

[Back](#)

21

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]

P.412

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.

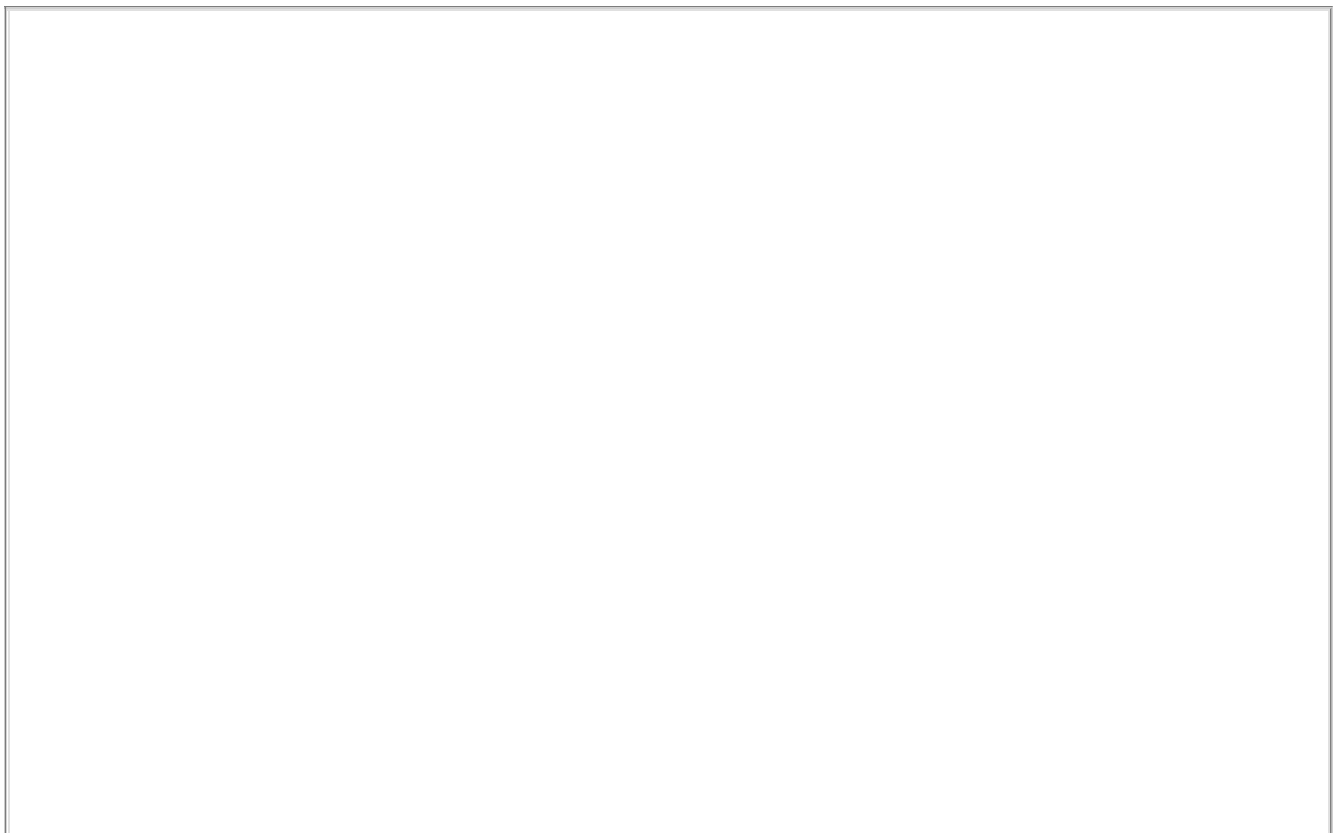
In short, our perceptions are not direct records of the world around us. Rather, they are constructed internally according to constraints imposed by the architecture of the nervous system and its functional abilities. The philosopher Immanuel Kant referred to these inherent brain properties as *a priori* 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

