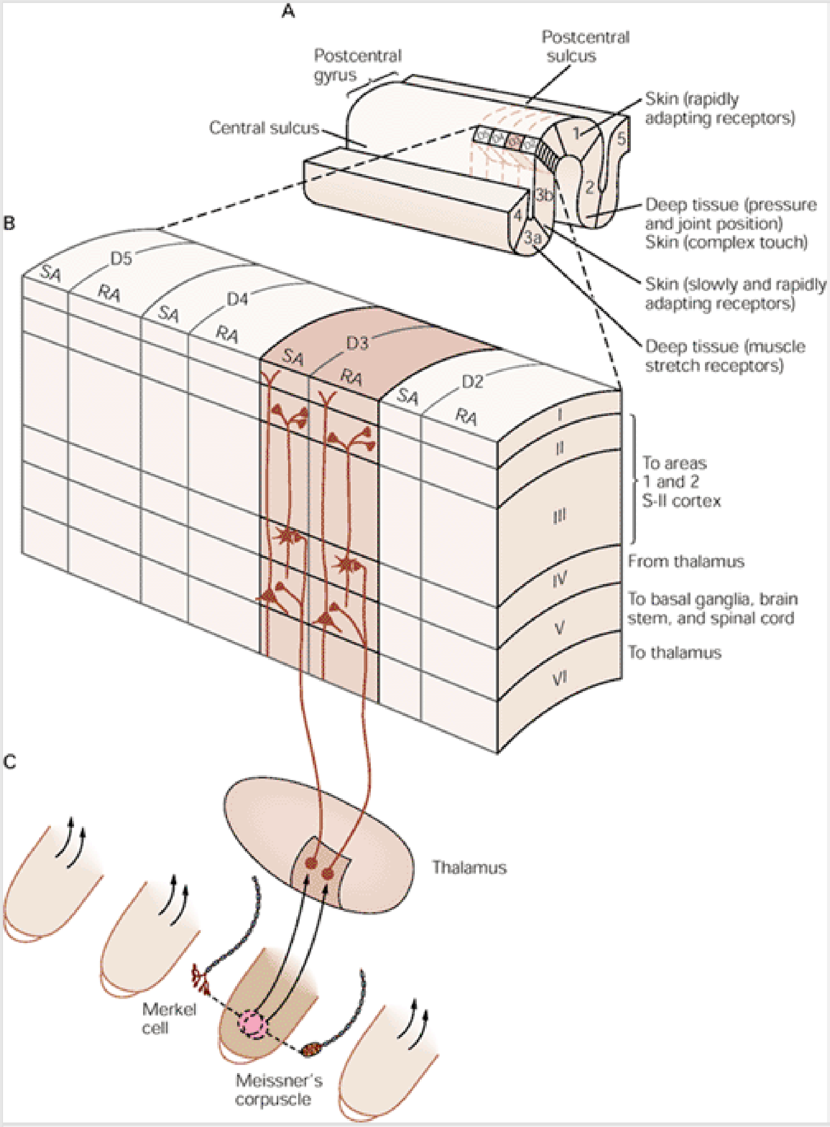

Figure 23-7 Each region of the somatic sensory cortex receives inputs from primarily one type of receptor.

A. In each of the four regions of the somatic sensory cortex—Brodmann's areas 3a, 3b, 1, and 2—inputs from one type of receptor in specific parts of the body are organized in columns of neurons that run from the surface to the white matter. (Adapted from Kaas et al. 1981.)

B. Detail of the columnar organization of inputs from digits 2, 3, 4, and 5 in a portion of Brodmann's area 3b. Alternating columns of neurons receive inputs from rapidly adapting (**RA**) and slowly adapting (**SA**) receptors in the superficial layers of skin. (Adapted from Sur et al. 1984.)

C. Overlapping receptive fields from RA and SA receptors project to distinct columns of neurons in area 3b.

Spatial Resolution in the Cortex Is Correlated With the Innervation Density of the Skin

The somatotopic arrangement of somatosensory inputs in the human cortex is called a *homunculus;* it corresponds closely to the somatotopic maps of cortical columns determined by single neuron recordings in monkeys. However, the internal representation of the body within the homunculus does not duplicate the spatial topography of the skin exactly. Rather, the image of the body in the brain exaggerates certain body regions, particularly the hand, foot, and mouth and compresses more proximal body parts.

Each part of the body is represented in the brain in proportion to its relative importance to sensory perception. The map represents the *innervation density* of the skin rather than its total surface area. In humans a large number of cortical columns receive input from the hands, particularly from the fingers. About 100 times as much cortical tissue is devoted to a square centimeter of skin on the fingers as to a square centimeter of skin on the abdomen. Similarly, large numbers of cortical neurons receive input from the foot and face. More than any other part of the body, the hands, face, and feet are important sensors of the properties of objects and thus have the highest density of touch receptors. The proximal portions of the limbs and trunk are much less densely innervated; correspondingly, fewer cortical neurons receive inputs from these regions.

