Third Edition

FOUNDATIONS OF SENSATION AND PERCEPTION

George Mather

A Psychology Press Book

COMPANION WEBSITE

ROUTLEDGE

Foundations of Sensation and Perception

Do you wonder how movies—sequences of static frames—appear to move, or why 3-D films look different from traditional movies? Why does ventriloquism work, and why can airliner flights make you feel disoriented? The answers to these and other questions about the human senses can be found within the pages of *Foundations of Sensation and Perception*.

Early chapters allow students to grasp fundamental principles in relation to the relatively simple sensory systems (smell, taste, touch, and balance) before moving on to more complex material in hearing and vision. The text has been extensively updated, and this new edition includes:

- a new chapter devoted to attention and perception
- over 200 new references
- over 30 new figures and improved, more colorful, visual presentation
- a new companion website with a range of resources for students and lecturers

The book contains a range of pedagogical features, including accessible tutorial sections at the end of each chapter. This distinctive feature introduces areas of the subject which are rarely included in student texts, but are crucial for establishing a firm foundation of knowledge. Some tutorials are devoted to more advanced and technical topics (optics, light measurement, Bayesian inference), while others cover topics a little outside of the mainstream (music perception, consciousness, visual art).

Foundations of Sensation and Perception will enable the reader to achieve a firm understanding of the processes that underlie our perception of the world and will be an invaluable resource for those studying psychology, neuroscience, and related disciplines.

George Mather is Professor of Vision Science at the University of Lincoln, UK. He has published over 60 research papers, 4 books, and 7 book chapters and his main research interests are in motion perception, visual after-effects and the perception of visual art. His research has attracted funding by a number of UK research councils and charities.

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Foundations of Sensation and Perception

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Preface to the third edition

The third edition has given me the opportunity to update the text and to incorporate the many helpful comments I received on the second edition. I hope that the changes significantly improve the book as a resource for students of sensation and perception.

As in previous editions, the book starts with the so-called minor senses and then moves on to hearing and vision, before dealing with several topics that span the senses: multisensory processing, attention, and individual differences. However I've made two changes to the sequence of chapters in the text. The chapter on color vision has moved from Chapter 12 to Chapter 8 so that rather than following on from motion perception, it now follows on more coherently from the material on visual physiology in Chapter 7. Also there is a new chapter (14) on attention and perception, which replaces and significantly expands the material on attention which was covered in the tutorial section of Chapter 13. In addition, three other chapters have been restructured, with new and/or reordered chapter sections to add material and improve the flow of the discussion: Chapter 1 (introduction), Chapter 11 (depth perception), and Chapter 12 (motion perception).

In this third edition I have tried to stay true to the aims I had in mind when writing the first and second editions. When reading other textbooks I was often less than satisfied with assertions about specific aspects of sensation and perception which were made without reference to a source, a primary reference which the reader could consult for confirmation and for more detail. So, by the second edition the text included over 600 references and I have added a further 200 references in this edition. I certainly would not expect any one reader to consult a significant proportion of these references but they are there to give the reader the option to do so as and when they need more detail and a primary source.

Another aim I had in mind was to introduce areas of the subject which are not normally covered in student texts, yet which are crucial for anyone wishing to understand or conduct research. Lack of knowledge in these areas can lead to misunderstandings and misconceptions becoming entrenched. Some of the tutorials are intended to fill this gap. For example, there are introductory tutorials in the hearing and vision chapters on the basic principles of Fourier analysis. This mathematical technique is fundamental in many areas of science and engineering, but textbook coverage of it usually assumes a high degree of mathematical competence. The Fourier tutorials assume relatively little formal training in math. Similarly there are non-technical tutorials on optics, light measurement, and Bayesian inference which are not in themselves essential for understanding the text but become much more important when one wishes to understand some of the details of research studies. Apart from these more technical topics, other tutorials discuss areas which tend not to be covered in student texts because they are slightly outside of the mainstream or are more controversial. Examples include music perception, consciousness, and individual differences in artists.

I am indebted to all of the reviewers who provided such detailed and helpful comments on the second edition, which I have tried to incorporate in the third edition. I am also grateful to the editorial and production team at Psychology Press, who have done an excellent job as usual. Though the fault for any remaining errors and problems with readability and intelligibility is entirely my own.

Finally, I would like to dedicate the book to Anne, whose patience and support were so important during the production of all three editions.

The companion website

Web-based supplementary materials to accompany *Foundations of Sensation and Perception, Third Edition*

The companion website offers an array of supplementary materials for students and instructors.

Student Resources include:

- Animations and simulations of key perceptual phenomena
- Chapter summaries
- Multiple-choice and gap-fill quizzes
- Flash cards to test definitions of key terms.
- A comprehensive chapter-by-chapter glossary of key terms used in the book.

Access to the Student Resources is freely available and free-of-charge.

Instructor Resources include:

- A testbank of multiple-choice questions.
- A set of short-answer questions per chapter to stimulate discussion
- The figures from the book.

Access to the Instructor Resources is restricted to instructors only by password protection. These resources are free of charge to qualifying adopters.

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General principles

1

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INTRODUCTION

From a subjective standpoint, there seems to be little to explain about perception. Our perception of the world is direct, immediate, and effortless, and there is no hint of any intervening operations taking place in the brain. The apparent simplicity of perception is reinforced by the fact that our perceptions are almost always accurate. We rarely make mistakes when identifying people by their face or voice, or in judging how hot a cup of tea is, or in navigating a flight of steps. Moreover, our own perceptions nearly always agree with those of other people. Sounds, sights, and smells seem to be “out there” in the world, not constructed in our head.

Despite appearances to the contrary, our perceptual world is constructed in the brain by a huge mass of neurons performing complex, but hidden, operations. Three observations hint at the complexity of the brain processes involved in perception. First, a large proportion of the brain’s most highly developed structure, the cerebral cortex, is devoted entirely to perception. Vision alone consumes over half of the neurons in the cortex. Second, despite the complexity and power of modern computer technology, computer scientists have not yet succeeded in building general-purpose systems with the perceptual proficiency of even an infant. Relatively confined problems, such as detecting abnormalities in medical images, identifying a face or a voice, or guiding an autonomous vehicle, have proven to be formidable problems to solve by computer (see Huang, 2005). Third, as a result of brain damage through injury or disease, a small number of unfortunate individuals suffer deficits in their perceptual capabilities. These deficits can be very specific and debilitating, but also dramatic and perplexing to other people. It seems difficult to believe that someone can fail to recognize their own face reflected in a mirror (**prosopagnosia**), or cannot judge the position of their limbs without looking directly at them. Such people remind us of the sophisticated brain processes serving perceptual abilities that most of us take for granted.

KEY TERM

Prosopagnosia
A clinical condition resulting from brain damage, in which a patient is unable to recognize familiar faces.

Spectator sports provide a very clear example of the reliability, and occasional fallibility, of the information extracted by our perceptual systems. Everyone involved—participants, referees/umpires, and spectators—must make perceptual judgments in order to interpret events on the sports field, and to decide what should happen next. Did the tennis ball bounce out of court? Did the football cross the goal line and enter the goal? All those involved nearly always agree on what happened, because their perceptual systems arrive at the same decisions. Sporting activities would not be viable either for participants or for spectators without reliable perceptual systems. Certain critical judgments do require special skills and observation conditions. For instance, net-cord judges were once used in professional tennis tournaments to decide whether the ball delivered by the serving player had struck the top edge of the net (the net-cord) on its way across the court. They relied on a combination of three senses—sight (deflection of the ball in flight), sound (the impact of the ball on the net), and touch (vibration of the net). As a result, the net-cord judge could detect the slightest of contacts between ball and net that were missed by most or all of the spectators. Professional courts now use an electronic net-cord sensor rather than a human observer; the sensor picks up the tiny vibrations caused by the ball (the first version of the sensor, introduced in the 1970s was the pick-up from an electric guitar).

? *Think of other reasons for disagreements between spectators about the same sporting incident.*

FIGURE 1.1
Fine sensory discriminations during sporting activities probe the limits of our perceptual abilities. Disagreements can arise from the inherent variability of sensory signals. Copyright © Brian Snyder/Reuters/Corbis.

Perceptual judgments are not infallible, as demonstrated by the disagreements between participants or observers that can and do arise in many sports. Such disagreements can offer hints about the nature of the underlying perceptual processes (as well as providing additional entertainment; see Figure 1.1). Common sources of disagreement involve decisions about whether a ball crossed a line on the sports field, such as whether a tennis ball bounced inside a court line. Participants often reach contradictory decisions in “close” calls. This disagreement is not simply a reflection of differences in skill or concentration level, or gamesmanship, but a natural consequence of the inherent variability in our perceptual decisions. In optimal conditions, perceptual responses are highly reliable, both within and between observers. When a ball bounces some distance to one side of a line, there is no disagreement as to where it bounced. However,

psychophysical research has taught us that in marginal conditions when stimuli are very close together or indistinct, perceptual responses are probabilistic. When a ball bounces slightly to the left of a line, the response of the perceptual system itself will sometimes lead to a "left" response, and other times lead to a "right" response. As a result, different observers are likely to disagree a certain proportion of the time. Perceptual research aims to estimate the precise degree of uncertainty attached to perceptual judgments, and to identify its likely causes (see Mather, 2008).

SENSATION, PERCEPTION, AND SENSORY MODALITY

Sensations are simple conscious experiences generated by stimulation of a sense organ such as the eye: Your awareness of the brightness of a camera flash, or the sourness of a lemon, or the sharpness of a pinprick are all sensations. Perceptions are complex, meaningful experiences of objects and events. Sensations are immediate and automatic, whereas perceptions can take time to reach a stable state, and may require effort. For instance, at one of the sports events described earlier you may sense the green color of the grass, or the loudness of the public address system, but you perceive the identities of the players on the court or pitch, and the way their actions are interconnected.

Philosophers and psychologists call simple sensations **qualia** because they relate to the qualities of conscious experiences. By their very nature, qualia are private, and accessible only to the person who has them. Most researchers believe that qualia map onto specific brain states or functions of brain states. For example, there is a specific brain state associated with the sensation of the color red. If your sensation of color changed to, say, green, there would be a corresponding change in brain state. The assumed link between sensations and brain states lies at the very foundation of modern theories of perception, as will become clear below. However, an "explanatory gap" (Levine, 1983, 1999) remains between the physical world (brain states) and the mental world (sensations). No one has been able to explain precisely how the qualitative nature of sensation can be explained by reference to neural activity.

Qualia divide up the sensory world into qualitatively different modes of sensation, also known as **sensory modalities**. The sensations evoked by light, for example, are qualitatively different from those evoked by sounds, touches, or smells. There is no possibility of us confusing a visual sensation with an auditory one, but it is possible to confuse one auditory sensation with another (for instance, within limits you cannot discriminate between two sounds of different intensities). One of the most fundamental questions one can ask about sensation is: "How many different sensory modalities do we have?" The answer is important because it determines the divisions which perceptual science should respect when seeking explanations. For instance, we cannot investigate how the different senses interact (as we do later in the book) without first distinguishing between them as separate modalities.

Since the time of Aristotle, common sense has divided the sensory world into five modalities—seeing (vision), hearing (audition), touch (somatosensation), smell (olfaction), and taste (gustation)—on the basis of visible sense organs (eye, ear, skin,

KEY TERMS

Psychophysics
The scientific study of the relationship between physical stimulation and perceptual experience.

Qualia
Primitive mental states, such as sensory impressions induced by stimulation of a sense organ (e.g., loudness, brightness, heat).

Sensory modality
A mode of sensation that is qualitatively different from other modes, so its sensations cannot be confused with those of other modalities; for example, the experience of seeing is qualitatively different from that of hearing or touching.

nose, tongue). However we must consider another four candidate modalities for this list, none of which have visible sense organs. The sense of balance (vestibular sense) is now recognized as a distinct modality, for reasons that will become clear below, and three more modalities relate to sensory awareness of the body: The sense of body position (proprioception), the sense of body motion (kinesthesis), and the sense of pain (nociception).

The criteria for distinguishing between the different sensory modalities are summarized in Table 1.1. Seeing, hearing, and balance are easy to distinguish in physical terms, because they detect different forms of energy (electromagnetic radiation, air pressure waves, and motive force, respectively). Although smell and taste both detect chemical contact, they qualify as different modalities in the sense that they have different neural pathways. Touch, body position, and body motion do not really qualify as distinct modalities because they share a neural pathway and cortical destination. The status of pain as a distinct sensory modality is not clear-cut because it does have separate receptors and pathways but it shares the same cortical destination as the other body senses. Overall we can enumerate seven major sensory modalities, which are listed in Table 1.1 according to their scientific name: Audition (hearing), gustation (taste), nociception (pain), olfaction (smell), somatosensation (touch), the vestibular sense (balance), and vision (seeing). Nociception, somatosensation, and the vestibular sense will be discussed together in Chapter 3 as "the body senses."

All the senses require receptor cells which convert energy from the outside world (light, sound, and so on) into electrical nerve impulses. As the third column of Table 1.1 shows, there are just four basic types of receptor, though the number of receptor cells varies markedly between the modalities. Audition is based on surprisingly few receptors (about three and a half thousand in each ear), in contrast to the 125 million photoreceptors in each eye. Later chapters will consider what information is carried in the receptor signals, and how the brain interprets them.

Receptor signals are carried to the brain along a number of different pathways, with signals in each modality arriving at a specific area of the **cerebral cortex**. The cortex is a crumpled sheet of cells 2.5 mm thick and 1000 cm^2 in surface area (Braitenberg & Schuz, 1991). It contains approximately 20,000,000,000 cells. Figure 1.2 (top) shows a drawing of the human brain, identifying the receiving areas for different pathways. In the early 1900s the German anatomist Korbinian Brodmann distinguished over 50 different areas of the cerebral cortex, numbering them from BA1 to BA52. His numbering system has become the standard way of referencing the cortex. Table 1.1 shows the Brodmann cortical area (and Brodmann number) which receives incoming fibers from the nerves in each sensory pathway. It is important to note that Table 1.1 and Figure 1.2 indicate only the cortical *receiving* areas. Many other cortical areas are also devoted to the senses, by virtue of connections between cortical cells. There are interesting species differences in the total extent of cortical surface devoted to different senses. In primates, including humans, the visual cortex is the largest sensory area in the brain. Figure 1.2 (bottom) shows the relative area of cortex devoted to vision, hearing, and touch in two other species as well as in primates. Auditory cortex is dominant in bats, and somatosensory cortex is dominant in moles. The relative area of cortex devoted to different senses is indicative of their relative importance to the survival of each animal.

KEY TERM

Cerebral cortex
The outer layer of the human brain; approximately 2.5 mm thick, it contains the millions of neurons thought to underlie conscious perceptual experience.

? *Think of other reasons for differences in brain area devoted to different senses.*

The right-hand column of Table 1.1 lists the most important functions served by the sensory systems, in terms of the computations they perform. The concept of computation will be discussed later in the chapter.

