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.
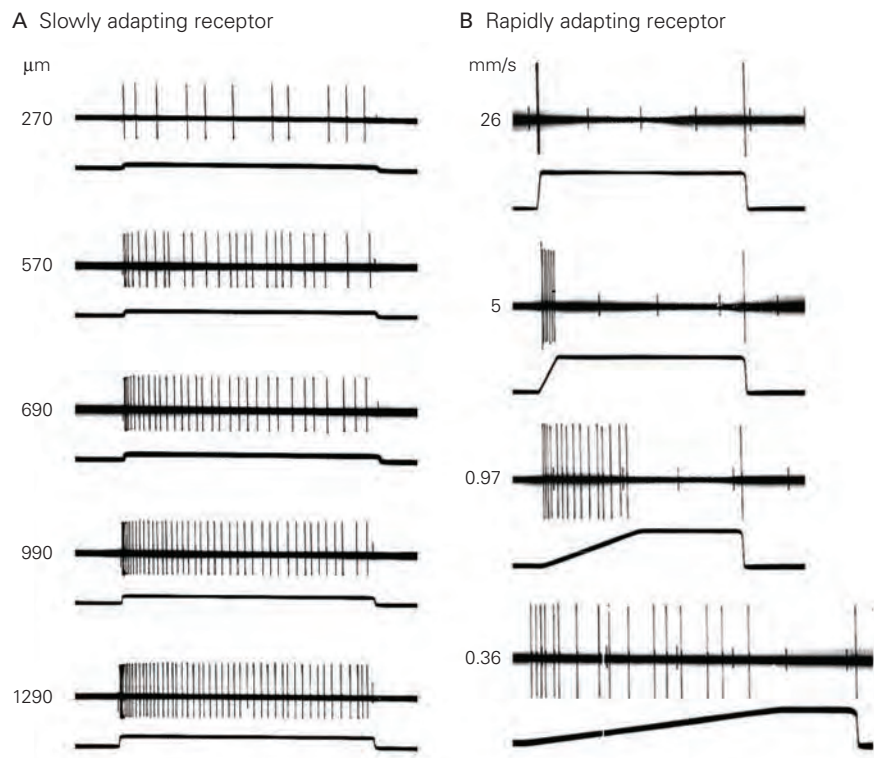
A Slowly adapting receptor

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.
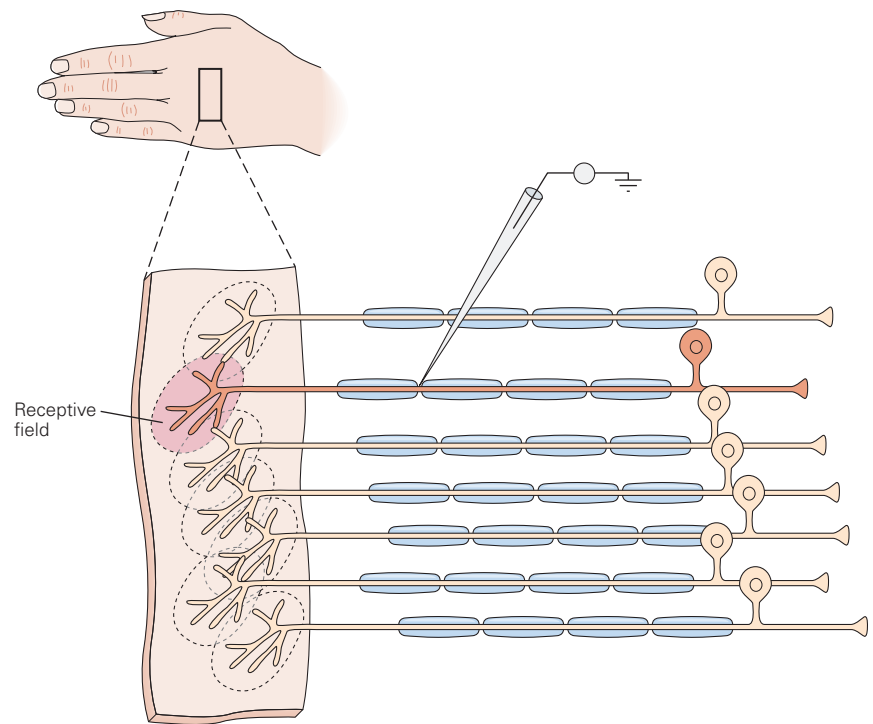
fovea, the population of neurons transmits a very detailed representation of the visual scene. Ganglion cells in the periphery of the retina have larger receptive fields because the receptor density is much lower. The dendrites of these ganglion cells receive information from a wider area of the retina, 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).