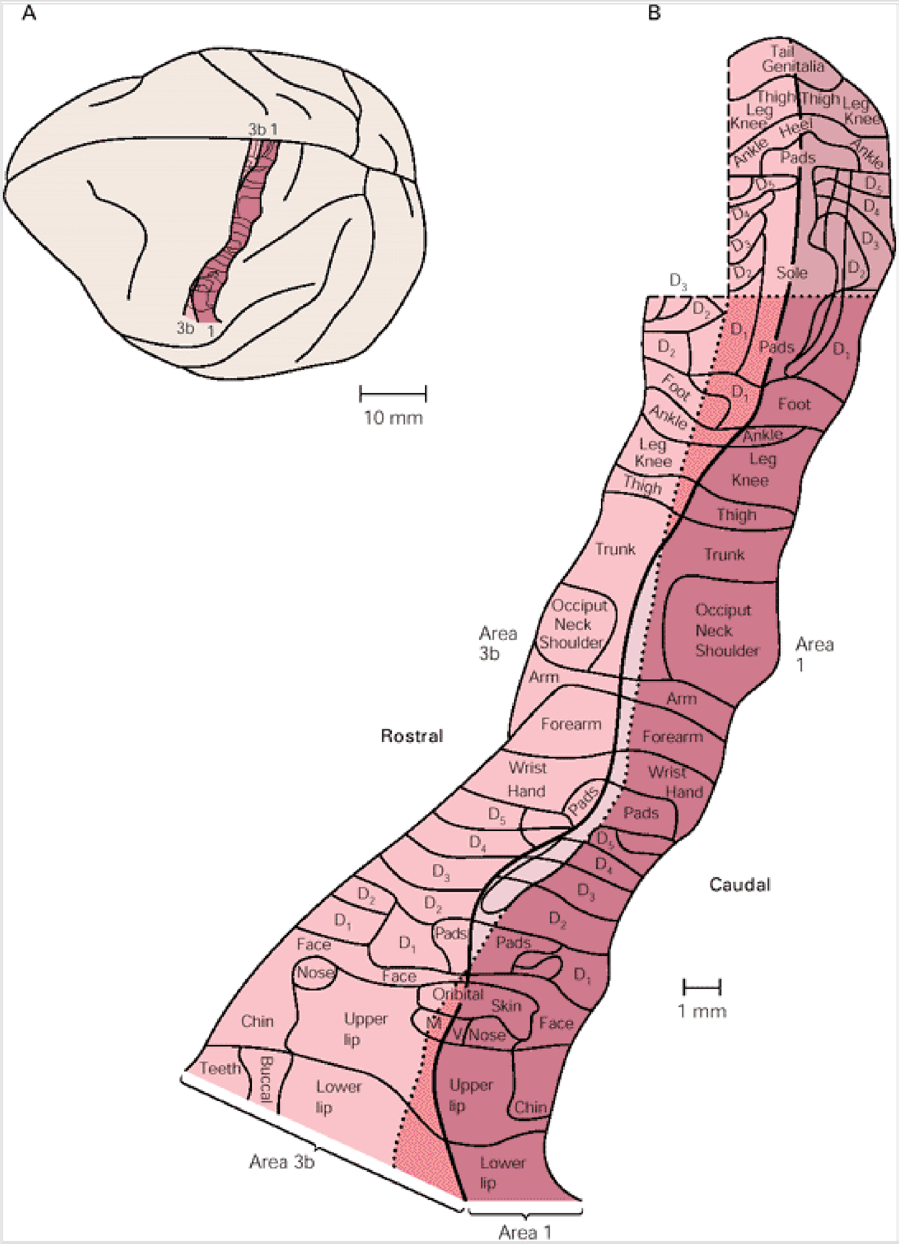

Figure 23-8 Each of the four regions of the primary somatic sensory cortex contains a complete map of the body surface. (Adapted from Nelson et al. 1980.)

A. Location of the primary somatosensory cortex in the brain of the macaque monkey. The body surface is mapped to the surface of the cortex as rostrocaudal strips arranged in the order of the spinal dermatomes.

B. Enlarged view of the body maps in areas 3b and 1 of the macaque primary somatic sensory cortex. The cortex is unfolded in this diagram along the central sulcus (**dotted line**, which parallels the border between 3b and 1), and at the medial wall of the hemisphere (**dashed line** at the edge of the foot representation). The sacral and lower lumbar segments are represented on the medial wall of the hemisphere. More rostral segments are mapped more laterally; the most lateral portions of the cortex contain the representation of the neck, face, mouth, and tongue. The largest portion of the cortical map is devoted to the glabrous surface of the hand and foot; each finger has its own separate representation along the medial-to-lateral axes of the cortex. The maps in areas 3b and 1 form mirror images of the distal-proximal or dorsal-ventral axes of each dermatome. (**M** = mandible or lower jaw, **V** = maxilla or upper jaw.)

In lower species the hand representation in the brain is smaller than in primates, as these animals use other body parts to probe the environment. For example, rodents use their whiskers for tactile exploration rather than their hands. The representation of the whisker fields in the cortex is larger than that of the paw, forming distinct morphological structures called barrels (Box 23-2).

An important consequence of the magnification of the hand representation in the cortex is that the size of individual peripheral receptive fields on the hand cover a much smaller area of skin than receptive fields on the arm, which are smaller than receptive fields on the trunk. For example, receptive fields in the hand region may cover the tips of one or more fingers (Figure 23-3)

whereas receptive fields on the forearm may span the entire ulnar surface (Figure 23-4). The large receptive fields for proximal portions of the body (due to the low innervation density) grow proportionally greater at each successive relay.

Box 23-2 The Cortical Representation of Whiskers in Rodents Is Precisely the Same From Animal to Animal

In rodents the whiskers are the principal tactile receptors. Thus the region surrounding the mouth is more extensively represented in the cortex than are the paws. Each whisker is innervated by a separate vibrissal nerve containing about 100 myelinated fibers, which are activated by movements of the whiskers in specific directions.

The cortical representation of the whiskers has a unique structure. The neurons of layer IV are arranged in discrete functional units called barrels, so-called because when the cortex is cut tangentially, parallel to the cortical surface, the cell bodies of layer IV appear to form barrel-shaped arrays around a neuropil of axons and dendrites (Figure 23-9). Each barrel processes tactile input principally from a single whisker. The number of barrels is the same as the number of vibrissae on the contralateral side of the face, and the barrels are arranged in a pattern that corresponds to the topography of the whiskers.

The fact that each barrel represents a morphologically distinct group of tactile receptors makes it useful for studying plasticity of the cortical maps. Selective removal of vibrissae or vibrissal follicles, or distinctive patterns of stimulation of specific vibrissae, result in alterations in neuronal firing patterns in both the test and adjacent barrel fields. There is also a dynamic interaction between adjacent whiskers in the supragranular and infragranular layers of the cortex.

The unique morphology of the rodent barrel fields allows experimenters to correlate specific cortical locations with function without having to perform direct electrophysiological recordings. Thus measurements can be made of cytochemical, morphological, and metabolic changes related to altered sensory input.

