17

Sensory Coding

OUR SENSES ENLIGHTEN AND EMPOWER US. Through sensation, we form an immediate and relevant picture of the world and our place in it, informed by our past experience and preparing us for probable futures. Sensation provides immediate answers to three ongoing and essential questions: *Is something there? What is it?* and *What's changed?* To answer these questions, all sensory systems perform two fundamental functions: *detection* and *discrimination*. Because our world and our needed responses to it change with time, sensory systems can both *preferentially respond* and *adapt* to changing stimuli in the short term, and also *learn* to modify our responses to stimuli as our needs and circumstances change.

Since ancient times, humans have been fascinated by the nature of sensory experience. Aristotle defined five senses—vision, hearing, touch, taste, and smell—each linked to specific sense organs in the body: eyes, ears, skin, tongue, and nose. Pain was not considered to be a specific sensory modality but rather an affliction of the soul. Intuition, often referred to colloquially as a "sixth sense," was not yet understood to depend upon the experience of the classic sensory systems. Today, neurobiologists recognize intuition as inferences derived from previous experience and thus the result of cognitive as well as sensory processes.

In this chapter, we consider the organizational principles and coding mechanisms that are universal to all sensory systems. *Sensory information* is defined as neural activity originating from stimulation of receptor cells in specific parts of the body. Our senses include the classic five senses plus a variety of modalities not recognized by the ancients but essential to bodily function: the *somatic* sensations of pain, itch, temperature, and proprioception (posture and movement of our own body); *visceral* sensations (both conscious and

unconscious) necessary for homeostasis; and the *vestibular* senses of balance (the position of the body in the gravitational field) and head movement.

Sensation informs and enriches all life, and the fundamentals of sensory processing have been conserved throughout vertebrate evolution. Specialized receptors in each of the sensory systems provide the first neural representation of the external and internal world, transforming a specific type of stimulus

energy into electrical signals (Figure 17–1). All sensory information is then transmitted to the central nervous system by trains of action potentials that represent particular aspects of the stimulus. This information flows centrally to regions of the brain involved in the processing of individual senses, multisensory integration, and cognition.

The sensory pathways have both serial and parallel components, consisting of fiber tracts with
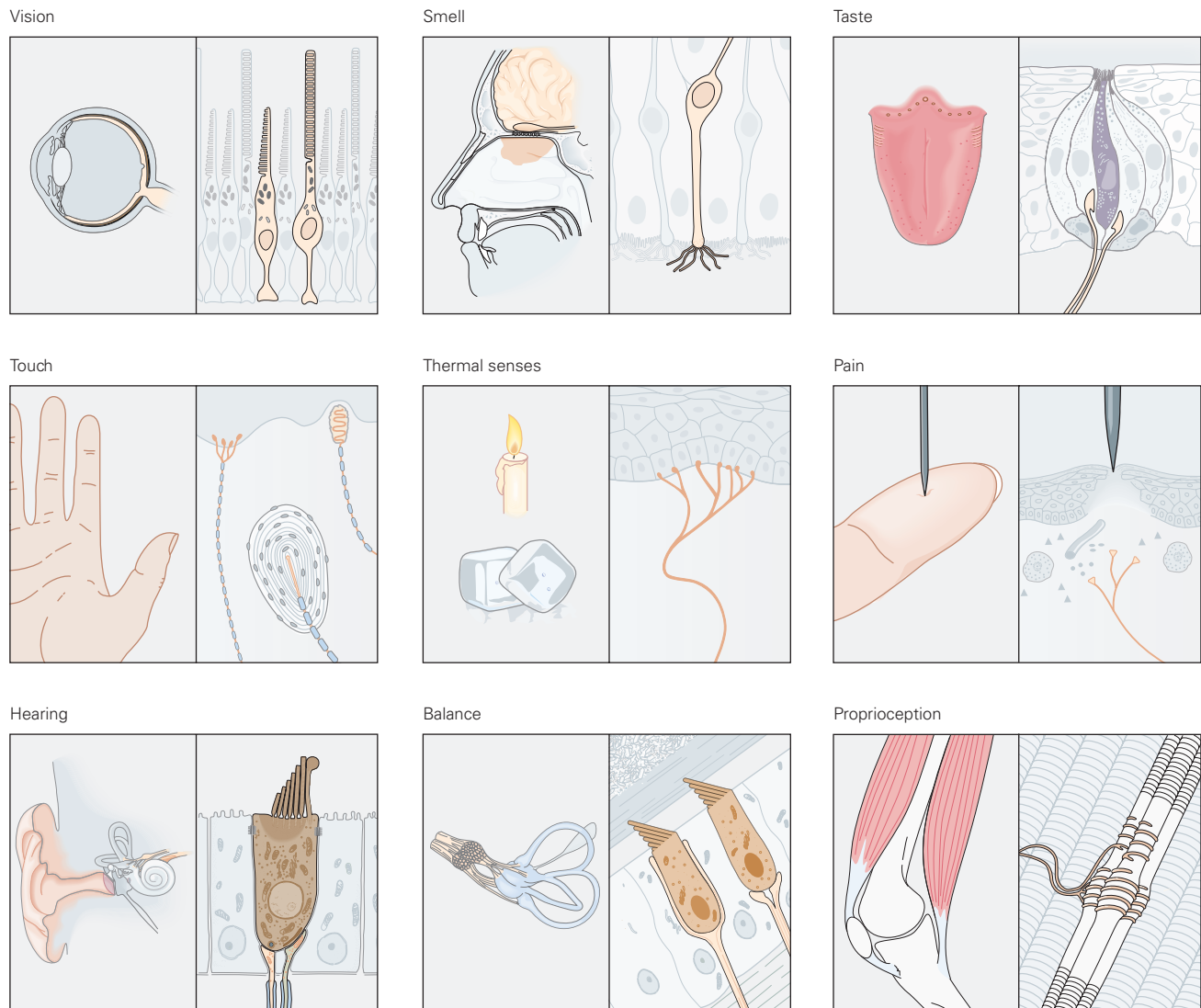
Figure 17–1 The major sensory modalities in humans are mediated by distinct classes of receptor neurons located in specific sense organs. Each class of receptor cell transforms one type of stimulus energy into electrical signals that are encoded as trains of action potentials (see Figure 17–4). The principal receptor cells include photoreceptors (vision), chemoreceptors (smell, taste, and pain), thermal receptors, and mechanoreceptors (touch, hearing, balance, and proprioception). The classic five senses—vision, smell, taste, touch, and hearing—and the sense of balance are mediated by receptors in the eye, nose, mouth, skin, and inner ear, respectively. The other somatosensory modalities—thermal senses, pain, visceral sensations, and proprioception—are mediated by receptors distributed throughout the body.

thousands or millions of axons linked by synapses that both transmit and transform information. Relatively simple forms of neural coding of stimuli by receptors are modulated by complex mechanisms in the brain to form the basis of cognition. Sensory pathways are also controlled by higher centers in the brain that modify and regulate incoming sensory signals by feeding information back to earlier stages of processing. Thus, perception is the product not simply of "raw" physical sensory information but also cognition and experience.

Both scientists and philosophers have examined the extent to which the sensations we experience accurately reflect the stimuli that produce them, and how they are altered by our inherently subjective and imprecise knowledge of the world. In prior centuries, the interest of European philosophers in sensation and perception was related to the question of human nature itself. Two schools of thought eventually dominated: empiricism, represented by John Locke, George Berkeley, and David Hume, and idealism, represented by René Descartes, Immanuel Kant, and Georg Wilhelm Friedrich Hegel.