TABLE 1.1 Criteria for distinguishing sensory modalities

Modality	Physical stimulus	Receptor type	Number	Afferent path	Synapses	Cortical receiving area (Brodmann number)	Computation
Audition	Air pressure waves	Mechano-	3.5K	Vestibulocochlear nerve, cochlear division (VIII)	5	Heschl's gyrus (BA 41)	Auditory object location & recognition, orienting, social communication
Gustation (taste)	Chemical contact	Chemo-	1M	Facial, glossopharyngeal, vagus nerves (VII, IX, X)	3	Primary gustatory cortex (BA 43)	Substance edibility, nutrition
Nociception (pain)	Mechanical or chemical contact	Noci-	~100K	Spinothalamic tract Trigeminal nerve (V)	3	Primary somatosensory cortex (BA 1-3)	Harm, injury
Olfaction (smell)	Chemical contact	Chemo-	6M	Olfactory nerve (I)	2	Primary olfactory cortex (BA 28)	Stimulus approach/avoidance, substance edibility
Somatosensation (touch) Proprioception (body position) Kinesthesis (body movement)	Mechanical force	Mechano-	~100K	Lemniscal tract Trigeminal nerve (V)	3	Primary somatosensory cortex (BA 1-3)	Haptic object segregation & recognition, body position and movement
Vestibular sense (balance)	Motive force	Mechano-	~20K	Vestibulocochlear nerve, vestibular division (VIII)	3	Posterior parietal operculum (BA 40)	Head position & acceleration, visual stability, body posture & equilibrium
Vision	Electromagnetic radiation	Photo-	125M	Optic nerve (II)	4	Striate cortex (BA 17)	Visual object segregation, location, & recognition, self-motion, scene layout, orienting

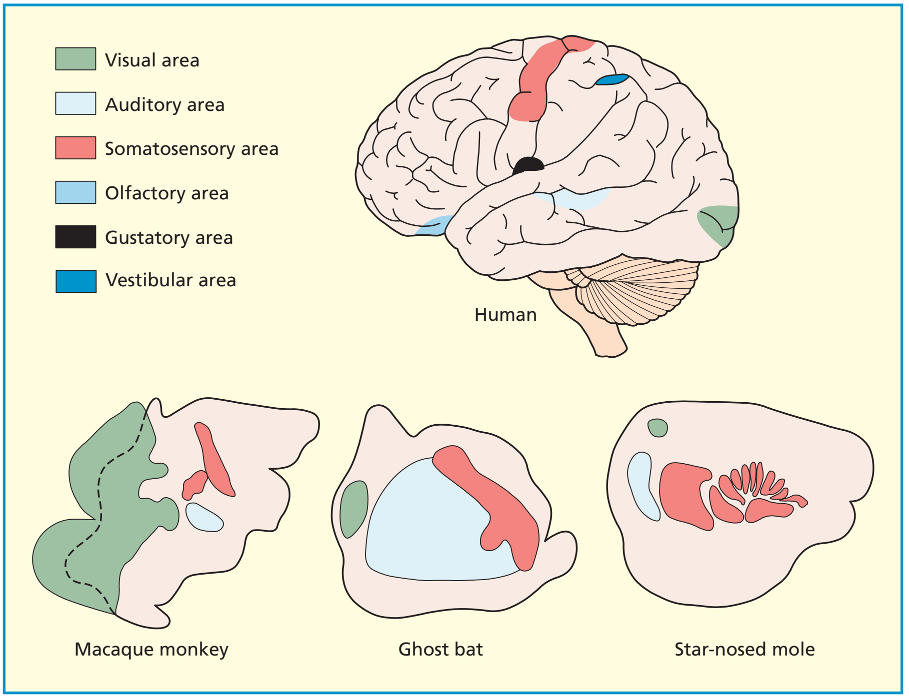

FIGURE 1.2
Cortical representation of the senses. Top: Cortical receiving areas in the human brain. Bottom: Total cortical area devoted to three senses in three different animals (redrawn from Krubitzer, 1995). The broken line identifies the cortical receiving area in macaque monkey. Copyright © 1995 Elsevier. Reproduced with permission.

PSYCHOPHYSICS

Figure 1.3 shows the three key elements of sensation and perception. When external stimuli arrive at a sensory organ (1) they generate a neural response in sensory receptors (2) which leads to sensory and perceptual experiences (3). In this section we consider the psychophysical techniques used to study the relationship between stimuli and perceptual responses. In the following section we will turn our attention to the neuroscientific techniques that are used to study the relationship between stimuli and neural responses. Notice that there is also a direct link between neural responses and perception; neural responses are thought to underlie

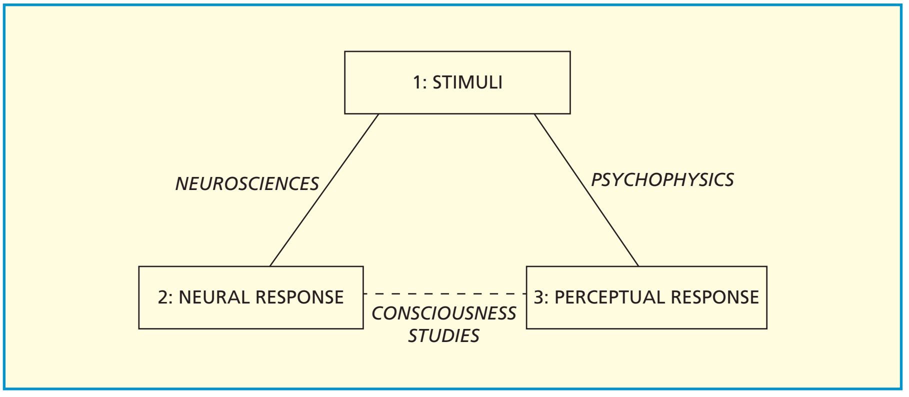

FIGURE 1.3
The three key elements of perception: (1) Sensory stimulation (light, sound, etc.); (2) Neural responses to stimulation; (3) Perceptual experiences which correlate with neural responses. Neuroscience studies the relation between stimuli and neural responses, and psychophysics studies the relation between stimuli and perceptual experiences. Psychophysical linking hypotheses bridge the gap between neural activity and perception.

all conscious perceptual experience. Hypotheses that link these two elements are known as **psychophysical linking hypotheses**, though no one knows how and why the link exists at all (the issue of consciousness is discussed in the tutorial at the end of Chapter 14).

KEY TERM

Psychophysical linking hypothesis
A linking proposition positing a specific causal link between neural activity in the brain and perceptual experience.

WEBER AND FECHNER

Psychophysical methods are so-called because they study the relation between mental events (perceptions) and physical stimulation. They were first developed by Ernst Weber and Gustav Fechner working at Leipzig University in the mid-1800s. Weber studied the ability of experimental participants to judge small differences in the heaviness of handheld weights. More specifically, he measured the smallest difference between a "standard" weight and another "comparison" weight that could be reliably detected, known as the "just noticeable difference" or JND. Weber found that the JND was a constant fraction of the standard weight. For example, if the JND for a weight of 1000g was measured at 50g, then the JND for a weight of 2000g would be 100g; a JND of 1/20. When discrimination was measured for many other sensory judgments (brightness, loudness, and so on), they were all characterized by a specific JND. This rule became known as Weber's Law, and the JND became known as Weber's Fraction. Fechner extended Weber's initial discoveries in his research into how our perception of the magnitude of a stimulus grows with stimulus intensity. Fechner reasoned that a sequence of stimuli that grows in steps that correspond to JNDs is equally spaced in terms of sensory increments though not equally spaced in terms of stimulus intensity. For example, assuming that weights must increase in steps of 1/20 in order for them to be discriminable (a JND of 1/20), the following sequence of weights is spaced at equally discriminable sensory increments: 1000g, 1050g, 1102.5g, 1157.6g, 1215.5g, 1276.3g, 1340g, and so on. The difference between the first two weights is 50g (1/20th of 1000), while the difference between the last two weights is 63.7g (1/20th of 1276.3g). So a small increment to a relatively light weight would produce the same change in perceived weightiness as a larger increment to a relatively heavy weight. This rule became known as Fechner's Law.

Fechner developed a set of experimental methods known as psychophysical methods for measuring the relation between mental and physical events. The tutorials section at the end of the chapter offers an introduction to the principles underlying these important techniques.

The discoveries made by Weber and Fechner laid the foundations of experimental psychology. They demonstrated that, using psychophysical techniques, it is possible to discover universal laws governing relationships between mental events and physical events; in other words, the link between boxes 1 (stimuli) and 3 (perceptual responses) in Figure 1.3. Given the assumption that neural responses (box 2) are also linked to perceptual responses, then psychophysical data can be used to make inferences about the neural processes underlying perceptual responses. These inferences are known as "psychophysical linking hypotheses."

? *Why are special experimental techniques required to study perception?*

SENSORY THRESHOLDS

Figure 1.4 shows data from an experiment to measure the detectability of a small light increment against a uniform background. The participant was shown a series of trials containing different increments, and at each presentation was asked to report whether they detected the increment. The horizontal axis shows the magnitude of

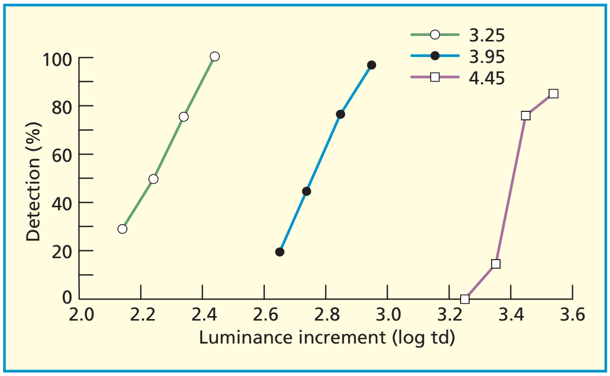

FIGURE 1.4
Psychometric function plotting the probability of a "yes" response to the presentation of a small light increment against a uniform background. The horizontal axis represents the magnitude of the light increment, and the three curves represent data obtained at three different background intensities. Adapted from Mueller (1951).

the light increment and the vertical axis shows the percentage of trials in which the participant detected the increment. The three curves represent data using three different background light levels. Each curve (also called a **psychometric function**) shows a smooth transition between no-detection and detection as stimulus level increases. This kind of detection function is called "probabilistic" rather than "all-or-none": As the size of the increment increases there is a gradual increase in the probability that the participant will detect it, rather than a sudden switch from no-detection to detection. Similarly, experiments that measure the ability of a participant to discriminate between two similar stimuli such as lights at different intensities find a smooth, probabilistic transition from perceiving no difference to perceiving a clear difference. There is no single stimulus value at which there is a step change in response from no detection or discrimination to certain detection/discrimination so there is uncertainty as to what stimulus level corresponds to the threshold for seeing it. In the face of this inherent uncertainty in the decision, the usual convention in psychophysical research is to select a given response level, such as 75% correct, as representing the threshold between no detection/discrimination and detection/discrimination. There has been a long debate as to the best explanation for the probabilistic nature of sensory thresholds, which is summarized in the tutorials section.

SENSORY MAGNITUDE

Variation in intensity affects not only the detectability of a stimulus, but also its sensory magnitude. For example, the brightness of a light, the loudness of a sound, or the heaviness of a weight increases as stimulus magnitude increases. An experimental technique called **magnitude estimation** allows us to establish the precise relationship between physical stimulus magnitude and sensory magnitude. The subject is initially presented with a standard stimulus at moderate intensity, and asked to assign an arbitrary number to it, such as 100. Other stimuli are then presented one at a time, and the subject is asked to estimate the magnitude of each relative to the standard stimulus using the same numerical scale. If, for example, a stimulus appears twice as intense as the standard (twice as bright or twice as loud), then the subject should assign the number 200 to it. The technique has been applied to a wide range of sensory stimuli. Representative data are shown on the left of Figure 1.5. The relationship between stimulus intensity and sensory magnitude is not linear.

In some sensory judgments, such as brightness, sensory magnitude increases rapidly at low stimulus intensities, but flattens off or saturates at higher intensities. In others, sensory magnitude shows the opposite pattern. If the data are plotted on logarithmic axes rather than linear axes, they fall along straight lines in the graph (right of Figure 1.5). This means that sensory magnitude data conform to a mathematical power law, in which sensory magnitude grows in proportion to stimulus intensity raised to a power

KEY TERMS

Psychometric function
A graph relating stimulus value (e.g., intensity) to the response rate of an experimental subject (e.g., proportion of "yes" responses).

Magnitude estimation
A psychophysical technique in which the subject estimates the magnitude of a given stimulus by assigning it a position along an arbitrary numerical scale (e.g., 0–100).

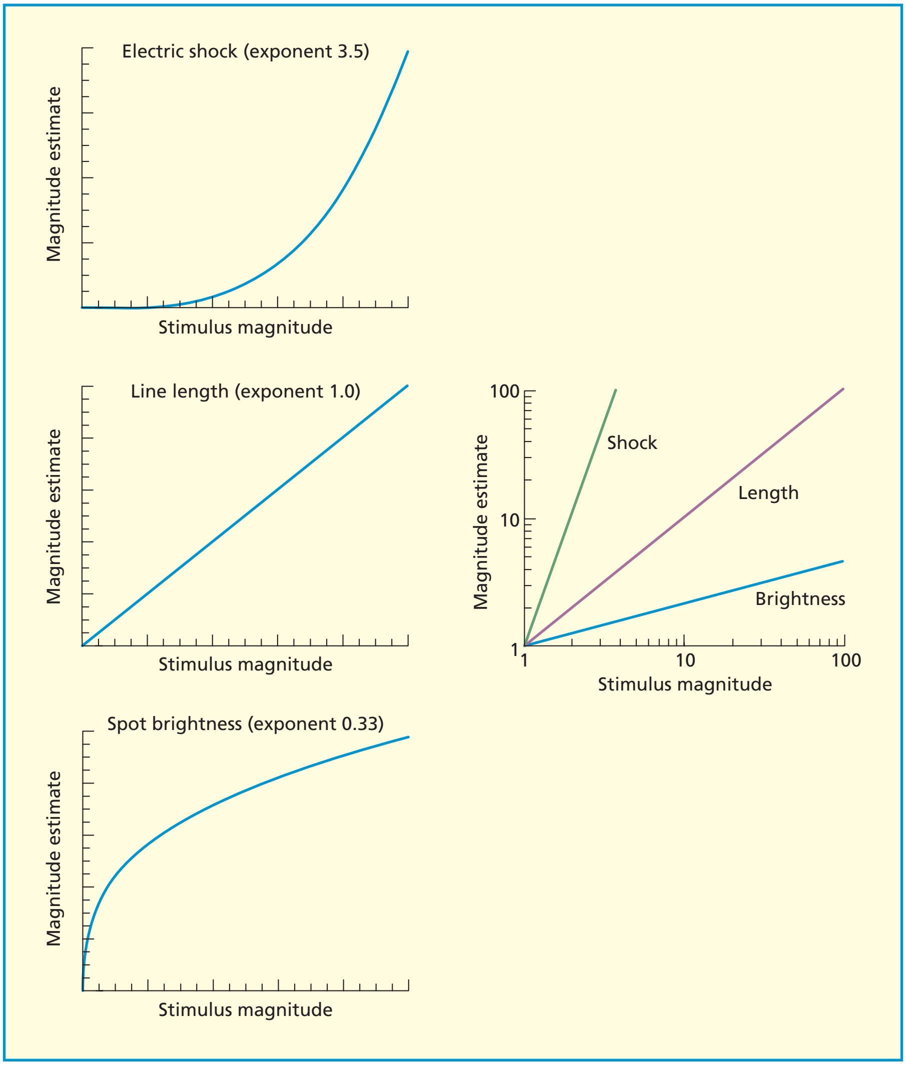

FIGURE 1.5
The relationship between stimulus intensity and sensory magnitude. The left-hand graphs are plotted using linear axes—sensory magnitude increases nonlinearly at different rates in different senses. The right-hand graph shows the same data plotted on logarithmic axes—sensory magnitude now increases linearly, showing the power-law relationship between stimulus intensity and sensory magnitude. Exponents of the plots were taken from Stevens (1961).

(the slope of each line in the logarithmic graph corresponds to the power or exponent to which intensity must be raised for that sensation). This property of sensory magnitude data is known as "**Stevens's power law**" (e.g., Stevens, 1961). The power-law relation between stimulus intensity and sensory magnitude means that equal ratios of intensity correspond to equal ratios of sensory magnitude. For example, each time light intensity increases by a factor of eight, brightness increases by a factor of two, at all levels of intensity. It seems that the sensory systems provide information about *changes* in the level of stimulation rather than about the absolute level of stimulation. Stevens's power law of sensory magnitude is closely related to Fechner's Law of JNDs.

SENSORY ADAPTATION

If there was a fixed relation between sensory magnitude and stimulus level, each stimulus level would be uniquely associated with a specific sensory magnitude. However research has shown that the relation between stimulus and sensation

KEY TERM

Stevens's power law
A nonlinear relationship between stimulus intensity and perceived magnitude, in which equal ratios of intensity produce equal ratios of magnitude.

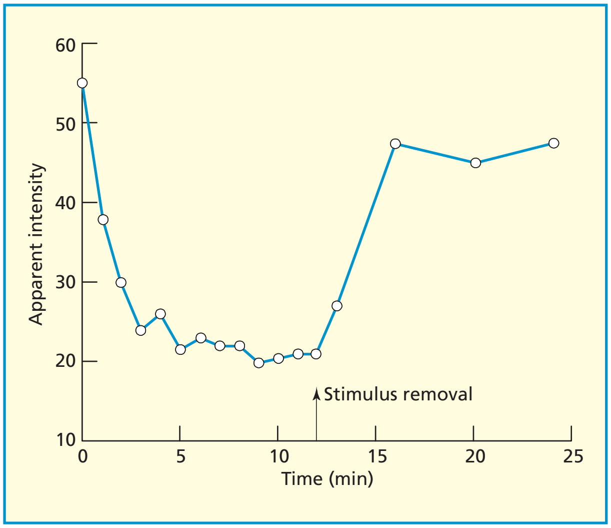

FIGURE 1.6
Adaptation to an odor. Sensory magnitude of an odor sensation was measured at regular intervals during a 12-minute exposure, showing adaptation to a constant stimulus. Once the stimulus was removed, sensory magnitude gradually recovered to former levels. From Ekman et al. (1967). Reproduced with permission from John Wiley and Sons.

is not fixed and unchanging, but varies: Any one stimulus level can give rise to a range of different sensory magnitudes; depending on the prevailing stimulus conditions. The sensory systems **adapt**. For instance, when you enter a dark cinema from a bright street, you are initially unable to see, but your visual system soon adapts to the new, dim level of illumination (and vice versa; after the film the street initially appears startlingly bright). Continuous exposure to a sustained stimulus actually has three consequences for sensation. First, sensitivity changes so that a different level of stimulus intensity is required to induce a given sensory response after adaptation than before adaptation. For example, after you have adapted to the dim cinema you require much less light to see than you did upon first entering. Second, the apparent intensity of the stimulus changes (the cinema initially appears extremely dark, but after adaptation it appears not so dark; see also the example of odor adaptation in Figure 1.6). Third, the rate at which sensory magnitude increases with stimulus level usually steepens. The response capacity of each sensory system is limited, in that it can only respond to a certain range of stimulus levels at any one time. Adaptation ensures that this restricted response is well matched to the prevailing stimulation.