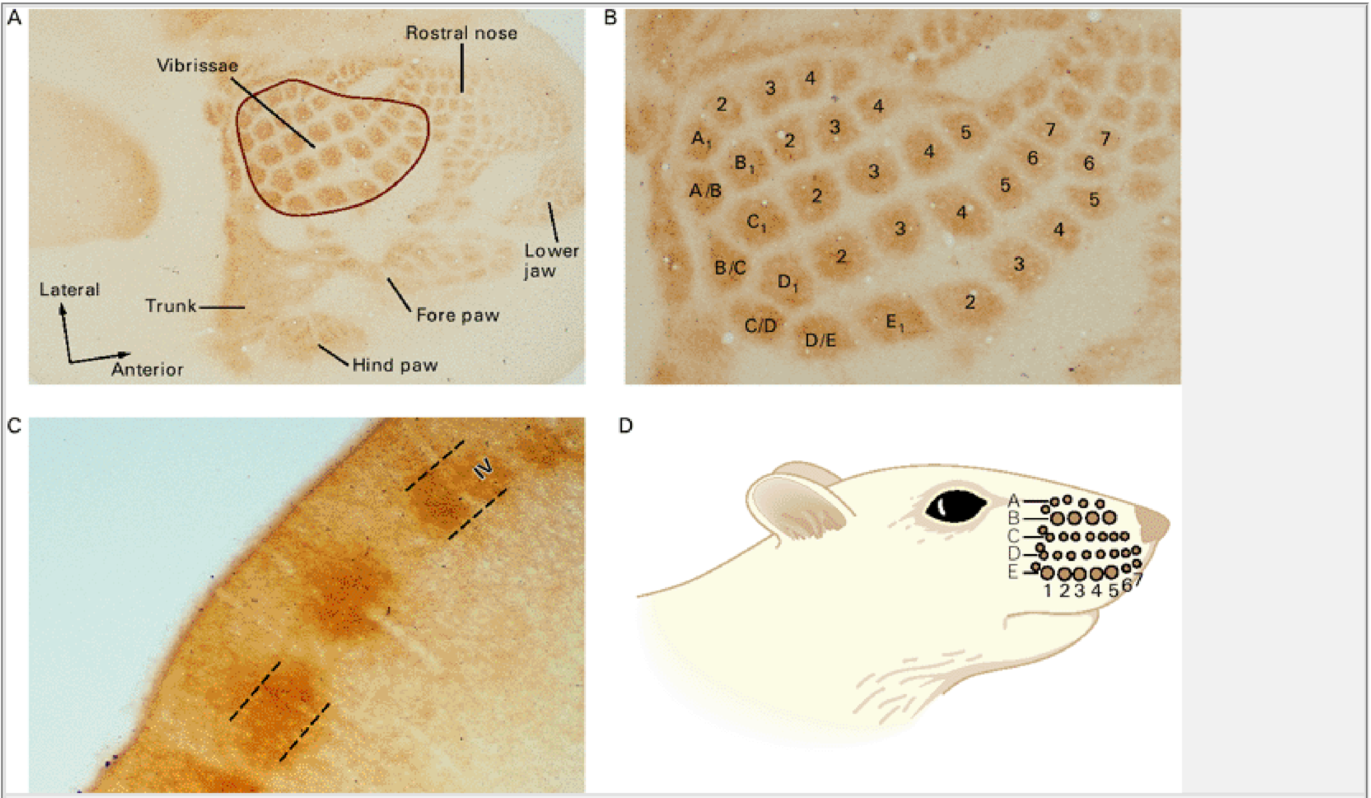

Figure 23-9 The representation of whiskers in the somatosensory cortex of the rat. (Adapted from Bennett-Clarke et al. 1997).

A. Photomicrograph of a horizontal section through layer IV of the somatosensory cortex of a juvenile rat that has been stained for serotonin. The dark immunoreactive patches correspond to the cortical representations of specific parts of the body. The largest part of the cortical map is devoted to the face representation (whiskers, nose, and lower jaw).

B. Enlarged view of the whisker representation. Neurons that receive projections from the whisker fields are arranged in discrete circular units called *barrels.* Each barrel is most responsive to a single whisker.

C. Coronal section through the rat somatosensory cortex. The barrels form dense patches localized to layer IV of the cortex.

D. The topographic arrangement of the barrels in the cortex corresponds to the spatial arrangement of the whiskers in discrete rows and columns on the face.

Cortical Receptive Fields Are Altered by Use of the Hand

An important feature of somatotopic maps is that they are not fixed but can be altered by experience. While the general medial-to-lateral and rostral-to-caudal arrangement of cortical columns is the same in all individuals, the details of the map vary between individuals. A tennis champion will develop a larger proportion of cortical neurons devoted to sensory inputs from the arm than a pianist, who needs to differentiate inputs from individual fingers. As we saw in Chapter 20, the configuration of the map in individual animals can be altered experimentally by fusing adjacent digits or by increased stimulation of a particular finger.

Inhibitory Networks Sharpen Spatial Resolution by Restricting the Spread of Excitation

For somatotopic mapping of cortical function it is enough to know which neurons respond to a stimulus at a particular site on the body. For this purpose the receptive fields of individual neurons are identified by touching the skin with a small probe. A more complex receptive field structure emerges when the skin is touched at two or more points simultaneously. Stimulation of regions of skin surrounding the excitatory region of the receptive field of a cortical neuron may reduce the responsiveness of the neuron to an excitatory stimulus because afferent inputs surrounding the excitatory region are inhibitory. These regions of the receptive field of a cortical neuron are called the *inhibitory surround.* This spatial distribution of excitatory and inhibitory activity serves to sharpen the peak of activity within the brain.

The inhibitory responses observed in the cortex are generated by interneurons in the dorsal column nuclei, the ventral posterior lateral nucleus of the thalamus, and the cortex itself. Inhibitory interneurons in relay nuclei form circuits that tend to limit the spatial spread of excitation through divergent connections (see Figure 21-12). Peripheral receptors in the somatic sensory system are not themselves inhibited (Figure 23-10A). At the first relay point in the somatic sensory system the afferent fibers inhibit the activity of cells in the dorsal column nuclei that surround the cells they excite (Figure 23-10B). Inhibition generated by activity of the most intensely activated receptors reduces the output of projection neurons that are less strongly excited. It permits a winner-take-all strategy, which ensures that the strongest of two or more competing responses is expressed. In addition, the most active output neurons use recurrent collateral fibers to limit the activity of adjacent neurons. This lateral inhibition further sharpens the contrast between the active cells and their neighbors (Figure 23-10C).

Lateral Inhibition Can Aid in Two-Point Discrimination

Inhibitory interactions are particularly important for fine tactile discrimination such as reading Braille. We can understand how this is accomplished by considering the simplest example of spatial discrimination: the ability to distinguish two closely placed point stimuli. We are able to perceive two points rather than one because two distinct populations of neurons are activated. Stimuli applied to two widely spaced positions on the skin set up excitatory gradients of activity in two cell populations at every relay nucleus.