Locke, the preeminent empiricist, advanced the idea that the mind at birth is a blank slate, or *tabula rasa*, void of any ideas. Knowledge, he asserted, is obtained only through sensory experience—what we see, hear, feel, taste, and smell. Berkeley extended this topic by questioning whether there was any sensory reality beyond the experiences and knowledge acquired through the senses. He famously asked: Does a falling tree make a sound if no one is near enough to hear it?

Idealists argued that the human mind possesses certain innate abilities, including logical reasoning itself. Kant classified the five senses as categories of human understanding. He argued that perceptions were not direct records of the world around us but rather were products of the brain and thus depended on the architecture of the nervous system. Kant referred to these brain properties as *a priori knowledge*.

Thus, in Kant's view, the mind was not the passive receiver of sense impressions envisaged by the empiricists. Rather, it had evolved to conform to certain universal conditions such as space, time, and causality. These conditions were independent of any physical stimuli detected by the body. For Kant and other idealists, this meant that knowledge is based not only on sensory stimulation alone but also on our ability to organize and interpret sensory experience. If sensory experience is inherently subjective and personal, they said, it may not be subject to empirical analysis. As the empirical investigation of perception matured, both schools proved partially correct.

Psychophysics Relates Sensations to the Physical Properties of Stimuli

The modern study of sensation and perception began in the 19th century with the emergence of experimental psychology as a scientific discipline. The first scientific psychologists—Ernst Weber, Gustav Fechner, Hermann Helmholtz, and Wilhelm Wundt—focused their experimental study of mental processes on sensation, which they believed was the key to understanding the mind. Their findings gave rise to the fields of psychophysics and sensory physiology.

Psychophysics describes the relationship between the physical characteristics of a stimulus and attributes of the sensory experience. *Sensory physiology* examines 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 both human and animal studies. For example, functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) have been used in controlled experiments to identify regions of the human brain involved in the perception of pain or the identification of specific types of objects or particular persons and places.

Psychophysics Quantifies the Perception of Stimulus Properties

Early scientific studies of the mind focused not on the perception of complex qualities such as color or taste but on phenomena that could be isolated and measured precisely: the size, shape, amplitude, velocity, and timing of stimuli. Weber and Fechner developed simple experimental paradigms to study how and under what conditions humans are able to distinguish between two stimuli of different amplitudes. They quantified the intensity of sensations in the form of mathematical laws that allowed them to predict the relationship between the magnitude of a stimulus and its detectability, including the ability to discriminate between different stimuli.

In 1953, Stanley S. Stevens demonstrated that the subjective experience of the intensity (I) of a stimulus (S) is best described by a power function. Stevens's law states that,
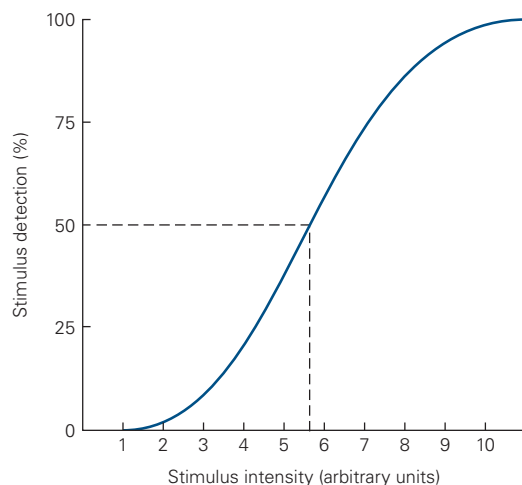
$$I = K(S - S_0)^n,$$

where the *sensory threshold* (S_0) is the lowest stimulus strength a subject can detect, and K is a constant. For some sensations, such as the sense of pressure on

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.

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.

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.

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

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.

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?"

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

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

B
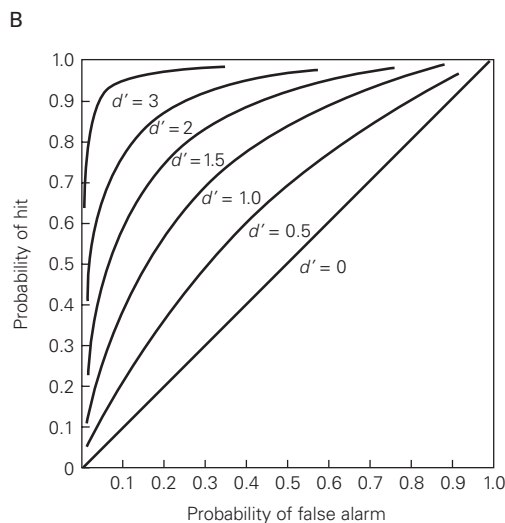
Figure 17–3B A receiver operating characteristic (ROC) plot displays the results of sets of trials, each collected in matrices such as those in Figure 17–3A. The vertical axis plots the fraction or probability of hits as a function of fraction or probability of false alarms on the horizontal axis. It 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.

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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

