Foundations of Perception

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PREFACE

My primary aim in writing this book has been to provide a coherent, up-to-date introduction to the basic facts and theories concerning human sensory perception. A full appreciation of perception requires some understanding of relevant physical stimuli and a basic grasp of sensory physiology. Therefore, the physical and physiological aspects of each sensory modality are considered before its perceptual characteristics. Emphasis is placed on how perceptual experience relates to the physical properties of the world and to physiological constraints in the brain.

The first chapter introduces some of the techniques used to study perception, and some important general principles that apply equally to all the sensory systems. These principles are first applied to the minor senses in the following two chapters: smell and taste (Chapter 2), and touch and balance (Chapter 3). More space is devoted to hearing (Chapters 4 and 5), and yet more to vision (Chapters 7 to 12), reflecting the relative importance of the senses to humans. The final chapter considers individual differences in perception relating to age, sex, culture, and expertise.

The bulk of each chapter is devoted to fundamental material that all students should read. Each chapter also contains a Tutorial section covering more advanced or controversial material, or newly developing areas, to offer an opportunity for further study and a bridge to more advanced texts. For example, tutorials in Chapters 4 and 8 introduce Fourier analysis; tutorials in Chapter 9 discuss Bayesian inference as well as the debate about active versus passive processing; a tutorial in Chapter 13 surveys recent research on sensory integration.

The manuscript has been improved significantly as a result of the critical comments offered by a number of people including Chris Darwin, Graham Hole, Ian Howard, Linda Murdoch, Romi Nijhawan, Daniel Osorio, and several anonymous reviewers. I am very grateful to them all for their valuable contributions, but any remaining errors are of course down to me. I would also like to thank Mike Forster, Ruben Hale, Mandy Collison, and everyone else at Psychology Press for all their encouragement during the protracted period of writing.

Finally I would like to dedicate the book to Anne, Laura, and Luke for their patience and support during the preparation of the manuscript and associated material. Laura was particularly helpful in the preparation of the indexes.

CHAPTER 1

CONTENTS

1

General principles

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.

Yet 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, or identifying a face or a voice, have proven to be formidable problems to solve by computer. 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 recognise their own face reflected in a mirror (**prosopagnosia**), or cannot judge the position of their limbs without looking directly at them. Such cases remind us of the sophisticated brain processes serving perceptual abilities that most of us take for granted.

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 judgements 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 enter the goal net? 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.

KEY TERM
Prosopagnosia: A clinical condition resulting from brain damage, in which a patient is unable to recognise familiar faces.

FIG. 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 © Giampìero Sposito/Reuters/Corbis.

Certain critical judgements do require special skills and observation conditions. For instance, the judge who decides whether a tennis ball strikes the top edge of the net during a serve often uses 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 judge can detect the slightest contacts between ball and net that are missed by most or all of the spectators. Disagreements between participants or observers can and do arise, and 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, or whether a football crossed a goal line. Participants often reach opposite decisions in "close" calls. This disagreement is not simply a reflection of differences in skill or concentration level, 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 on 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 judgements, and to identify its likely causes.

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

CLASSIFICATION OF THE SENSES

The senses can be divided into five major groups, as shown in Table 1.1, on the basis of the particular form of environmental stimulation they detect.

TABLE 1.1 CLASSIFICATION OF THE SENSES

Sense	Stimulus	Receptor	Sensory structure	Cortex
Vision	Electromagnetic energy	Photoreceptors	Eye	Primary visual cortex
Hearing	Air pressure waves	Mechanoreceptors	Ear	Auditory cortex
Touch	Tissue distortion	Mechanoreceptors, thermoreceptors	Skin, muscle, etc.	Somatosensory cortex
Balance	Gravity, acceleration	Mechanoreceptors	Vestibular organs	Temporal cortex
Taste/smell	Chemical composition	Chemoreceptors	Nose, mouth	Primary taste cortex, olfactory cortex