If the two stimuli are brought close together, the activity in the two populations tends to overlap, and the distinction between the two peaks might become blurred. However, the inhibition produced by each stimulus also summates in the zone of overlap. As a result of this more effective inhibition, the peaks of activity in the two responding populations become sharpened, thereby separating the two active populations spatially (Figure 23-11B). This sculpturing role of the inhibition thus preserves the spatial distinction between the two stimuli.

Spatial Detail Is Accurately Represented in the Cortex

How far does this fidelity of the sensory stimulus extend? Studies of cortical neurons using Braille dot patterns, or embossed letters touched by the fingers, indicate that the signal transmitted to the cortex faithfully reproduces the stimulus features encoded by the receptors in the skin. As we saw in Chapter 22, both Merkel disk receptors and Meissner's corpuscles transmit a faithful neural image of such patterns (see Figure 22-8). These sharp sensory images are preserved up to the first stage of cortical processing in area 3b of the somatic sensory cortex. Neurons in area 3b fire bursts as each line segment of a letter is scanned across the receptive field and together faithfully signal its shape (Figure 23-12).

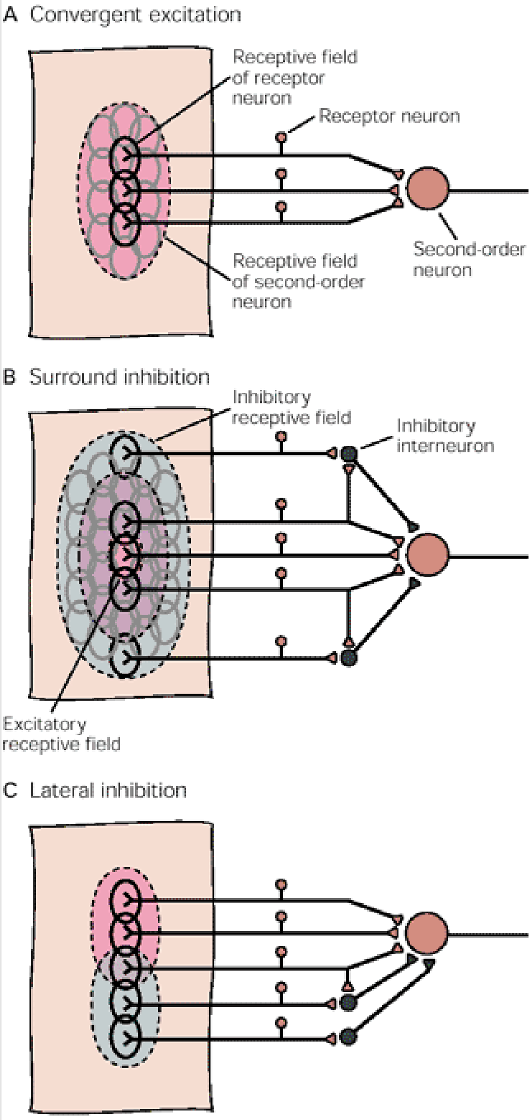

Figure 23-10 The receptive field of a higher-order neuron in the dorsal column nuclei has a characteristic pattern of excitation and inhibition that increases spatial resolution.

A. Many peripheral receptors converge onto a single second-order sensory neuron in the dorsal column nuclei. As a consequence, the excitatory receptive field of the central neuron is made up of the receptive fields of all the presynaptic cells.

B. The receptive field of a neuron in the dorsal column nuclei and in the ventral posterior nuclei of the thalamus typically has a central excitatory receptive field surrounded or flanked by an inhibitory region. The addition of inhibitory interneurons (**gray**) narrows the discharge zone. Feed-forward inhibition sharpens the representation of a punctate stimulus by limiting the spread of excitation through convergent neural networks. On either side of the excitatory region the discharge rate is driven below the resting level by inhibition.

C. The asymmetric distribution of inhibitory interneurons produces lateral inhibition. In this schematic network, stimulation in the upper portion of the receptive field produces strong excitation of the relay neuron. Stimulation of the lower portion of the receptive field inhibits firing because the interneurons produce feed-forward inhibition. Stimulation in the zone of overlap of excitation and inhibition reduces the responsiveness of the relay neuron to the stimulus. Lateral inhibition is particularly important for feature detection.

The cortical representation of each letter is further sharpened by a pause in firing as the moving edges exit the excitatory receptive field and enter its inhibitory surround. The contrast between the spike bursts and subsequent silent intervals permits the letters to stand out from the noisy background activity.

Neurons in area 3b are able to signal the precise shape of the letters moved over the finger because their receptive fields are smaller than the letters. The individual line segments that characterize each letter are viewed one at a time as they cross the neuron's receptive field. The spatial arrangement of stimulated and unstimulated regions of skin is represented in the cortex in columns of active and silent neurons.

In later stages of cortical processing, however, the responses are more abstract. For example, activity in neurons in area 1 does not reproduce the shape of the letters but instead signals specific features common to groups of letters, such as the presence of vertical or horizontal line segments. Since certain cortical neurons represent letter stimuli faithfully and neurons at a later stage do not, it should be possible to determine the intermediate step by which the initial representation becomes abstracted.

Neurons in Higher Cortical Areas Have Complex Feature-Detecting Properties

To produce a coherent sensation of an object the nervous system must integrate information from a large number and variety of receptors as well as the modalities of touch, proprioception, and temperature. How is this integration accomplished? At least four factors are involved:

(1) The size of the receptive field becomes larger at each level of processing, so that eventually the entire object rather than a single edge is sensed by a neuron. (2) The profile of activity in the active population of neurons changes through the action of inhibitory networks. (3) At successive levels of sensory processing in the cortex individual neurons respond to more complex inputs. (4) The submodalities converge on individual neurons in association cortical areas.

