Preceding Page

In Plato's "Allegory of the Cave," which addresses the origin of knowledge, his early insight into the constructive nature of perception offers illuminating metaphors for the process. The parable begins with the premise that a group of prisoners has never seen the outside world. Their experience is limited to shadows cast upon the wall of the cave by objects passing before a fire. The causes of those shadows—even the fact that they are shadows—is unknown to the prisoners. Nonetheless, over time, the shadows become imbued with meaning in the prisoners' minds. Metaphorically, the shadows represent sensations, which are fleeting and incoherent. The assignment of meaning represents the construction of intelligible percepts. The prisoner turning the corner of the wall has been freed to witness the larger world of causes, which he reports back to those still imprisoned. In a novel metaphorical take on this ancient story, this returning prisoner represents the field of modern neuroscience, which sheds light on the relationship between our shadowy sensations and our rich perceptual experience of the world. (Plato's Cave, 1604. Jan Pietersz Saenredam, after Cornelis Cornelisz van Haarlem. National Gallery, Washington D.C.)

IV Perception

> I understood that the world was nothing: a mechanical chaos of casual, brute enmity on which we stupidly impose our hopes and fears. I understand that, finally and absolutely, I alone exist. All the rest, I saw, is merely what pushes me, or what I push against, blindly—as blindly as all that is not myself pushes back. I create the whole universe, blink by blink…. Nevertheless, something will come of all this.[1]

JOHN GARDNER'S HEARTRENDING TALE OF THE TORMENTED MONSTER Grendel's perspective on life captures the fundamental nature of perceptual experience: It is a construct that we alone impose. Or, as Grendel keenly observes, "The mountains are what I define them as." Isolated and tortured by loneliness, Grendel sees the world as do the shackled prisoners in Plato's Cave, where mere shadows are what is sensed, but those shadows are imbued with meaning, utility, agency, beauty, joy, and sadness, all through the constructive process of perception: "What I see, I inspire with usefulness . . . and all that I do not see is useless, void."

Like the prisoner who escapes from Plato's Cave to view a larger world of causes, or the all-knowing dragon who fills Grendel with ideas from another dimension—"But dragons, my boy, have a whole different kind of mind. . . . We see from the mountaintop: all time, all space"—modern neuroscience promises a mountaintop understanding of perceptual experience, an understanding not simply of the things we construct from our shadowy sensations, but how we do so, and for what purpose.

This section on perception offers that expansive mountaintop view. For each of the sensory modalities in turn, these chapters begin by examining environmental stimuli—light, sound, gravity, touch, and chemicals—that are the origins of human experience and knowledge of the world. In hierarchical fashion, the chapters survey the mechanisms that enable stimulus detection and discrimination, the perceptual processes that fill evanescent sensations with meaning, and the operations that support attention, decision, and action, based on what is perceived.

Vision—a sense both particularly well understood and heavily utilized by humans—acquires information through properties of light. Light reflected from objects in the environment varies in wavelength and intensity and fluctuates over space and time, and through

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[1] Gardner J. 1971. *Grendel*. Alfred A. Knopf, New York.

those physical properties conveys evidence of the world around us. Cast as patterned images upon the retina, luminous energy is transduced into neuronal signals by dedicated receptor cells. The evidential properties of these images are detected by a collection of specialized neuronal systems that sense forms of contrast and convey this information to the rest of the brain.

Similarly, the auditory system acquires information about the world through the simple compression and rarefaction of air, as caused by spoken language, music, or environmental sounds. This sensory evidence is detected—even in minute quantities and with incredibly precise timing—by an extraordinarily intricate amplification system consisting of small drums, levers, tubes, and hair cells, whose bendable stereocilia transduce mechanical energy into neuronal signals. Similar motion-detecting hair cells serve the vestibular senses of balance, acceleration, and rotation of the head.

The somatosensory system acquires information about physical stimuli impinging on the body in the form of pressure, vibration, and temperature—and, in the extreme, pain—as would be caused by touch, movement of the skin across a textured surface, or contact with a source of heat. The peripheral nerve endings of a variety of specialized detector neurons embedded in skin, viscera, and muscle transduce this mechanical energy into neuronal signals, which are carried via the spinal cord and cranial nerves to the brain.