A Chemoreceptor

Odorants

B Photoreceptor

Light

C Mechanoreceptor

Pressure
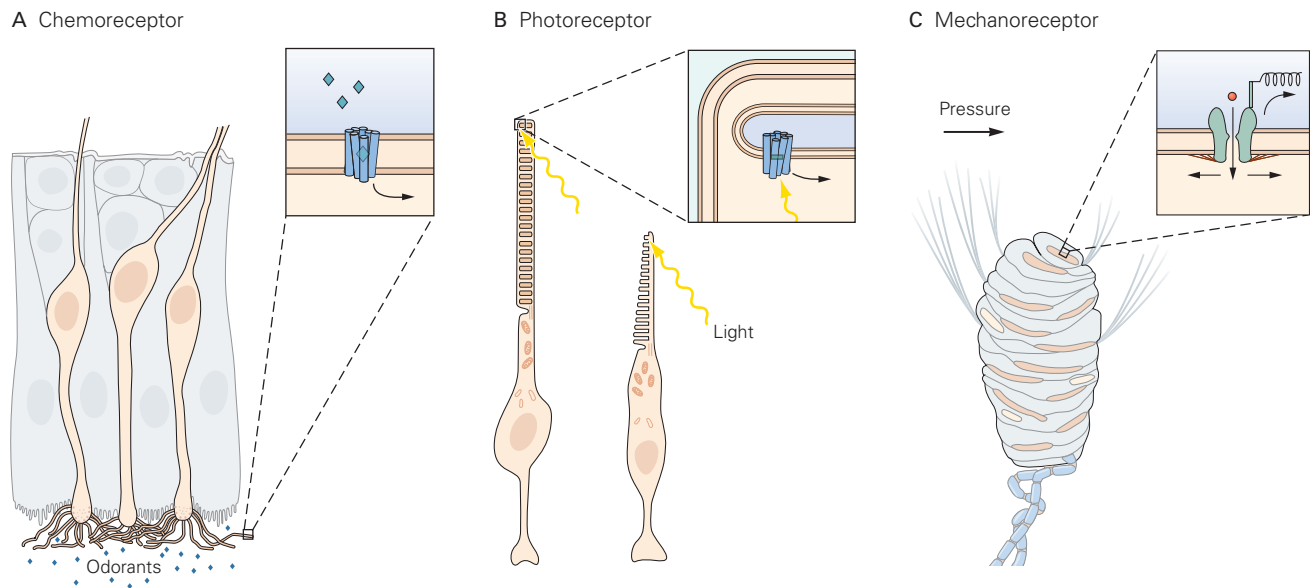
Figure 17–4 Sensory receptors are specialized to transduce a particular type of stimulus energy into electrical signals. Sensory receptors are classified as chemoreceptors, photoreceptors, or mechanoreceptors depending on the class of stimulus energy that excites them. They transform that energy into 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
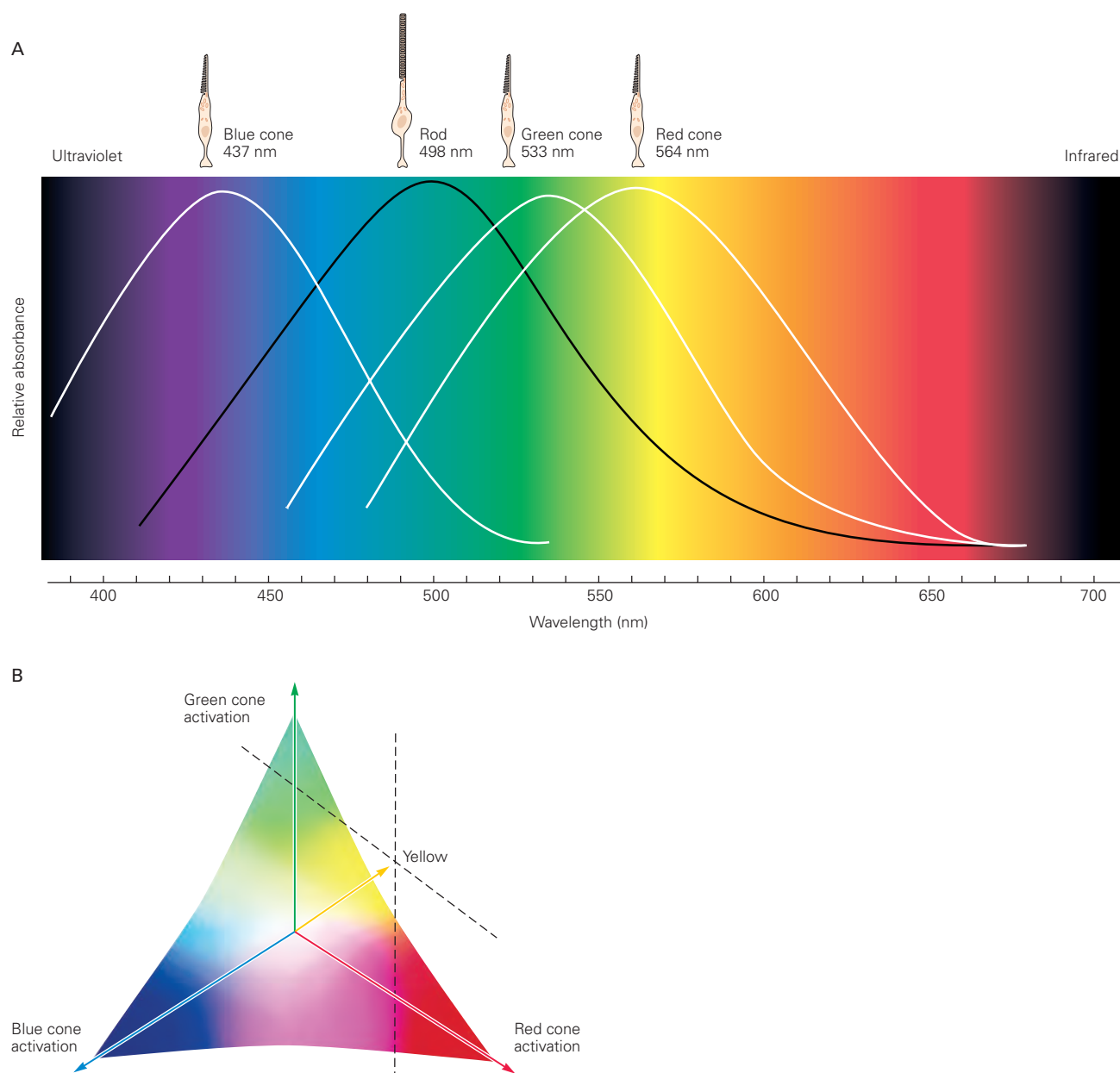
Figure 17–5 Human perception of colors results from the simultaneous activation of three different classes of photoreceptors in the retina.

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

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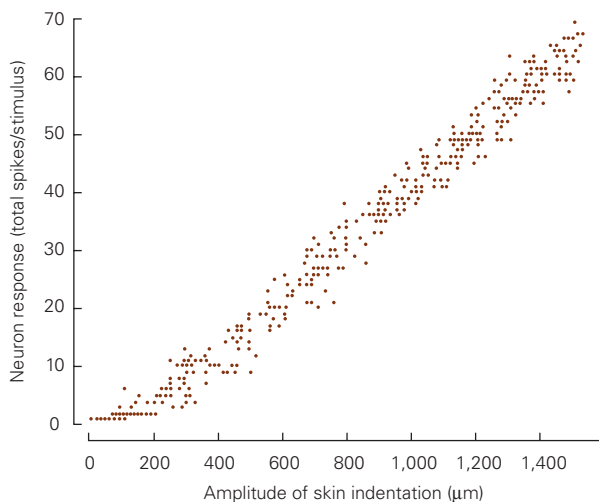
B Perceived sensation intensity
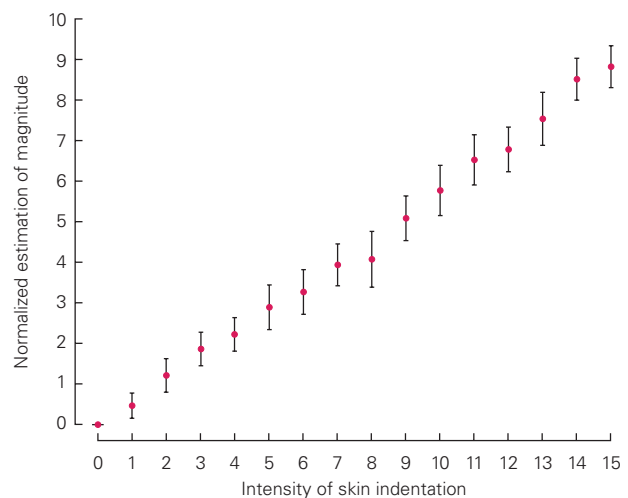
Figure 17–6 The firing rates of sensory neurons encode the stimulus magnitude. The two plots indicate that the neural coding of stimulus intensity is faithfully transmitted from peripheral receptors to cortical centers that mediate conscious sensation. (Adapted, with permission, from Mountcastle, Talbot,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

A Slowly adapting receptor

B Rapidly adapting receptor
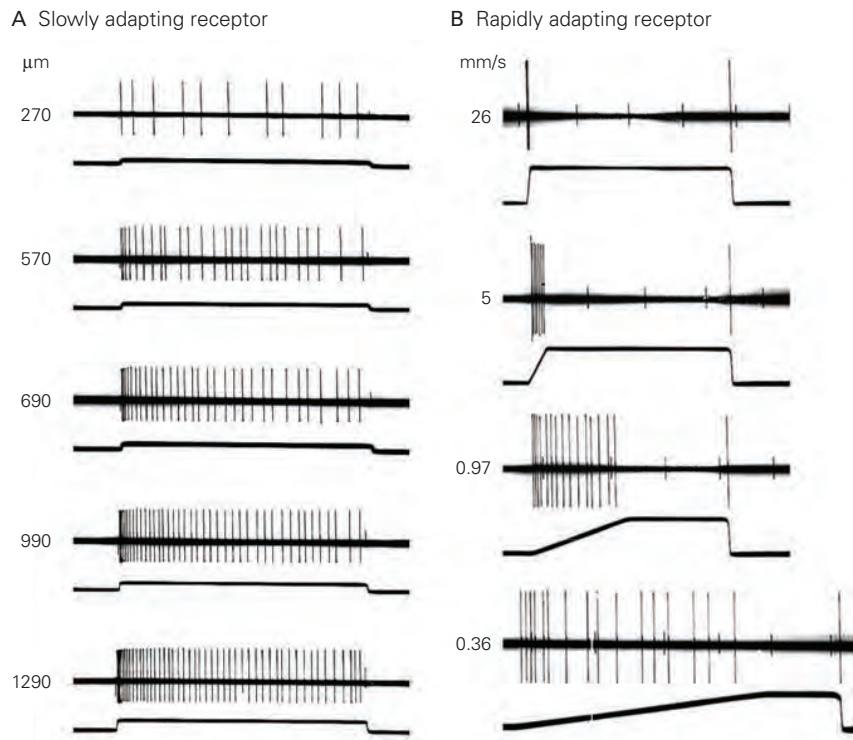
Figure 17–7 Firing patterns of sensory neurons convey information about the stimulus intensity and time course. These records illustrate responses of two different classes of touch receptors to a probe pressed into the skin. The stimulus amplitude and time course are shown in the lower trace of each pair; the upper trace shows the action potentials recorded from the sensory nerve fiber in response to the stimulus.