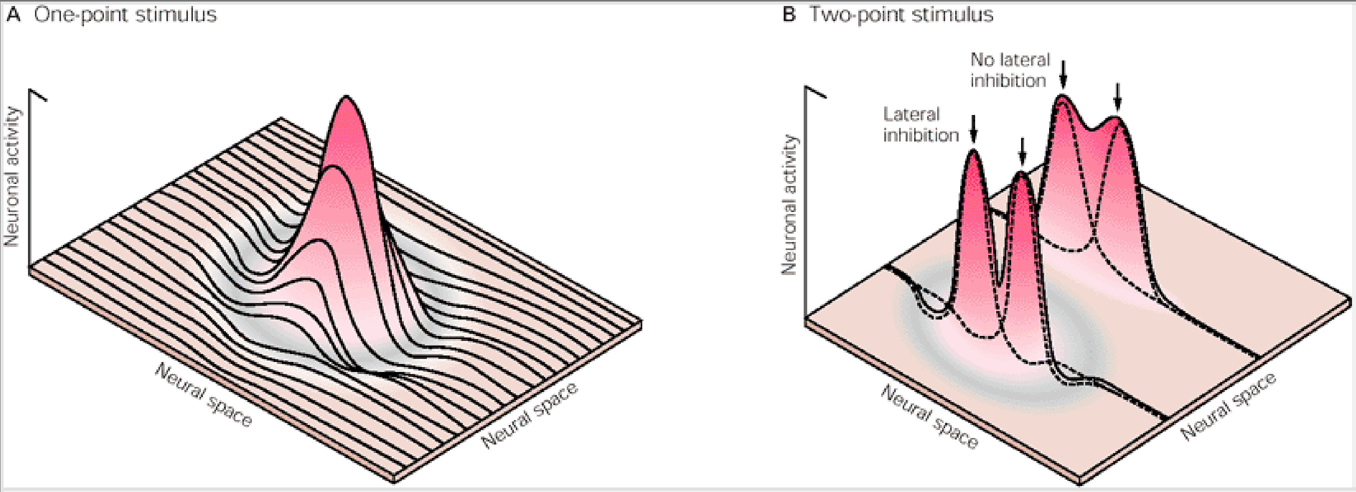

Figure 23-11 Two-point discrimination depends on separation of the signals from each source. (Adapted from Mountcastle and Darian-Smith 1968.)

A. Stimulation of a single point on the skin activates one population of cells in the cortex. Maximal activity is in the center of the population. These neurons are surrounded by a band of neurons whose firing rates are depressed below normal tonic levels by the actions of interneurons that form lateral inhibitory networks.

B. Stimulation of two adjacent points activates two populations of receptors, each with a peak of activity (**dotted lines**). Normally the convergence of the two active populations in the central nervous system would result in a single large group of undistinguished inputs (all excitatory). However, lateral inhibitory networks suppress excitation of the neurons between the points, sharpening the central focus and preserving the spatial clarity of the original stimulus (**solid line**).

We have seen that neurons in area 3b provide a detailed representation of the properties of an individual object such as an embossed letter. They respond to a particular form and amount of energy at a specific location in space and together reproduce its shape. As information flows from the initial stages of cortical processing toward higher-order cortical areas, specific combinations of stimuli or stimulus patterns are needed to excite individual neurons. Neurons in areas 1 and 2 are concerned with more abstract properties of tactile stimuli than simply the site of stimulation. These cells ignore many of the myriad details of a stimulus and instead detect regularities amid the confusion. Their firing patterns signal features such as the orientation of edges, the direction of motion across the skin, the surface curvature of objects, or the spatial arrangement of repeated patterns that form textures. Feature detection is a basic principle of cortical processing that allows the brain to find patterns common to stimuli of a particular class.

Experiments using alert animals have revealed a variety of feature-detection neurons in the cortex. Some cortical neurons in area 2 respond preferentially to specific combinations of simultaneously stimulated receptors. Such *orientation-sensitive* neurons sense the angle of edges contacted by the skin (Figure 23-13A). This information is extremely important in reconstructing the shapes of objects. Other cells are *direction sensitive.* They respond vigorously when the skin is stroked in a preferred direction and are unresponsive when the same region of skin is stroked in the opposite direction (Figure 23-13B). Some neurons in area 2 are even more specialized, sensing the spacing or alignment of ridges in a grating when the hand is rubbed over its surface.

The ability of a cortical neuron to detect the orientation of an edge or direction of motion results from the spatial arrangement of its input neurons (Figure 23-14). The excitatory receptive fields of the input neurons are aligned along the preferred axis and produce a strong excitatory response when the stimulus orientation matches that of the receptive fields. In addition, the inhibitory receptive fields are placed to one side of the excitatory fields, suppressing inputs with the "wrong" orientation or approaching from the "wrong" direction.

The convergent projections from areas 3a and 3b onto areas 1 and 2 permit neurons in area 2 to respond to other complex features, such as the shape of objects. Whereas neurons in 3b and 1 respond only to touch, and neurons in areas 3a respond only to position sense, certain neurons in area 2 have both inputs. These neurons respond best when an object of a specific shape is grasped by the hand. Some of these cells respond more vigorously to round objects than to objects with distinct edges, while others are activated selectively by rectangular objects. As we shall see below, this information is thought to provide the necessary tactile clues for skilled movement of the fingers.

Figure 23-12 The spatial characteristics of embossed letters are accurately represented by neurons in area 3b of the primary somatic sensory cortex but not in area 1. (Adapted from Phillips et al. 1988.)

A. Spatial event plots (see Figure 22-8A) for the principal tactile afferent fibers of the hand: the slowly adapting (**SA**) Merkel disk receptors and rapidly adapting (**RA**) Meissner's corpuscles. Both SA and RA receptors accurately encode the shape of each letter.

B. Spatial event plots for neurons in areas 3b and 1 of an awake monkey. In area 3b slowly adapting (SA) receptors continue to signal the shape of the letters, but rapidly adapting (RA) neurons are more sensitive to the vertical leading edges. In area 1 SA neurons sense particular features of the letter (in this case the vertical but not horizontal components) while the RA neuron illustrated failed to represent form.

Detection of the direction of movement and of other features of the stimulus is not apparent in neurons in the dorsal column nuclei, in the thalamus, or even in areas 3a and 3b. Feature-detecting neurons sensitive to stimulus direction and orientation are first found in area 1 and are represented more extensively in area 2, the areas concerned with stereognosis (the three-dimensional perception of objects) and with discriminating the direction of movement of objects on the skin. Thus, these complex stimulus properties arise not from thalamic input but from cortical processing of more elementary inputs.

In the posterior parietal cortex (areas 5 and 7) the somatosensory responses are even more complex and are often integrated with other sensory modalities. These association cortical areas play an important role in the sensory guidance of movement and are consequently organized functionally rather than topographically (Chapter 19). Many neurons in area 5 receive inputs from several adjacent joints or groups of muscles that provide information about the posture of the entire hand or arm, particularly when monkeys reach out their hands to grasp objects. Other cells integrate tactile and postural information and are most vigorously activated when the monkey preshapes the hand to grasp and acquire objects, or plucks food morsels from a small container.