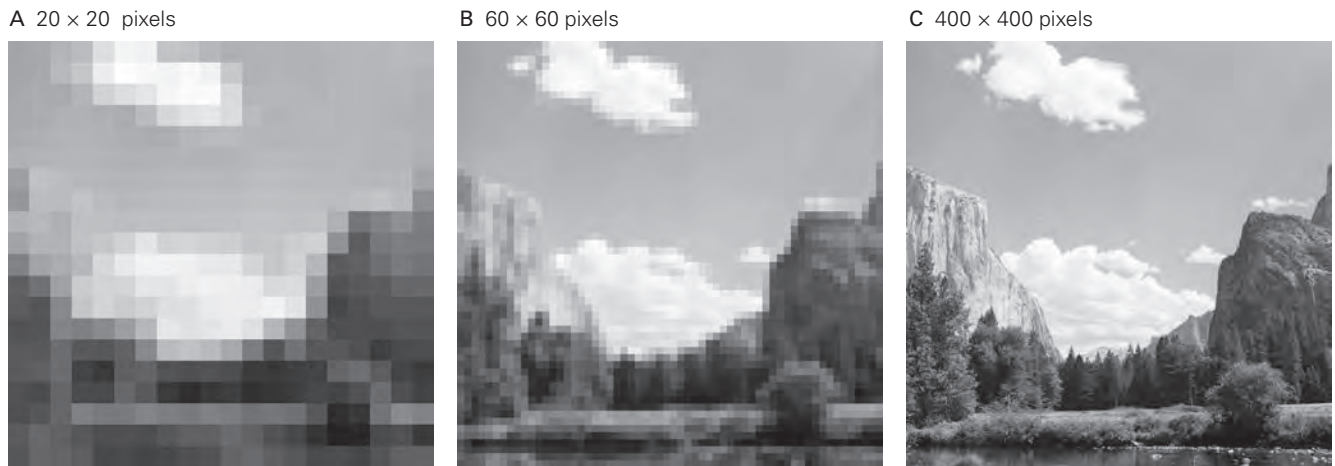
A 20 × 20 pixels   B 60 × 60 pixels   C 400 × 400 pixels

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
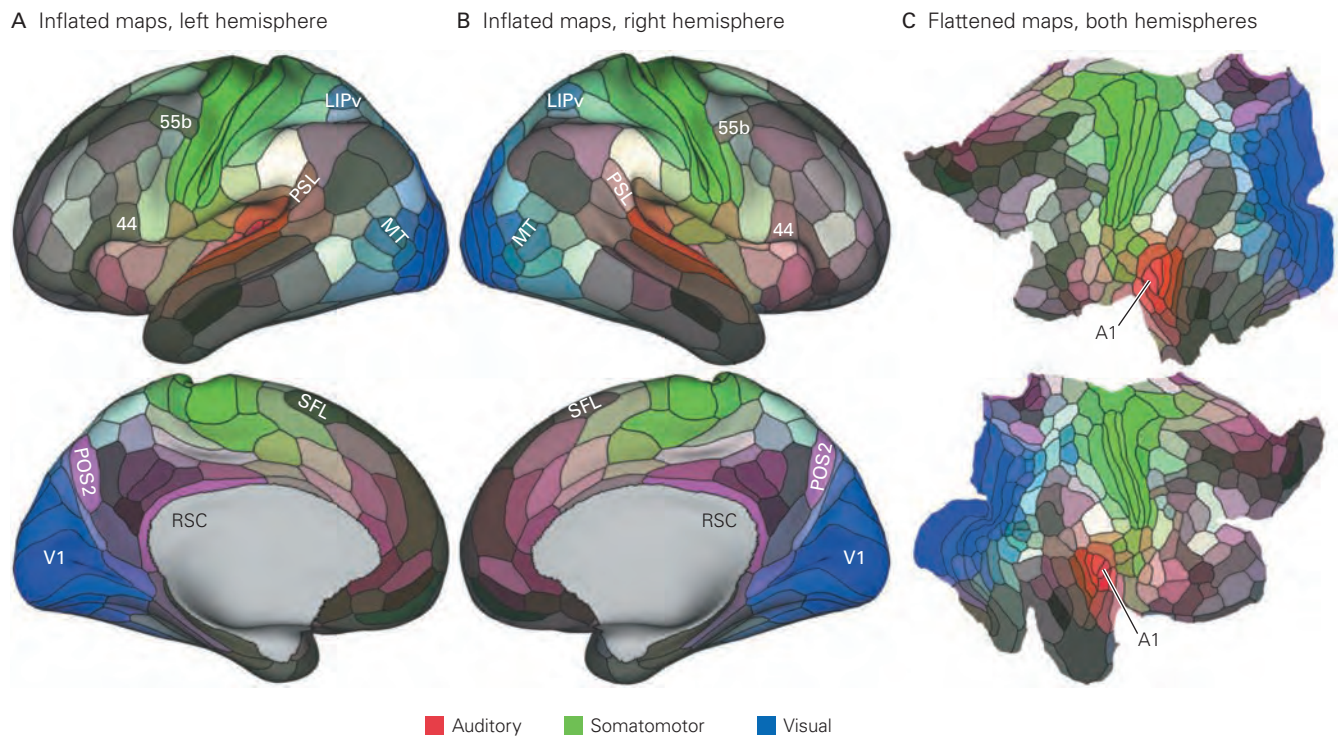
A Inflated maps, left hemisphere

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
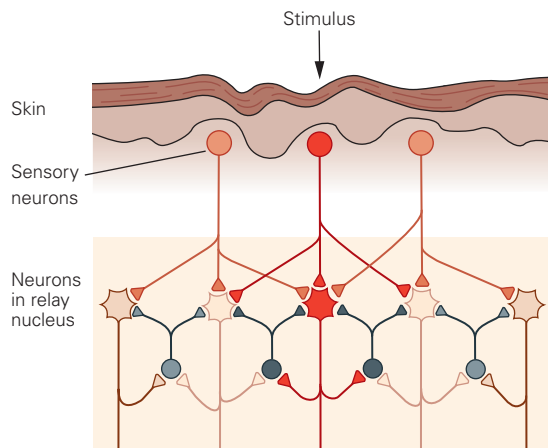
