the hand, the relationship between the stimulus magnitude and its perceived intensity is linear, that is, a power function with a unity exponent ($n = 1$).

All sensory systems have a threshold, and thresholds have two essential functions. First, by asking if a sensation is large enough to have a high enough probability of being of interest or relevance, they reduce unwanted responses to noise. Second, the specific nonlinearity introduced by thresholds aids encoding and processing, even if the rest of the primary sensory response scales linearly with the stimulus. Sensory thresholds are a feature, not a bug. 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* (Figure 17–2). By convention, threshold is defined as the stimulus amplitude detected in half of the trials.

The measurement of sensory thresholds is a useful technique for diagnosing sensory function in individual modalities. An elevated 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 by emotional or psychological factors related to the conditions in which stimulus detection is measured. 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 detectable or an increasing stimulus becomes detectable. This technique is widely used in audiology to measure hearing thresholds.

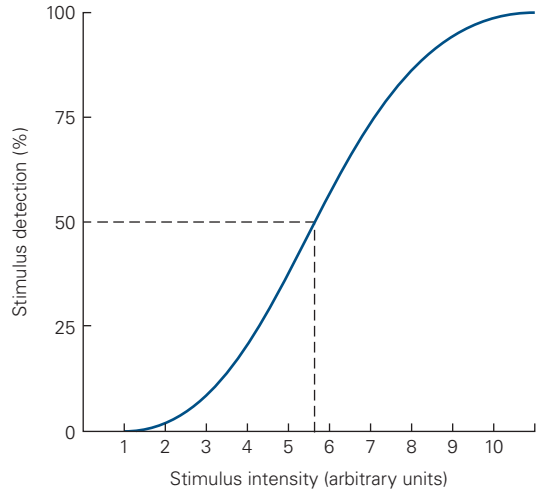

Figure 17–2 The psychometric function. The psychometric function plots the percentage of stimuli detected by a human observer as a function of the stimulus magnitude. Threshold is defined as the stimulus intensity detected on 50% of the trials, which in this example would be about 5.5 (arbitrary units). Psychometric functions are also used to measure the *just noticeable difference* (JND) between stimuli that differ in intensity, frequency, or other parametric properties.

Subjects can also provide nonverbal responses in sensory detection or discrimination tasks using levers, buttons, or other devices that allow accurate measurement of decision times. Experimental animals can be trained to respond to controlled sensory stimuli using such devices, allowing neuroscientists to investigate the underlying neural mechanisms by combining electrophysiological and behavioral studies in the same experiment. Methods for quantifying responses to stimuli are summarized in Box 17–1.

Stimuli Are Represented in the Nervous System by the Firing Patterns of Neurons

Psychophysical methods provide objective techniques for analyzing sensations evoked by stimuli. These quantitative measures have been combined with neurophysiological techniques to study the neural mechanisms that transform sensory neural signals into percepts. The goal of sensory neuroscience is to follow the flow of sensory information from receptors toward the cognitive centers of the brain, to understand the processing mechanisms that occur at successive synapses, and to decipher how this shapes our internal representation of the external world. The neural coding of sensory information is better understood at the early stages of processing than at later stages in the brain.

This approach to the *neural coding problem* was pioneered in the 1960s by Vernon Mountcastle, who showed that single-cell recordings of spike trains from peripheral and central sensory neurons provide a statistical description of the neural activity evoked by a physical stimulus. He then investigated which quantitative aspects of neural responses might correspond to the psychophysical measurements of sensory tasks and, just as important, which do not.

The study of neural coding of information is fundamental to understanding how the brain works. A neural code describes the relationship between the activity in a specified neural population and its functional consequences for perception or action. Sensory systems are ideal for the study of neural coding because both the physical properties of the stimulus input and the neural or behavioral output of these systems can be precisely defined and quantified in a controlled setting.

Box 17–1 Signal Detection Theory: Quantifying Detection and Discrimination

Two major functions of our sensory systems are to tell us if something is there and what it is. To test our ability and the ability of our sensory systems to answer these questions, experimental protocols, tools, and methods have been developed to quantify the response of sensory systems to stimuli. These include *decision theory* and *signal detection theory*. Each uses statistical methods to quantify the variability of subjects' responses.

In an "Is something there?" task, for example, subjects or experimental animals can correctly detect a specific stimulus (a "hit" or "true positive"), respond incorrectly in the absence of that stimulus ("false positive" or "false alarm"), fail to respond to a true stimulus ("miss"), or correctly decline to respond in the absence of the stimulus ("true negative" or "correct rejection"). With repeated presentations, these choices can be tabulated in a four-cell stimulus–response matrix (Figure 17–3A).

This quantifies *sensitivity*, defined as the number of true positives divided by the number of stimuli presented, and *specificity*, defined as the number of true negatives divided by the number of presentations without a stimulus.