Neurons in area 7 of the posterior parietal cortex integrate tactile and visual stimuli that overlap in space and play an important role in eye-hand coordination. They respond more vigorously when the monkey is able to observe its hand while manipulating objects of interest than when simply looking at the object or handling it in the dark. Such neurons are used to monitor visually guided hand movements rather than to convey detailed sensory information concerning the exact position or intensity of touch.

Stimulus Features Are Processed in Parallel by Distinct Areas of Cortex

We have seen that specific stimulus features are represented in discrete somatosensory cortical areas. Neurons

in area 3b with small receptive fields sense which finger is contacted and indeed which individual phalanx touches the object. Neurons in area 1 with multi-finger receptive fields sense the object size; they fire at higher rates if several fingers are touched and at lower rates if only a small portion of the receptive field is contacted. Neurons in area 2 sense even more complex features, such as the direction of motion across the hand, the curvature of surfaces, the orientation of edges, or the spacing of ridges on textured surfaces. Neurons in area 5 integrate tactile inputs from the skin with proprioceptive postural information from the fingers to encode the shape of objects grasped in the hand. Neurons in the posterior parietal cortex integrate the tactile and pro-prioceptive information with visual properties of the objects touched.

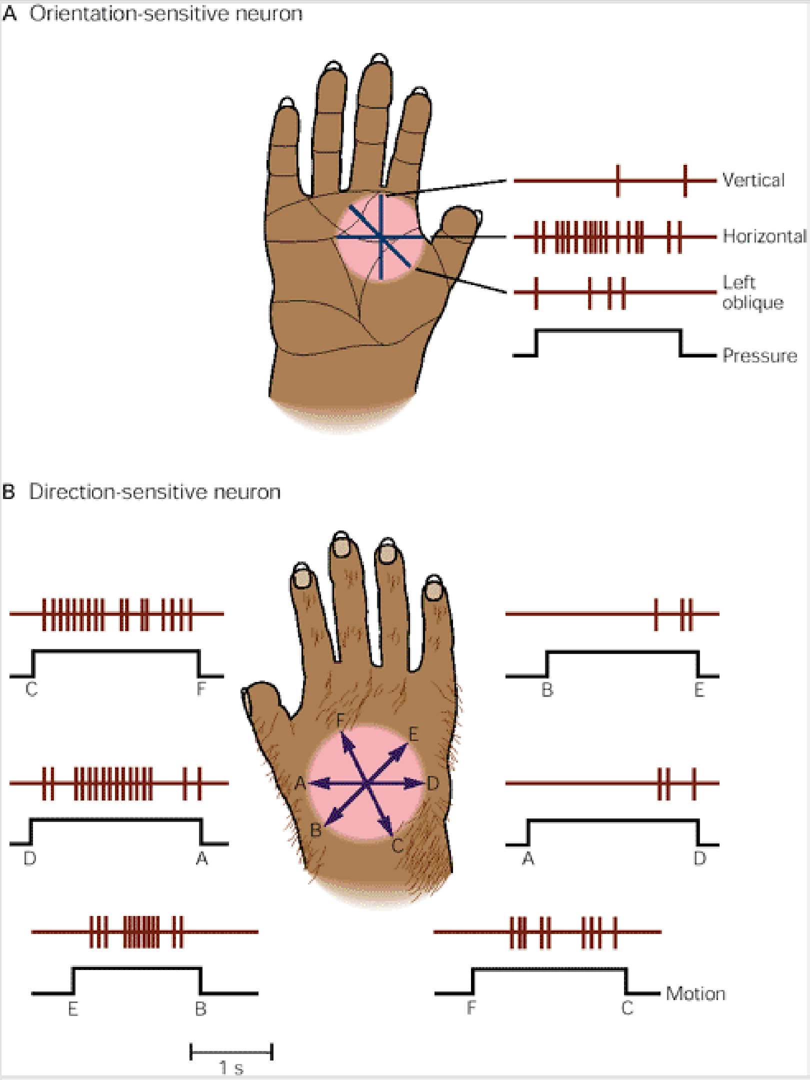

Figure 23-13 Feature-detection neurons in area 2 of the primary somatic sensory cortex respond to highly specific features of a stimulus. The examples shown here are from a macaque monkey.

A. This orientation-sensitive neuron distinguishes horizontal and vertical edges pressed on the palm. The neuron responds vigorously when the edge is oriented horizontally but is nearly silent when the edge is oriented vertically. Responses to the oblique orientation are weaker than those to the horizontal position. (Adapted from Hyvärinen and Poranen 1978.)

B. This direction-sensitive neuron responds most vigorously to movement across the hand toward the thumb and index finger. The neuron displays its strongest responses to motion in the radial direction (D to A and E to B); the weakest responses occur in the ulnar direction (A to D and B to E). Responses to distal movements toward the fingers (C to F) are more vigorous than responses to proximal movements toward the wrist (F to C). The trace below each cell record shows the duration of motion and the start and end points of the path. (Adapted from Costanzo and Gardner 1980.)