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

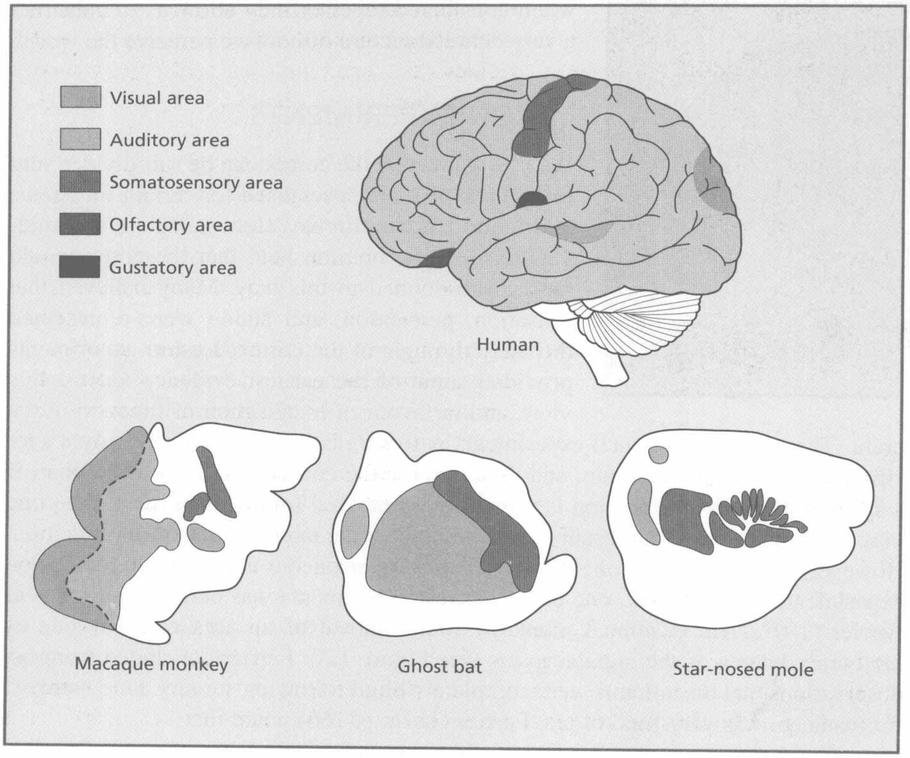

FIG. 1.2 Cortical representation of the senses. Top: Cortical receiving areas in the human brain. Bottom: Total cortical area devoted to three senses in three different animals (re-drawn from Krubitzer, 1995). The broken line identifies the cortical receiving area in macaque monkey. Copyright © 1995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

Receptor cells convert environmental energy into electrical nerve impulses. A variety of methods are used to achieve this **transduction**, including molecular changes in photoreceptors triggered by light absorption, and mechanical deflection of tiny hairs by fluid currents in the inner ear. Receptors in each sense are connected to cells in different specialised areas of the **cerebral cortex** of the brain, as shown in the right hand column of the table. 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 area for each sense. Activity of cells in these cortical areas is thought to lead to conscious perceptual experience. It is important to note that Figure 1.2 shows only the *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.

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

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

METHODS USED TO STUDY PERCEPTION

A number of techniques have been used to study perception over the last 200 years. Each technique has particular advantages and limitations, but no one technique is to be preferred over the others. Different techniques complement each other, so that

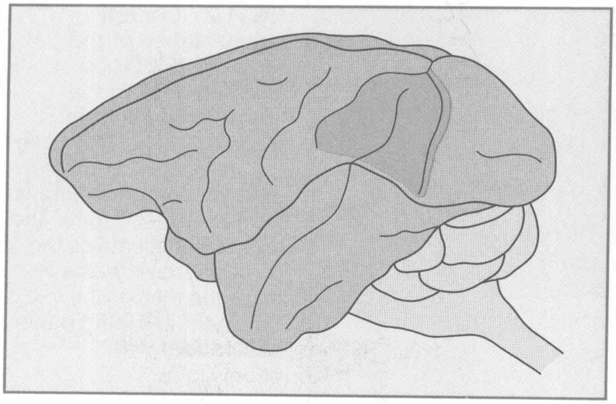

FIG. 1.3 Site of the lesion in Ferrier's monkeys (re-drawn from Glickstein, 1985). Copyright © 1985 Elsevier. Reproduced with permission.

when considered together they allow us to construct a very detailed picture of how we perceive the world.