In 1927, L. L. Thurstone proposed that the variability of sensations evoked by stimuli could be represented as normal or Gaussian probability functions, equating the physical distance between the amplitudes of two stimuli to a psychological scale value of inferred intensity called the *discrimination index* or *d'*.

Decision theory methods were first applied to psychophysical studies in 1954 by the psychologists Wilson Tanner and John Swets. They developed a series of experimental protocols for stimulus detection that allowed accurate calculation of *d'* as well as techniques for quantitative analyses of sensations in both human and animal subjects. Such studies can be designed to measure not just "Is something there?" as in the earlier example, but also comparative judgments of a physical property of a stimulus such as its intensity, size, or temporal frequency, thereby measuring a *two-alternative forced-choice* analog of "What is it?"

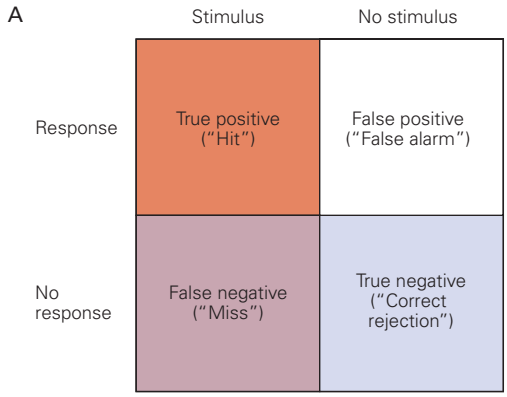

Figure 17–3A The stimulus–response matrix for data collected during a yes–no stimulus detection task ("Is a particular stimulus there?"). Each trial updates one of the four totals. For example, correct detection of the stimulus would update the count of true positives (hits), but an incorrect positive response in the absence of the stimulus would count as a false positive. From such a table, important measures such as the sensitivity and false-positive rate can be calculated.

When subjects are asked to report whether the second stimulus is stronger or weaker, higher or lower, larger or smaller, or same or different than the first stimulus, responses in each trial can again be tabulated in a four-cell stimulus–response matrix similar to the one in Figure 17–3A, but with the terms "stimulus" or "no stimulus" replaced by the two distinct stimuli.

(*continued*)

By recording neuronal activity at various stages of sensory processing, neuroscientists attempt to decipher the mechanisms used by various sensory modalities to represent information and the transformations needed to convey these signals to the brain encoded by sequences of action potentials. Additional analyses are performed of the transformation of signals by neural networks along pathways to and within the cerebral cortex. Neuroscientists can also modify activity within sensory circuits by direct stimulation with electrical pulses, chemical neurotransmitters, and modulators, or can use genetically encoded light-activated ion channels (optogenetics) to depolarize or hyperpolarize sensory neurons. How sensory stimuli are encoded by neurons may lead to insight into the coding principles that underlie cognition.

It is often said that the power of the brain lies in the millions of neurons processing information in parallel. That formulation, however, does not capture the essential difference between the brain and all the other organs of the body. In the kidney or a muscle, most cells do similar things; if we understand typical

Box 17–1 Signal Detection Theory: Quantifying Detection and Discrimination (continued)

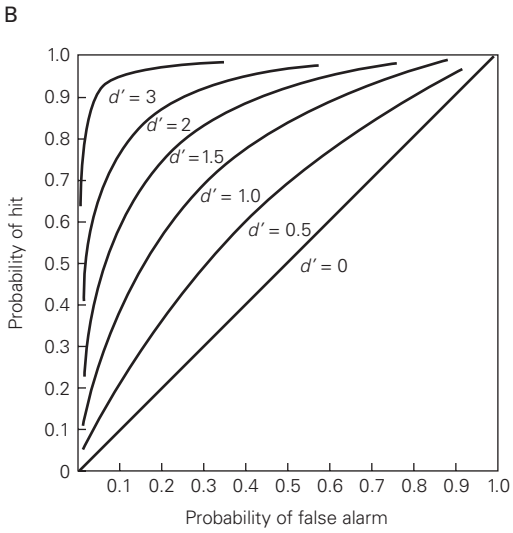

Figure 17–3B A receiver operating characteristic (ROC) plot displays the results of sets of trials, each collected in matrices such as those in Figure 17–3A. The vertical axis plots the fraction or probability of hits as a function of fraction or probability of false alarms on the horizontal axis. It is also common to label the vertical axis TPR (true-positive rate), or sensitivity, and the horizontal axis FPR (false-positive rate), or (1 – specificity). A set of trials in which yes or no responses are delivered randomly (discriminability [d'] = 0) plots as a straight line from the origin to the upper right corner. The area under such an ROC curve (AUC) would be 0.5. A perfect set of trials, in which observers accurately detect the presence of every stimulus and fail to be fooled by any trials without stimuli ($d' > 3$), would rise sharply along the left axis, and the AUC would be 1.0. AUC values are increasingly quoted as single-number measures of confidence. The (theoretical) curves shown demonstrate how higher values of d' result in larger AUC. (Adapted, with permission, from Swets 1973. Copyright © 1973 AAAS.)