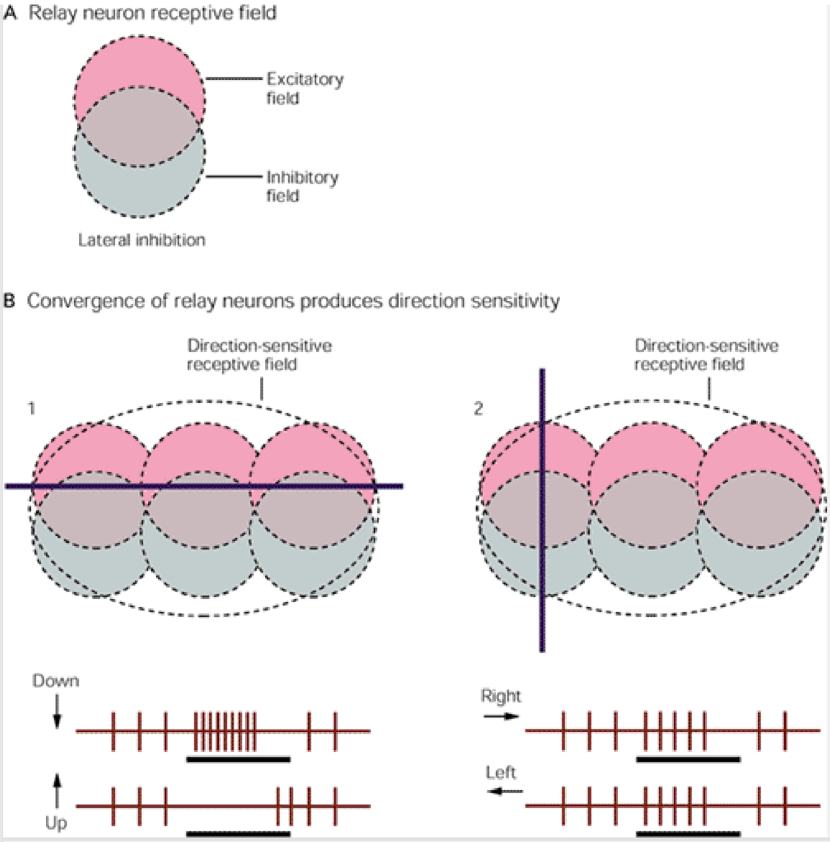

Figure 23-14 The spatial arrangement of presynaptic inputs to a cortical neuron determined which specific features of a stimulus will activate the neuron.

A. Stimuli moving across the receptive field of a relay neuron receiving lateral inhibition (see Figure 23-10) are more effective when the excitatory field is stimulated first because the inhibitory responses are longer in duration than the excitatory responses. Stimuli starting from the excitatory field produce a burst of action potentials followed by inhibition as the stimulus moves into the inhibitory field. Motion in the opposite direction is less effective because the long-lasting inhibitory postsynaptic potential evoked from the inhibitory field decreases the ability of the cell to respond when the stimulus moves into the excitatory field.

B. Convergence of three relay neurons with the same arrangement of excitatory and inhibitory fields confers direction sensitivity on a cortical neuron. In this example the preferred stimulus is a horizontal bar moving downward. **1.** Motion of a horizontal bar across the cortical receptive field (**solid line** below the spike trace). Downward motion of the bar produces a strong excitatory response because it crosses the excitatory fields of all three relay neurons simultaneously. Upward motion of the bar strongly inhibits firing because it enters all three inhibitory fields first. The neuron responds poorly to upward motion through the excitatory field because the initial inhibition outlasts the stimulus. **2.** Motion of a vertical bar across the cortical receptive field evokes a weak response because it crosses excitatory and inhibitory fields of the relay neurons simultaneously. Motion to the left and right are not distinguished in this example.

The somatosensory information necessary for stereognosis is processed in parallel in these areas because palpation involves repetitive touching of the object for several seconds. Such information is not simply relayed from point to point in the brain, as are the somatosensory evoked potentials after a brief shock to the nerve. Instead, tactile sensory information transmitted to higher cortical areas must be compared with more recent information being processed at the early stages. Thus, the activity that occurs simultaneously in different cortical areas is produced by events that happen at different moments in time. Responses in areas 3a and 3b occur 20 ms after touch or movement and therefore reflect stimuli in the immediate past. The more posterior cortical areas receive sensory information at longer latencies, processing stimuli presented 30-100 ms earlier.

How does the brain put together all of these features to form a coherent percept of an object? The firing patterns of neurons in separate cortical areas interact in ways we do not fully understand. The problem of binding together activity in different regions of the cerebral cortex has been studied more extensively for vision than for touch. Those studies of the visual system indicate that the brain may bind together the various stimulus features by synchronizing firing in different cortical areas.

The Behavioral Relevance of a Tactile Stimulus Modifies Cortical Responses

Selective attention can modify firing patterns at the higher stages of cortical processing. Although neurons in S-II are activated by embossed letters scanned across their receptive fields, they do not signal the spatial properties of the letters as do neurons in area 3b. Instead, neuronal responses in S-II depend on behavioral context or motivational state. For example, the firing rates can be altered by varying the letters that are reinforced with rewards or by distracting the monkey with an unrelated visual or auditory discrimination task. These same changes in circumstance have little effect on the spatial information conveyed by neurons in S-I.

The S-II cortex provides the gateway to the temporal lobe via the insular cortex. We shall learn in a later chapter that regions of the medial temporal lobe, particularly the hippocampus, are vital to the formation of memories. We do not store in memory every scintilla of tactile information that enters the nervous system, only information that has some behavioral significance. The demonstration that the firing patterns of S-II neurons are modified by selective attention suggests that S-II serves as a decision point for determining whether a particular bit of tactile information is remembered.

Lesions in Somatosensory Areas of the Brain Produce Specific Sensory Deficits

The earliest information about the function of the somatic sensory system came from the analysis of disease states and traumatic injuries of the spinal cord. For example, one of the late consequences of syphilitic infection in the nervous system is a syndrome called *tabes dorsalis*, which destroys the large-diameter neurons in the dorsal root ganglia, causing degeneration of myelinated afferent fibers in the dorsal columns. Patients who have this degeneration as a result of tabes dorsalis have severe deficits in touch and position sense but often little loss of temperature perception and of nociception.

Additional information about the somatic afferent system has come from studies of the behavioral defects produced by transection of the dorsal columns of the spinal cord in experimental animals or by trauma in humans. Injury to the afferent somatosensory pathways in the dorsal columns results in a chronic deficit in certain tactile discriminations, such as detecting the direction of movement across the skin, the frequency of vibration, the relative position of two cutaneous stimuli, and two-point discrimination. The deficit is ipsilateral to the lesion and occurs at levels below the lesion. Interestingly, some simple spatial discriminations, such as differentiating the size of probes pressed on the skin, can be recovered after extensive retraining and rehabilitative therapy. However, perception of stimuli with complex spatio-temporal patterns, such as distinguishing letters drawn on the skin (*graphesthesia*), is permanently impaired.

In addition to sensory deficits, lesions of the dorsal columns distort natural hand movements. For example, macaque monkeys with a lesion of the cuneate fascicle show major deficits in the control of fine finger movements during grooming, scratching, and manipulation of objects. A similar but reversible deficit in the execution of skilled movements can be produced experimentally in monkeys by pharmacological inhibition of neural activity in area 2 of the cortex. When muscimol (a GABA agonist that inhibits cortical cells) is applied to the hand representation of area 2, the monkey is unable to assume normal functional postures of the hand or coordinate the fingers for picking up small objects (Figure 23-15).