PSYCHOPHYSICAL LINKING HYPOTHESES

Psychophysical data establish the relationship between stimuli and sensory experiences. But as indicated in Figure 1.3 these experiences are also linked to the neural responses generated by stimulation. Brindley (1960) recognized that any rigorous theory of sensation and perception should express this linkage in terms of explicit propositions that he called *psychophysical linking hypotheses*. More recently, Teller (1984) defined a linking proposition as “a claim that a particular mapping occurs, or a particular mapping principle applies, between perceptual and physiological states” (Teller, 1984, p. 1235).

Rigorous theories of perception usually contain at least one linking proposition of this kind. An example of such a proposition is that the loudness of a sound is coded by the rate of firing of certain cells in the auditory system. However, perceptual theories do not always spell out explicitly their linking propositions, but it is important to be aware that such propositions must form part of any theory that attempts to relate neural events to perceptual events.

KEY TERM

Adaptation
A change in the response of a system to a sustained stimulus.

COGNITIVE NEUROSCIENCE

The neurosciences can be defined as a set of scientific disciplines which are devoted to the study of the nervous system. Two branches of neuroscience are particularly relevant for sensation and perception. Cognitive neuroscience studies the parts of the nervous system that are involved in cognition, which includes sensation and perception; computational neuroscience studies the computations performed by the nervous system.

A wide range of techniques have been used in cognitive neuroscience over the last 200 years to study perception. Each technique has its particular advantages and limitations, but no one technique is preferred over the others. Different techniques complement each other, so that when considered together they allow us to construct a very detailed picture of how we perceive the world.

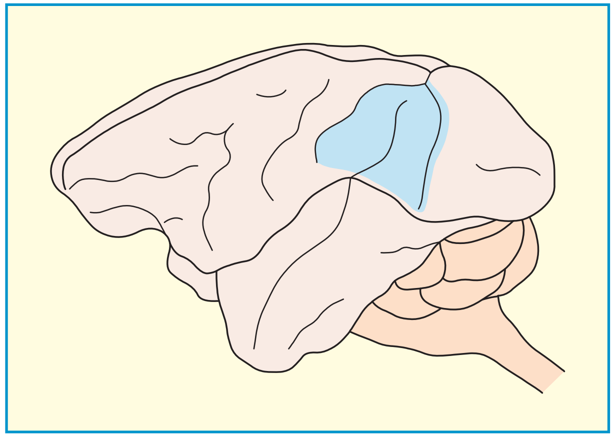

FIGURE 1.7
Site of the lesion in Ferrier's monkeys (redrawn from Glickstein, 1985). Copyright © 1985 Elsevier. Reproduced with permission.

LESIONS

The cerebral cortex of the brain can be subdivided into many areas which specialize in certain cognitive functions, as Figure 1.2 has already shown. But in the mid-1800s, scientific opinion was that the cortex could not be subdivided in this way. Many believed that sensation, perception, and action were represented diffusely throughout the cortex. **Lesion** experiments provided some of the earliest evidence against this view, and in favor of localization of function in the brain. The procedure in such experiments is to surgically remove or destroy a specific area of an animal's brain, and then observe the consequences for behavior. If a specific behavioral function is impaired or removed following surgery, then we may infer that the relevant brain area is crucial for the maintenance of that function. However, care is needed to avoid drawing erroneous conclusions from lesion experiments. For example, one of the earliest experiments was performed by David Ferrier (1876). He examined monkeys after removal of an area on each side of the cortex known as the angular gyrus (see Figure 1.7). Ferrier concluded from his observations that the animals were completely blind following surgery. One monkey, for instance, was very fond of tea. Ferrier (1876, p. 166) noted that:

> *On placing a cup of tea close to its lips it began to drink eagerly. The cup was then removed from immediate contact, and the animal though intensely eager to drink further, as indicated by its gestures, was unable to find the cup, though its eyes were looking straight towards it.*

? *How well could you infer the function of a car's components using "lesions" (disconnecting or removing components)?*

Later experiments, some of which are described below, indicate that Ferrier was mistaken in concluding from his observations that the monkeys were blinded by the lesion. Blindness is now known to be associated with damage to the occipital cortex, not the angular gyrus (occipital cortex is at the very back of the brain). According to Glickstein (1985), Ferrier's lesions had disrupted visually guided action, not vision itself. The monkey he described could probably see the cup, but could not perform the actions needed to drink from it. Despite such early mistakes, lesion studies have played an important part in establishing **localization of function** as a basic principle of cortical organization.

KEY TERMS

Lesion
An abnormality in structure or function in any part of the body.

Localization of function
The view that neurons underlying a specific sensory or cognitive function are located in a circumscribed brain area.

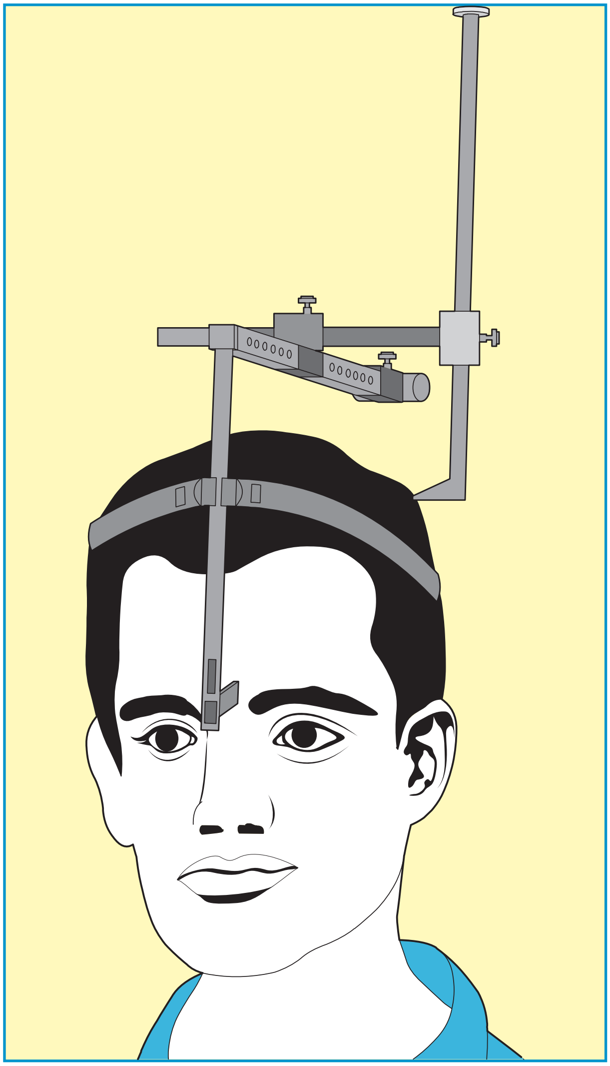

FIGURE 1.8
Inouye's instrument for tracing the path of a bullet in head wounds suffered by Japanese soldiers (drawing based on Glickstein & Witteridge, 1987).

CLINICAL CASES

Research on localization of function in humans has relied largely on clinical investigation into the consequences of accidental damage or disease to specific brain areas. The usefulness of these studies is very similar to that of lesion experiments, in that they allow inferences to be drawn about localization of function. Some of the earliest work to establish the importance of the occipital cortex for vision was undertaken by Tatsuji Inouye in the early 1900s. Inouye was a Japanese army physician, who studied soldiers wounded during combat in the Russo-Japanese war. His job was to assess their degree of blindness following bullet wounds to the head, as this determined the size of their pension (see Glickstein & Whitteridge, 1987). Inouye devised an instrument to locate precisely in three-dimensions the position of entry and exit wounds (see Figure 1.8).

Assuming a straight path for the bullet, he was then able to identify the areas of the brain that were damaged, and relate them to the impairments observed in the soldiers. Inouye was among the first to show that the visual field is mapped in a very ordered way on the surface of the human occipital cortex (see below).

Clinical studies of the consequences of brain damage are necessarily less controlled than lesion studies, since the researcher has no control over the location and extent of the damage. As a result, the inferences that can be drawn from clinical studies are limited. However, clinical studies have led to many important discoveries concerning localization of function.

SINGLE-UNIT RECORDINGS

Although a great deal was known about anatomy and about localization of function prior to the 1950s, nothing was known for certain about how individual nerve cells contributed to sensory processing. As David Hubel (1988, p. 4) remarked:

> *I can well remember, in the 1950s, looking at a microscopic slide of visual cortex, showing the millions of cells packed like eggs in a crate, and wondering what they all could conceivably be doing.*

In partnership with Torsten Wiesel, David Hubel performed a series of ground-breaking experiments based on single-cell recordings from cells in the visual system of the cat. They were later awarded a Nobel prize for these discoveries.

Early theories of perception were inspired largely by the anatomical features of the sensory systems. The brain was known to contain huge numbers of cells, that are massively interconnected (but only over short distances) in circuits that are anatomically similar over the whole cortex. This anatomy prompted the Electrical Field Theory of perception, in which visual patterns were thought to impress corresponding patterns or fields of electrical activity on the surface of the cortex, analogous to the patterns imprinted on a photographic plate. Perceptual organization in complex displays was thought to be governed by interactions between fields of current extending across the cortical surface. Experimental tests of the theory included attempts to short-circuit the electrical fields by pinning metallic strips across the surface of the cortex in rhesus monkeys, and then performing tests of visual functioning (e.g., Lashley, Chow, & Semmes, 1951).

In the early 1950s, Stephen Kuffler was among the first to use a new **microelectrode recording** technique to monitor the activity of single sensory cells. He inserted electrodes (very fine insulated wires) through the white of the eye in an awake, anesthetized cat, and was able to record activity generated in individual retinal ganglion cells by simple visual stimuli placed in front of the animal. Kuffler's (1953) work on the cat retina, along with work by Barlow (1953) on the frog retina, and by Hubel and Wiesel (1959) on the cat visual cortex, provided the first detailed information on the way that individual sensory cells respond preferentially to certain stimuli. We now know that, despite being anatomically the same, the functional properties of individual cells vary hugely. For example, some retinal cells respond best to small, bright spots of light, while others respond best to large, dark spots. In the cortex, individual cells respond in a highly selective way to specific line orientations, or movement directions, colors, sizes, and so on (see Figure 1.9).

KEY TERM

Microelectrode recording
A technique in which electrical activity is recorded from single cells in a live animal using fine insulated wires.

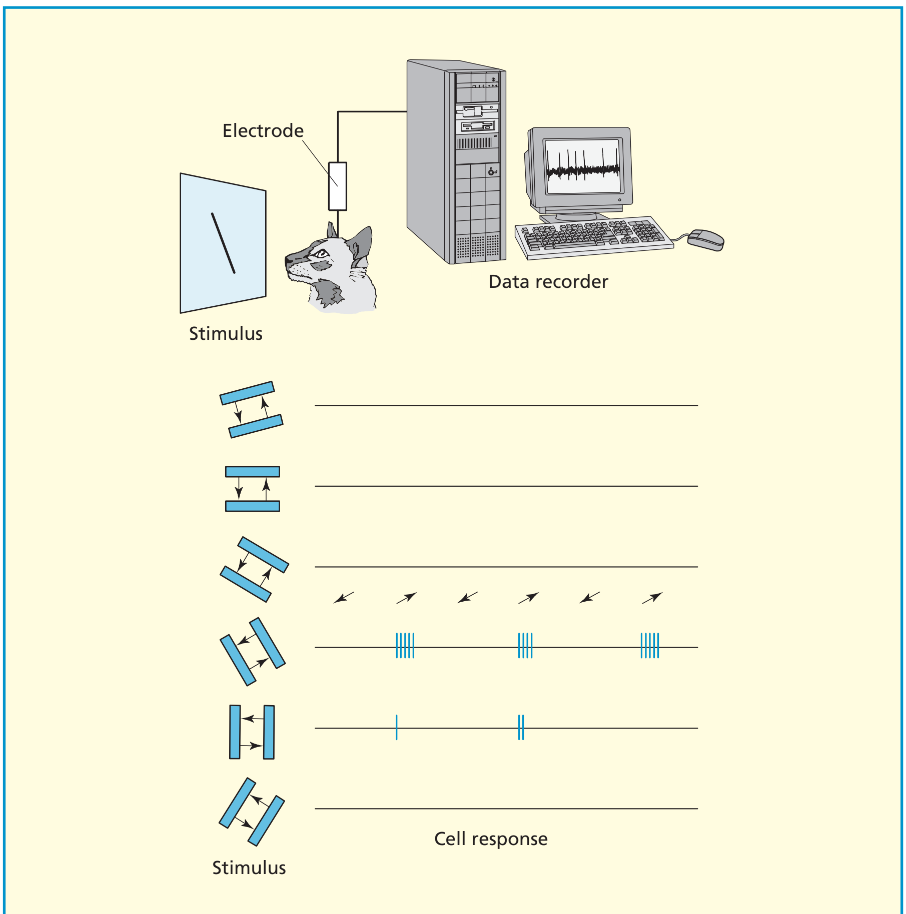

FIGURE 1.9
Single-unit recording. A stimulus is presented to the animal (in this case a visual stimulus) while a fine electrode registers activity from cells in the sensory system. The activity is recorded and analyzed by special-purpose equipment, in this case a computer equipped with appropriate hardware and software.

KEY TERMS

Feature detector
The view that individual neurons in the brain act as detectors for individual stimulus features.

Computerized tomography (CT) scan
A medical technique in which X-rays are passed through the body at different angles, and the resulting data are processed by a computer to create detailed images of body structure.

The key word is specialization rather than uniformity of function. These discoveries led to theories of pattern recognition based on neural "feature detectors." However, as we shall see in later chapters, this view of single cells as **feature detectors** is rather too simple. One must also be wary of drawing conclusions about the functioning of a huge mass of neurons on the basis of responses in single units. Indeed some argue that it is not possible to infer the functional properties of a large sensory system from knowledge of individual cell properties, however detailed (Churchland & Sejnowski, 1992). Nevertheless, single-cell recording data have had a profound influence on theories of perception.

NEUROIMAGING

Neuroimaging techniques were developed in the 1970s, primarily for use in medicine. The earliest technique to be developed was **computerized tomography** (CT). The subject is placed bodily in a long, thin, cylindrical tube (see Figure 1.10).

X-ray emitters and detectors are positioned around the circumference of the tube. A highly focused X-ray beam is emitted from one side of the cylinder so that it passes through the subject's body before being collected by detectors at the opposite side. X-rays are passed through the head from many directions around the tube. From the resulting pattern of X-ray transmission, sophisticated data analysis procedures can build up a detailed picture of the different structures inside the head, as shown in Figure 1.10. CT scans reveal areas of brain damage, and are therefore particularly useful in combination with clinical investigations into the behavioral consequences of brain damage.

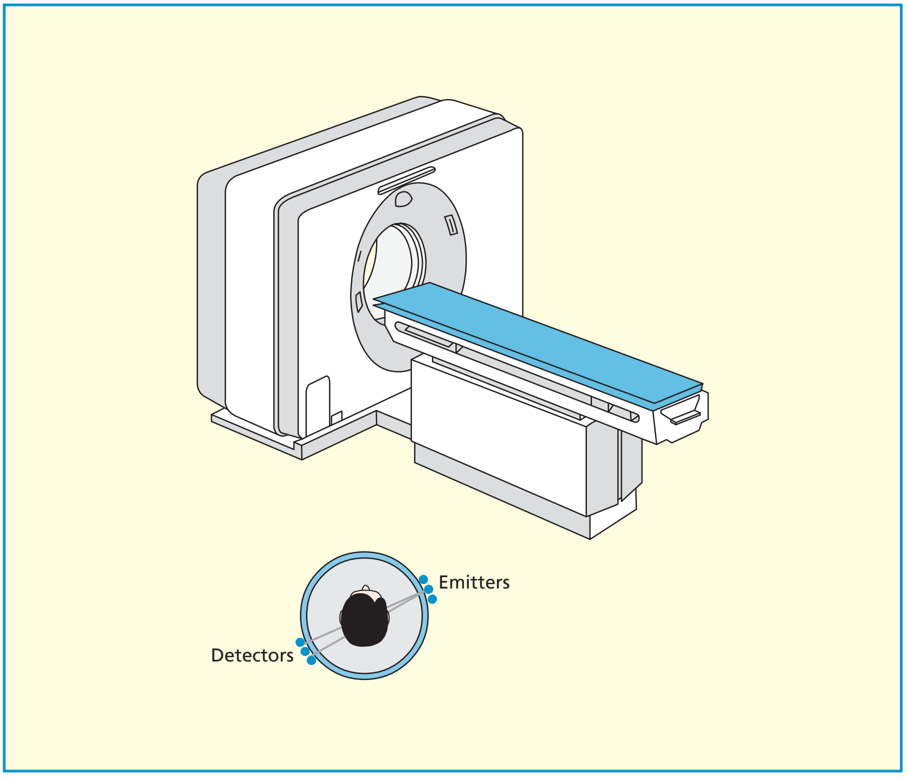

FIGURE 1.10
CT scanner. The patient lies on a table that can be slid inside the scanner (left). The walls of the scanner are lined with X-ray emitters and detectors. X-rays are emitted from one side of the scanning tube so that they pass through the patient's body before being registered by detectors on the opposite side. A detailed image of the brain can be constructed from the pattern of X-ray transmission in all directions around the head.