A. A slowly adapting mechanoreceptor responds as long as pressure is applied to the skin. The total number of action potentials discharged during the stimulus is proportional to the amount of pressure applied to the skin. The firing rate is higher

at the beginning of skin contact than during steady pressure, as this receptor also detects how rapidly pressure is applied to the skin. When the probe is removed from the skin, the spike activity ceases. (Adapted, with permission, from Mountcastle, Talbot, and Kornhuber 1966.)

B. A rapidly adapting mechanoreceptor responds at the beginning and end of the stimulus, signaling the rate at which the probe is applied and removed; it is silent when pressure is maintained at a fixed amplitude. Rapid motion evokes a brief burst of high-frequency spikes, whereas slow motion evokes a longer-lasting, low-frequency spike train. (Adapted, with permission, from Talbot et al. 1968.)

The Receptive Fields of Sensory Neurons Provide Spatial Information About Stimulus Location

The position of a sensory neuron's input terminals in the sense organ is a major component of the specific information conveyed by that neuron. The skin area, location in the body, retinal area, or tonal domain in which stimuli can activate a sensory neuron is called its *receptive field* (Figure 17–8). The region from which a sensation is perceived to arise is called the neuron's *perceptive field*. The two usually coincide.

The dimensions of receptive fields play an important role in the ability of a sensory system to encode detailed spatial information. The objects that we see with our eyes or hold in our hands are much larger than the receptive field of an individual sensory neuron,

and therefore stimulate groups of adjacent receptors. The size of the stimulus therefore determines the total number of receptors that are activated. In this manner, the spatial distribution of active and silent receptors provides a neural image of the size and contours of the stimulus.

The spatial resolution of a sensory system depends on the total number of receptor neurons and the distribution of receptive fields across the area covered. The projection neurons for regions of the body with a high density of receptors, such as the retinal ganglion cells representing the central retina (the fovea), have small receptive fields because they receive inputs from a small number of bipolar cells, each of which receives input from a few closely packed photoreceptors. Because of the high density of receptors in the

Figure 17–8 The receptive field of a sensory neuron. The receptive field of a touch-sensitive neuron denotes the region of skin where gentle tactile stimuli evoke action potentials in that neuron. It encompasses all of the receptive endings and terminal branches of the sensory nerve fiber. If the fiber is stimulated electrically with a microelectrode, the subject experiences touch localized on the skin. The area from which the sensation is perceived to arise is called the *perceptive field*. A patch of skin contains many overlapping receptive fields, allowing sensations to shift smoothly from one sensory neuron to the next in a continuous sweep. The axon terminals of sensory neurons in the central nervous system are arranged somatotopically, providing an orderly map of the innervated region of the body.
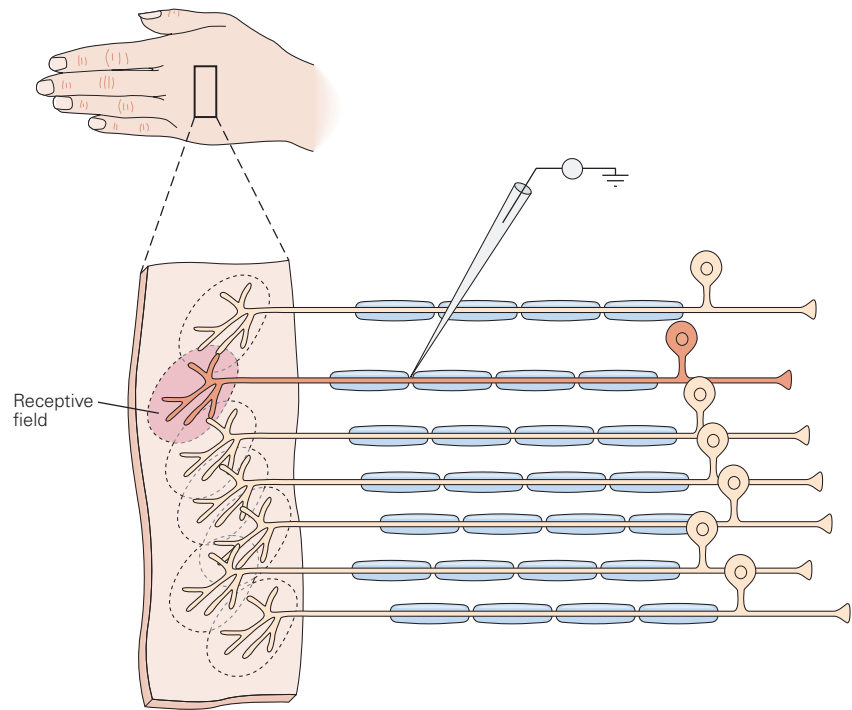
Receptive field

fovea, the population of neurons transmits a very detailed representation of the visual scene. Ganglion cells in the periphery of the retina have larger receptive fields because the receptor density is much lower. The dendrites of these ganglion cells receive information from a wider area of the retina, and thus integrate light intensity over a greater portion of the visual field. This arrangement yields a less detailed image of the visual scene (Figure 17–9). Similarly, the region of the body most often used to touch objects is the hand. Not surprisingly, mechanoreceptors for touch are concentrated in the fingertips, and the receptive fields on the hand are smaller than those on the arm or trunk.

Central Nervous System Circuits Refine Sensory Information

The central connections of a sensory neuron determine how that neuron's signals influence our sensory experience. Action potentials in nerve fibers of the cochlea, for example, evoke the sensation of a tone whether they are initiated by sound waves acting on hair cells or by electrical stimulation with a neural prosthesis.

The parcellation of a stimulus into its components, each encoded by an individual type of sensory receptor or projection neuron, is an initial step in sensory processing. These components are integrated into a representation of an object or scene by neural networks in the brain. This process allows the brain to select certain abstract features of an object, person, scene, or external event from the detailed input of many receptors. As a result, the representation formed in the brain may enhance the saliency of features that are important at the moment while ignoring others. In this sense, our percepts are not merely reflections of environmental events, but also constructs of the mind.

How we experience the sensations reported by primary receptors is also subject to modification or learning. Initially aversive odors and tastes, for example, can become attractive over time because of familiarity or changes in context or association. The pleasure elicited by photos of a respected baseball player can be converted to disdain should he subsequently appear in the uniform of a rival team.