LESION EXPERIMENTS

We now know that the cortex can be sub-divided into many areas that are specialised for certain functions, as Figure 1.2 has already shown. But in the mid-1800s, scientific opinion held that the cortex could not be sub-divided 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 favour of localisation 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 behaviour. If a specific behavioural function is impaired or removed following surgery, then one may infer that the relevant brain area is crucial for the maintenance of that function. However, care is needed if one is 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 1.3). 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 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 **localisation of function** as a basic principle of cortical organisation.

CLINICAL STUDIES

Research on localisation 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 localisation 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).

KEY TERMS

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

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

Inouye devised an instrument to locate precisely in three-dimensions the position of entry and exit wounds (see Figure 1.4).

Assuming a straight path for the bullet, he was then able to identify the brain areas 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 highly ordered way on the surface of human occipital cortex (see below).

Clinical studies of the consequences of brain damage are necessarily more untidy 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 localisation of function.

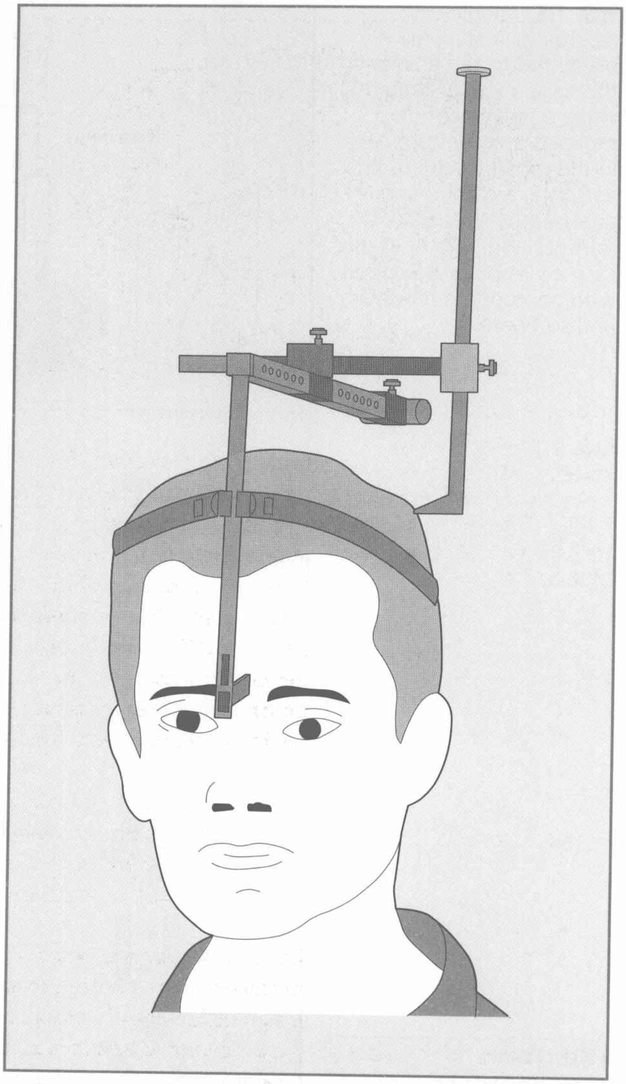

FIG. 1.4 Inouye's instrument for tracing the path of a bullet in head wounds suffered by Japanese soldiers (re-drawn from Glickstein & Witteridge, 1987).

SINGLE-UNIT RECORDINGS

Although a great deal was known about anatomy and about localisation 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.*

Theories of perception were inspired largely by anatomy. The brain was known to contain huge numbers of cells, massively interconnected (but only over short distances) in circuits that are similar over the whole cortex. As we have seen, studies of localised brain damage showed that the visual cortex was mapped **topographically**. These facts inspired the Electrical Field Theory of perception. Visual patterns were thought to set up corresponding fields of electrical activity across the surface of the cortex. Perceptual organisation in complex displays was said 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, anaesthesised 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

KEY TERMS

Topographic map: A spatial arrangement of neurons in a neural structure (e.g. the cortex) in which nearby cells respond to nearby locations in the visual field of view.