Experimental lesions of the various somatic areas of the cortex have also provided valuable information about the function of different Brodmann's areas concerned with somatic sensibility. Total removal of S-I (areas 3b, 3a, 1, and 2) produces deficits in position sense and the ability to discriminate size, texture, and shape. Thermal and pain sensibilities usually are not abolished, but are altered. In addition, serious motor deficits in hand function occur following major lesions in S-I.

Small lesions in the cortical representation of the hand in Brodmann's area 3b produce deficits in the discrimination of the texture of objects as well as their size and shape. Lesions in area 1 produce a defect in the assessment of the texture of objects, whereas lesions in area 2 alter the ability to differentiate the size and shape of objects. This is consistent with the idea that area 3b receives information about texture as well as size and shape (area 3b, together with 3a, is the principal target for the afferent projections from the ventral posterior lateral nucleus of the thalamus). Area 3b projects to both areas 1 and 2. The projection to area 1 is concerned primarily with texture, whereas the projection to area 2 is concerned with size and shape.

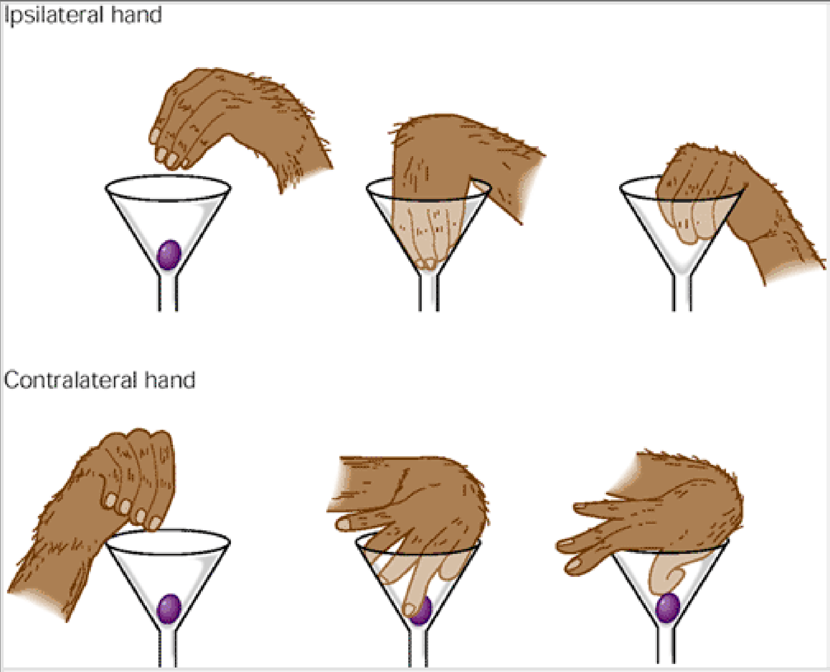

Figure 23-15 A monkey's finger coordination is disrupted when synaptic transmission in the somatic sensory cortex is inhibited. Muscimol, a GABA agonist, was injected into Brodmann's area 2 on the left side of a monkey brain. Within minutes after injection of muscimol, the finger coordination of the right hand (contralateral) is severely disorganized. The monkey is unable to remove a grape piece from a funnel. The injection effects are known to be specific to the injected hemisphere because the left hand (ipsilateral) continues to perform normally. (Adapted from Hikosaka et al. 1985.)

Because S-II receives inputs from all areas of S-I, removal of S-II causes severe impairment in the discrimination of both shape and texture and prevents monkeys from learning new tactile discriminations based on the shape of an object.

Finally, as we saw in Chapter 20, damage to the posterior parietal cortex produces complex sensorimotor abnormalities. These include the inability to accurately process stimuli in the contralateral visual field or contralateral half of the body. Poor motor coordination and poor eye-hand coordination during reaching, grasping, and hand orientation lead to neglect in usage of the hand.

An Overall View

To perceive how the world impinges on our bodies, the brain is organized to represent the tactile sensory system of the skin. The receptive fields of cortical neurons become progressively more complex with each stage of information processing, thus extracting more cohesive features of a stimulus at each stage. Cortical receptive fields are larger than those of peripheral receptors due to convergence of inputs from simultaneously stimulated areas of skin.

Cortical neurons are functionally organized in columns, so that all six layers of the cortex in any column receive information representing the same location and modality. The columns are arranged topographically, projecting a precise representation of the external body surface onto the cortical surface. Somatotopy, the orderly projection of the sensory sheet in the brain, permits orderly intracortical connections. However, the somatosensory map or homunculus is not an exact representation of the body surface but is distorted. The finger tips, for example, are represented by a much greater cortical area than are regions like the back. The cortical map represents the density of innervation, hence the functional importance of different areas of the skin.

The body surface has at least eight distinct neural maps in the parietal cortex, four in S-I, two in S-II, and two in the posterior parietal cortex. Each of the four subregions in S-I contains its own map of the body surface, specific to a particular somatic sensory modality. Area 3a receives input primarily from muscle stretch receptors; area 3b receives cutaneous receptor input; area 1 receives input from rapidly adapting receptors; and area 2 contains a map of both cutaneous and deep receptors. As a result, these different regions are responsible for different aspects of somatic sensation. Areas 3b and 1 are involved in sensing surface texture, while area 2 is responsible for sensing the size and shape of objects.

Neurons in areas 2, 5, and 7 are involved in the later stages of somatosensory processing, have more complex feature-detecting properties, receive convergent input from several submodalities, and have larger receptive fields than first-order cortical neurons. At least four types of higher-order somatosensory cells have been found: direction-sensitive, orientation-sensitive, texture-sensitive, and shape-sensitive neurons. Even more complicated processing seems to be carried out by neurons activated when the hand is manipulating an object; these neurons project to the motor cortex for sensory-motor integration. Finally, the S-I cortex sends outputs to the posterior parietal cortex, where integration with other senses and the opposite limb occurs and where an overall picture of the body is formed.

Why are there so many representations of the body surface? Somatic sensation involves the parallel analysis of different stimulus attributes in different cortical areas. Parallel processing in the brain is a form of processing that we shall encounter repeatedly in the sensory systems. It is designed not to achieve multiplication of

identical circuitry but to allow different neuronal pathways and brain relays to deal with sensory information in slightly different ways.

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