Discriminability (d') in these studies is measured with *receiver operating characteristic* (ROC) analyses that compare the neural firing rates or choice probability evoked by pairs of stimuli that differ in some property. The assumption is that one of the two stimuli evokes higher responses than the other. ROC graphs of neural or psychophysical data plot the proportion of trials judged correctly (hits) and incorrectly (false positives) when the decision criteria are set at various firing levels or choice rates (Figure 17–3B). The area under the ROC curve provides an accurate estimate of d' for each stimulus pair.

Signal detection methods have been applied by William Newsome, Michael Shadlen, and J. Anthony Movshon in studies of neural responses to visual stimuli that differ in orientation, spatial frequency, or coherence of motion in order to correlate changes in neural firing rates with sensory processing. The neurometric function, plotting neural discriminability as a function of stimulus differences, corresponds closely to the psychometric function obtained in forced-choice paradigms testing the same stimuli, thereby providing a physiological basis for the observed behavioral responses.

Many of these tools, developed in part to study sensory systems, have been generalized to apply broadly beyond neuroscience. ROC curves, sensitivity, and specificity are essential in quantification of diagnosis and treatment of disease. The area under an ROC curve, or *AUC*, is today used much more than d'. Values of AUC close to 1 characterize high sensitivity and high specificity. The *false positive rate* (1 – specificity, or the number of false positives divided by the number of presentations without a stimulus) is, for many experiments or clinical investigations in which true positive findings are rare, a more meaningful measure than the classical p value.

muscle cells, we essentially understand how whole muscles work. In the brain, millions of cells each do something *different*. To understand the brain, we need to understand how its tasks are organized in networks of neurons.

Sensory Receptors Respond to Specific Classes of Stimulus Energy

Functional differences between sensory systems arise from two features: the different stimulus energies that drive them and the discrete pathways that compose each system. Each neuron performs a specific task, and the train of action potentials it produces has a specific functional significance for all postsynaptic neurons in that circuit. This basic idea was expressed in the theory of specificity set forward by Charles Bell and Johannes Müller in the 19th century, and remains one of the cornerstones of sensory neuroscience.

When analyzing sensory experience, it is important to realize that our conscious sensations differ qualitatively from the physical properties of stimuli because,

as Kant and the idealists predicted, the nervous system extracts only certain features of each stimulus while ignoring others. It then interprets this information within the constraints of the brain's intrinsic structure and previous experience. Thus, we *receive* electromagnetic waves of different frequencies, but we *see* them as colors. 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 odors and tastes. Colors, tones, odors, and tastes are mental creations constructed by the brain out of sensory experience. They do not exist as such outside the brain but are linked to specific physical properties of stimuli.

The richness of sensory experience begins with millions of highly specific sensory receptors. Sensory receptors are found in specialized epithelial structures called sense organs, principally the eye, ear, nose, tongue, and skin. Each receptor responds to a specific kind of energy at specific locations in the sense organ and sometimes only to energy with a particular temporal or spatial pattern. The receptor transforms the stimulus energy into electrical energy; thus, all sensory systems use a common signaling mechanism. The amplitude and duration of the electrical signal produced by the receptor, termed the *receptor potential*, are related to the intensity and time course of stimulation of the receptor. The process by which a specific stimulus energy is converted into an electrical signal is called *stimulus transduction*.

Sensory receptors are morphologically specialized to transduce specific forms of energy, and each receptor has a specialized anatomical region within the sense organ where stimulus transduction occurs (Figure 17–4). Most receptors are optimally selective for a single type of stimulus energy, a property termed