Magnetic resonance imaging (MRI) scanners detect the magnetic properties of brain molecules, revealed by passing radio waves through the head in all directions. Functional MRI (fMRI) scanning techniques use MRI scanners to detect minute magnetic changes in hemoglobin induced by variation in blood oxygen concentration (blood oxygen level-dependent or BOLD response). Since variation in blood oxygen concentration is related to neural activity (activity consumes energy) fMRI scans can inform us about brain *function*. The primary inferences from brain scanning data concern localization of function. Studies using fMRI scans often compare scans obtained while the subject is performing different tasks, in order to identify the brain areas that are associated with those tasks. An important recent development is fMRI adaptation. Repeated presentation of two similar stimuli causes a reduction in BOLD response in cortical regions containing cells responsive to both stimuli. Little or no reduction is observed if the stimuli activate different cells. So fMRI adaptation studies allow us to draw inferences about stimulus selectivity in small cortical regions (see Grill-Spector, Henson, & Martin, 2006). Neuroimaging studies are making an increasingly important contribution to sensory research, though they have also attracted a good deal of controversy about “blobology” (identification of hotspots in brain activity with little regard to their functional significance) which is being addressed using new techniques (see Poldrack, 2012).

DIRECT BRAIN STIMULATION

In recent years there has been rapid growth in other techniques to stimulate the intact human brain in a fairly localized manner, in the hope of revealing the function of the underlying neural tissue. For example, transcranial magnetic stimulation (TMS) involves directing a brief, powerful but focused magnetic pulse at the subject’s head, as a way of interfering with the electrical activity of neurons in a specific brain region. Transcranial direct current stimulation (tDCS) delivers a low-level current directly to a brain region via small electrodes. This technique has known therapeutic benefits for sufferers of Parkinson’s Disease, tinnitus, and damage caused by strokes, but is also being taken up as an experimental technique to interfere with brain activity.

BASIC CONCEPTS IN COGNITIVE NEUROSCIENCE

Neural impulses and transduction

Information in the nervous system is conveyed by streams of electrical signals (**neural impulses**) passed from one cell to another through the system. These impulses travel from a cell’s **dendrites** and body to its **terminal buttons**, typically via an **axon**. The terminal buttons connect to the dendrites of another cell or cells at **synapses**. When the

KEY TERMS

Magnetic resonance imaging (MRI) scan
A medical technique in which short bursts of powerful radio waves are passed through the body at different angles, and signals emitted by body molecules are processed by a computer to create detailed images of body structure.

Neural impulse
A brief, discrete electrical signal (also known as an action potential) that travels rapidly along a cell’s axon.

Dendrite
The branched tree-like structure projecting from a neuron’s cell body, which makes contact with the terminal buttons of other cells.

Terminal button
A bud at the branched end of an axon, which makes contact with the dendrites of another neuron.

Axon
The long, thin wire-like structure that conveys neural impulses from a neuron’s cell body to its terminal buttons.

Synapse
The junction between the terminal button of one neuron and the dendrite of another neuron.

impulse reaches a synapse, it causes the release of **neurotransmitter** chemicals that affect the electrical state of the receiving neuron. The neurotransmitter can be excitatory (e.g., acetylcholine, ACh), or inhibitory (e.g., gamma amino butyric acid, GABA). Excitatory neurotransmitters increase the probability that the receiving neuron will generate an impulse. Inhibitory neurotransmitters decrease the probability that the receiving neuron will fire an impulse.

Energy from the environment takes a number of forms, as Table 1.1 showed. Each sense requires specialized cells that receive one particular form of energy and convert or transduce it into neural signals. The eye, for example, contains **photoreceptors**, each of which contains photopigments (two examples are shown in Figure 1.11). The breakdown of these photopigments when struck by light results in the generation of a receptor voltage that is transmitted to neurons in the retina. The **mechanoreceptors** of the inner ear contain hair-like outgrowths (cilia). Vibrations initiated by sound pressure waves arriving at the outer ear deflect the cilia and trigger an electrical change in the receptor.

KEY TERMS

Neurotransmitter
A chemical secreted across a synapse to pass on electrical signals from one cell to another.

Photoreceptor
A specialized nerve cell that produces electrical signals when struck by light.

Mechanoreceptor
A specialized nerve cell that produces electrical signals when subjected to mechanical deformation.

Transduction
The process by which sensory receptor cells convert environmental energy (e.g., light, sound) into electrical neural signals.

Hierarchical processing

Neural signals generated during **transduction** are transmitted to several structures in the brain. A common feature of all the senses is that ultimately at least some of the signals arrive at a receiving area in the cortex of the brain, as described earlier and pictured in Figure 1.2.

In between transduction and arrival at the cortex, signals from each sense organ pass through a series of synapses at successively higher levels of neural processing.

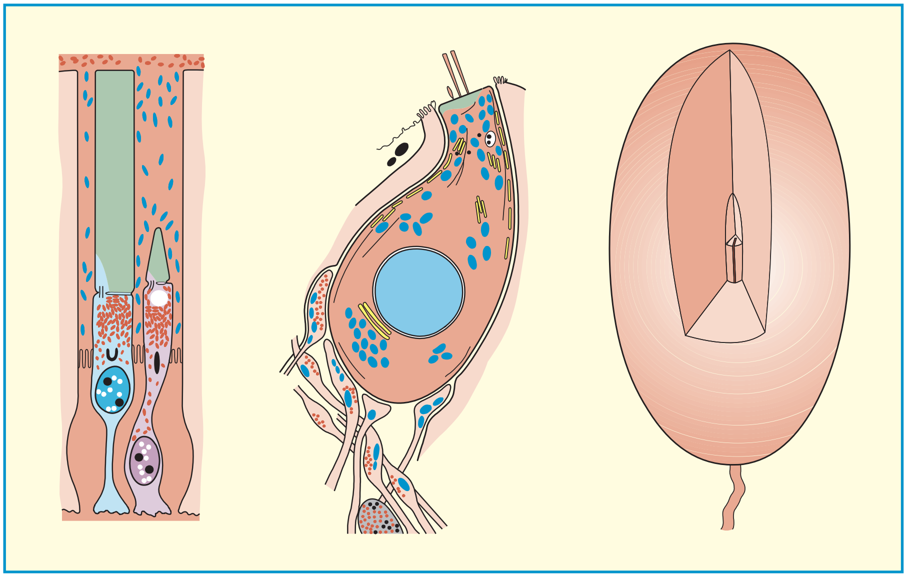

FIGURE 1.11
Sensory receptors. Left: Visual photoreceptors (a rod on the left, and cone on the right). Middle: Auditory inner hair cell. Right: Somatosensory Pacinian corpuscle.

In the case of hearing, for example, there are five synapses on the route from hair cells to cortex. In the case of vision there are four levels of synapse between photoreceptors and brain. In all the senses except olfaction, one of the synapses on the route from sense organ to brain is located in the **thalamus** (olfactory signals are an exception because they pass directly from olfactory bulb to cortex). After the sensory signals arrive at a **receiving area** in the cortex, they are passed on to other cortical areas, often called **association areas**. Figure 1.12 summarizes the successive hierarchical stages characteristic of sensory processing.

Arrows in Figure 1.12 identify the direction of flow of neural signals through the system. In most cases signal flow is unidirectional up to the thalamus (at least in mammals), and bidirectional thereafter. Each stage of processing (each box in Figure 1.12) contains a large population of cells, often extensively interconnected. The input signal that arrives at each stage is modified by interactions that take place between the cells in that stage. As a result, the output signal that is passed on to the next stage differs in some way from the input signal—it has undergone a transformation during its passage through the processing stage. The successive transformations that occur as the sensory signal progresses through the hierarchy of processing refine the information it contains. For example, useful information is selectively retained and elaborated, while less useful information is lost. What information is "useful"? Theories in computational neuroscience attempt to answer this question, and are discussed later.

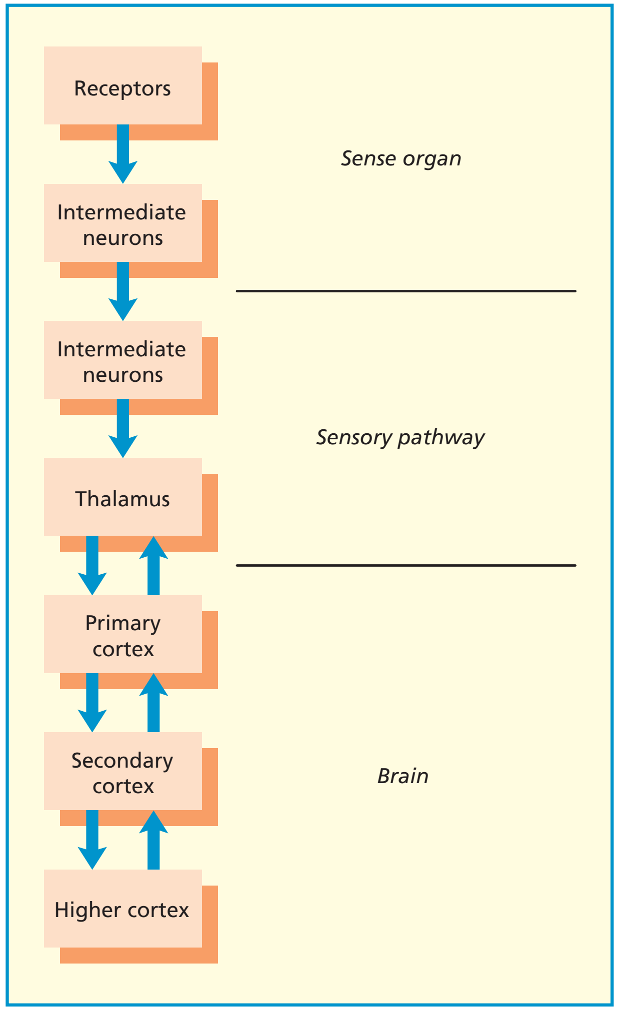

FIGURE 1.12 Hierarchical stages of sensory processing. Neural signals originate in sensory receptors and pass through a series of processing stages. Each stage consists of a large population of interconnected neurons. Arrows denote the direction of flow of the signals.

Specific nerve energy

All sense organs generate the same kind of electrical signals, as we have seen. After transduction, there is no feature of the neural signals that marks them as coming from one of the sense organs rather than any of the others. How, then, can they evoke different experiences? Differences between the senses are not reflected in the nature of the sensory signals themselves, but in their destination in the brain. As Table 1.1 and Figure 1.2 showed, signals in different sensory systems arrive at different cortical receiving areas. It is the destination that marks a particular signal as arising from a specific sense, giving the signal a characteristic sensory quality. Johannes Muller introduced this idea in 1838, and described it as the law of **specific nerve energy**.

Dramatic and direct support for the idea of specific nerve energy can be drawn from observations made during neurosurgery. The neurosurgeon removes a section of skull to expose an area of the cortex. In order to navigate the dense folds of the

? *Why are there so many processing stages in the sensory systems?*

KEY TERMS

Thalamus
A large dual-lobed mass of neurons lying in the middle of the brain at the top of the brainstem and below each cerebral cortex, which relays information to the cortex from diverse brain regions.

Cortical receiving area
An area of the cortex where afferent (incoming) fibers from a sense organ terminate; also known as primary sensory cortex.

Cortical association area
An area of the cortex that receives information from neurons in a cortical receiving area; also known as secondary sensory cortex.

Specific nerve energy
The idea that neural signals in the senses are differentiated by their pathways in the nervous system, rather than by differences in the nature of the signals themselves.

Hz
The abbreviation of hertz, the unit of frequency in a repetitive, time-varying waveform such as a musical sound; each repetition of the waveform is a single cycle.

cortical surface safely (avoiding damage to important functions), small electrical signals are often applied directly to the cortex while the patient is awake but anesthetized. This stimulation evokes sensations associated with the particular sense organ connected to that part of the cortex, such as visual or tactile sensations (see Chapter 3).

Selectivity

Neurons in the sensory systems generally respond only to a particular range of stimuli; they are highly selective. The human auditory system, for example, responds to sound pressure wave frequencies between 20 **Hz** and 16,000 Hz. Sounds outside this range are not detectable (though they may be detectable to other organisms; dogs, for example, can detect frequencies higher than 16,000 Hz). The range of effective stimuli for a particular system can be described as its sensory space. Within this sensory space, stimuli can vary along many different dimensions or parameters. A single spot of visible light can vary in, for example, its horizontal position in the visual field, its vertical position, its size, its intensity, and its wavelength characteristics. Single-unit recording techniques allow us to take an individual neuron at any one level of processing in a sensory system, and examine the particular range of stimuli within the system's sensory space to which that cell responds. Single-unit recording data reveal that sensory cells are highly selective in their response. A specific cell in the visual system, for instance, may respond only when a spot of light is presented at a specific location in the visual field, and has a particular size and color. A change in any one of these parameters causes a reduction in the cell's response (see Figure 1.13).

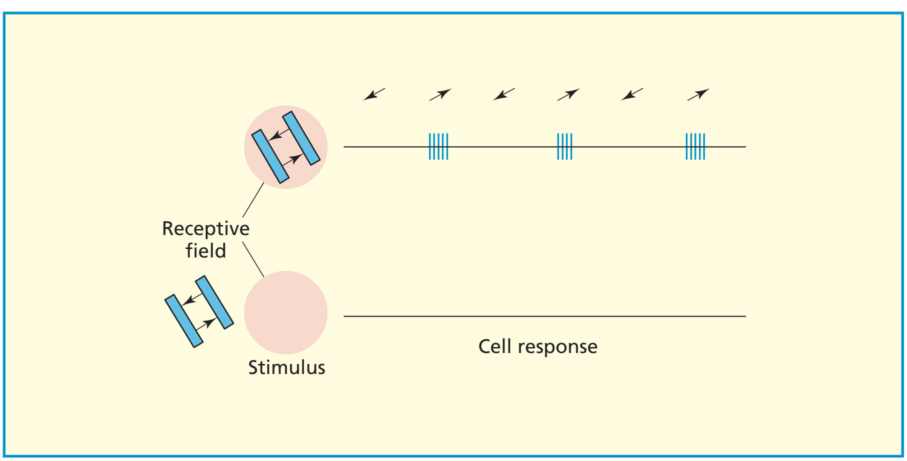

FIGURE 1.13
Selectivity in neural responses. The visual stimulus was a tilted bar that oscillated back and forth repeatedly (left). The upper trace on the right shows the neural impulses (short vertical lines) recorded from a cat cortical cell by Hubel and Wiesel. Time is plotted horizontally, and arrows represent the two phases in the bar's movement. The cell responded only when the bar moved up and to the right. When it moved out of the cell's receptive field (lower trace), then no response at all was recorded.

Such selectivity is a universal property of sensory cells. Different cells have different stimulus preferences, so a stimulus change that results in a reduction in one cell's response is likely to result in an increase in another cell's response. A given cell responds to stimulation only in a limited spatial area of, for example, the visual field or body surface. This is usually called the cell's **receptive field.** Different cells have receptive fields in different locations. So as the stimulus moves about in visual space, or across the surface of the body, different cells respond to it.

Univariance and Population Coding

Although sensory neurons respond in a highly selective way to sensory stimuli, there is still an unavoidable ambiguity in their response which was first described by Naka and Rushton (1966). They measured the graded change in electrical potential produced by photoreceptors when they are struck by light, and observed that the response depends jointly on two stimulus parameters, namely the intensity of light and its wavelength. Photoreceptor response increases with intensity, but a given photoreceptor also responds more strongly to some light wavelengths than to others (as discussed in Chapter 8). The receptor has one **univariant** kind of response (electrical potential) which depends on two stimulus parameters. One cannot "read" the response to infer either intensity or wavelength unambiguously because any one response level can be produced by different combinations of the two variables. Univariance is a universal problem in sensory coding. For instance the response of many visual neurons depends on a whole constellation of stimulus parameters including position, size, contrast, orientation, and motion direction as indicated in Figure 1.13.