Finally, the senses of taste and smell acquire information about the chemical composition of the world, in the form of form of food, drink, and airborne molecules. From one of the most exciting and rapidly developing areas of sensory biology today, we now know that there are hundreds of olfactory receptors that have unique patterns of affinity for airborne molecules, which accounts for the human ability to detect and discriminate a staggering number and diversity of odors.

All of these receptive systems serve as filters, characterized by neural "receptive fields" that highlight certain forms of information and restrict others. These selective filters are tunable over different timescales, enhancing attention to salient stimuli and adapting to the statistics of the sensory world. This flexibility accommodates variations in both behavioral goals and environmental conditions.

Like the shackled prisoners in Plato's cave, our sensory systems initially convey simple filtered representations of sensory input, which are fundamentally ambiguous, noisy, and incomplete. Alone they have no meaning. Quite remarkably, our brain enables us to ultimately experience this sensory information as the environmental objects and events that *cause* those patterns. The constructive transition from a world of sensory evidence to one of meaning lies at the heart of perception and has long been one of the most engaging mysteries of human cognition. The 19th-century English philosopher John Stuart Mill wrote "perception reflects the permanent possibilities of sensation," and in doing so reclaims from transient sensory events the enduring structural and relational properties of the world.

This section reveals how perception overcomes the vagaries of sensory evidence to develop hypotheses or inferences about the causes of sensation, by reference to past knowledge. Much of this happens through the machinery of the cerebral cortex, where sensory signals are linked both within and between modalities and to feedback from the memory store. Like a detective viewing a crime scene, informed by memory and context, the activity of cortical neurons begins to yield what William James aptly called the "perception of probable things."

With this perceptual transformation also comes the ability to recognize objects familiar to us. We readily generalize across different sensory manifestations of the same or similar objects, in the form of perceptual constancies and categorical percepts, and we link these with other meaningful events. The sound of the coffee grinder in the morning, the smell of a lover's perfume or the sight of her face expands our experience beyond the immediate to a realm of recall and imagination. The chapters in this collection review the brain structures and computations that underlie these associative functions, which include highly specialized neuronal systems for recognizing and interpreting complex and behaviorally significant objects, such as faces.

Perceptual experience of the world around us is a prerequisite for meaningful interaction with that world. Decisions are made based on the accumulation of sensory evidence in support of one percept versus another. Is that my suitcase on the carousel? Is this where we turn? Was that aria from Wagner or Strauss? Is that the fragrance of jasmine or gardenia? Cortical neurons form salience maps, which represent the outcome of these perceptual decisions with respect to behavioral goals and rewards and prioritize actions accordingly.

Perception is generally treated—as it is herein—as a distinct subdiscipline of neuroscience. Increasingly we see this compartmentalization breaking down. The relationship of perception to other brain functions—learning, memory, emotion, motor control, language, development—is ever clearer with the explosive growth of new concepts and experimental methods for monitoring and manipulating brain structure and function, and for revealing the extensive anatomical and functional neural connections between seemingly distinct brain regions. Thus have we begun to fully appreciate how the brain's system for acquiring and interpreting information, for becoming aware of and understanding the world—for *perceiving*—is the functional centerpiece of human cognition and behavior.