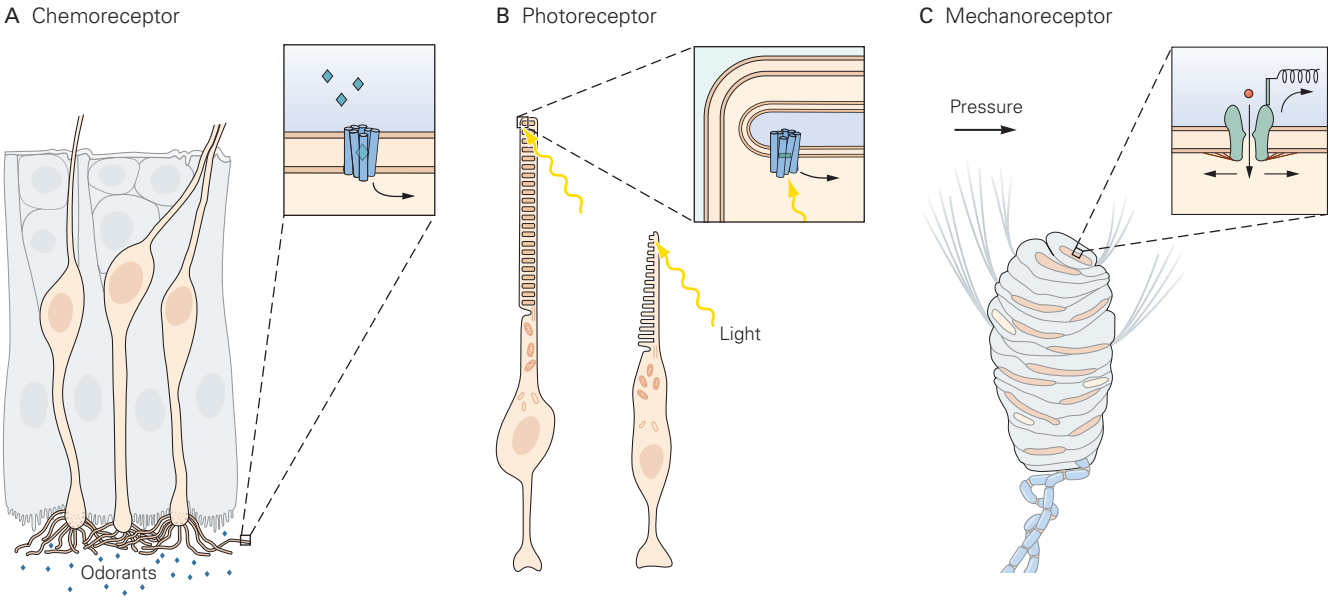

Figure 17–4 Sensory receptors are specialized to transduce a particular type of stimulus energy into electrical signals. Sensory receptors are classified as chemoreceptors, photoreceptors, or mechanoreceptors depending on the class of stimulus energy that excites them. They transform that energy into an electrical signal that is transmitted along pathways that serve one sensory modality. The inset in each panel illustrates the location of the ion channels that are activated by stimuli.

A. The olfactory hair cell responds to chemical molecules in the air. The olfactory cilia on the mucosal surface bind specific odorant molecules and depolarize the sensory nerve through a second-messenger system. The firing rate signals the concentration of odorant in the inspired air.

B. Rod and cone cells in the retina respond to light. The outer segment of both receptors contains the photopigment rhodopsin, which changes configuration when it absorbs light of particular wavelengths. Stimulation of the chromophore by light reduces the concentration of cyclic guanosine 3′,5′-monophosphate (cGMP) in the cytoplasm, closing cation channels and thereby hyperpolarizing the photoreceptor. (Adapted from Shepherd 1994.)

C. Meissner's corpuscles respond to mechanical pressure. The fluid-filled capsule (**pale blue**) surrounding the sensory nerve endings (**pink**) is linked by collagen fibers to the fingerprint ridges. Pressure or motion on the skin opens stretch-sensitive ion channels in the nerve fiber endings, thus depolarizing them. (Adapted, with permission, from Andres and von Düring 1973.)

receptor specificity. We see particular colors, for example, because we have receptors that are selectively sensitive to photons with specific ranges of wavelengths, and we smell particular odors because we have receptors that bind specific odorant molecules.

In all sensory systems, each receptor encodes the type of energy applied to its receptive field, the local stimulus magnitude, and how it changes with time. For example, photoreceptors in the retina encode the hue, brightness, and duration of light striking the retina from a specific location in the visual field. Hair cell receptors in the cochlea encode the tonal frequency, loudness, and duration of sound-pressure waves hitting the ear. The neural representation of an object, sound, or scene is therefore composed of a mosaic of individual receptors that collectively signal its size, contours, texture, temporal frequency, color, and temperature.

The arrangement of receptors in the sense organ allows further specialization of function within each sensory system. Mammalian sensory receptors are classified as mechanoreceptors, chemoreceptors, photoreceptors, or thermoreceptors (Table 17–1). Mechanoreceptors and chemoreceptors are the most widespread and the most varied in form and function.

Four different kinds of *mechanoreceptors* that sense skin deformation, motion, stretch, and vibration are responsible for the sense of touch in the human hand and elsewhere (Chapters 18 and 19). Muscles contain three kinds of mechanoreceptors that signal muscle length, velocity, and force, whereas other mechanoreceptors in the joint capsule signal joint angle (Chapter 31). Hearing is based on two kinds of mechanoreceptors, inner and outer hair cells, that transduce motion of the basilar membrane in the inner ear (Chapter 26). Other hair cells in the vestibular labyrinth sense motion and acceleration of the fluids of the inner ear to signal head motion and orientation (Chapter 27). Visceral mechanoreceptors detect the distension of internal organs such as the bowel and bladder. Osmoreceptors in the brain, which sense the state of hydration, are activated when a cell swells. Certain mechanoreceptors report extreme distortion that threatens to damage tissue; their signals reach pain centers in the brain (Chapter 20).