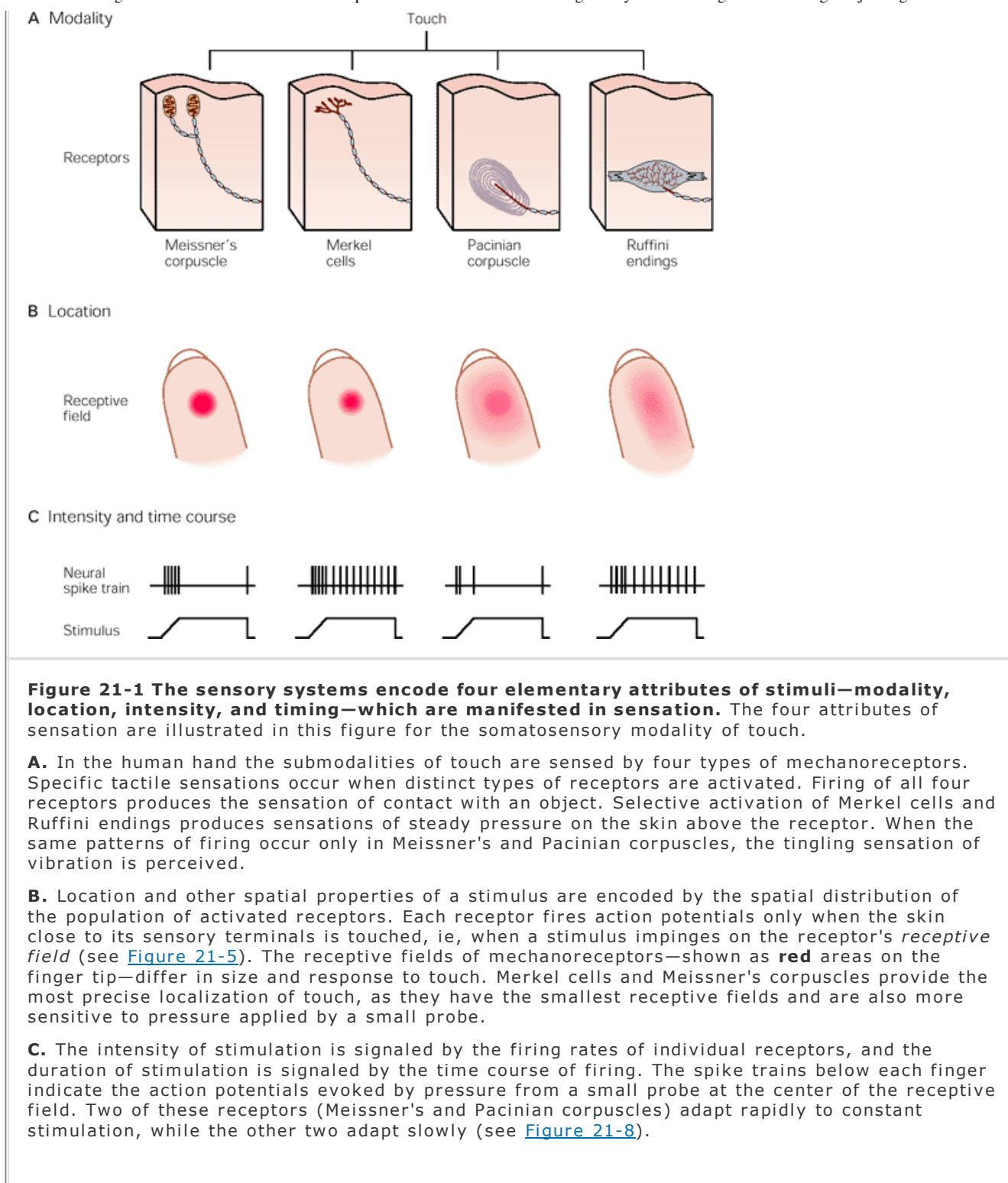
As we shall see later, the dialectical tension between Kant's idealism and Comte's empirical positivism continues to reverberate in studies of perception. Kant's concept of a priori knowledge left its mark on *Gestalt psychology*, which holds that aspects of perception are the product of the brain's 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.





P.413

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,

P.414

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 class¹	Receptor cell types²
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

P.415

P.416

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.

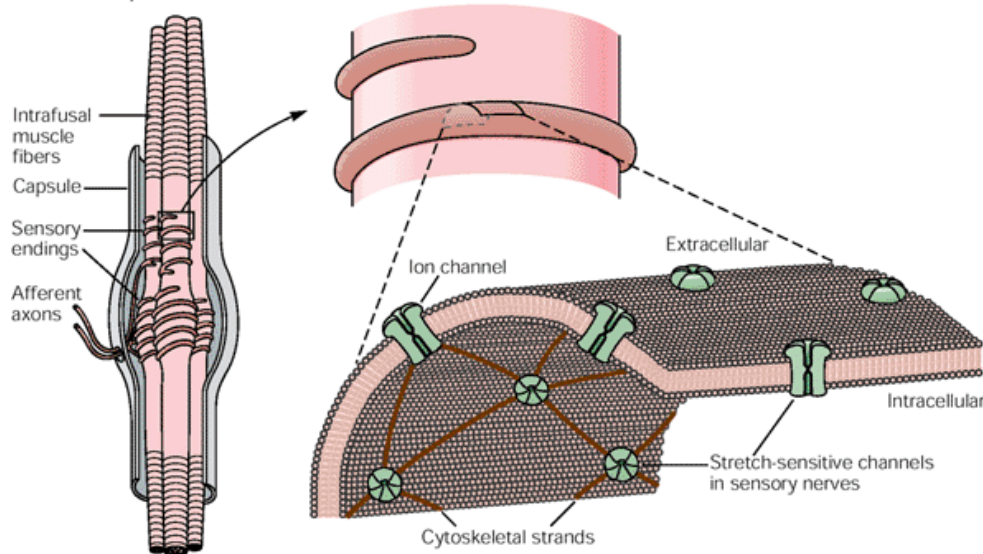
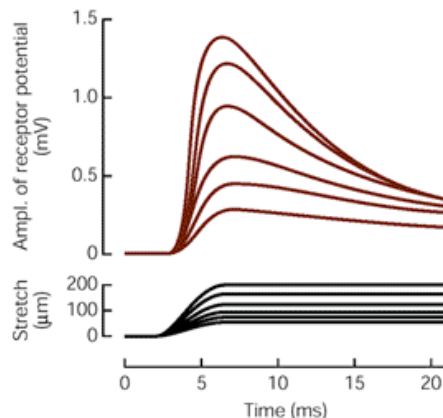
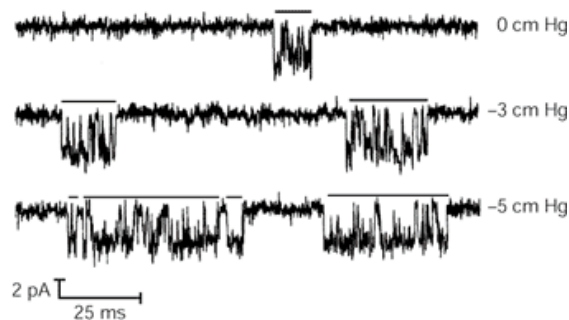
A Muscle spindle**B Receptor potential in nerve****C Single-channel response to stretch**