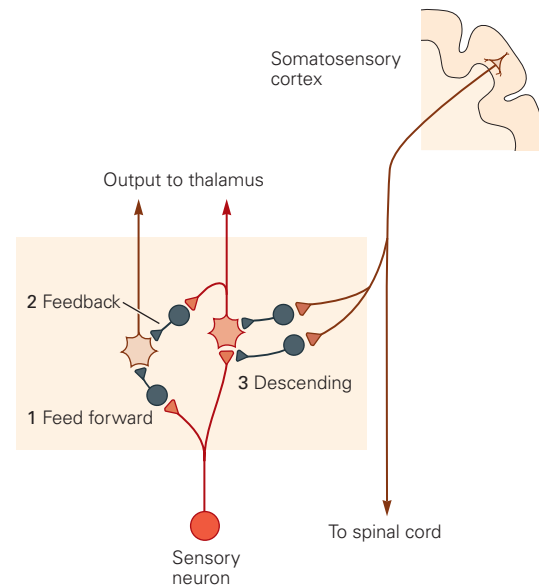B Spatial distribution of excitation and inhibition among relay neurons

C Types of inhibition in relay nuclei
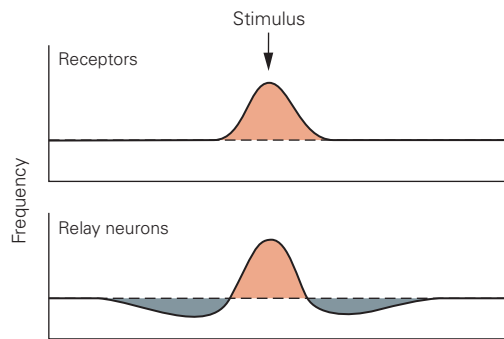
Figure 17–11 Relay neurons in sensory systems integrate a variety of inputs that shape stimulus information.