Table 17–1 Classification of Sensory Receptors

Sensory system	Modality	Stimulus	Receptor class	Receptor cells
Visual	Vision	Light (photons)	Photoreceptor	Rods and cones
Auditory	Hearing	Sound (pressure waves)	Mechanoreceptor	Hair cells in cochlea
Vestibular	Head motion	Gravity, acceleration, and head motion	Mechanoreceptor	Hair cells in vestibular labyrinths
Somatosensory				Cranial and dorsal root ganglion cells with receptors in:
	Touch	Skin deformation and motion	Mechanoreceptor	Skin
	Proprioception	Muscle length, muscle force, and joint angle	Mechanoreceptor	Muscle spindles, Golgi tendon organs, and joint capsules
	Pain	Noxious stimuli (thermal, mechanical, and chemical stimuli)	Thermoreceptor, mechanoreceptor, and chemoreceptor	All tissues except central nervous system
	Itch	Histamine, pruritogens	Chemoreceptor	Skin
	Visceral (not pain)	Wide range (thermal, mechanical, and chemical stimuli)	Thermoreceptor, mechanoreceptor, and chemoreceptor	Cardiovascular, gastrointestinal tract, urinary bladder, and lungs
Gustatory	Taste	Chemicals	Chemoreceptor	Taste buds, intraoral thermal, and chemoreceptors
Olfactory	Smell	Odorants	Chemoreceptor	Olfactory sensory neurons

Chemoreceptors are responsible for olfaction, gustation, itch, pain, and many visceral sensations. A significant part of pain is due to chemoreceptors that detect molecules spilled into the extracellular fluid by tissue injury and molecules that are part of the inflammatory response. Several kinds of *thermoreceptors* in the skin sense skin warming and cooling. Another thermoreceptor, which monitors blood temperature in the hypothalamus, is mainly responsible for whether we feel warm or cold.

Vision is mediated by five kinds of *photoreceptors* in the retina. The light sensitivities of these receptors define the visible spectrum. The photopigments in rods and cones detect electromagnetic energy of wavelengths that span the range of 390 to 670 nm (Figure 17–5A), the principal wavelengths of sunlight and moonlight reaching the earth and informing our visual world. Unlike some other species, such as birds or reptiles, humans do not detect ultraviolet light or infrared radiation because we lack receptors that detect the appropriate short or long wavelengths. Likewise, we do not perceive radio waves and microwave energy bands because we have not evolved receptors for these wavelengths.

Multiple Subclasses of Sensory Receptors Are Found in Each Sense Organ

Each major sensory system has several *submodalities*. For example, taste can be sweet, sour, salty, savory, or bitter; visual objects have qualities of color, shape, and pattern; and touch includes qualities of temperature, texture, and rigidity. Some submodalities are mediated by discrete subclasses of receptors that respond to limited ranges of stimulus energies of that modality; others are derived by combining information from different receptor types.

The receptor behaves as a filter for a narrow range or bandwidth of energy. For example, an individual photoreceptor is not sensitive to all wavelengths of light but only to a small part of the spectrum. We say that a receptor is *tuned* to an optimal or best stimulus, the *preferred* stimulus that activates the receptor at low energy and evokes the strongest neural response. As a result, we can plot a *tuning curve* for each receptor based on physiological experiments (see the light absorbance curves for photoreceptors in Figure 17–5A). The tuning curve shows the range of sensitivity of the receptor, including its preferred stimulus. For example, blue cone cells in the retina are most sensitive to light of 430 to 440 nm, green cone cells respond best to 530 to 540 nm, and red cone cells respond most vigorously to light of 560 to 570 nm. Responses of the three cone cells to other wavelengths of light are weaker as the incident wavelengths differ from these optimal ranges (Chapter 22).

Each rod and cone cell thus responds to a wide spectrum of colors. The graded sensitivity of photoreceptors encodes specific wavelengths by the amplitude of the evoked receptor potential. However, this amplitude also depends upon the intensity or brightness of the light, so a green cone responds similarly to bright orange or dimmer green light. How are these distinguished? Stronger stimuli activate more photoreceptors than do weaker ones, and the resulting population code of multiple receptors, combined with receptors of different wavelength preferences, distinguishes intensity from hue. Such neural ensembles enable individual visual neurons to multiplex signals of color and brightness in the same pathway.

Additionally, because the tuning curve of a photoreceptor is roughly symmetric around the best frequency, wavelengths of greater or lesser values may evoke similar responses. For example, red cones respond similarly to light of 520 and 600 nm. How does the brain interpret these signals? The answer again lies with multiple receptors, in this case the green and blue cones. Green cones respond very strongly to light of 520 nm, as it is close to their preferred wavelength, but respond weakly to 600 nm light. Blue cones do not respond to 600 nm light and are barely activated at 520 nm. As a result, 520 nm light is perceived as green, whereas 600 nm is seen as orange. Thus, through varying combinations of photoreceptors, we are able to perceive a spectrum of colors.