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](#)).

P.417

P.418

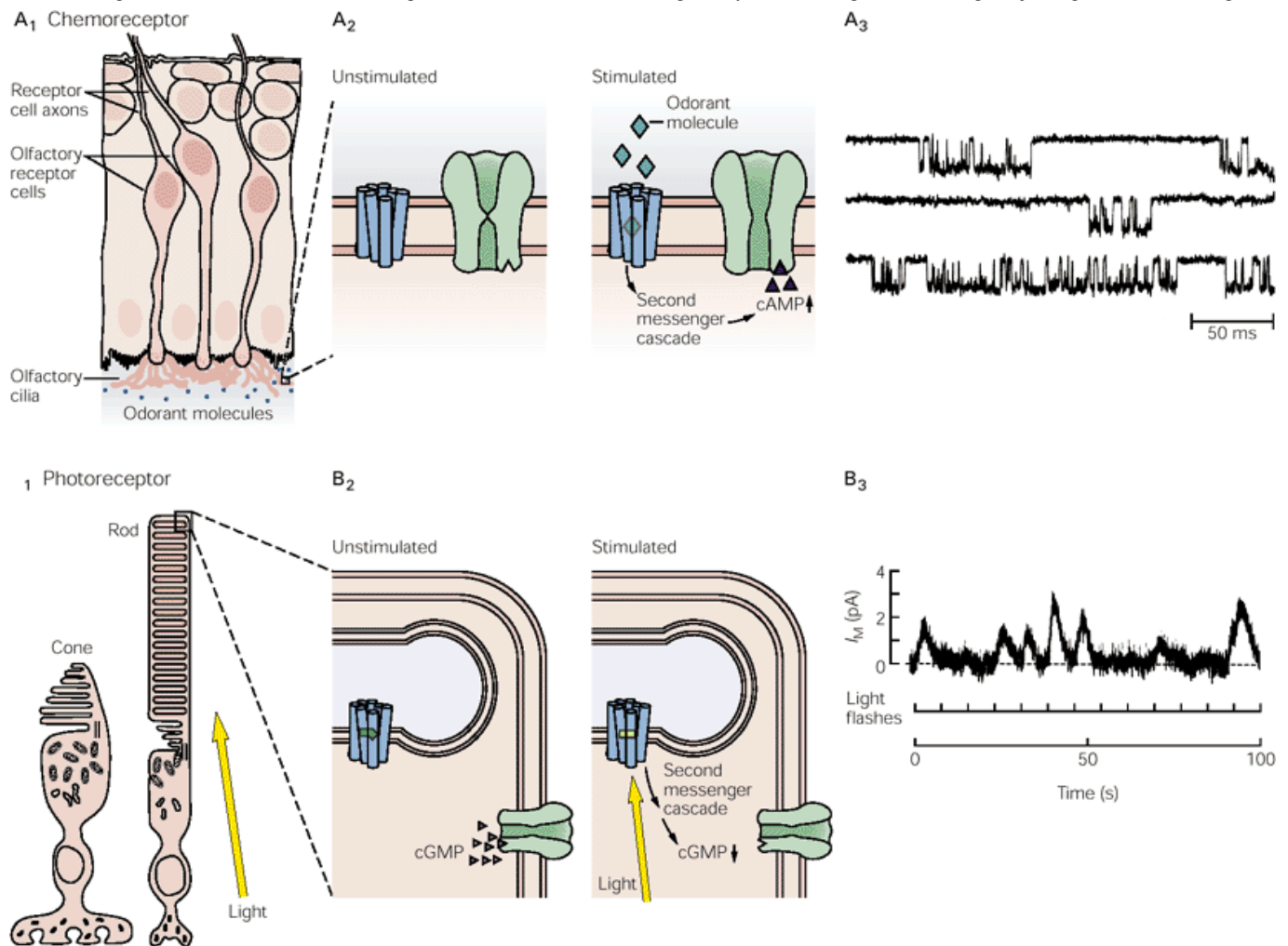


Figure 21-3 Transduction of stimulus energy into neural activity by chemoreceptors and photoreceptors requires intracellular second messengers. (Adapted from [Shepherd 1994](#).)