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,
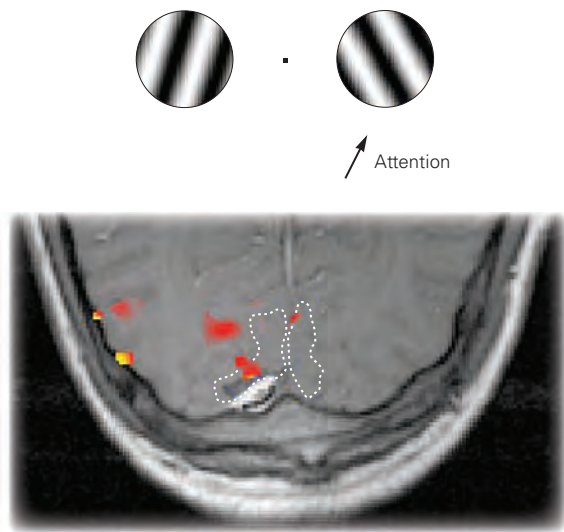
Figure 17–12 Attention to a visual stimulus alters responses of neurons in visual cortical areas. When we pay attention to a stimulus, we select certain sensory inputs for cognitive processing and ignore or suppress other information. Functional MRI is used in this study to measure the effects of attention 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
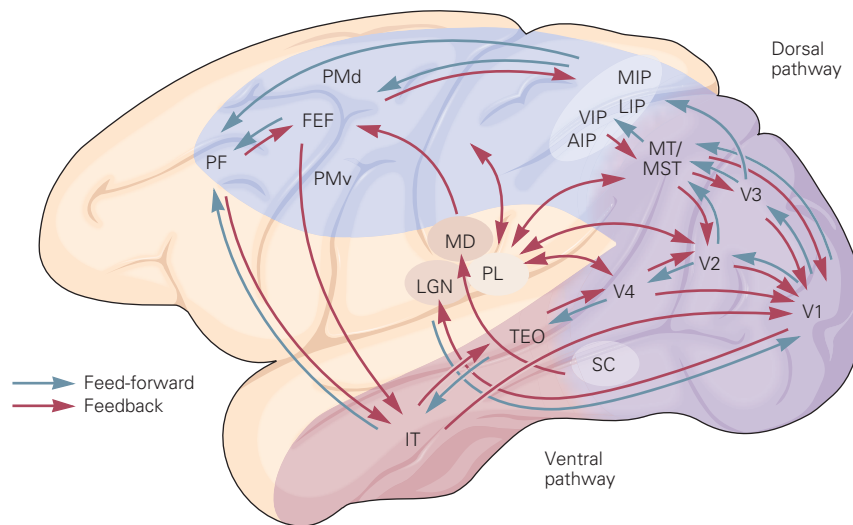
Figure 17–13 Visual stimuli are processed by serial and parallel networks in the cerebral cortex. When you read this text, the spatial pattern of the letters is sent to the cerebral cortex through successive synaptic links comprising photoreceptors, bipolar cells of the retina, retinal ganglion cells, 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.