In the early stages of sensory information processing in the central nervous system, each class of peripheral receptors provides input to clusters of neurons in relay nuclei that are dedicated to one sensory modality. That is, each sensory modality is represented by an ensemble of central neurons connected to a specific class of receptors. Such ensembles are referred to as *sensory systems*, and include the somatosensory, visual, auditory, vestibular, olfactory, and gustatory systems (see Table 17–1).
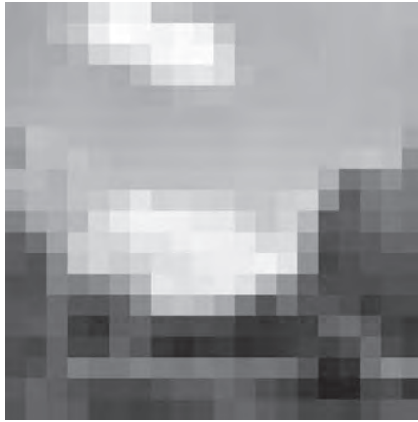
A 20 × 20 pixels   B 60 × 60 pixels   C 400 × 400 pixels

Figure 17–9 The visual resolution of scenes and objects depends on the density of photoreceptors that mediate the image. The resolution of detail is inversely correlated with the area of the receptive field of individual neurons. Each square or pixel in these images represents a receptive field. The gray scale in each pixel is proportional to the average light intensity in the corresponding receptive field. If there are a small number of neurons, and each spans a large area of the image, the result is a very schematic representation of the scene (**A**). As the density of neurons increases, and the size of each receptive field decreases, the spatial detail becomes clearer (**B, C**). The increased spatial resolution comes at the cost of the larger number of neurons required to transmit the information. (Photographs reproduced, with permission, from Daniel Gardner.)
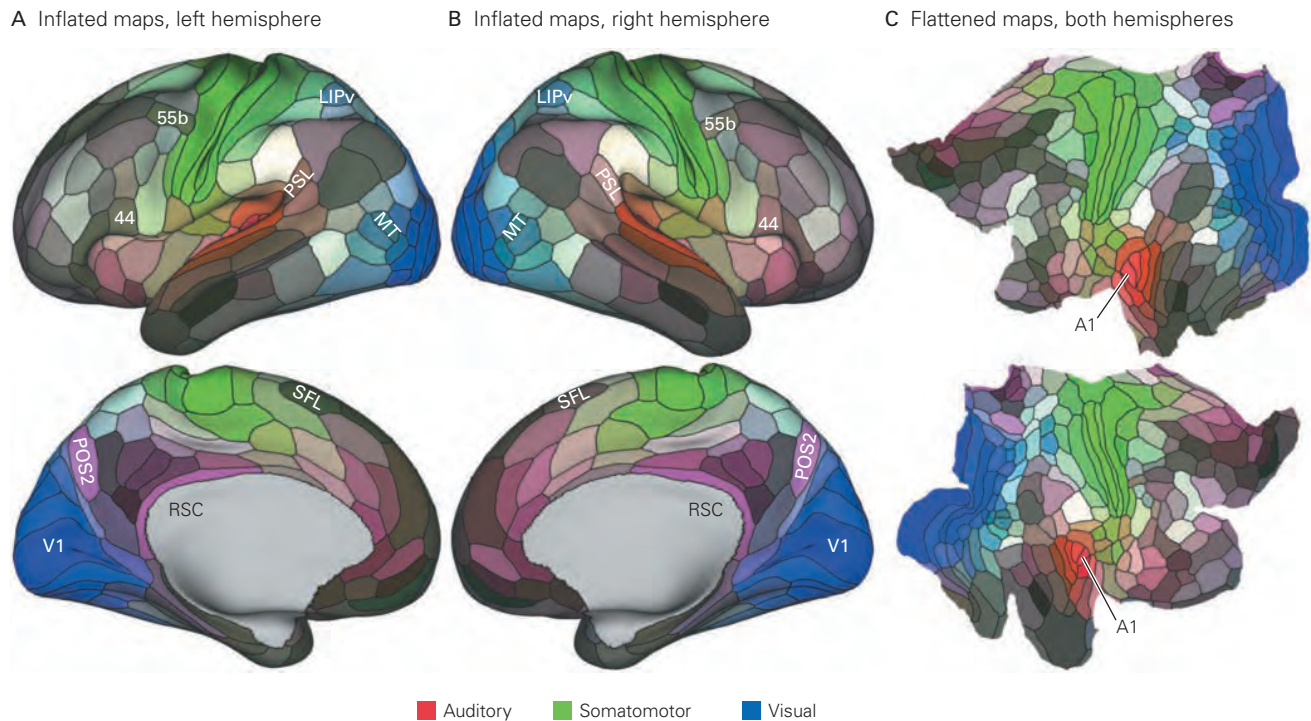
The brain has evolved to process and respond to this rich ensemble of sensory information. The activation of sensory, cognitive, and motor systems in the human brain can be visualized in real time with fMRI techniques. Maurizio Corbetta, Marcus Raichle, and colleagues discovered coherent fluctuations in low-frequency (0.01–0.1 Hz) components of the blood oxygen level–dependent (BOLD) signal during the "resting" state in brain areas that are anatomically connected and activated together during specific behaviors. Figure 17–10 highlights three functionally specialized networks of brain areas that respond to auditory (in red), somatomotor (in green), and visual (in blue) inputs. Other areas are multisensory, integrating information from several different modalities. Spontaneous correlation of firing of these networks in the absence of direct sensory stimuli or performance of motor tasks suggests that excitability within resting state sensory or motor networks may signal readiness to process information for future sensation or action. Deficits in sensory, cognitive, or motor function following local brain injury may result not just from impairment of one specific area, or node, but rather disruption of the circuit or circuits that include that node.

Synapses in sensory pathways provide an opportunity to modify the signals from receptors. Most neurons in relay nuclei receive convergent excitatory inputs from many presynaptic neurons (Figure 17–11A), integrate those inputs, combine them with inhibitory and top-down signals, and transmit the processed information to higher brain areas. Horace Barlow proposed that sensory systems demonstrate *efficient coding*, which includes sensory relays recoding sensory messages so that their redundancy is reduced, but comparatively little information is lost. Likewise, each receptor neuron excites multiple postsynaptic relay neurons.

Convergent excitatory networks provide a mechanism for spatial summation of inputs, strengthening signals of functional importance. One example of how such circuits are used is detection of synchronous inputs from multiple nearby locations but not others, thereby providing the first step toward *orientation tuning* of central neurons. Relay neurons are also interconnected with their neighbors, forming recurrent excitatory connections that amplify sensory signals. Such *recurrent networks* are also a feature of some deep learning algorithms used by artificial neural networks to classify sensory patterns.

A relay neuron's receptive field is also shaped by inhibitory input. The inhibitory region of a receptive field provides an important mechanism for enhancing the contrast between stimuli, giving the sensory system additional power to resolve spatial detail. Inhibitory interneurons modulate the excitability of neurons in relay nuclei, thereby regulating the amount of sensory information transmitted to higher levels of

A Inflated maps, left hemisphere   B Inflated maps, right hemisphere   C Flattened maps, both hemispheres

Auditory   Somatomotor   Visual

Figure 17–10 Distinct regions of the human brain process information for individual sensory modalities, multisensory systems, motor activity, or cognitive function. The human cerebral cortex has been divided into 180 functional areas by the Human Connectome Project based largely on a variety of fMRI techniques and neuroanatomy. Early auditory areas (**red**), somatosensory and motor areas (**green**), and visual areas (**blue**) are shaded in primary colors. Mixed colors indicate multisensory areas: visual and somatosensory/motor (**blue-green, LIPv, MT**); or visual and auditory (**pink to purple, POS2, RSC**). Language networks include areas 55b, 44, SFL, and PSL in both hemispheres. Gray-scaled regions serve cognitive functions; they comprise the anticorrelated "task-positive" (**light shading**) and "default mode" (**dark shading**) networks. The maps show brain regions located on the surface gyri and within adjacent cortical sulci. Note the similarity of brain organization

between the two hemispheres. Data available at https://balsa.wustl.edu/study/RVVG. (Reproduced, with permission, from Glasser et al. 2016. Copyright © 2016 Springer Nature.)