Similarly, the complex flavors we perceive when eating are a result of combinations of chemoreceptors with different affinities for natural ligands. The broad tuning curves of a large number of distinct olfactory and gustatory receptors afford many combinatorial possibilities.

The existence of submodalities points to an important principle of sensory coding, namely that the range of stimulus energies—such as the wavelength of light—is deconstructed into smaller, simpler components whose intensity is monitored over time by specialized receptors that transmit information in parallel to the brain. The brain eventually integrates these diverse components of the stimulus to convey an ensemble representation of the sensory event. The ensemble hypothesis is even more important when we examine the representation of sensory events in the central nervous system. Although most studies of sensory processing have examined how individual neurons respond to temporally varying stimuli, the current challenge is to decipher how sensory information is

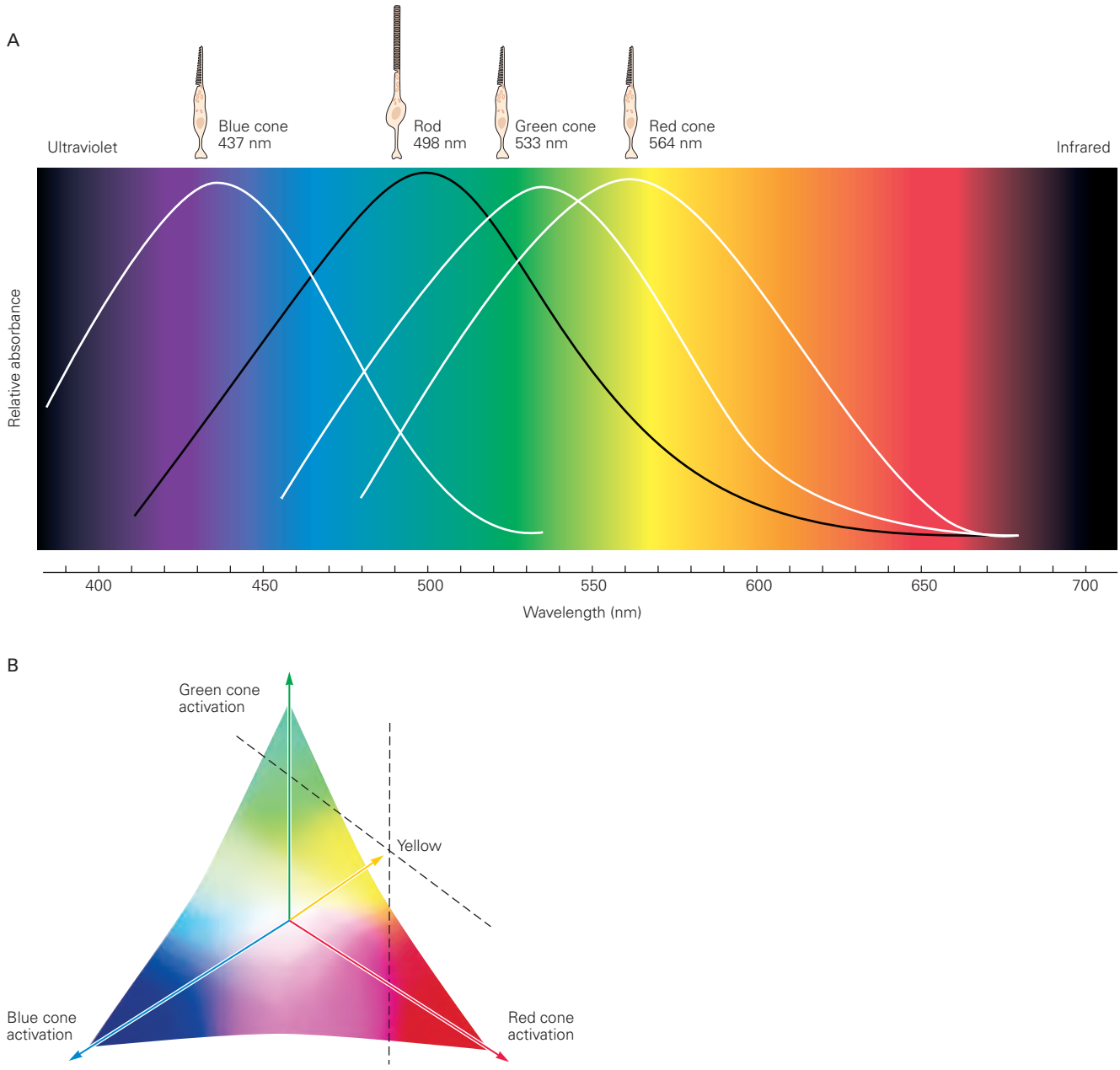

Figure 17–5 Human perception of colors results from the simultaneous activation of three different classes of photoreceptors in the retina.