According to the principle of univariance, any given neuron responds to many different stimuli. The converse is also true: Any given stimulus induces activity in many different neurons. This consequence of univariance is the basis for a form of coding known as **population coding**. Neurons are activated to a greater or lesser extent by different stimuli, so the value of a given stimulus can be inferred from the relative activity of the whole population of neurons. For example, the downward visual movement of a waterfall will excite a large number of cortical cells in the visual system which respond to movement, but some cells will respond much more than others (the cells which are tuned to downward motion). People walking across your field of view from left to right will induce a different pattern of activity in the population of cells, with cells tuned to rightward motion responding the most. Population coding is thought to be ubiquitous in the sensory systems (see Pouget, Dayan, & Zemel, 2000) as you will read in later chapters.

Organization

In general, cells that respond to similar stimuli tend to be located near to each other in the brain. The most dramatic examples of this organization are so-called

KEY TERMS

Receptive field
The area of a stimulus field in which presentation of a stimulus causes a change in the firing rate of a given sensory neuron.

Univariance
A principle of neural coding in which any one level of excitation in a neuron can be produced by different combinations of stimulus values.

Population coding
A general principle of sensory processing, according to which different values of a perceptual attribute are coded by different patterns of activity in a whole population of neurons.

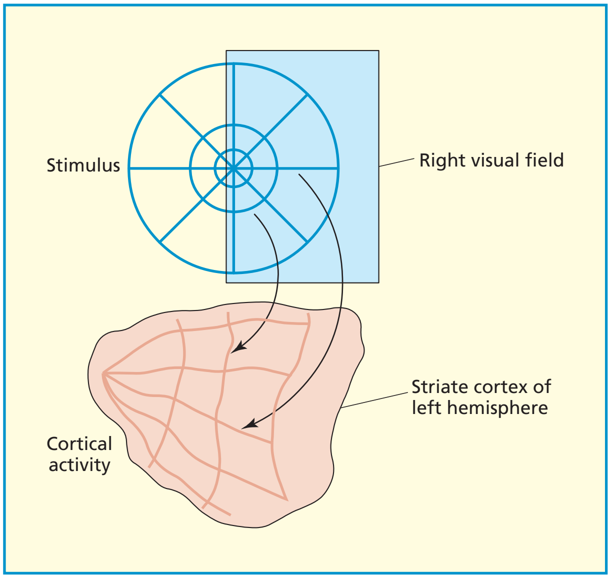

FIGURE 1.14
Topographic map in the visual system. The bull's-eye pattern in the upper part of the figure was presented to a monkey so that the area enclosed by the rectangle appeared in its right-hand visual field. The lower part of the figure is a flattened view of the animal's left cerebral hemisphere. A physiological staining technique highlights any cells that were active while the pattern was being viewed (dark areas). The pattern of activity is highly organized, and demonstrates how the animal's visual field is laid out topographically across the surface of the cortex. Based on Tootell et al. (1982).

topographic maps. Figure 1.14 shows an example from vision.

The upper bull's-eye pattern was presented to a monkey so that the area outlined by the rectangle appeared in the animal's right visual field (i.e. fixation at the center of the pattern). The lower image is a map of the left hemisphere of the monkey's cortex, showing only a portion at the rear of the hemisphere (the area where visual signals arrive—striate cortex). Tootell et al. (1982) used a physiological **staining** technique to identify which cells in this area of cortex were active while the animal viewed the bull's-eye. Regions containing active cells are darker. Neurons with receptive fields at nearby retinal positions are clearly located near to each other in the cortex, since the active regions are grouped together. The pattern of activity is so well ordered that it constitutes a map of the projection from the retina (often called a topographical cortical map). Notice that the cortical map is distorted. The small region of the image near to fixation (innermost ring of the bull's-eye) occupies a relatively large proportion of the cortical surface (left-hand third of the cortical map). This property of organization is called **cortical magnification**, and is a common feature across the senses.

KEY TERMS

Topographic map
A systematic projection from one neural structure to another, which preserves the spatial arrangement of neural connections (e.g., from the retina to the cortex).

Staining
A technique for identifying substances in and around cells, using chemical stains that are selectively taken up by certain kinds of tissue (e.g., cell bodies).

Cortical magnification
The exaggerated cortical representation of one part of a sensory dimension or surface compared to another.

Plasticity

The neural mechanisms that acquire and process sensory information are modifiable during development and during adulthood. As a human infant grows, the dimensions of his or her body change progressively. Limbs become longer and heavier, the eyes move apart. Sensory systems must be capable of adapting to these changes. Research has shown that the brain is able to tune itself into the changing sensory environment of the developing organism. Although this plasticity is only possible for a limited period during development (sometimes called a "critical period"; see Blakemore and Cooper, 1970; Maurer et al., 1999). Over much shorter time periods, each sensory system is also able to adapt itself to the specific sensory environment that the individual finds him or herself in. For example, as the sun sets the visual system's sensitivity changes progressively to match the prevailing illumination level, or, if you wear a particularly coarse-textured shirt, the initial feeling of itchiness conveyed by touch receptors in the skin soon subsides as the receptors adapt to their new environment.

? *Is adaptation just a by-product of depleted resources?*

The graph in Figure 1.15 shows the change in response of touch receptors to a steadily applied stimulus over a period of 40 seconds. **Neural adaptability** is a universal feature of sensory systems, and is the source of the sensory adaptation effects described earlier.

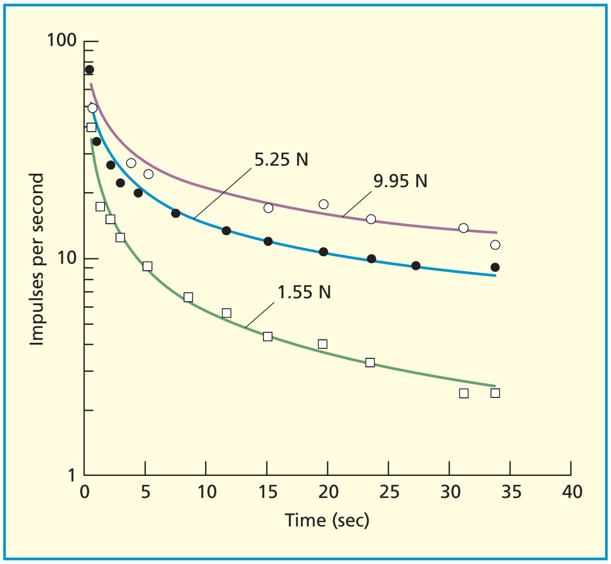

FIGURE 1.15
Time-course of the response of a pressure receptor to stimuli at three different intensities. Response rate is initially high, but declines steadily over a period of 40 seconds. Redrawn from Schmidt (1981, p. 88).

Noise

The activity level of a neuron can be measured in terms of the frequency with which it generates electrical impulses. Activity level can vary between zero (no impulses at all) to approximately 800 impulses per second, though the typical rate for a very active cell is 100–200 impulses per second. In the example shown in Figure 1.15, the initial activity level of the touch receptor was about 100 impulses/s. Neural signals show a certain degree of variability, even in the absence of adaptation or short-term plasticity. The response to repeated presentation of identical stimuli differs randomly from presentation to presentation. This kind of variability is usually called "noise" because it bears no systematic relation to the incoming stimulation, or signal. There are two sources of variability (White, Rubinstein, & Kay, 2000). First, there are fluctuations in the electrical excitability of neurons, caused mainly by random opening and closing of **ion channels**. Second, there are fluctuations in synaptic transmission caused by, among other factors, the random nature of diffusion and chemical reaction across synapses.

We need to be able to detect changes in neural response since they reflect changes in the state of the outside world. However, any measure of change in neural response must take account of the inherent variability in the sensory signal. Theories of sensory coding must, as we shall see, accommodate neural noise.

? *In what sense, if any, can one regard the brain as a computer?*

COMPUTATIONAL NEUROSCIENCE

Three twentieth century mathematicians laid the foundations for the modern field of computational neuroscience: Alan Turing (1912–1954), Claude Shannon (1916–2001), and David Marr (1945–1980). Turing is most famous for his work as a code-breaker during the Second World War, but he also foresaw the development of modern computers. He developed the notion of universal **computation**, according to which all sufficiently powerful computing devices are essentially identical. Any one device can emulate the operation of any other device. If we accept that the brain is a form of computational device, then it follows that it can be emulated by other such devices, namely computers. This is the conceptual basis for computational neuroscience.

KEY TERMS

Adaptability
The ability of a sensory system to vary its response characteristics to match prevailing stimulation.

Ion channel
A specialized protein molecule that allows certain ions (e.g., sodium, potassium) to enter or leave a cell, so altering its electrical state.

Computation
The manipulation of quantities or symbols according to a set of rules.

Shannon was working for a US telecommunications company at about the same time as Turing was working in the UK. He developed a rigorous mathematical theory of how information is transmitted across telecommunications systems. Shannon's basic conceptual unit consists of three parts: A signal source, a transmission line or channel to carry the signal, and a receiver. Shannon identified several key properties that govern the behavior of any such system:

- Channel capacity—the number of signals it can transmit simultaneously
- Transmission rate—how quickly the signals travel along the channel
- Signal redundancy—the amount of information carried in the signal
- Noise—intrusion of information that is unrelated to the signal.

Shannon defined each of these properties in precise mathematical terms to create his "Information Theory," which has since been used to design and analyze telecommunications networks. For example, signal redundancy allows signals to be compressed with no loss of information:

> *The redundancy of ordinary English, not considering statistical structure over greater distances than about eight letters, is roughly 50%. This means that when we write English half of what we write is determined by the structure of the language and half is chosen freely.*
>
> *(Shannon, 1948, p. 392)*

Modern text messages can omit certain letters without loss of information (mny wrds cn b abbrvtd in ths wy). Cognitive scientists soon recognized that the "source–transmitter–receiver" concept can be applied to neural systems as well as to electronic systems. The neural processing stages in Figure 1.12 can be considered as a succession of source–transmitter–receiver units, and Information Theory provides the mathematical tools to analyze their behavior. For example, the concept of redundancy helps us to understand stimulus selectivity and adaptation in sensory neurons. High levels of activity incur an energy cost, so neurons tend to respond only when the activity provides the most useful (least redundant) information.

According to Information Theory, perception is above all an information processing task. David Marr accepted this view wholeheartedly. He was trained in mathematics and physiology at Cambridge in the UK before moving to the MIT Artificial Intelligence laboratory in the 1970s. Marr had initially developed mathematical models of the cerebellum, hippocampus, and cortex, before switching his attention to the visual system. Marr argued that an adequate theory of any information processing system like the visual system had to consider three levels of analysis (Marr, 1982, p. 25):

Computational theory "What is the goal of the computation, why is it appropriate, and what is the logic of the strategy for carrying it out?"

Representation and algorithm "How can this computational theory be implemented? In particular, what is the representation of the input and output, and what is the algorithm for the transformation?"

Hardware implementation "How can the representation and algorithm be realized physically?"

Cognitive neuroscience studies the hardware level of neural processing, computational neuroscience is concerned with computational theories, and psychophysics investigates the middle level of representation and algorithm. The three levels are loosely connected. A given theory can be implemented using different algorithms, which can in turn be realized in different physical systems. Indeed Turing's concept of universal computation argues that a given computation can be implemented in many different ways.

Marr's computational approach to building theories of perception has been highly influential. Some of the key concepts in computational neuroscience are unpacked in the next section.

BASIC CONCEPTS IN COMPUTATIONAL NEUROSCIENCE

Representation

Representation sits in the very center of Marr's three levels of analysis. It has long been accepted that, although the world appears to be "out there," it is in fact a pattern of neural activity evoked in our head during the act of perceiving. As Boring (1950) noted: "The immediate objects of the perception of our senses are merely particular states induced in the nerves" (p. 82).

A specific internal state of the brain, in the form of a particular pattern of neural activity, in some sense *represents* the state of the outside world. Perception must involve the formation of these **representations** in the brain. Most modern computational theories of perception are in essence theories about how the brain builds and uses representations of the world. Earlier in the chapter we discussed the idea that neural signals in sensory systems pass through a series of processing stages. According to the notion of representation, each of these stages must contain a representation of the state of the world. The transition through a series of neural processing stages can be viewed as a transition through a series of internal representations.

The idea that the state of one physical system (e.g., the brain) can in some sense represent the state of another system (e.g., the world) is very general, and can be applied to many systems. For example, the reading on a thermometer represents the current temperature; the display on a wristwatch represents the current time. As time moves on, the watch's display changes accordingly. A distinction can be drawn between two basic forms of representation, **analog** and **symbolic**. In an analog representation, magnitudes in one physical system map onto analogous magnitudes in another system. For example, height in a mercury thermometer represents temperature; the moving progress bar you see on your computer while downloading a file represents the data downloaded so far. Analog representations seem to be very common in sensory systems. One of the earliest examples was discovered by Adrian and Zotterman (1926), who measured the firing rate of sensory nerves in a frog's muscle as a function of the mechanical load on the muscle. Firing rate increased with load, so creating an analog representation of muscle load. As later chapters will show, analog **rate codes** of this kind are thought to represent many sensory dimensions such as brightness, loudness, pressure, and head acceleration. Morgan (2003) provides a detailed account of how analog spatial representations (maps) in the brain are the basis of our perception of space.

KEY TERMS

Representation
The idea that the state of one physical system can correspond to the state of another physical system; each state in one system has a corresponding state in the other.

Analog representation
A representation in which magnitudes in one system, such as spatial position or response rate, map onto analogous magnitudes in another system.

Symbolic representation
A representation in which discrete symbols in one system, such as characters or words, act as tokens to denote states or entities in another system.

Rate code
Neural coding principle in which the firing rate of a neuron carries information about the stimulus; it is associated with neural coding of magnitude (light intensity, loudness, mechanical pressure, or stretch).

? *Think of another example of how the same information can be represented in both analog and symbolic form.*

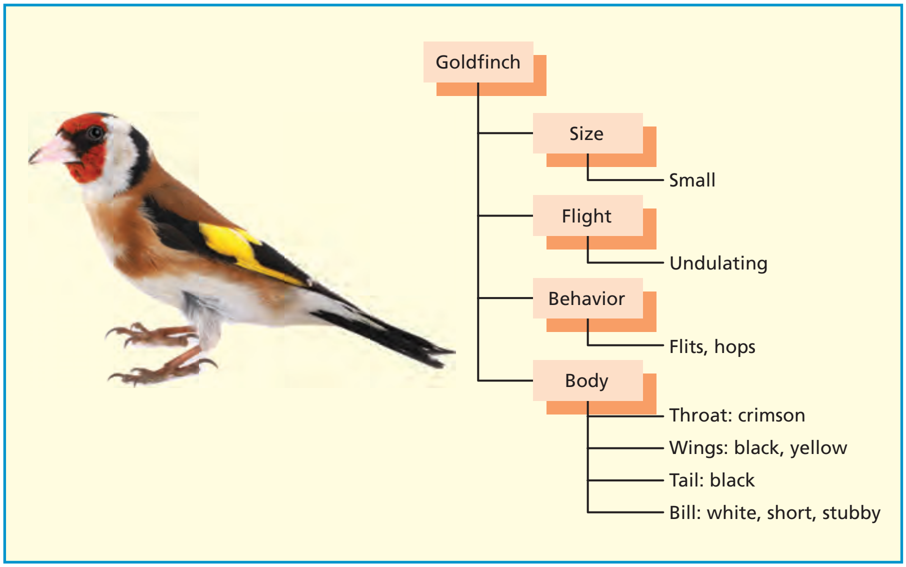

FIGURE 1.16
Entry for a goldfinch in a bird-spotter's handbook. The pictorial image of the bird constitutes an analog representation, while the list of attributes on the right constitutes a symbolic representation. Photo © panbazil/ Shutterstock.com.

In a symbolic representation a limited vocabulary of arbitrary symbols in one system maps onto states or entities in the other system. A digital watch display represents time using the digits from 0 to 9, for example. Similar displays can be used to represent temperature, vehicle speed, altitude, and so on. As an example of the distinction between analog and symbolic representation, consider how a bird-spotter's handbook might represent a specific species of bird. The entry for that species may contain a still image of the bird, and a text list of its attributes, as illustrated in Figure 1.16. A multimedia text may also contain an audio clip of the bird's call, and a movie clip of the bird's flight. The image, audio clip, and movie clip are clearly analog representations, since they represent the bird in terms of its patterns of light or sound values. The text list of attributes is an abstract symbolic representation of the bird.

Computation

The concept of computation lies alongside the concept of representation at the heart of most present-day theories of perception (see Churchland & Sejnowski, 1992). In an abstract sense, computation can be defined as the manipulation of quantities or symbols according to a set of formal rules. It follows from this abstract definition of computation that a neural process that produces an analog quantity such as brightness, or a perceptual symbol such as an object property, can be described as a computational process. The formal rules used in computations are sometimes called **algorithms**. The idea that neural processing is a form of computation originated from the work of Alan Turing, as mentioned earlier. According to Turing, the brain can be considered as a computing device in the sense that it manipulates quantities and symbols according to sets of rules.