A. Inflated maps of the left hemisphere. The top map is a lateral view and the bottom map is a medial view.

B. Similar maps of the right hemisphere.

C. Flattened maps show the functional organization of both hemispheres (left at top, right at bottom).

(Abbreviations: **A1,** primary auditory cortex; **LIPv,** lateral intraparietal area, ventral portion; **MT,** middle temporal area; **POS2,** parieto-occipital sulcus area 2; **PSL,** perisylvian language area; **RSC,** retrosplenial complex; **SFL,** superior frontal language area; **V1,** primary visual cortex; **Area 55b,** newly identified language area; **Area 44,** part of Broca's area.)

a network (Figure 17–11B). Inhibitory circuits are also useful for suppressing irrelevant information during goal-directed behaviors, thereby focusing attention on specific task-related inputs. Additionally, inhibitory networks allow the context of a stimulus to modify the strength of excitation evoked by that stimulus, an important process called *normalization*.
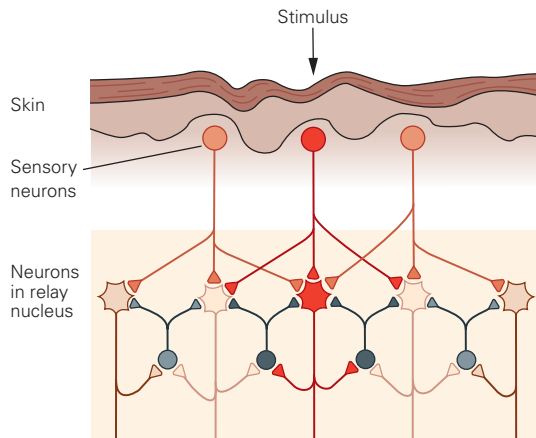
The responses of central neurons to sensory stimuli are more variable from trial to trial than those of peripheral receptors. Central sensory neurons also fire irregularly before and after stimulation and during periods when no stimuli are present. The variability of the evoked central responses is a result of several factors: the subject's state of alertness, whether attention

is engaged (Figure 17–12), previous experience of that stimulus, and recent activation of the pathway by similar stimuli. Similarly, the context of stimulus presentation, subjective intentions, motor plans that may require feedback, or intrinsic oscillations of the neuron's membrane potential can all modify incoming sensory information.
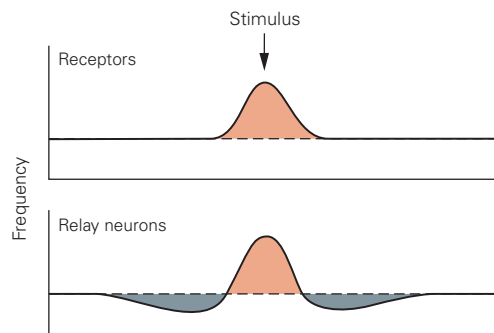
The Receptor Surface Is Represented Topographically in the Early Stages of Each Sensory System

The axons of sensory projection neurons terminate in the brain in an orderly manner that retains their spatial arrangement in the receptor sheet. Sensory neurons for
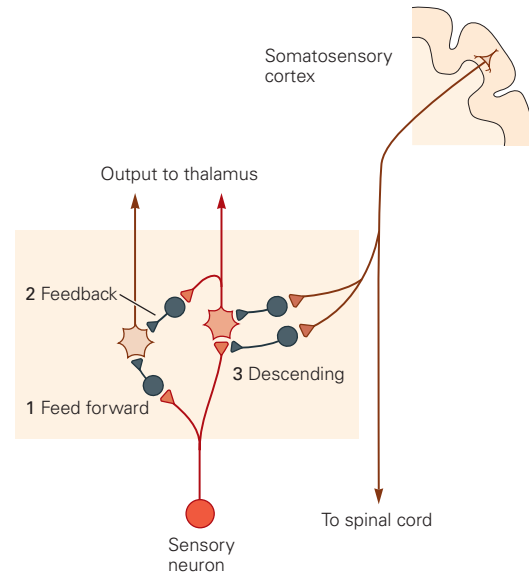
A Typical neural circuit for sensory processing

C Types of inhibition in relay nuclei

B Spatial distribution of excitation and inhibition among relay neurons

Figure 17–11 Relay neurons in sensory systems integrate a variety of inputs that shape stimulus information.

A. Sensory information is transmitted in the central nervous system through hierarchical processing networks. Neural signaling initiated by a stimulus to the skin reaches a large group of postsynaptic neurons in relay nuclei in the brain stem and thalamus and is most strong in neurons in the center of the array of postsynaptic cells (**red neuron**). (Adapted, with permission, from Dudel 1983.)

B. Inhibition (**gray areas**) mediated by local interneurons (**gray**) confines excitation (**orange area**) to the central zone in the array of relay neurons where stimulation is strongest. This pattern of inhibition within the relay nucleus enhances the contrast between strongly and weakly stimulated relay neurons.

C. Inhibitory interneurons in a relay nucleus are activated by three distinct excitatory pathways. **1. Feed-forward** inhibition is initiated by the afferent fibers of sensory neurons that terminate on the inhibitory interneurons. **2. Feedback** inhibition is initiated by recurrent collateral axons of neurons in the output pathway from the nucleus that project back to interneurons in the source nucleus. The interneurons in turn inhibit nearby output neurons, creating sharply defined zones of excitatory and inhibitory activity in the relay nucleus. In this way, the most active relay neurons reduce the output of adjacent, less active neurons, thus ensuring that only one of two or more active neurons will send out signals. **3. Descending** inhibition is initiated by neurons in other brain regions such as the cerebral cortex. The descending commands allow cortical neurons to control the afferent relay of sensory information, providing a mechanism by which attention can select sensory inputs.

touch in adjacent regions of the skin project to neighboring neurons in the central nervous system, and this topographic arrangement of receptive fields is preserved throughout the early somatosensory pathways. Each primary sensory area in the brain thus contains a topographic, spatially organized map of the sense organ. This topography extends to all levels of a sensory system. Within these maps, specificity—the qualities to which neurons are most narrowly tuned—provides clues to the functional organization of that region of the brain.

In the first and subsequent relay nuclei of the somatosensory, visual, and auditory systems, adjacent neurons represent adjacent areas of the body,
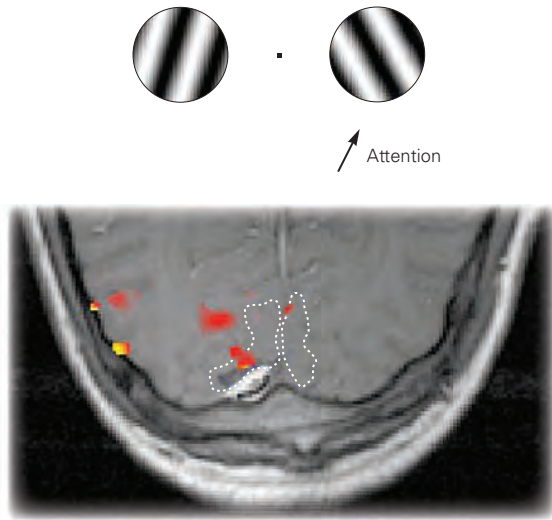
Figure 17–12 Attention to a visual stimulus alters responses of neurons in visual cortical areas. When we pay attention to a stimulus, we select certain sensory inputs for cognitive processing and ignore or suppress other information. Functional MRI is used in this study to measure the effects of attention to visual stimuli on neural responses in human primary visual (V1) cortex (**white dashed lines** on the brain anatomical section, **lower panel**). Moving grating stimuli (**upper panel**) were presented simultaneously to the right and left visual fields while subjects stared at a central fixation point (**black dot**). The subjects performed a motion discrimination task, attending (without moving their eyes) to one of the two oriented gratings. When stimuli were attended in the right visual field, neural activity (**red**) increased significantly in the left hemisphere, but not in the right hemisphere, even though the stimuli were presented to both eyes. When the subject attended to the grating in the left visual field, a similar focus of activity occurred in the right V1 cortex, and activity dropped in the left hemisphere (not shown). (Adapted from Gandhi, Heeger, and Boynton, 1999.)

retina, and cochlea, respectively. The organization of these nuclei is thus said to be somatotopic, retinotopic, or tonotopic. Nuclei in the auditory system are tonotopic because the cochlear hair cells of the inner ear are arranged to create an orderly shift in frequency sensitivity from cell to cell (Figure 26–2). Neurons in the primary sensory areas of the cerebral cortex maintain these location-specific features of a stimulus, and the functional maps of these early cortical areas are likewise somatotopic, retinotopic, or tonotopic.