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.)

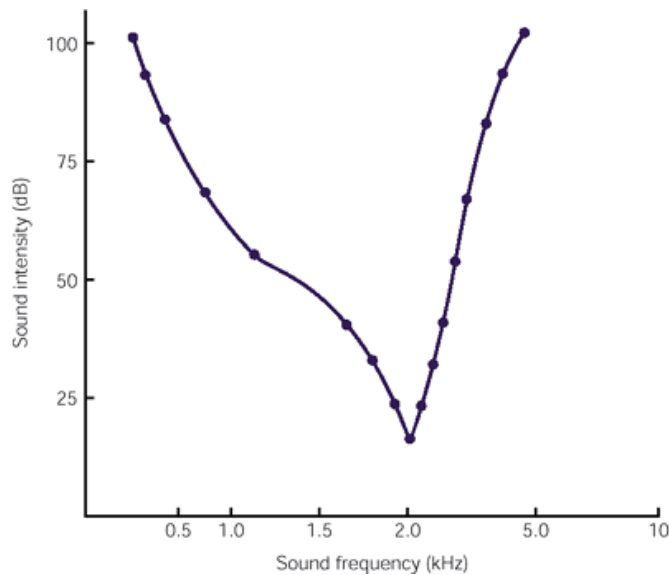


Figure 21-4 Tuning curves of sensory receptors measure the minimum amplitude of stimulation needed to activate a sensory receptor over a range of stimulus energies. Each sensory receptor responds optimally to a narrow range of intensities of a single type of energy. The tuning curve shown here is for 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

P.419

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.