KEY TERM

Algorithm
A specific computational procedure used to transform one representation into another.

How exactly does the concept of computation apply to perception? We have seen that perceptual systems can be considered as *representational* systems—internal brain states represent the state of the outside world. Perceptual analysis proceeds through a series of representations, produced by a series of neural processing stages. The representation received at each processing stage is transformed into a new representation by a computational operation, and then passed onto the next stage as depicted in Figure 1.17 (a modification of Figure 1.12).

The nature of the computation that transforms one representation into the next depends on what form the two representations take, analog or symbolic. Computations performed on analog representations involve the creation and manipulation of *quantities* according to a set of rules, sometimes called signal processing. The computations involve mathematical manipulations of the values stored in the original representation. Computations performed on symbolic representations involve the creation and manipulation of *symbols* according to a set of rules. The computations involve comparisons between symbols to test for equality, and the combination of symbols to create new symbol structures. For example, the first representation may contain the symbols illustrated in Figure 1.16 (Size = Small; Flight = Undulating; etc.). The perceptual system may contain a rule that states that (IF Size = Small AND Flight = Undulating AND . . . THEN Bird = Goldfinch). An instance of the symbol for “goldfinch” would be created at the next level of representation in the processing hierarchy.

Symbolic representations and computations have traditionally been associated with human cognition, such as problem solving (Newell & Simon, 1972), and seem a natural choice for high-level perceptual representations relating to object identity. Initial perceptual representations, such as those in sense organs and cortical receiving areas, are probably best considered to be analog in form, because they involve rate codes of relatively simple stimulus properties such as intensity. Representations of perceptual objects are thought to be symbolic, but it is not yet clear where and how perceptual representations shift from analog to symbolic.

Notice the direction of the arrows in Figure 1.17. Some arrows point “upward” indicating that information flows from the bottom (receptors) to the top (cortex), so-called bottom-up processing. Other arrows point “downward,” indicating that information flows back down from higher levels of analysis to lower levels, so-called top-down processing. The top-down route allows for some strategic control of processing based on, for example, context or attention.

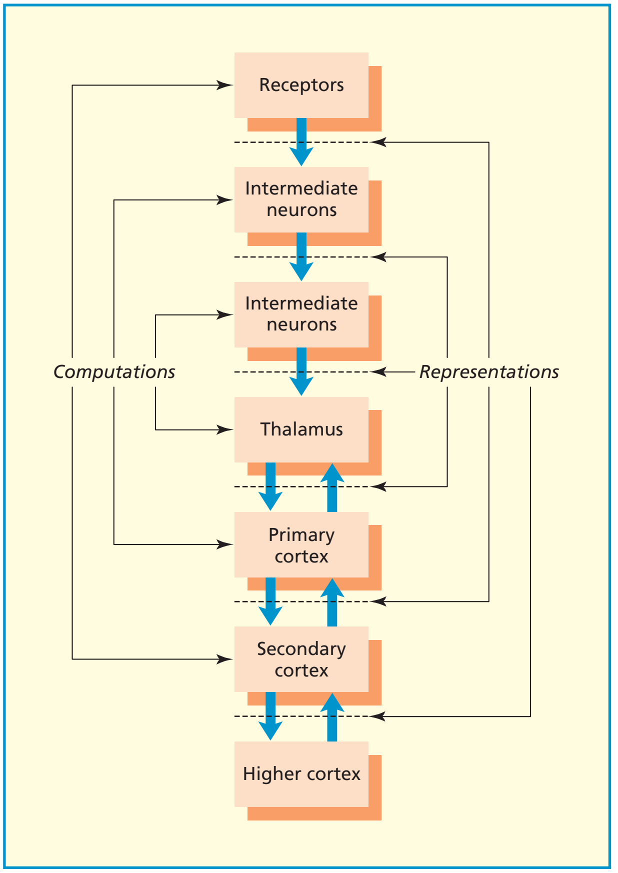

FIGURE 1.17
Representation and computation in relation to the hierarchical processing scheme depicted in Figure 1.12. Each processing stage receives a representation of the sensory stimulus as its input and creates a new representation that is passed on to the next processing stage. The modification that takes place at each processing stage can be considered as a computational operation that transforms one representation into another.

CHAPTER SUMMARY

Perception involves highly complex neural processes that consume a substantial proportion of the brain's cerebral cortex.

SENSATION, PERCEPTION, AND SENSORY MODALITY

Sensations (also known as qualia) are primitive mental states or experiences induced by sensory stimulation. Perceptions are complex, organized, and meaningful experiences of objects or events. Qualia can be divided into seven distinct sensory modalities: Audition, gustation, nociception, olfaction, somatosensation, the vestibular sense, and vision.

The modalities differ in terms of the physical stimuli that excite them, the neural structures involved in transduction and sensory analysis, and the functions they serve. In humans, a much greater area of cortex is devoted to vision than to the other senses.

The three key elements of perception are:

1. Stimuli
2. Neural responses
3. Perceptions.

Stimuli generate neural responses which in turn lead to perceptual experiences. Psychophysics studies the relation between stimuli and perceptual experience, whilst neuroscience studies the relation between stimuli and neural responses. Psychophysical linking hypotheses propose specific links between perception and neural responses, as part of theories in computation neuroscience.

PSYCHOPHYSICS

Psychophysical methods to study perception were developed by Weber and Fechner in the 1800s, who established some fundamental laws governing the relation between sensory stimuli and sensation. Basic concepts in psychophysics include:

- Sensory thresholds
- Sensory magnitude
- Sensory adaptation
- Psychophysical linking hypotheses.

COGNITIVE NEUROSCIENCE

Methods used to study sensation and perception include:

- Lesion experiments
- Clinical cases

- Single-unit recordings
- Neuroimaging
- Direct brain stimulation.

Basic concepts include:

- Neural impulses and transduction
- Hierarchical processing
- Specific nerve energy
- Selectivity
- Univariance
- Organization
- Plasticity
- Noise

COMPUTATIONAL NEUROSCIENCE

The foundations of computational neuroscience were laid by three mathematicians:

- Alan Turing introduced the concept of universal computation
- Claude Shannon developed Information Theory
- David Marr introduced the three-level distinction between computational theory, representation, and hardware implementation.

Basic concepts include:

- Analog and symbolic representation
- Computation.

TUTORIALS

PSYCHOPHYSICAL METHODS

As we saw earlier in the chapter, certain physical stimuli evoke perceptual experiences ranging from simple sensations such as “redness” or “loudness” to complex perceptions such as facial identity. How can we study the relationship between physical stimuli and perceptual experience? The simplest method is to use verbal reports, such as “it looks red” or “that is my grandmother.” This phenomenological approach is severely limited in its usefulness, for several reasons. First, it obviously requires subjects who can describe their experiences in words, so excludes infants and animals. Second, even when restricted to subjects who can talk, it is contaminated by differences in the way different people use words. Third, it is open to bias introduced by each individual’s assumptions, expectations, and desires.

We need precise, accurate measures of perception that can be used to establish the limits of perceptual ability, to monitor how these limits change with stimulus conditions, and to test the predictions of perceptual theories. Ideally these measurement methods should be immune to the effects of verbal ability, expectation, and attitude. Over the last 100 years or so a body of experimental techniques has been developed to provide the required measurements. Since these techniques provide quantitative, physical measures of psychological phenomena, they are called *psychophysical* methods.

Psychometric functions

Any plot relating a quantifiable response to a physical stimulus measure is known as a psychometric function. One might plot, for example, sound intensity against the probability that the subject will detect the presence of the sound. What is the typical shape of a psychometric function in a detection experiment? One might expect that below a certain stimulus level the sound is never heard, and above it, the sound is always heard—a step function. Real psychometric functions always show a gradual shift from no-detection to detection as stimulus level increases, rather than a sudden shift (as shown earlier in the chapter in Figure 1.4). Why?

Classical psychophysical theory and the psychometric function

The concept of the threshold is crucial to classical psychophysical theory. A threshold marks a transition from one perceptual experience to another, usually as a result of a simple change in the physical stimulus. For example: How intense must a sound be for us to detect it? How fast must something move for us to see the movement? How different in distance must two objects be for us to tell that one is nearer? There are two kinds of threshold, the **absolute threshold** and the **differential threshold**. The absolute threshold marks the smallest amount of stimulus energy required for an observer to just detect its presence (e.g., the minimum sound intensity or movement velocity required for detection). The differential threshold marks the minimum change in stimulus energy that can be detected by an observer. This threshold is also known as the “just noticeable difference,” or JND, as discussed earlier in the chapter (e.g., the small change in sound intensity required for the observer to notice a change in loudness). Classical psychophysical methods were basically developed to measure JNDs accurately and reliably.

Classical psychophysical theory explains smooth real-world psychometric functions (as in Figure 1.4) with the following three assumptions. First, there is an ideal threshold function that relates the internal response of the sensory system (“sensory magnitude”) to stimulus level. This function is a step function with two levels, “low,” and “high.” Second, when the internal

KEY TERMS

Absolute threshold
A measure of the smallest amount of stimulus energy required for a subject reliably to detect its presence.

Differential threshold
A measure of the smallest change in stimulus level required for a subject reliably to discriminate the direction of stimulus change.

response is "high," the observer always reports detection of the stimulus, and when the internal response is "low," the observer never reports detection of the stimulus. Third, the exact position of the threshold in relation to stimulus level is subject to some random fluctuation, due to momentary variations in neural sensitivity, arousal level, and so on. Although the threshold tends, on average, to cluster around a specific stimulus level, it occasionally falls below or above this level, so that the probability that the threshold will fall at a particular stimulus level conforms to a bell-shaped curve or **normal distribution**, as in Figure 1.18 (left).

In the figure, at a low stimulus level (top-left graph), the probability that the threshold will be lower than this level is small (arrowed area), so detection rates are low. As the stimulus level increases, the likelihood of detection improves because there is a much greater probability that the threshold will be lower than the stimulus level (lower-left graph). Consequently, if we plot probability of detection against stimulus level, a typical psychometric function is obtained (right-hand graph). At what stimulus level is threshold reached? According to classical theory, the "true" threshold coincides with the mean of the probability distribution in Figure 1.18. Since, by definition, 50% of the distribution lies below the mean, and 50% lies above it, the most logical place on the psychometric function to locate the threshold is

KEY TERM

Normal distribution
A distribution in which scores fall symmetrically and predictably on either side of the mean score.

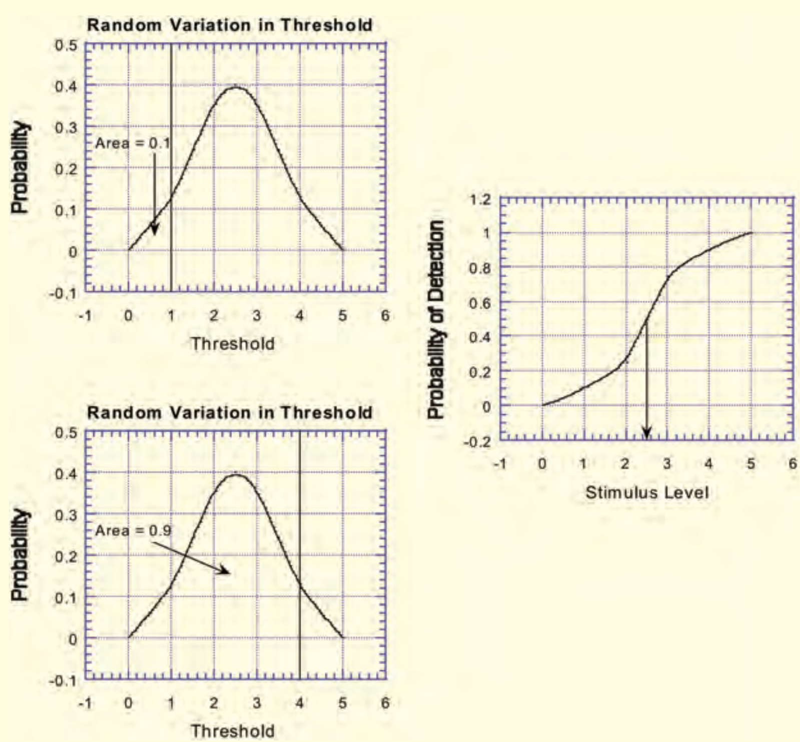

FIGURE 1.18
Explanation of the empirical psychometric function, according to classical psychophysical theory. The stimulus level at which sensory response reaches threshold is subject to some degree of random variation (left-hand graphs). A low intensity stimulus (e.g., 1.0 in the upper-left graph) is unlikely to be detected (probability 0.1), because only rarely does the threshold drop to such a low stimulus level. A high intensity stimulus (e.g., 4.0 in the lower-left graph) is very likely to be detected (probability 0.9), because most of the time the threshold is lower than this level. As a result detection rates improve gradually with stimulus level (right-hand graph).

KEY TERMS

Method of adjustment
A psychophysical procedure in which subjects adjust the value of a stimulus to estimate their threshold.

Method of constant stimuli
A psychophysical procedure in which preselected stimuli are presented to the subject in random order over a series of trials; the subject makes a binary response after each trial.

at the 50% point. This account of thresholds applies to both absolute and differential thresholds.

Classical psychophysical methods

All classical methods aim to measure the observer's threshold. Some methods provide an estimate of the whole psychometric function. Others provide an estimate of just one point on the function, usually the 50% point. A number of classical methods were developed at the turn of the 19th century, but this tutorial will describe the only two methods that are still in use, the **method of adjustment** and the **method of constant stimuli**.

Method of adjustment

In this procedure, the observer is given control of the stimulus (e.g., a dial that controls stimulus intensity), and asked to adjust it until it is just detectable. This method is quick and easy to use, but rather unreliable. The observers have direct control of the stimulus, so are free to apply some degree of bias to their settings. Some observers may try to impress with their high sensitivity, and tend to bias dial settings toward low stimulus levels. Other observers may prefer to be cautious and careful, tending to bias their settings toward high stimulus levels.

Method of constant stimuli

The experimenter selects a range of stimulus levels at the start of the experiment. These different levels are presented to the subject repeatedly in random order, in a series of experimental trials. After each presentation, the subject is required to respond "yes" if the stimulus (or a difference between stimuli) was detected in that trial, or "no" if it was not detected. This method is more trustworthy than adjustment, since the subject has no direct knowledge of the stimulus level presented. It constructs the full psychometric function, so is reliable but more labor-intensive than the method of adjustment. Computers can be used to take care of stimulus selection, increasing the efficiency of the method.