Part Editors: Thomas D. Albright and Randy M. Bruno

Part IV

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

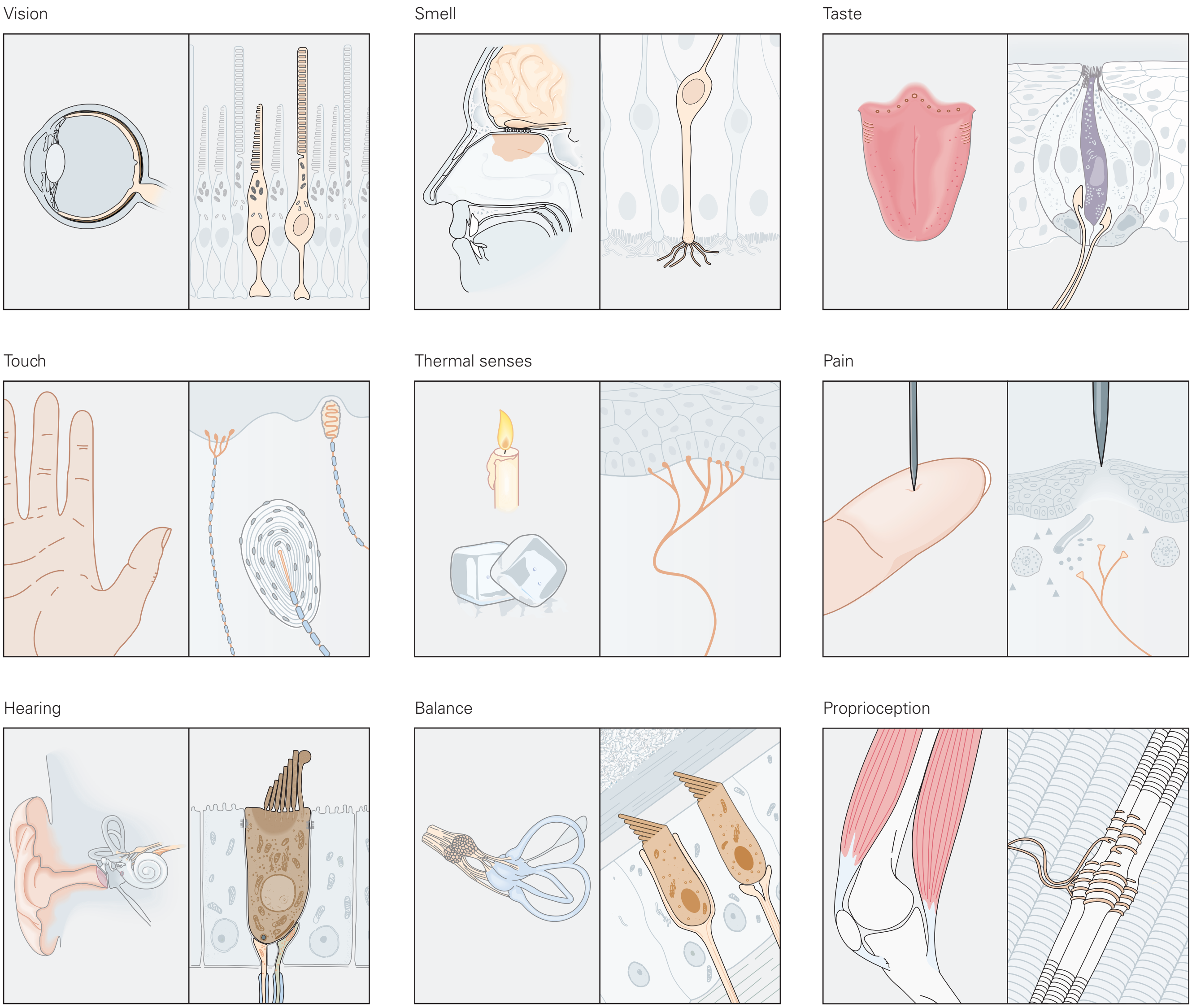

Figure 17–1 The major sensory modalities in humans are mediated by distinct classes of receptor neurons located in specific sense organs. Each class of receptor cell transforms one type of stimulus energy into electrical signals that are encoded as trains of action potentials (see Figure 17–4). The principal 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

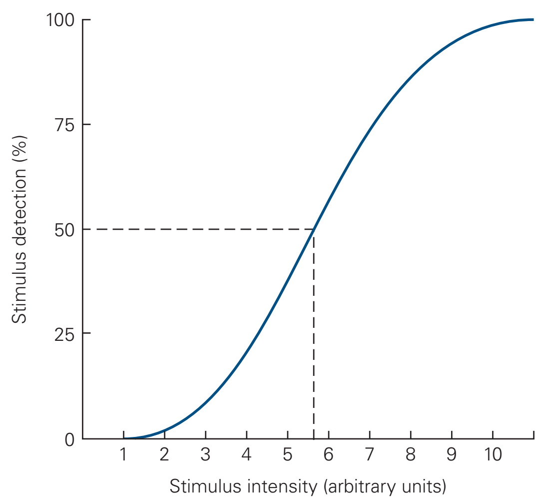

Figure 17–2 The psychometric function. The psychometric function plots the percentage of stimuli detected by a human observer as a function of the stimulus magnitude. Threshold is defined as the stimulus intensity detected on 50% of the trials, which in this example would be about 5.5 (arbitrary units).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

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.