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

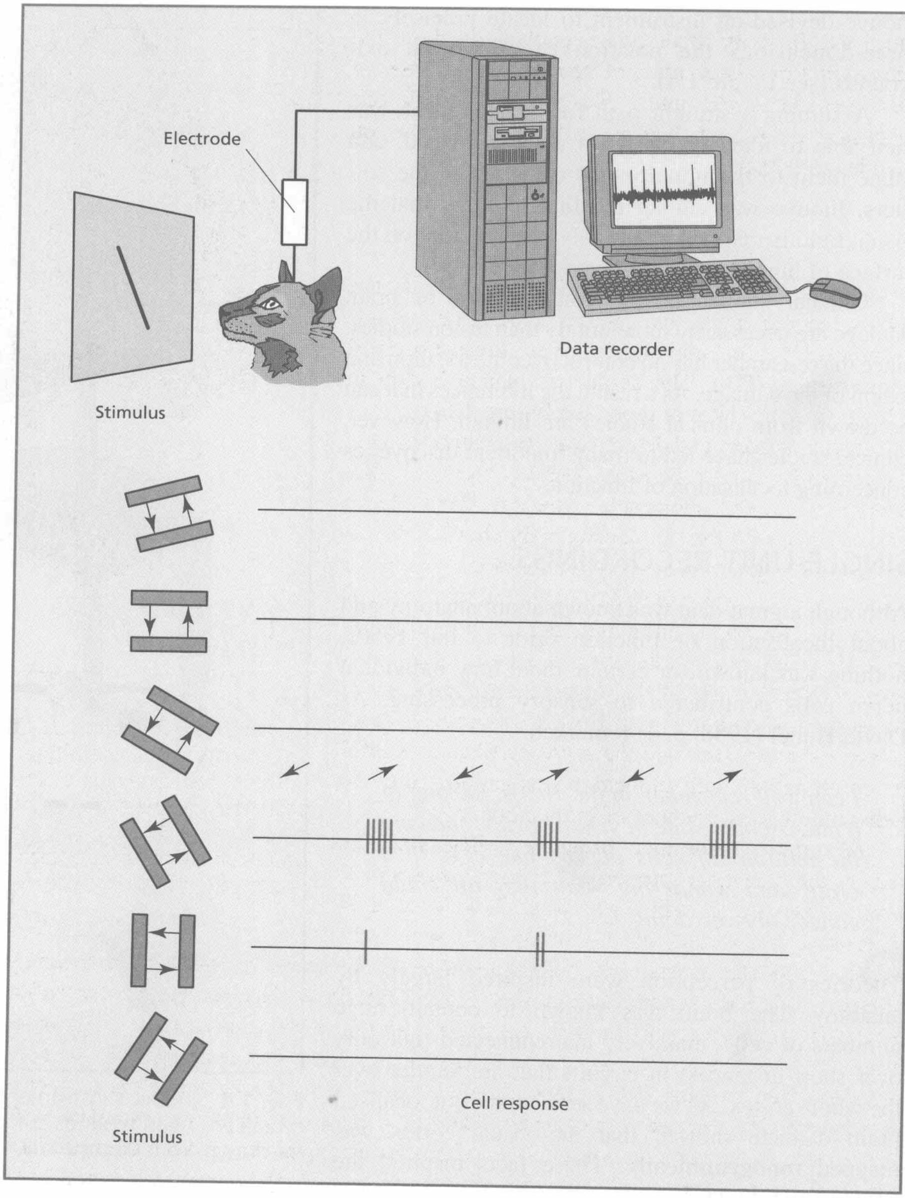

FIG. 1.5 Single-unit recording. A stimulus is presented to the animal (in this case a visual stimulus) while a fine electrode registers activity from cells in the sensory system. The activity is recorded and analysed by special-purpose equipment, in this case a computer equipped with appropriate hardware and software.

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

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.