Sensory information flows serially through hierarchical pathways, including multiple levels of the cerebral cortex, before ending in brain regions that are concerned with cognition and action. Forming the percepts that inform these regions requires integration of lower-level inputs that report only information from

small areas of the sense organ. Neurons in the cerebral cortex are specialized to integrate and so detect specific features of stimuli beyond merely their location in the sense organ. Such neurons are said to be *tuned* to combined stimulus features represented by ensembles of sensory receptors. These neurons respond preferentially to stimulus properties such as the orientation of edges (eg, simultaneous activation of specific groups of receptors), direction of motion, or tonal sequences of frequencies (temporal pattern of receptor activation). Central auditory neurons are less selective for frequency and more selective for certain kinds of sound. For example, some neurons are specific for vocalizations by members of the same species. In each successive stage of cortical processing, the spatial organization of stimuli is progressively lost as neurons become less concerned with the descriptive features of stimuli and more concerned with properties of behavioral importance. Details of these central sensory transformations are presented in succeeding chapters that describe specific sensory systems.

Sensory Information Is Processed in Parallel Pathways in the Cerebral Cortex

Distributed spatial coding is ubiquitous in sensory systems for two reasons. First, it takes advantage of the parallel architecture of the nervous system. There are approximately 100 million neurons in each primary sensory area of the cerebral cortex, and the possible number of combinatorial patterns of neural activity far exceeds the number of atoms in the universe. Second, each neuron codes the intensity and timing of a stimulus as well as its location in the receptor sheet. It fires only when many of its excitatory synapses receive action potentials and most of the inhibitory synapses do not, firing in response to specific patterns of stimulation but not to others. Since many cortical neurons receive input from 1,000 to 10,000 synapses, the information coding potential is enormous.

One of the most important insights into feature detection in the cortex arose from combined physiological and anatomical studies of the cortical visual pathways by Mortimer Mishkin and Leslie Ungerleider in the early 1980s. They discovered that sensory information arriving in the primary visual areas is divided in two parallel pathways.

One pathway carries information needed for classification of images, while the other conveys information needed for immediate action. Visual features that identify *what* an object is are transmitted in a *ventral pathway* to the temporal lobe and eventually to the hippocampus and entorhinal cortex. Visual information
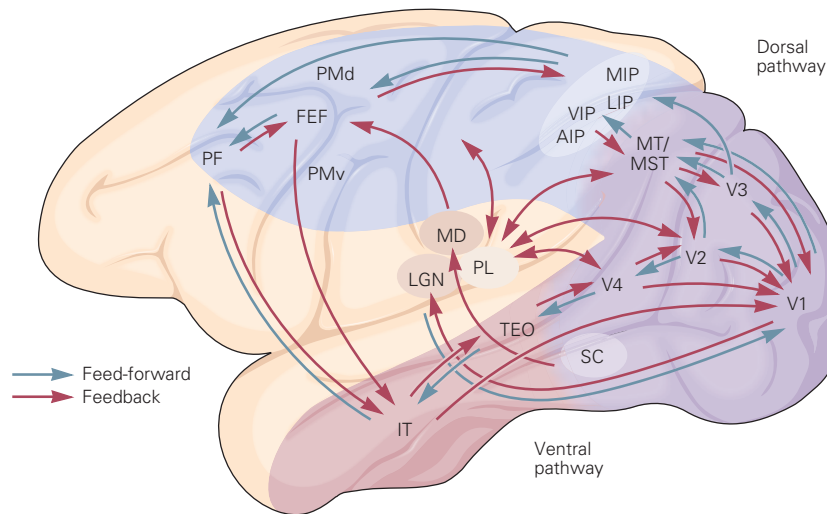
Figure 17–13 Visual stimuli are processed by serial and parallel networks in the cerebral cortex. When you read this text, the spatial pattern of the letters is sent to the cerebral cortex through successive synaptic links comprising photoreceptors, bipolar cells of the retina, retinal ganglion cells, cells in the lateral geniculate nucleus (**LGN**) of the thalamus, and neurons of the primary visual cortex (**V1**). Within the cortex, there is a gradual divergence to successive processing areas called ventral and dorsal streams that are neither wholly serial nor parallel. The ventral stream in the temporal lobe (**red shading**) analyzes and encodes information about the form and structure of the visual scene and objects within it, delivering this information to the parahippocampal cortex (not shown) and prefrontal cortex (**PF**). The dorsal stream in the parietal lobe (**blue shading**) analyzes and represents

information about stimulus location and motion and delivers this information to motor areas of the frontal cortex that control movements of the eyes, hand, and arm. The anatomical connections between these areas are reciprocal, involving both feedforward and feedback circuits. The zone of overlap (**purple**) shows that both pathways originate from the same source in **V1**. Connections to subcortical structures in the thalamus and midbrain are defined in Figure 21–7B. (Abbreviations: **V1**, **V2**, **V3**, and **V4**, occipital visual areas; **MT**, middle temporal; **MST**, medial superior temporal; **AIP**, **VIP**, **LIP**, and **MIP**, anterior, ventral, lateral, and medial intraparietal; **TEO**, temporal-occipital; **IT**, inferior temporal; **PMd** and **PMv**, dorsal and ventral premotor; **FEF**, frontal eye fields.) (Adapted from Albright and Stoner 2002.)

about *where* an object is located, its size and shape, and *how* it might be acquired and used is transmitted in a more *dorsal pathway* to the parietal lobe and eventually to the motor areas of frontal cortex (Figure 17–13).

Ventral and dorsal streams are evident in other sensory systems as well. In the auditory system, acoustic information from speech is transmitted to Wernicke's area in the temporal lobe, which has a strong role in language comprehension, and to Broca's area in the frontal cortex, which is involved in speech production. In the somatosensory system, information about an object's size and shape is transmitted to ventral areas of parietal cortex for object recognition. Tactile information about object size, weight, and texture is also communicated to posterior parietal and frontal motor areas, where it is needed to plan the handling of the object.

Ventral and dorsal streams of sensory information also contribute to two major forms of memory: semantic (also called explicit) memory, which we use to talk about objects or persons, and procedural (also

called implicit) memory, which we use to interact with objects, persons, or the immediate environment.

Ventral stream information generates *nouns* that we use to identify and classify persons, places, and objects, such as spheres, bricks, and cars. Dorsal stream information motivates *verbs* enabling the actions performed based on sensory inputs and subjective intentions, such as grasping, lifting, or driving.

Feedback Pathways From the Brain Regulate Sensory Coding Mechanisms

Sensory systems are not simply automated assembly lines that reassemble fragmented neural representations of environmental events (eg, light, sound, odor) into more coherent percepts. We have enormous control over our own experience of sensation and perception, and even our conscious attention.

We can to some extent control which sensations reach our consciousness. We may, for example, watch television to take our minds off the pain of a sprained ankle.