The problem of bias in classical methods

In classical psychophysics, the subject's response to the stimulus is assumed to depend only on their sensitivity, the stimulus level at which the internal response shifts from low to high. However, responses are also likely to reflect uncontrolled bias effects. The problem is most severe using the method of adjustment, but may also intrude in the method of constant stimuli. Since a stimulus is presented in every trial, the observers are free to apply some degree of bias to their responses. They may, for example, be feeling uncooperative or lacking in confidence, and so unwilling to respond "yes" unless they are very confident of being correct. As a result, the

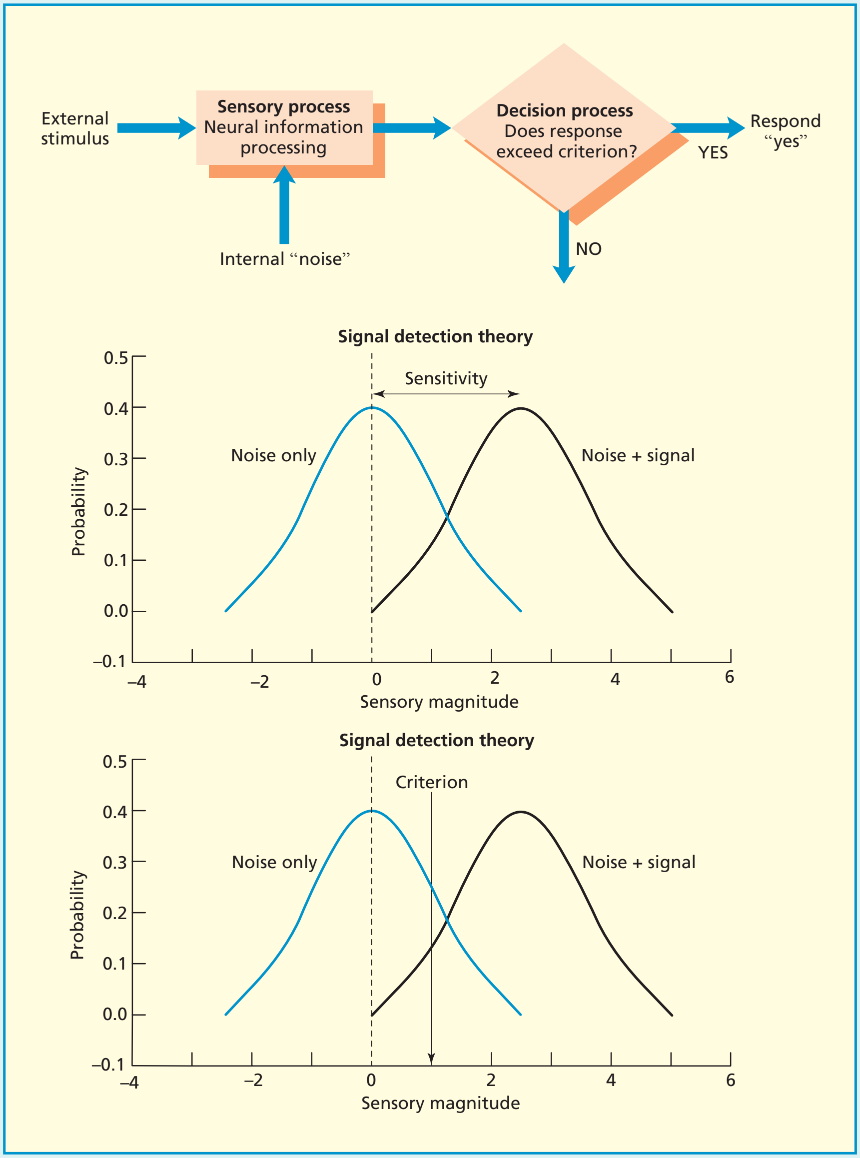

FIGURE 1.19 Signal detection theory (SDT). Top: Two hypothetical stages in detection, according to SDT. Middle: According to SDT, both stimulus-absent ("noise only") and stimulus-present ("noise + signal") trials generate a response in the sensory process of the detection system. Each response is subject to some random variation due to internal noise, shown by the two distributions. The observer's sensitivity to the stimulus is characterized by the difference between the means of the two distributions. Bottom: The decision process receives a response from the sensory process, and must decide whether the response came from the noise only distribution or from the noise + signal distribution. A specific response level is selected ("criterion"), above which the decision is that the response came from the noise + signal distribution.

measured threshold will not be a pure estimate of the subject's sensitivity to the stimulus, but will reflect some unknown combination of sensitivity and bias. Signal detection theory was developed specifically to address the problem of bias effects.

Signal detection theory (SDT)

Signal detection theory (SDT) acknowledges the importance of bias effects by assuming that stimulus detection is a two-stage process (Figure 1.19, Top). The first stage is a purely sensory process in which a specific stimulus level produces an internal sensory response that depends on the intensity

KEY TERM

Signal detection theory
A theory of performance in psychophysical experiments in which subjects' decisions are determined jointly by their sensory response and by a tendency to respond in a certain way.

of the stimulus and the sensitivity of the sensory system. This internal response is subject to random internal “noise” of the kind described earlier in the chapter. The second stage is a decision process in which the sensory response magnitude is compared to an internally set criterion. If the response magnitude exceeds this criterion, the decision process decides that a stimulus was present. If the internal response falls below the criterion, then the decision process decides that no stimulus was present. The position of the criterion is influenced by all the factors described earlier that affect bias. Highly motivated subjects may adopt a low criterion, reflecting a bias in favor of accepting rather weak stimuli. Subjects who lack confidence in their judgments may adopt a high criterion, because they are biased toward accepting only relatively intense stimuli. The experimenter is interested primarily in the sensitivity of the sensory system, rather than the subject’s bias, but SDT provides methods of estimating both sensitivity and bias.

SDT methodology: Yes/no and forced-choice tasks

In classical psychophysical methods, every stimulus presentation in the experiment contains a stimulus. In SDT methods only *half* of the presentations contain stimuli, randomly selected. For example, if the subject is required to detect the presence of a visual pattern against a uniform background, then only half of the presentations contain the pattern and background, while the other half contain only the background. Presentations containing a stimulus are called *noise + signal* presentations, for reasons that will become obvious, and presentations not containing a stimulus are called noise presentations. The subject must discriminate between noise + signal presentations and noise presentations. Two kinds of task are commonly used. In a **yes/no task**, the subject is presented with a single stimulus event in each experimental trial, which may or may not contain a signal. The subject must respond “yes” if he or she decides that a stimulus was presented in that trial, and “no” otherwise. In a **forced-choice task**, the subject is usually presented with two stimulus events in each trial, side by side or one after the other. In a vision experiment, for example, two stimulus patches may be presented side by side. In a hearing experiment, two sounds may be presented sequentially. Only one event contains the stimulus to be detected. The subject must decide which of the two events contained the stimulus, and respond “left” or “right,” or “one” or “two” as appropriate. Tasks of this kind are commonly called two-alternative forced choice or 2AFC tasks.

Notice that in SDT tasks the subject has no direct knowledge of which event contains the required stimulus. This reduces the possibility of bias, because when the stimulus is not detectable the subject is forced to guess as to which event contained the stimulus. However, in yes/no tasks there is a possibility of some bias in favor of “yes” responses, because of a social aversion to saying “no.” Many researchers prefer to use forced-choice tasks wherever possible, because the alternative responses are fairly neutral (Green & Swets, 1966).

KEY TERMS

Yes/no task
A psychophysical procedure in which only 50% of presentations contain a stimulus, and the subject must respond “yes” or “no” after each.

Forced-choice task
A psychophysical procedure in which each presentation contains two intervals, only one of which (randomly selected) contains the stimulus; the subject must select the correct interval.

SDT measures of sensitivity and bias

This brief description of SDT measures is based on a yes/no task, but also applies (with appropriate modifications) to forced-choice tasks. SDT theory assumes that both noise + signal and noise events generate an internal response in the sensory process of the detection system, because this process is subject to internal noise (Figure 1.19). Noise events reflect only the contribution of internal noise to the response. Noise + signal events reflect contributions from both internal noise and external stimulation. The probability distribution of the response to each event can be plotted, as shown in Figure 1.19. Each distribution simply plots the relative probability of that event generating a specific response magnitude. The noise distribution reflects only the variable level of internal noise, which tends to cluster around a mean value (the peak of the distribution). The noise + signal distribution contains contributions from both internal noise and external stimulation. The effect of the external stimulus is to add a constant value to the noise distribution, displacing it toward higher response magnitudes. The distance over which noise + signal distribution is shifted relative to the noise distribution depends on the system's sensitivity to the stimulation. The difference between the means of the two distributions is taken as a measure of the sensitivity of the system to the stimulus, and is known as **d′ (d-prime)**.

In any one trial of a yes/no task, the decision process receives a response at a particular magnitude, and must decide whether that response was drawn from the noise distribution or from the noise + signal distribution. SDT assumes that the decision process selects a specific criterion level of response, shown by the arrow in Figure 1.19. Response levels below this value are deemed to belong to the noise distribution, so are assigned a "no" response. Response levels above this value are deemed to belong to the noise + signal distribution, and are assigned a "yes" response. The level at which the criterion is set depends on biasing factors. It may be "unbiased," or midway between the two distributions, or biased in one direction or the other.

SDT provides various methods for making precise estimates of sensitivity or d′ independent of criterion level or **bias** (also known as β). However, bias effects are pervasive (see Witt et al., 2015). In 2AFC tasks, a simple measure of sensitivity is given by the proportion of correct responses recorded by the subject. Readers interested in the mathematical details of SDT measures are referred to Stanislaw and Todorov (1999), who provide formulae and procedures for performing the calculations using general-purpose software such as spreadsheets.

Evaluation

SDT was first applied to psychophysical problems by Tanner and Swets in the mid-1950s and, as we have seen, it discards the classical notion of the threshold in favor of d′. Fifty years later, despite the widespread acceptance

KEY TERMS

d-prime (d′)
A measure of stimulus sensitivity based on signal detection theory, it represents the increase in sensory response caused by the presence of stimulus.

Bias (β)
A measure of response bias based on signal detection theory. It represents the extent to which the subject is predisposed toward making a particular response, regardless of stimulus level.

in the scientific community of many of the ideas in SDT, much contemporary research still measures performance in terms of thresholds rather than d′ (Gordon, 1997). Why should this be so? Thresholds are still a very useful, and intuitively meaningful, way of summarizing the performance of a subject, reflecting the stimulus level that is just detectable by the subject. By contrast, d′ is a more abstract measure of sensitivity to a specific stimulus level, and is meaningful only if one appreciates the statistical concepts that underlie it. Despite the continuing attachment to thresholds, many researchers measure them using percentage correct responses in 2AFC tasks, having taken on board the concerns about bias effects raised by advocates of SDT.

THEORETICAL TRADITONS IN PERCEPTION RESEARCH

The previous tutorial on psychophysical methods introduced some of the techniques that have been developed for collecting perceptual data, and the rationale behind them. This second tutorial discusses the major theoretical movements that have motivated psychophysical experiments over the last 150 years. We must first define the essential properties of a theory, and discuss how the adequacy of different theories can be assessed.

At the very least, any scientific theory worthy of the name must have three properties (Popper, 1963). First, it must provide a framework for organizing and understanding the known facts in an economical manner. Second, it must attempt to provide explanations for the facts, or at least suggest causal links between them. Third, it must be capable of generating predictions that can be tested experimentally. If there are two competing theories to account for a particular set of facts, how can one select the theory that is to be preferred? Several criteria can be applied:

1. ***Empirical consistency*** One can compare the two theories according to their ability to explain the known facts. A theory is not much use if it cannot account for the data.
2. ***Logical consistency or computability*** If both theories pass the first test, one can judge their relative merits on the basis of logical consistency. Is the reasoning behind each theory tight and logically consistent? If a theory involves computational operations, can these operations be performed successfully? The inclusion of arbitrary (ad hoc) propositions, or computations that are difficult or impossible to implement, diminishes a theory's attractiveness.
3. ***Occam's Razor*** If both theories pass the first two tests, then one can apply the principle of Occam's Razor, which states that "Entities must not be multiplied beyond necessity." What this means is that the more parsimonious theory of the two is to be preferred. If a simple theory can explain the data as convincingly as a more complex theory then, other things being equal, the additional complexity is superfluous. Of course

this criterion begs the question: "What do you mean by simplicity?" One could interpret simplicity in computational terms, adopting a mathematical definition of computational complexity. On the other hand one could interpret simplicity in terms of the complexity of the neural structures which would be required to implement each theory.

4. ***Generality*** A final test of two competing theories concerns their generality. Some theories appear to exist in a vacuum, successfully accommodating the data they were devised to explain, but with no obvious connection to other phenomena or theories. Other theories attempt to place themselves in a wider context by, for example, making connections with other theories. In these circumstances, the better-connected theory is to be preferred. This criterion selects theories on the basis of higher order logical consistency. Are different theories invented ad hoc to explain phenomena in isolation, or is there some higher order rationale or structure that links different theories together? Examples of such higher order links would include energy efficiency, ecological validity.

If two competing theories cannot be separated on the basis of *any* of the four criteria, the only course of action is to return to the first criterion, empirical consistency. New predictions must be generated from each theory concerning the outcome of an experiment, formulated in such a way that (ideally) the results are bound to falsify one of the theories. In principle, the aim of any new theory is to provide the only true explanation for a particular phenomenon. However, it is worth remembering that few theories stand the test of time. Most new theories are ultimately discarded either because of empirical inconsistency, or because they prove to be unsatisfactory on the basis of one of the other criteria. Most theorists accept that the best they can hope for a particular theory is that it will provide a closer approximation to the truth than other available theories. Once a new theory appears that offers a better way of understanding the facts, then the old theory must be discarded. This does not mean that theorizing is futile and doomed to failure, for two reasons. First, it would be extremely difficult or impossible to arrive at the truth without having first absorbed the insights offered by previous theories. As Isaac Newton remarked: "If I have seen farther, it is by standing on the shoulders of giants" (letter to Hooke, 5 February 1675; see Turnbull, 1959, p. 416). Although Newton's own theories provided the foundation stones for most of the sciences, he acknowledged the debt he owed to predecessors such as Galileo and Kepler. Second, much empirical research would be aimless and trivial unless it was motivated by the need to test the predictions of new theories.

It should now be clear why it is important to understand some of the major theoretical movements in the scientific study of perception. As we shall see, each movement has made a valuable contribution to our understanding of perception. The major theoretical movements were developed in the context of vision, but the ideas can be taken to apply to all the senses. Modern theories of perception began with Structuralism 150 years ago.

KEY TERMS

Introspection
The act or process of self-examination; it provides information on one's own mental states, such as perceptual experiences.

Gestalt psychology
A theoretical movement which argued that complex perceptions are governed by a set of rules or laws that constrain the ways in which elementary components can be combined.

Structuralist approach

Structuralism drew inspiration from the chemical decomposition of complex substances into elements. It proposed that each complex perceptual experience could be decomposed into a large collection of elementary sensations. Structuralists used introspection to break down a particular perceptual experience into its sensory components. For example, Titchener (1902) decomposed the taste of lemonade thus: "The taste of lemonade is made up of a sweet taste, an acid taste, a scent (the fragrance of lemon), a sensation of temperature, and a pricking (cutaneous) sensation" (p. 62).

Introspection proved to be an unsatisfactory basis for theories of perception for reasons that, in retrospect, appear obvious. First, introspective data are inherently qualitative rather than quantitative. Second, observers frequently disagree in their introspections. Third, many important perceptual processes cannot be studied by introspection.

Gestalt approach

Gestalt psychologists rejected the basic principles of Structuralism, and proposed instead that when a collection of elementary sensations is combined together a new perceptual entity emerges—a Gestalt. The major exponents of Gestaltism (Wertheimer, Kohler, and Koffka) were German, and the German word "gestalt" means form, figure, or configuration. According to **Gestalt psychology**, perceptual systems are not passive recipients of isolated, elementary sensations, but dynamically organize these sensations into meaningful "wholes" or Gestalts. Gestaltism emphasized the importance of structure and organization in perception. It identified a number of organizing principles or laws to describe the variety of ways that perceptual systems achieve organization. The general theme of these laws is that isolated elements that share some property in common, such as spots of the same color, or shapes that move in the same direction, or notes of similar pitch, tend to be grouped together perceptually. Elements that form a "good figure" (*pragnanz*), such as dots falling along a smooth curve or forming an enclosed regular shape, also tend to group together perceptually.

The main weakness of Gestalt psychology was that its laws tended to be descriptive rather than explanatory. Its arguments tended to be circular. For example, Gestalt psychologists would explain why certain pattern elements group together by invoking the principle of good figure or *pragnanz*. But what is the principle of *pragnanz*? It is the tendency of elements forming a good figure to group together. Despite its limitations, Gestalt psychology made a valuable contribution to perceptual theory by emphasizing the way that entirely new perceptual entities can emerge from the organization of simpler elements. Gestaltism is no longer at the forefront of perceptual theorizing, but is still influential, particularly in European psychology, and is relevant to present-day computational theories.

Constructivist approach

The German scientist Hermann von Helmholtz introduced the idea of "unconscious conclusion" in his monumental, three-volume *Treatise on Physiological Optics* published between 1856 and 1866:

> *The psychic activities that lead us to infer that there in front of us at a certain place there is a certain object of a certain character, are generally not conscious activities, but unconscious ones. In their result they are equivalent to a conclusion . . . it may be permissible to speak of the psychic acts of ordinary perception as unconscious conclusions.*
>
> *(1962 translation of Vol. III, p. 4)*

To expand on this idea, Helmholtz used the example of an astronomer "who computes the positions of the stars in space, their distances, etc." from his conscious knowledge of the laws of optics. He argued that "there can be no doubt" that perception involves the same kind of computation as that used by the astronomer, but at an unconscious level. Helmholtz went further, stating confidently that:

> *Our ideas of things cannot be anything but symbols, natural signs for things which we learn how to use in order to regulate our movements and actions.*
>
> *(1962 translation of Vol. III, p. 19)*

Helmholtz therefore advocated the view that sensory systems construct some kind of internal representation of the world, and that this representation mediates perceptual experience. Related views on the indirect and inferential nature of perception have been promoted by, among others, Gregory (1980), and Rock (1983).

It is fair to say that constructivism has had a profound impact on theories of perception. Most modern theoretical approaches rely heavily on the notions of representation and computation. Helmholtz's ideas on symbolic representation were remarkably prescient, since they appeared 100 years before representation became a cornerstone of computational neuroscience.

Ecological approach

Perception begins with physical stimulation and ends with perceptual experience. In between the two, according to the Gestalt psychologists and constructivists, are sophisticated processes that construct internal representations from the sensory information. Perceptual experience has only an indirect relationship to the sensory data. James J. Gibson took the opposite view, in rejecting entirely the need for internal representation (Gibson, 1950). He argued instead that there is sufficient information

KEY TERM

Optic flow field
The highly structured movement in the spatial pattern of light reaching the observer, caused by relative movement between the observer and the environment.