(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 stimulus preferences of individual sensory cells. We now know that, despite anatomical uniformity, functional properties vary hugely from cell to cell. For example, some retinal cells prefer small, bright spots of light, while others prefer large, dark spots. In the cortex, individual cells are highly selective for line orientation, movement direction, colour, size, and so on (see Figure 1.5).

The key word is specialisation rather than uniformity of function. These discoveries led to theories of pattern recognition based on neural "feature detectors". 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. Nevertheless, single-cell recording data have had a profound influence on theories of perception.

BRAIN IMAGING

Brain-imaging techniques were developed in the 1970s, primarily for use in medicine. The earliest technique to be developed was **computerised tomography** (CT). The subject is placed bodily in a long, thin, cylindrical tube (see Figure 1.6).

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 1.6. CT scans reveal areas of brain damage, and are therefore particularly useful in combination with clinical investigations into the behavioural consequences of brain damage.

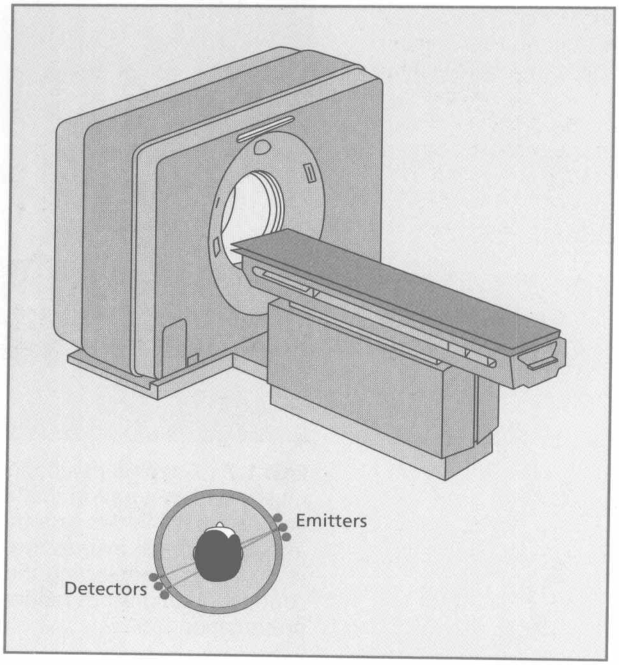

FIG. 1.6 CT scanner. The patient lies on a table that can be slid inside the scanner (left). The walls of the scanner are lined with X-ray emitters and detectors. X-rays are emitted from one side of the scanning tube so that they pass through the patient's body before being registered by detectors on 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 haemoglobin induced by variation in blood oxygen concentration. 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 localisation 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. Brain imaging is expensive and technically complex, and the data obtained require careful interpretation. However, the technique is likely to grow in importance as its use becomes more widespread, and data analysis techniques become more sophisticated still.

PSYCHOPHYSICS

Psychophysics is the scientific study of relationships between physical stimuli and perceptual phenomena. A typical psychophysical experiment involves carefully controlled stimuli, usually presented by a computer, and highly constrained responses from adult human observers. Figure 1.7 shows a typical psychophysical stimulus, presented on a computer monitor.

In this example, the stimulus is designed to study the subject's ability to discriminate small differences in stimulus contrast (the difference in intensity

KEY TERMS

Computerised 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.

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.