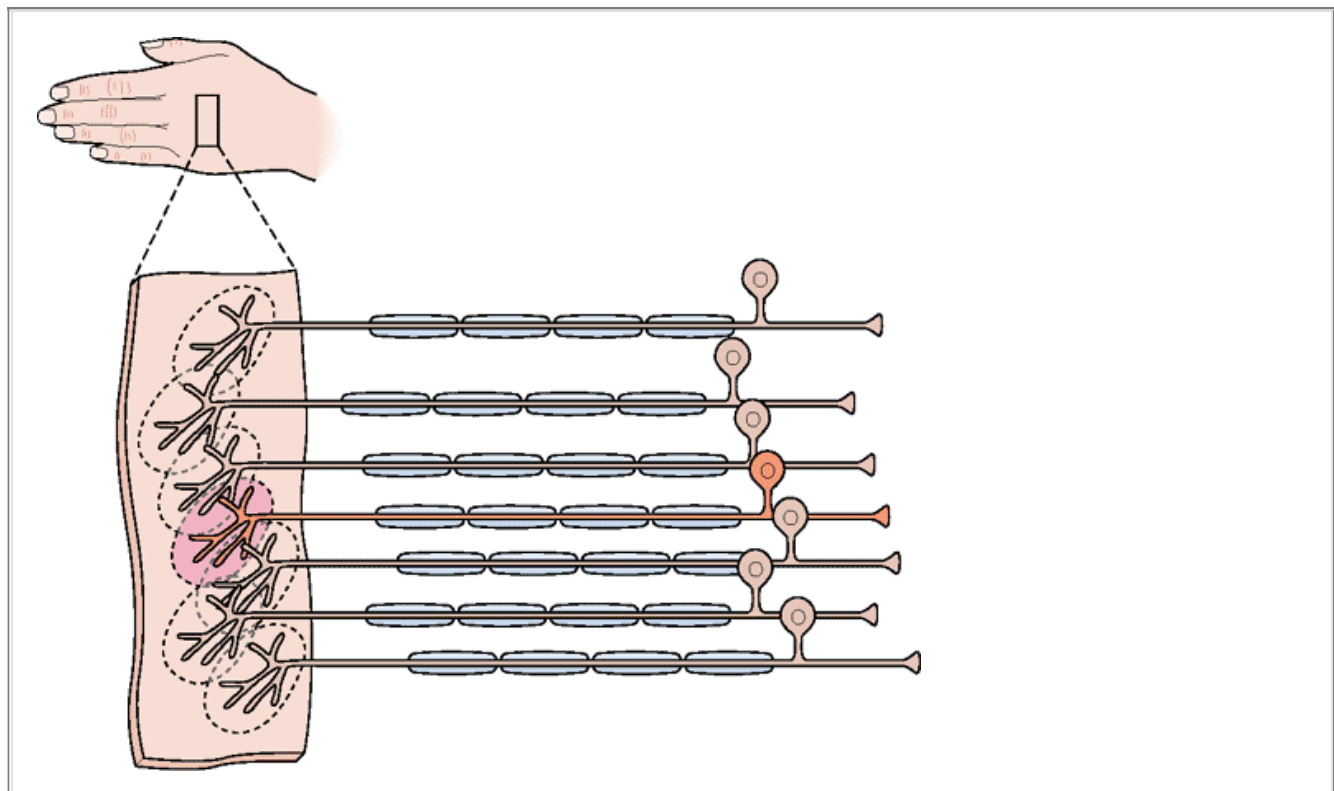


Figure 21-5 Structural basis of the receptive field of receptors for the sense of touch. The receptive field of a touch-sensitive neuron in the skin includes the sensory transduction apparatus in the nerve terminals and the surrounding skin in which the terminals are located. A patch of skin contains 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.

P.420
P.421



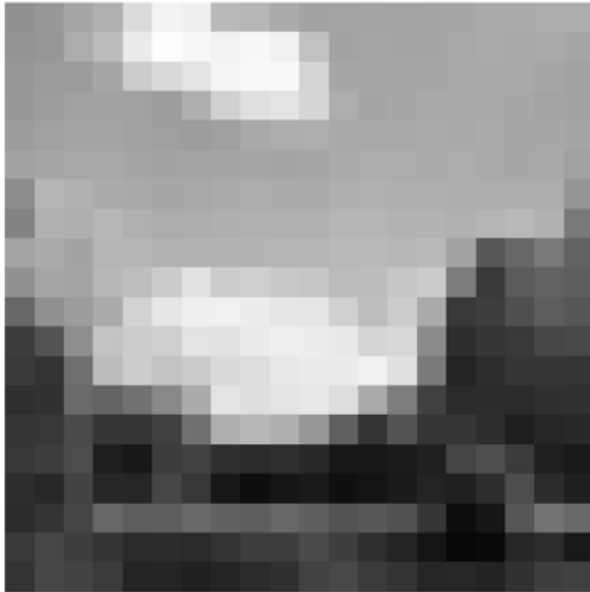
A 400 receptors**B 3,600 receptors****C 14,400 receptors****D 160,000 receptors**

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, Helmholtz, 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.

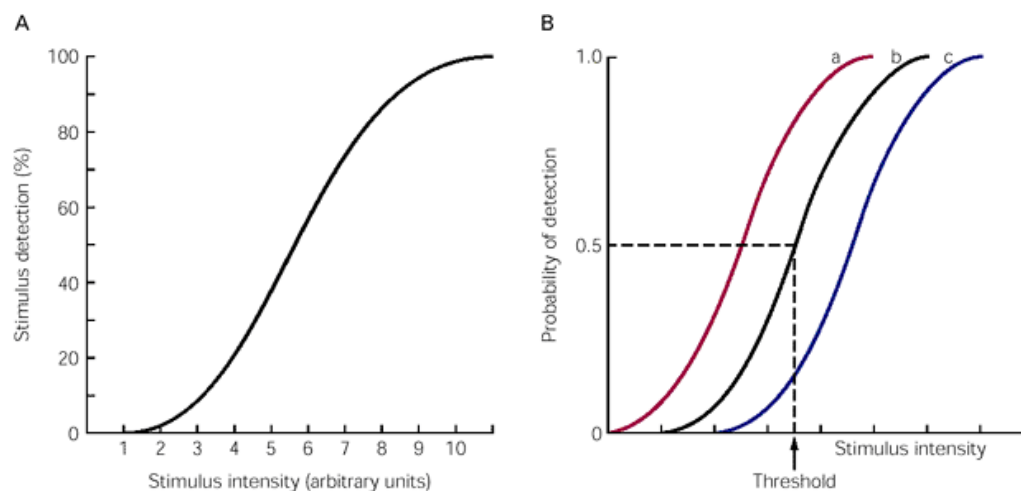


Figure 21-7 Sensory thresholds and the just noticeable difference (JND) between stimuli that differ in intensity, frequency, or other parametric features are quantifiable.

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.