Direct, volitional control of the sensory information that reaches consciousness can be readily demonstrated by suddenly directing your attention to a body part, such as the fingers of your left hand, to which you were initially oblivious as you were attending to this text. Sensations from the fingers flood consciousness until attention is redirected to the text. Neural recordings in somatosensory and visual cortex confirm that neurons change their sensitivity, as reflected in their firing rates, much more so than their selectivity for particular stimuli. At a more abstract level, for example, we can switch our attention from the subject matter of a painting to the artist's technique.

Each primary sensory area of cortex has extensive projections back to its principal afferent relay nucleus in the thalamus. In fact, the number of feedback axons exceeds the number of afferent axons from the thalamus to the cortex. These projections have an important function that is not yet clear. One possibility is that they modulate the activity of certain neurons when attention and vigilance change or during motor tasks.

Centers in the brain are also able to modulate the responsiveness of sensory receptors. For example, neurons in the motor cortex can alter the sensitivity of sensory receptors in skeletal muscle that signal muscle length. Activation of gamma motor neurons by corticospinal pathways enhances the sensory responses of muscle spindle afferents to stretch. Neurons in the brain stem can directly modulate the frequency sensitivity of hair cells in the cochlea. Thus, information about a stimulus sent from peripheral sensory neurons to the brain is conditioned by the entire organism.

Top-Down Learning Mechanisms Influence Sensory Processing

What we perceive is always some combination of the sensory stimulus itself and the memories it both evokes and builds upon. The relationship between perception and memory was originally developed by empiricists, particularly the associationist philosophers James and John Stuart Mill. Their idea was that sensory and perceptual experiences that occur together or in close succession, particularly those that do so repeatedly, become associated so that thereafter the one triggers the other. Association is a powerful mechanism, and much of learning consists of forging associations through repetition.

Contemporary neuroscientists using multineuronal recordings discovered that sensory events evoke sequences of neuronal activation. These patterns of neural activity are believed to trigger memories of previous experiences of such stimulation patterns. For example, as we hear a work of music over and over again, the circuits of our auditory system are modified by the experience, and we learn to anticipate what comes next, completing the phrase before it occurs. Familiarity with the phrasing and harmonies used by a composer allows us to distinguish the operas of Verdi from those of Mozart, and the symphonies of Bruckner from those of Brahms. Likewise, when we drive to an unknown destination, our visual system is initially overwhelmed by new landmarks, as we assess which are important and which are not. With repeated trips, the journey becomes second nature and seems to take less time.

Percepts are uniquely subjective. When we look at a work of art, we superimpose our personal experience on the view; what we see is not just the image projected on the retina, but its contextual meaning to us as individuals. For example, when we view a historic photograph of important events in our lives, or persons we admired or detested, we recall not only the event in the image but also the words spoken and our emotional reactions in the past. The emotional response is muted or absent if we did not experience a direct connection to the event or person illustrated.

How can a network of neurons "recognize" a specific pattern of inputs from a population of presynaptic neurons? One potential mechanism is called *template matching*. Each neuron in the target population has a pattern of excitatory and inhibitory presynaptic connections. If the pattern of arriving action potentials fits the postsynaptic neuron's pattern of synaptic connections even approximately—activating many of its excitatory synapses but mostly avoiding activating its inhibitory synapses—the target neuron fires. The codes may also be combinatorial: the overall activity of a region remains the same with different stimuli, but the specific subset of neurons that are active when a particular input is presented constitute a "tag" specifying that input.

Charles F. Stevens has identified these in very different sensory systems and noted that such *maximum entropy* codes are highly efficient, able to represent many different stimuli for a set number of neurons. Refining our understanding of efficient coding, the Carandini and Harris labs have recently shown that the neural code in mouse visual cortex is indeed efficient and preserves fine detail, but in a manner that retains the ability to generalize by responding similarly to closely related visual stimuli. Such computational or algorithmic views have great promise for our understanding of sensory systems. *Artificial neural networks*, simulated using computers, can be trained on images and taught to "see." Daniel L. Yamins and James J.

DiCarlo have pointed out that as these artificial networks evolve the ability to recognize objects and faces, the properties of neuron-like "units" in particular layers begin to resemble the distribution of activity seen in corresponding cortical areas. Such artificial neural networks are trained by machine learning algorithms that modify the connection strength between units, similar to neuronal learning with repetition and synapse modification.

Precisely how the brain solves the recognition problem is uncertain. There is currently much evidence that the neural representation of a stimulus in the initial pathways of sensory systems is an isomorphic representation of the stimulus. Successive synaptic regions transform these initial representations into abstractions of our environment that we are beginning to decipher. In contrast, we barely understand the top-down mechanisms by which incoming sensory information invokes memories of past occurrences and activates our prejudices and opinions.

One view of these processes is Bayesian: Our experience and understanding of the world inform a top-down *sensory prior* that describes our likely environment. The primary insight of Bayes's rule is that decisions are made by the likelihood ratio of current evidence from a test stimulus and the subject's previous experience of similar stimuli (priors), all modified by the task contingencies (rewards and hazards). Ongoing sensory information contributes immediate data, and the two combine to form an up-to-the-moment *posterior* estimate of our surroundings and our place in them. When we do understand these neural codes and the algorithms and mechanisms that generate and interpret them, it is likely that we will be on the verge of understanding cognition, the way in which information is coded in our memory and our understanding. That is what makes the study of neural coding so challenging and exciting.

Highlights

1. Our sensory systems provide the means by which we perceive the external world, remain alert, form a body image, and regulate our movements. Sensations arise when external stimuli interact with some of the billion sensory receptors that innervate every organ of the body. The information detected by these receptors is conveyed to the brain as trains of action potentials traveling along individual sensory axons.

2. 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 transformed 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.

3. The intensity and duration of stimulation are represented by the amplitude and time course of the receptor potential and by the total number of receptors activated. In order to transmit sensory information over long distances, the receptor potential is transformed into a digital pulse code, sequences of action potentials whose frequency of firing is proportional to the strength of the stimulus. The pattern of action potentials in peripheral nerves and in the brain gives rise to sensations whose qualities can be measured directly using a variety of psychophysical paradigms such as magnitude estimation, signal detection methods, and discrimination tasks. The temporal features of a stimulus, such as its duration and changes in magnitude, are signaled by the dynamics of the spike train.

4. The location and spatial dimensions of a stimulus are conveyed through each receptor's receptive field, the precise area in the sensory domain in which stimulation activates the receptor. The identity of the active sensory neurons therefore signals not only the modality of a stimulus but also the place where it occurs.

5. These messages are analyzed centrally by several million sensory neurons performing different, specific functions in parallel. Each sensory neuron extracts highly specific and localized information about the external or internal environment, and in turn has a specific effect on sensation and cognition because it projects to specific places in the brain that have specific sensory, motor, or cognitive functions. To maintain the specificity of each modality within the nervous system, receptor axons are segregated into discrete anatomical pathways that terminate in unimodal nuclei.

6. 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 nucleus integrates sensory inputs from adjacent receptors and, using networks of inhibitory neurons, emphasizes the strongest signals. After about a dozen synaptic steps in each sensory system, neural activity

converges on neuronal groups whose function is multisensory and more directly cognitive.

7. Processing of sensory information in the cerebral cortex occurs in multiple cortical areas in parallel and is not strictly hierarchical. Feedback connections from areas of the brain involved in cognition, memory, and motor planning control the incoming stream of sensory information, allowing us to interpret sensory stimulation in the context of past experience and current goals.

8. 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—requires the activation of large ensembles of receptors acting in parallel, each one signaling a particular aspect of a stimulus. The neural activity in a set of thousands or millions of neurons should be thought of as coordinated activity that conveys a "neural image" of specific properties of the external world.

9. Our sensory systems are increasingly appreciated as computational and algorithmic encoders, processors, and decoders of information. Insights from machine learning, information theory, artificial neural networks, and Bayesian inference continue to inform our understanding of what we perceive in our bodies and from the world around us.

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