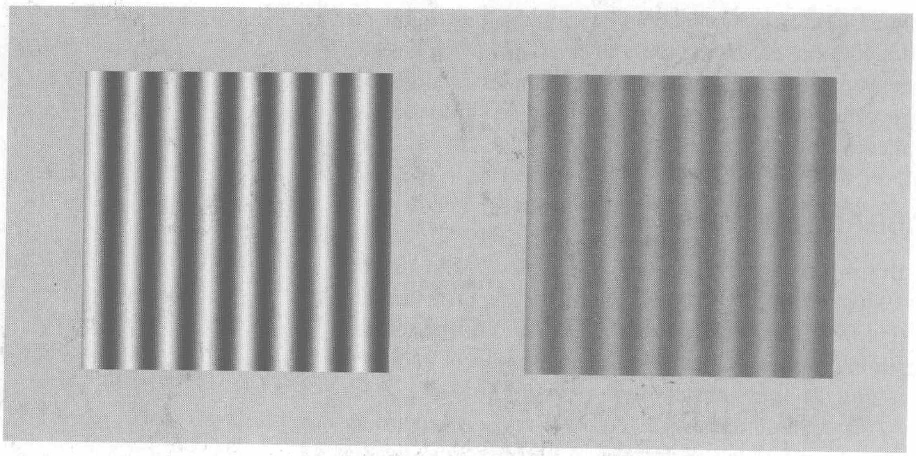

FIG. 1.7 A typical psychophysical stimulus, generated by a computer. The subject must select the grating that appears to have the higher contrast between its bright and dark bars. In this case the observer should select the left-hand grating. Responses are usually made by pressing one of two response buttons. The computer records each response before selecting the next stimulus to be displayed. The position of the higher contrast grating varies randomly between left and right from presentation to presentation.

between bright and dark bars). The subject is given a response pad containing two buttons, labelled "left" and "right". He or she is instructed to press the button corresponding to the stimulus that appears to have higher contrast. The contrast difference between the stimuli is manipulated to find the difference at which the subject achieves the required level of accuracy. A number of experimental techniques have been developed over the last 100 years to ensure that data obtained in psychophysical experiments are not contaminated by uncontrolled variables such as subject expectations or desires. In the example, the position of the higher contrast stimulus would be varied randomly between left and right from trial to trial, and the contrast difference may also vary randomly, without the subject's knowledge. The tutorial at the end of this chapter provides an introduction to the major psychophysical techniques, and their theoretical background. Psychophysical experiments are particularly useful for testing predictions from theories of perception. However, inferences about the neural structures mediating performance must be treated with some caution, and require cross-referencing against physiological data.

Why are special experimental techniques required to study perception?

KEY TERMS
Artificial intelligence (AI): A branch of computer science that aims to produce a device capable of behaviour normally associated with human cognition, such as language understanding, reasoning, and perception.
Computation: The manipulation of quantities or symbols according to a set of rules.

ARTIFICIAL INTELLIGENCE (AI)

In the 1930s the mathematician Alan Turing 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 AI approaches to brain function. But what does it mean to say that the brain is a computational device? The senses send information about the external world to the brain. The sensory stimulus can be measured and specified very precisely in mathematical terms, for example patterns of light and dark in optical images, or