A. The visible spectrum of light spans wavelengths of 390 to 670 nm. Individual photoreceptors are sensitive to a broad range of wavelengths, but each is most responsive to light in a particular spectral band. Thus, cone cells are classified as red, green, or blue type photoreceptors. Changes in the relative activation of each of the three cone types account for the perception of specific colors. (Adapted from Dowling 1987.)

B. The neural coding of color and brightness in the retina can be portrayed as a three-dimensional vector in which the strength of activation of each cone type is plotted along one of the three axes. Each point in the vector space represents a unique pattern of activation of the three cone types. Direction in the vector indicates the relative activity of each cone type and the color seen. In the example shown here, strong activation of **red cones** along with moderate stimulation of **green cones** and weak activation of **blue cones** produces the perception of **yellow**. The length of the vector from the origin to the point represents the intensity or brightness of light in that region of the retina.

distributed across populations of neurons responding to the same event at the same time.

Receptor Population Codes Transmit Sensory Information to the Brain

The receptor potential generated by an adequate stimulus produces a local depolarization or hyperpolarization of the sensory receptor neuron whose amplitude is proportional to the stimulus intensity. However, the sense organs are located at distances far enough from the central nervous system that passive propagation of receptor potentials is insufficient to transmit signals there. To communicate sensory information to the brain, a second step in neural coding must occur. The receptor potential produced by the stimulus must be transformed into sequences of action potentials that can be propagated along axons. The analog signal of stimulus magnitude in the receptor potential is transformed into a digital pulse code in which the frequency of action potentials is proportional to the intensity of the stimulus (Figure 17–6A). This is spike train *encoding*.

The recognition of an analog-to-digital transformation dates back to 1925 when Edgar Adrian and Yngve Zotterman discovered the all-or-none properties of the action potential in sensory neurons. Despite the simple recording instruments available at that time, Adrian and Zotterman discovered that the frequency of firing—the number of action potentials per second—varies with the strength of the stimulus and its duration; stronger stimuli evoke larger receptor potentials that generate a greater number and a higher frequency of action potentials. This signaling mechanism is termed *rate coding*.

In later years, as recording technology improved and digital computers allowed precise quantification of the timing of action potentials, Vernon Mountcastle and his colleagues demonstrated a precise correlation between sensory thresholds and neural responses, as well as the parametric relationship between neural firing rates and the perceived intensity of sensations (Figure 17–6B). They also found that the intensity of a stimulus is represented in the brain by all active neurons in the receptor population. This type of *population code* depends on the fact that individual receptors in a

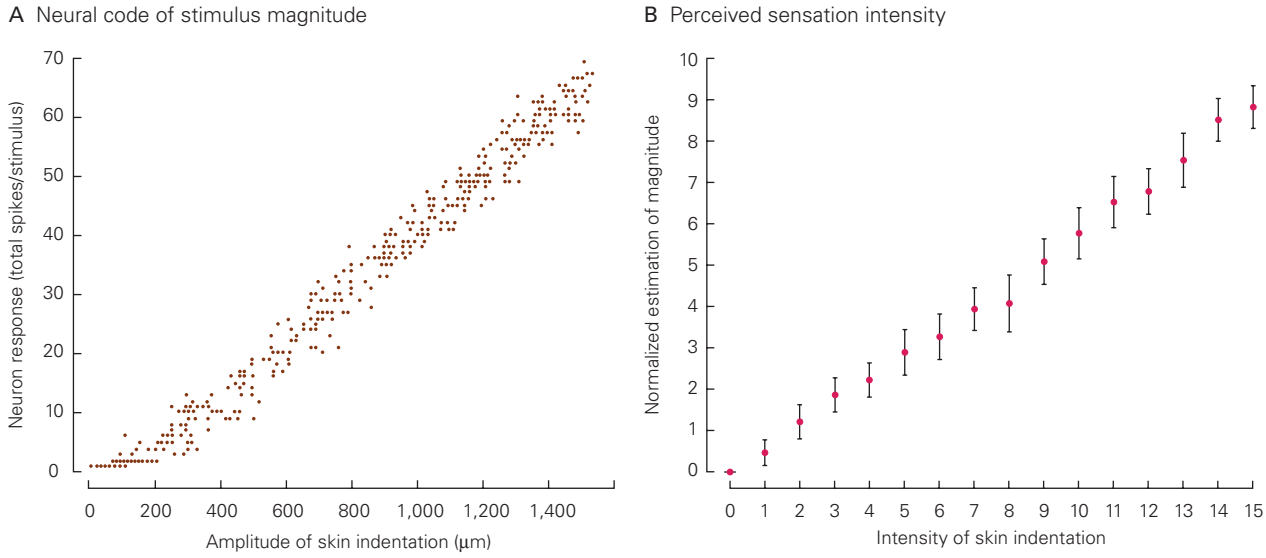

Figure 17–6 The firing rates of sensory neurons encode the stimulus magnitude. The two plots indicate that the neural coding of stimulus intensity is faithfully transmitted from peripheral receptors to cortical centers that mediate conscious sensation. (Adapted, with permission, from Mountcastle, Talbot, and Kornhuber 1966.)