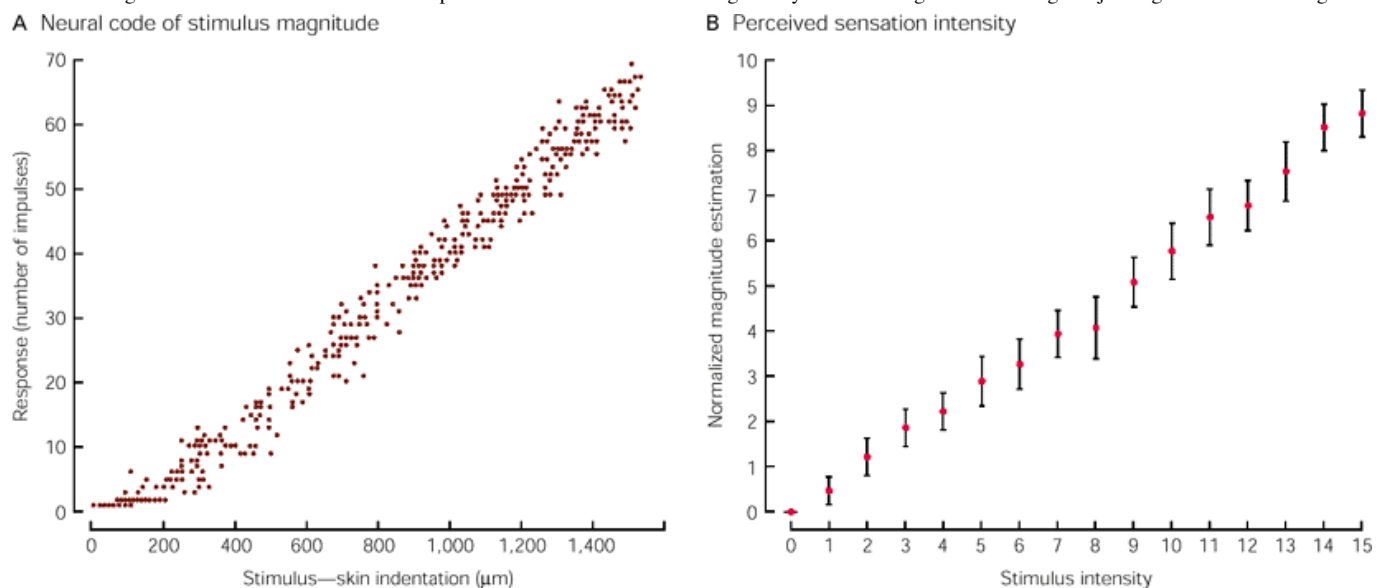


Figure 21-8 The firing rates of sensory nerves encode the stimulus magnitude. (Adapted from [Mountcastle et al. 1966.](#))

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.

P.422

P.423

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

P.424

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.