Artificial intelligence (AI)
A branch of computer science that aims to produce a device capable of behavior normally associated with human cognition, such as language understanding, reasoning, and perception.

available in the visual image for unambiguous perception to be derived directly, without the need for intervening processes. He suggested that the brain as a whole "picks up" the relevant information by some kind of "resonance." Gibson used an analogy with a radio set to explain this idea. Your immediate surroundings are almost certainly filled with low-energy electromagnetic radiation broadcast by TV and radio transmitters. A radio, properly tuned, will be able to pick up some of this information and produce intelligible sounds. Gibson would argue that in this situation all the components of the radio resonate with the information available in the electromagnetic radiation. There is no need to assume that some internal representation is constructed by the radio.

Gibson's ideas were inspired by his work in aircraft pilot training during the Second World War. He noticed that conventional treatments of depth cues were of little practical value, and became convinced that the highly structured patterns of movement pilots view from the cockpit were critical for aircraft control. As a plane comes in to land, surface details in the environment, such as markings on the runway, stream across the image projected into the pilot's eyes. They radiate out from the point in the image toward which the aircraft is heading, creating an **optic flow field**. Gibson correctly deduced that this flow field contains sufficient information to specify precisely where and when the aircraft would make contact with the ground. He argued that this information is somehow picked up directly by the sensory system. Gibson identified other properties of natural images, such as texture gradients, that can be used to specify surface depth, slant, and size. Due to its emphasis on natural images, Gibson's perspective became known as the ecological approach to perception. Its denial of the relevance of mediating processes also led to the label "direct perception."

Direct perception performed a valuable service in identifying some powerful sources of information in visual images, but it drastically underestimated the difficulty of the problem posed by picking up this information. Research on **artificial intelligence** (AI) has shown that the information available in visual images is usually not sufficient by itself to recover unambiguous information about the surfaces and objects that created the image.

Computational approach

The computational approach was anticipated by Helmholtz, in his analogy between astronomical calculations and perceptual conclusions. As mentioned earlier, firm foundations for the computational approach to perception were later laid by three mathematicians (Turing, Shannon, and Marr). Turing's notion of universal computation led to the idea that the brain was an information processing device that could be emulated by other such devices, namely computers. An information processing device receives input data and performs some processing operation on the data to produce an output. An electronic calculator is a good example of an information processing device. It receives input data in the form of a sequence of numbers and symbols, and processes this data to produce an output, usually the result of a calculation. In the case of perception, the input is environmental data such as a visual image. The output is perceptual data. Intervening processes transform one into the other. Modern computational neuroscientists attempt to discover the nature of the intervening processes given the input to the system, the output it produces, and some hints about the intervening neural operations. To continue the analogy with an electronic calculator, the task is similar to trying to discover the rules of arithmetic given only the sequence of numbers and symbols providing the input, and the numbers produced by the calculator as output.

Modern computational theories of human cognition began with Newell and Simon's information processing model of problem solving (e.g., Newell & Simon, 1972). Computational neuroscientists test their theories by attempting to implement them using computer programs. In a typical test of a theory in vision, the computer is given an image and attempts to produce the required output.

The computational approach has introduced a high degree of rigor into theories of perception, but it provides no account of consciousness. There is an explanatory gap between neural computations and conscious perceptual states, as mentioned earlier in the chapter (Levine, 1983, 1999).

Phenomenology

Phenomenology lies on the opposite side of the explanatory gap from computational theories. It is the study of consciousness from the first-person perspective—how the world appears to me. There is a long tradition of phenomenology in European philosophy and psychology, but it is sometimes dismissed as a legitimate approach to the study of perception, because it is inherently subjective. Scientific approaches are usually considered to require objective methods. However, phenomenological studies can be performed using a variant of standard empirical scientific methods, including hypothesis generation and observation. There are several key differences between conventional psychophysical observations and phenomenological observations. The convention in psychophysics is to keep subjects naive as to the purpose of the experiment, and give them a well-defined task with highly constrained responses such as "yes" versus "no" (see the previous tutorial). In phenomenological experiments subjects are often fully informed about the purpose of the experiment, and their task is kept relatively open with loosely constrained responses. Response classification may occur only after the data have been examined. A key check on validity in phenomenological experiments is *intersubjectivity*, or agreement among individuals about the nature of their perceptual experience.

Many important discoveries about perception have been made using phenomenological experiments. The Gestalt school discussed earlier was founded on phenomenological observations. Prominent figures in phenomenological studies of perception include the Belgian psychologist Albert

Michotte (1881–1965; perception of causality, discussed in Chapter 12), and eminent Italian psychologists such as Vittorio Benussi (1878–1927; lightness), Cesare Musatti (1897–1989; depth from motion), Fabio Metelli (1907–1987; transparency), and Gaetano Kanizsa (1913–1993; subjective figures).

Phenomenological aspects of perception are often underplayed in psychophysical research, but modern studies would make little sense without assuming the existence of a perceptual experience in the subject that could lead to a phenomenological report. Standard psychophysical techniques typically embed phenomenological experience in an artificial task requiring simple, constrained responses. So phenomenological observation frequently underlies the subject's responses. Indeed, initial interest in a research issue is often triggered by phenomenological observations made by the experimenter.

Evaluation

In its emphasis on a specific set of issues and ideas, each theoretical movement has made its own particular contribution to our understanding of human sensation and perception. Contemporary research adopts a pluralistic approach which combines both neuroscientific and psychophysical techniques. The cognitive and computational neurosciences provide a rich set of experimental techniques and theoretical approaches, while psychophysics supplies the essential link between stimulus characteristics and perceptual experience.

Yantis (2001) has collected together many of the key papers described in this tutorial, as well as other classic papers in visual perception, and offers an excellent opportunity to study the primary sources that laid the foundations of modern perceptual theories.

The chemical senses

2

Contents

INTRODUCTION

The senses of smell and taste are called chemical senses because they extract information from the environment by means of direct chemical interactions. Molecules from external substances interact with receptor molecules in the nose and mouth, resulting in the generation of neural signals. Chemical molecules are wafted to olfactory chemoreceptors in the nose by atmospheric currents, so the stimulating substance itself can be quite remote from the perceiver. Taste, on the other hand, is a contact sense; molecules have to be in a solution that makes direct contact with the chemoreceptors. In this chapter each sense will be considered first in terms of its anatomy and physiology, and second in terms of its perceptual and functional properties. Clear relationships between anatomy and physiology, on the one hand, and perceptual and functional properties, on the other, will emerge.

SMELL

Odors are crucial for many animals. They are used to detect prey and predators, identify potential mates or competitors, and judge the palatability of food. Although smell is generally considered to be a "minor" sense for humans, we are astonishingly good at detecting odors. On January 21, 2013, residents in the southeast of England flooded the police with calls about a noxious odor of rotten cabbage, which was so bad that many feared it may be poisonous. Health officials eventually pinpointed the source of the odor to a leak at a chemical factory owned by the firm Lubrizol in Rouen, Normandy, about 160 kilometers south of the UK coastline. The leak released a chemical called ethyl mercaptan, which is normally added to domestic gas to aid the detection of gas

FIGURE 2.1
Smells can evoke powerful memories of childhood experiences. Copyright © Wavebreak Media Ltd./Corbis.

leaks. The human nose is incredibly sensitive to the smell of this chemical: If three drops were added to the water in one of two Olympic-sized swimming pools, the odor would be sufficient for a human to detect which pool contained the chemical (Yeshurun & Sobel, 2010). The just noticeable difference (JND, discussed in Chapter 1) for odor is similar to that in other sensory systems, at about 5–7% (Cain, 1977).

Smell is also surprisingly effective in other ways. We can distinguish gender on the basis of breath, hand, or armpit smell (Doty et al., 1982; Schleidt, Hold, & Attili, 1981). Doctors have used the smell of a patient to help in the diagnosis of illnesses (Schiffman, 1983). Women who share accommodation have been found to synchronize their menstrual cycles as a result of chemical signals (see Wilson, 1992; Stern & McClintock, 1998).

? *Why is the emotional impact of smell so great?*

Odors are also very effective at evoking powerful emotional responses and memories. In many people, the smell of popcorn or hotdogs evokes vivid memories of fairgrounds or movie theaters, while the smell of disinfectants and medicines brings back painful or fearful memories of spells in hospital. The size of the perfumery industry, and the volume of body perfumes and "air fresheners" manufactured, are a testament to the huge emotional impact of smell. The fragrance market in Europe was worth about £1.5bn in 2014, and about $22bn globally (*Management Today*, November 27, 2014).

ANATOMY AND PHYSIOLOGY OF SMELL

Over the last 15 years olfaction has emerged from relative obscurity as a sensory system, due to major advances in our knowledge of the genetic and molecular basis of smell. The olfactory system is remarkable for its ability to signal the presence of just a few aromatic molecules, and to discriminate between thousands of different compounds.

Receptors

Olfactory receptor neurons are found in the roof of the nasal cavity, on a patch of tissue called the **olfactory epithelium** (see Figure 2.2). In humans this tissue area covers 2–4 square centimeters, and contains about 6 million receptors (Kratskin, 1995). Each olfactory receptor cell lasts approximately 60 days, so the receptor cells are being constantly renewed. The actual receptor sites are located on cilia. These are microscopic hair-like projections that extend from the surface of each receptor cell into the moist tissue lining the inside of the nose (the olfactory mucosa). Each cell possesses about 5–40 cilia. Molecules given off by volatile substances must dissolve in the olfactory mucus in order to arrive at the receptor sites on the olfactory cilia (see Schild & Restrepo, 1998; Smith, 2000). Olfactory receptors are neurons that generate

KEY TERMS

Olfactory receptor neuron
A specialized neuron that produces electrical responses to odor molecules.

Olfactory epithelium
A patch of mucous membrane in the roof of the nasal cavity (one for each nostril) containing olfactory receptor neurons; in humans it contains 6 million receptor neurons.

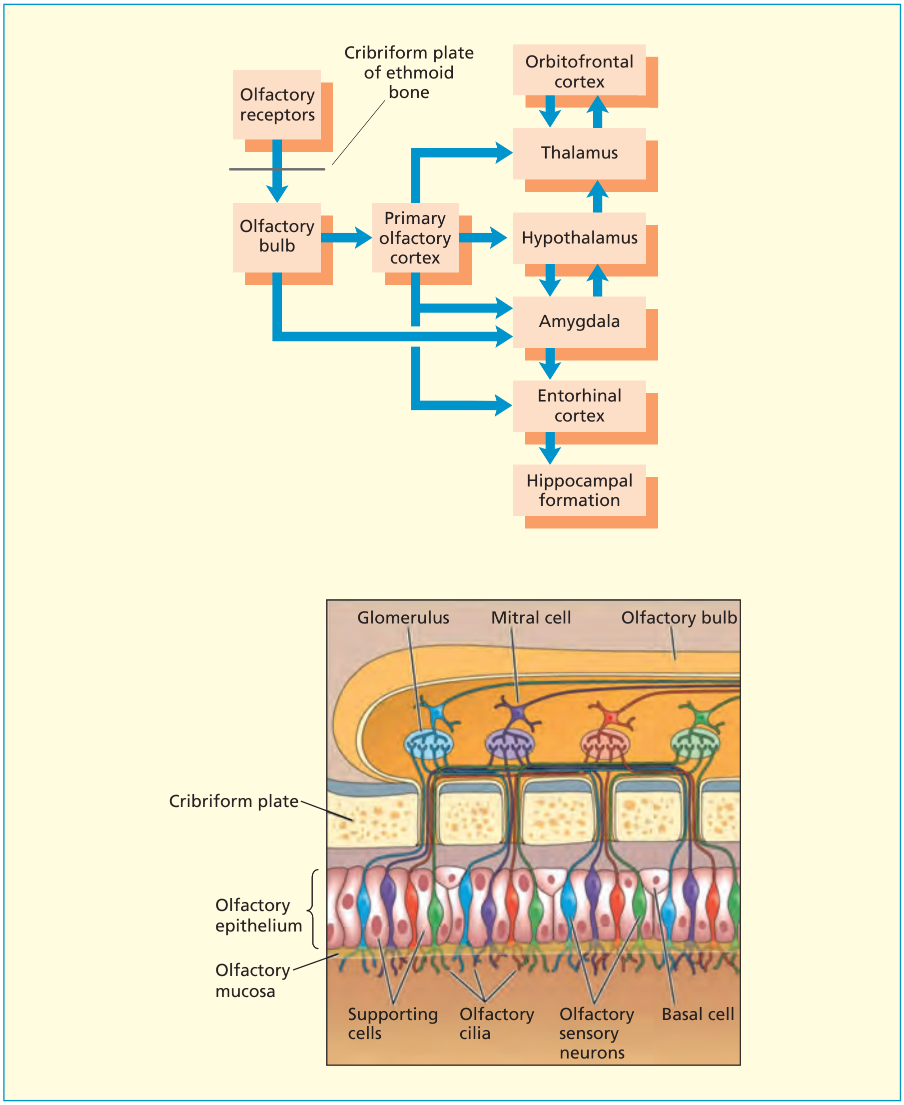

FIGURE 2.2
Sensory pathways for olfaction. Top: Flow diagram showing the organization of the pathways. Bottom: Peripheral anatomical components of the olfactory system.

an action potential when their resting potential of –65 mV depolarizes (the inside of the cell becomes positively charged) sufficiently to reach threshold. They effectively operate as molecule counters for particular kinds of chemical (Firestein, 2001).

As discussed in Chapter 1, the task of olfactory receptor neurons is to encode information about the chemical composition of odor molecules in neural signals. Small differences at the molecular level mean that different neurons are activated by different odor molecules (Ressler, Sullivan, & Buck, 1994). There are thought to be several hundred different olfactory receptor neuron types in humans. The olfactory mucosa also contains some **free nerve endings** that are

Our sense of smell is blunted when we have a cold because of the build-up of mucus in the nasal cavity that prevents odor molecules reaching the receptor cilia.

KEY TERM

Free nerve ending
A branch of a sensory nerve cell that has no specialized receptor process, but is embedded directly in tissue.

KEY TERMS

Mitral cell
A neuron in the olfactory bulb that receives signals from olfactory receptor neurons and relays them to the brain; there are 50,000 mitral cells in the human olfactory bulb.

Olfactory bulb
The mass of neural tissue protruding from the brain behind the nose, which conveys neural signals from the olfactory epithelium to the brain.

Olfactory glomerulus
A dense, spherical accumulation of dendrites and synapses, where approximately 200 olfactory receptors make contact with a single mitral cell.

Primary olfactory cortex
The cortical destination of mitral cell fibers, thought to mediate perception of smell.

Amygdala
A nucleus (dense group of neurons) lying deep in the brain, forming part of the limbic system; involved in emotional, sexual, and autonomic responses.

thought to mediate the sensations of coolness, tingling, and burning that arise from high concentrations of chemicals. Odorants are chemical compounds that have a smell or odor. Malnic et al. (1999) measured the response profiles of olfactory receptors and discovered that a single receptor responds to multiple odorants, by virtue of the fact that the odorants all contain the kind of molecule that excites the receptor. Conversely a single odorant excites multiple receptors because it contains many different kinds of molecule.

Sensory pathways

The axon of each receptor cell passes through a perforated bony plate in the skull (the cribriform plate) to project directly to a specific **mitral cell** in the **olfactory bulb**. The synapses between receptor cell axons and mitral cell dendrites bundle together to form 2000 **olfactory glomeruli** (Carlson, 2004; see Figure 2.2). Several thousand receptors converge on 5–25 mitral cells in each glomerulus (Firestein, 2001). The axons of mitral cells travel to the rest of the brain along the olfactory tract. Mitral cell axons project directly to the **primary olfactory cortex**, and also to the **amygdala**, which is associated with the generation of emotional responses.

Cortical processing

Severe blows to the head can result in a loss of the sense of smell, if the shearing force is sufficient to damage the receptor cell axons where they pass through the cribriform plate.

Smell is unique among the senses in that the neural projection from the olfactory tract is not relayed via the thalamus on the way to the cortex. This arrangement is thought to be a reflection of the relatively early appearance of olfaction during vertebrate evolution (Delcomyn, 1998). However a pathway running from the primary olfactory cortex to the orbitofrontal cortex (via the thalamus) is involved in the conscious perception of smell. Another unusual feature of olfaction is that both hemispheres of the cortex are activated by stimulation of only one nostril, whereas in other senses only one hemisphere tends to be activated by stimulation on one side of the body (usually the hemisphere on the opposite or contralateral side of the body to the stimulus). Cortical olfactory activity also seems to be modulated by breathing (see Lorig, 2002, for a review of cortical processing).

PERCEPTION AND FUNCTION OF SMELL

Detection

Some chemicals are detectable at concentrations thousands of times weaker than others. Humans are particularly sensitive to musk and to ethyl mercaptan but, for example, require concentrations up to a million times higher to detect methyl salicylate (the aromatic ingredient in the wintergreen plant).