A. The number of action potentials per second recorded from a touch receptor in the hand is proportional to the amplitude of skin indentation. Each dot represents the response of the receptor to pressure applied by a small probe. The relationship between the neural firing rate and the pressure stimulus is linear. This receptor does not respond to stimuli weaker than 200 μm, its touch threshold.

B. Estimates made by human subjects 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 physical strength resembles the relation between the discharge frequency of the sensory neuron and the stimulus amplitude.

sensory system differ in their sensory thresholds or in their affinity for particular molecules.

Most sensory systems have low- and high-threshold receptors. When stimulus intensity changes from weak to strong, low-threshold receptors are first recruited, followed by high-threshold receptors. For example, rod cells in the retina are activated by very low light levels and reach their maximal receptor potentials and firing rates in dim daylight. Cone cells do not respond in very dim light but do report differences in daylight brightness. The combination of the two types of photoreceptors allows us to perceive light intensity over several orders of magnitude. Parallel processing by low- and high-threshold receptors thus extends the dynamic range of a sensory system.

Distributed patterning of firing in neural ensembles allows the use of vector algebra to quantify how stimulus properties are distributed across populations of active neurons. For example, although humans possess only three types of cone cells in the retina, we can clearly identify colors across the entire spectrum of visible light. In Figure 17–5B, we see that the color yellow can be synthesized in the mind by specific combinations of activity in red, green, and blue cone cells (Figure 17–5B). Likewise, the color magenta results from other combinations of the same photoreceptor classes. Mathematically, the perceived hue can be represented in a three-dimensional vector space in which the strengths of activation of each receptor class are combined to yield a unique sensation.

High-dimensional multineuronal representation of stimuli across large populations of neurons is beginning to be analyzed as new techniques are developed for simultaneous recording and imaging of activity in neural ensembles. Ideally, the firing rates of each neuron in a population can be plotted in a coordinate system with multiple axes such as modality, location, intensity, and time. The neural components along these axes combine to form a vector that represents the population's activity. The vector interpretation is useful because it makes available powerful analytic techniques.

The possibilities for information coding through *temporal patterning* within and between neurons in a population are enormous. For example, the timing of action potentials in a presynaptic neuron can determine whether the postsynaptic cell fires. Two action potentials that arrive near synchronously will alter the postsynaptic neuron's probability of firing more than would action potentials arriving at different times. The relative timing of action potentials between neurons also has a profound effect on mechanisms of learning and synaptic plasticity, including long-term potentiation and depression at synapses (Chapter 54).

Sequences of Action Potentials Signal the Temporal Dynamics of Stimuli

The instantaneous firing patterns of sensory neurons are as important to sensory perception as the total number of spikes fired over long periods. Steady rhythmic firing in nerves innervating the hand is perceived as steady pressure or vibration depending upon which touch receptors are activated (Chapter 19). Bursting patterns may be perceived as motion. The patterning of spike trains plays an important role in encoding temporal fluctuations of the stimulus, such as the frequency of vibration or auditory tones, or changes in rate of movement. Humans can report changes in sensory experience that correspond to alterations within a few milliseconds in the firing patterns of sensory neurons.

Sensory systems detect *contrasts*, changes in the temporal and spatial patterns of stimulation. If a stimulus persists unchanged for several minutes without a change in position or amplitude, the neural response and corresponding sensation diminishes, a condition called *receptor adaptation*. Receptor adaptation is thought to be an important neural basis of perceptual adaptation, whereby a constant stimulus fades from consciousness. Receptors that respond to prolonged and constant stimulation—known as *slowly adapting* receptors—encode stimulus duration by generating action potentials throughout the period of stimulation (Figure 17–7A). In contrast, *rapidly adapting* receptors respond only at the beginning and end of a stimulus; they *cease* firing in response to constant amplitude stimulation and are active only when the stimulus intensity increases or decreases (Figure 17–7B). Rapidly and slowly adapting sensors illustrate another important principle of sensory coding: Neurons signal important properties of stimuli not only when they fire but also when they slow or stop firing.

The temporal properties of a changing stimulus are encoded as changes in the firing pattern, including the *interspike intervals*, of sensory neurons. For example, the touch receptors illustrated in Figure 17–7 fire at higher rates when a probe initially contacts the skin than when the pressure is maintained. The time interval between spikes is shorter when the skin is indented rapidly than when pressure is applied gradually. The firing rate of these neurons is proportional to both the speed at which the skin is indented and the total amount of pressure applied. During steady pressure, the firing rate slows to a level proportional to skin indentation (Figure 17–7A) or ceases entirely (Figure 17–7B). Firing of both neurons stops after the probe is retracted.