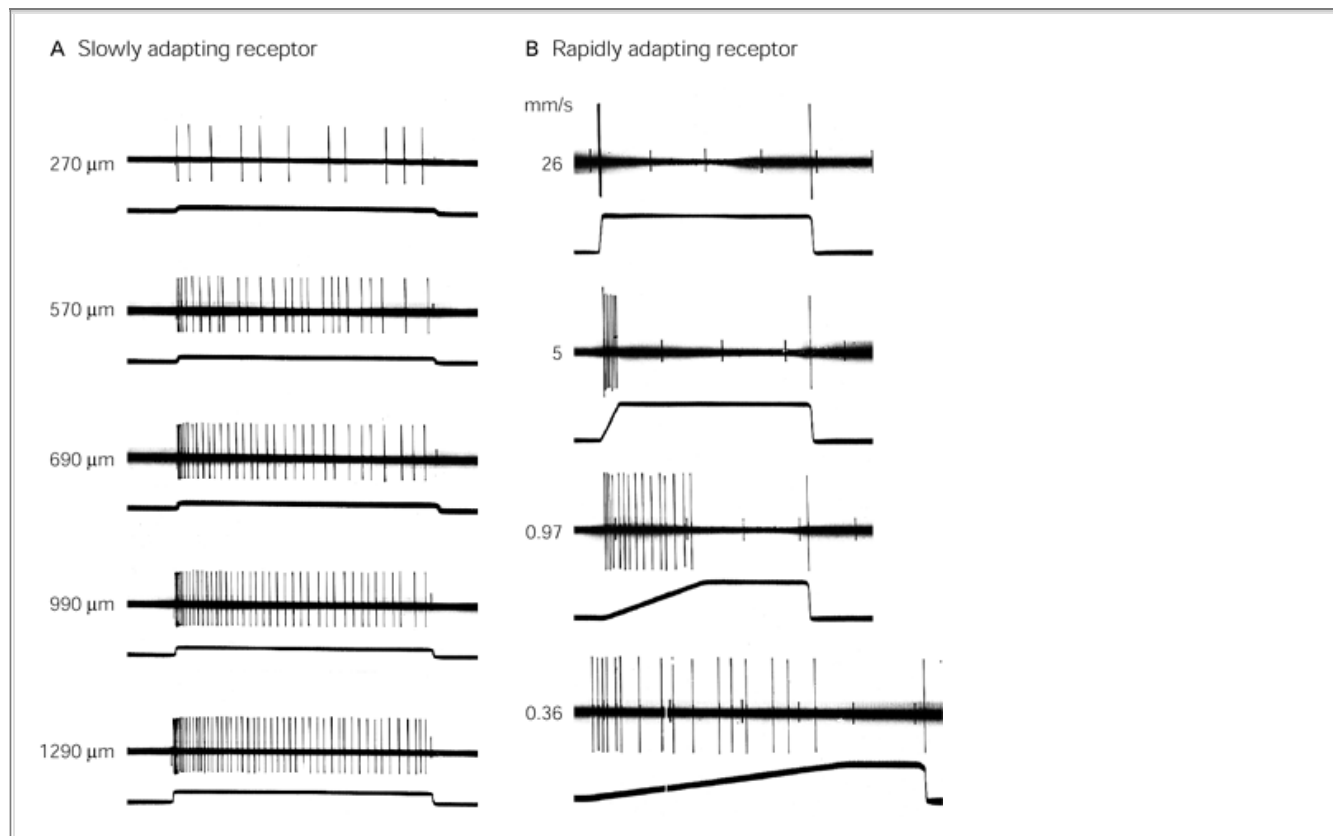


Figure 21-9 Measurements of firing rates quantify how sensory neurons represent the intensity of stimulation over time.

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

P.425

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.

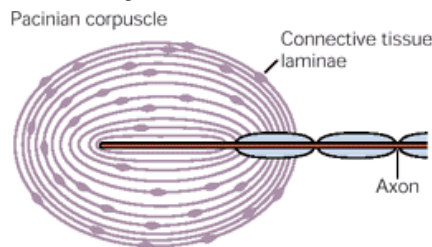
Some receptors *cease* firing in response to constant-amplitude stimulation and are active only when the stimulus intensity increases or decreases. These *rapidly adapting receptors* respond only at the beginning and end of a stimulus, signaling the rate or velocity of stimulation ([Figure 21-9B](#)). 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.

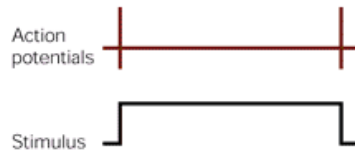
Many sensory receptors also sense spatial contrasts. In [Chapters 22](#) and [25](#) we will learn that certain neurons mediating touch and vision are particularly sensitive to edges. These neurons fire much faster if the spatial properties of a stimulus in their receptive field change abruptly than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



A Steady pressure



B 110 Hz vibration



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 mesentery 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.

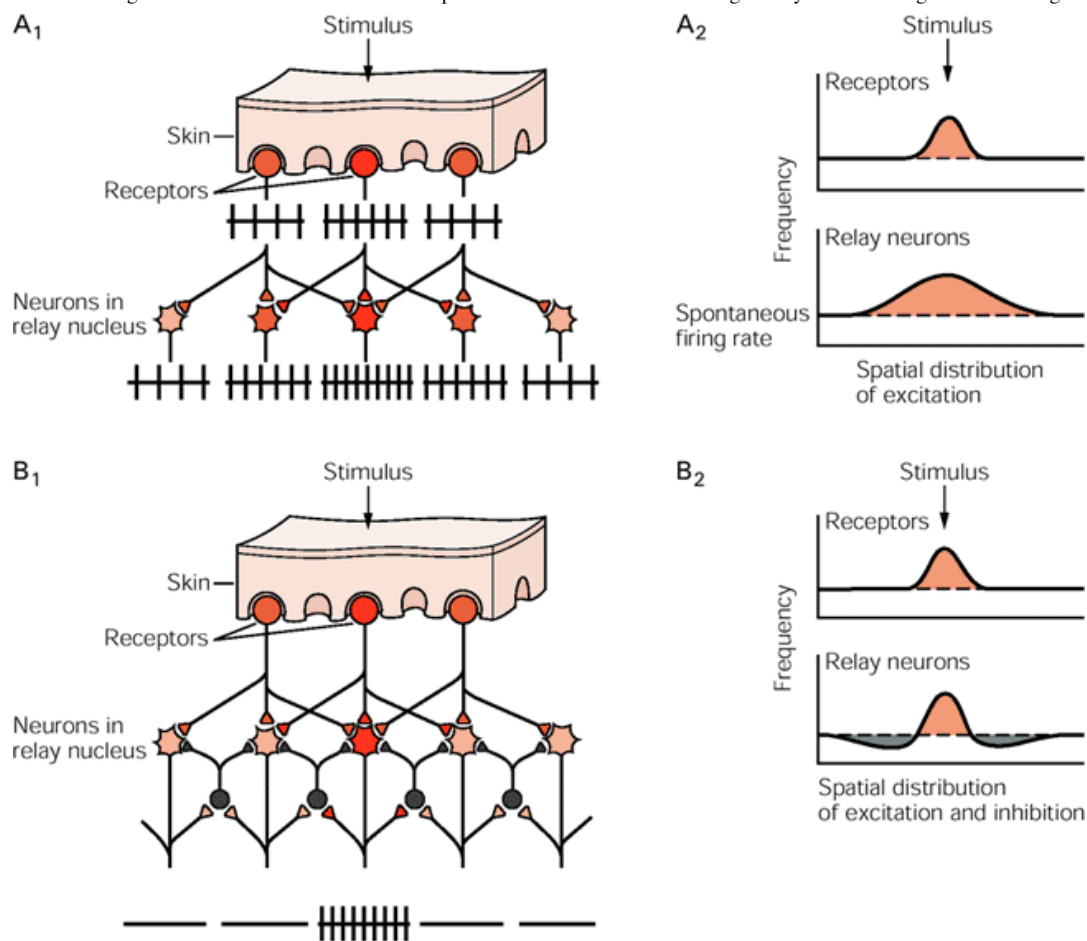


Figure 21-11 The functional and anatomical organization of sensory processing networks is hierarchical. Stimulation of a population of receptors initiates signals that are transmitted through a series of relay nuclei to higher centers in the brain (only one relay is shown). At each processing stage the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

P.426

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](#)).

P.427

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.

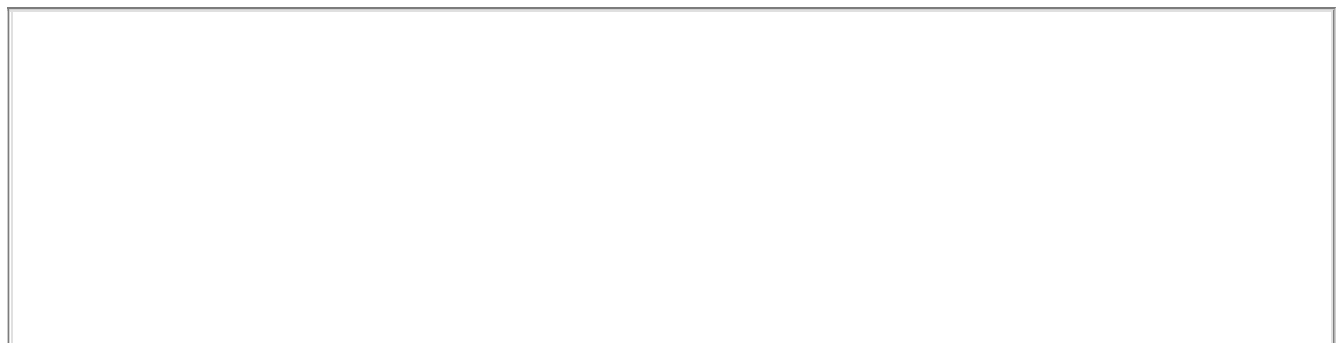
Like receptor neurons, neurons in each sensory relay nucleus have a receptive field. The receptive field of each relay neuron is defined by the population of presynaptic cells that converge on it. The receptive fields of second-order and higher-order sensory neurons are larger and more complex than those 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



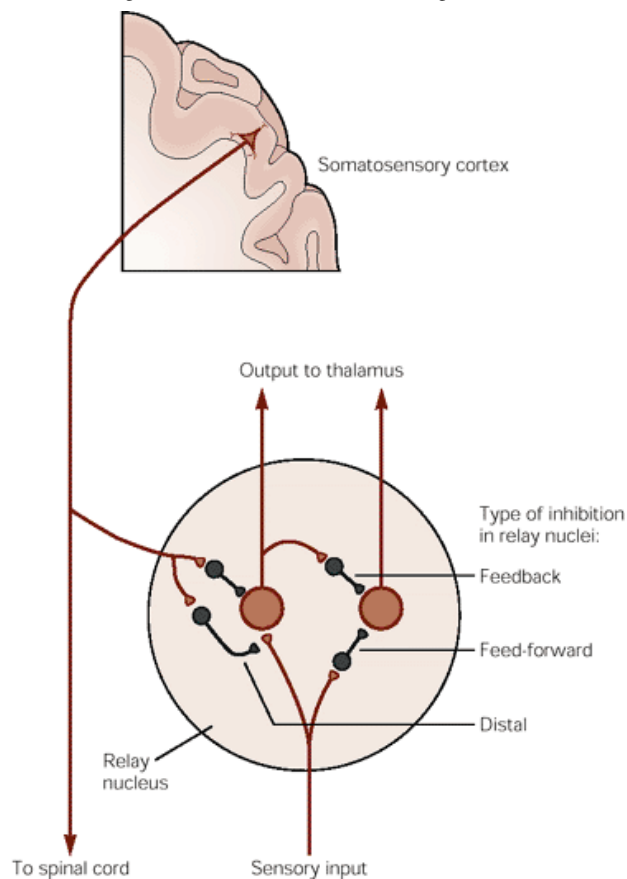


Figure 21-12 Inhibition of selected projection neurons in a sensory relay nucleus enhances the contrast between stimuli. The illustration shows three inhibitory pathways in the circuitry of the dorsal column nuclei, the first relay in the system for touch. The projection (or relay) cells (**brown**) 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.

P.428

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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