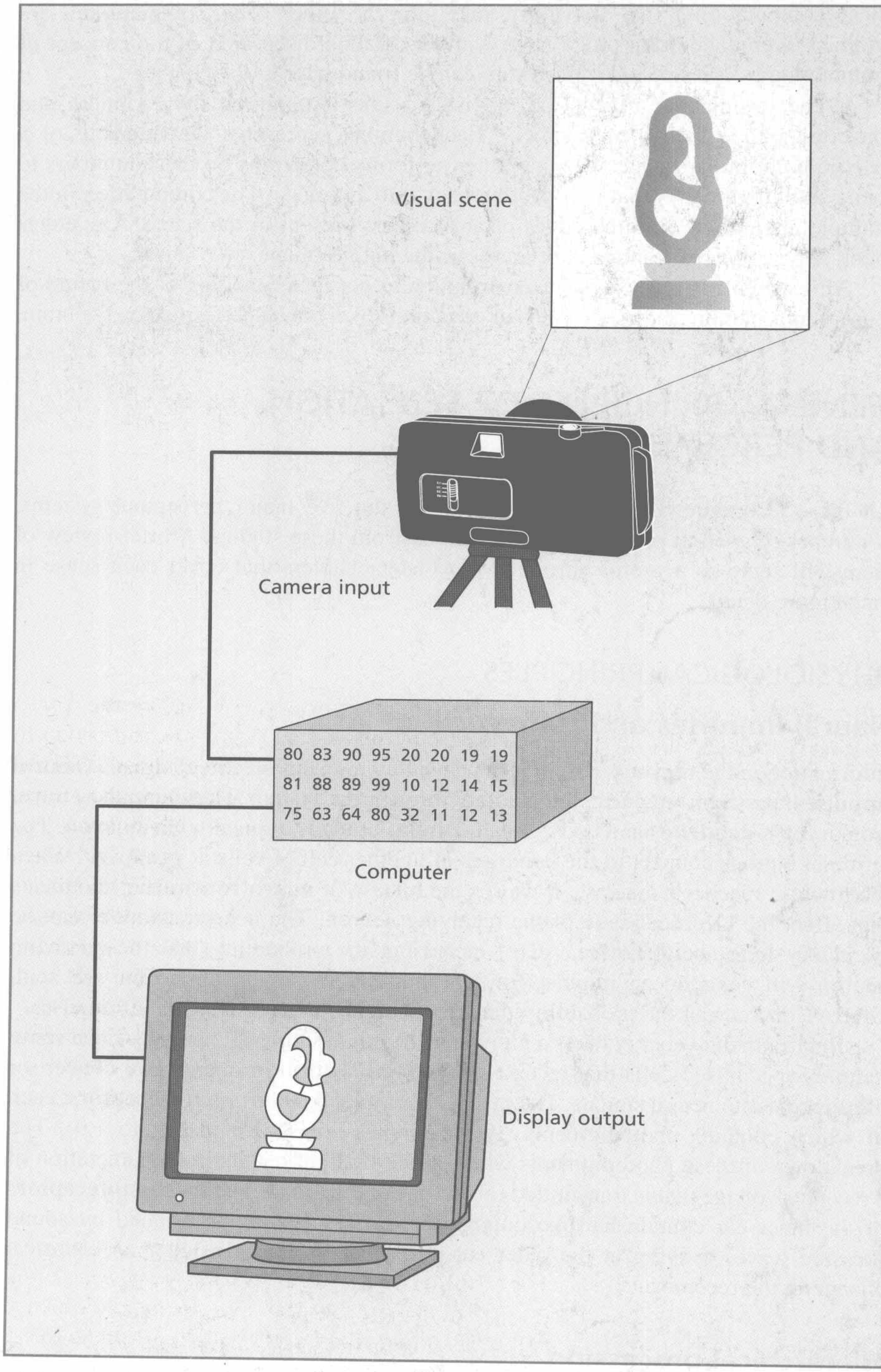

FIG. 1.8 Schematic illustration of a computer vision system. A visual scene is captured by a camera and fed into a computer. The scene is converted into a matrix of numbers. Each number represents the intensity of the light at a specific location in the scene. The computer performs computations on the matrix of numbers to create a new output matrix. The output matrix can be converted back into an image, again assuming that the magnitude of each number codes the intensity of light in the output image. In this example the computation has attempted to isolate all the edges of objects in the scene. Values in the output image that depart significantly from mid-grey represent the edges found.

sound-pressure waves entering the ear. The response of the brain can also be described in mathematical terms, for example patterns of neural activity, or consistent patterns of behaviour. Since both the input to the brain and its output can be expressed mathematically, AI researchers attempt to develop formal mathematical

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

rules (computations) that transform one into the other. The computations are assumed to emulate brain processing. A more detailed discussion of the concept of computation as it is applied to the brain can be found later in the chapter.

In the example in Figure 1.8, a visual scene is captured by a camera and converted into a matrix of numbers. Each number represents the intensity of a specific point in the image. The computer performs operations on these numbers to create an output matrix that is converted back into an image. The computation in the example attempts to find the edges of any objects present in the scene. Any edges found appear as very light or dark marks in the output image.

AI research has made a major contribution to our understanding of the nature of sensory information, and of the kinds of operations likely to be performed by the brain.

GENERAL PRINCIPLES OF SENSATION AND PERCEPTION

All these techniques have been used to study the five major perceptual systems. A number of general principles have emerged from these studies. A brief review of them will serve as a useful introduction to later chapters that cover each sense in much more detail.

KEY TERMS

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

Dendrite: The branched treelike 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.

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

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

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

PHYSIOLOGICAL PRINCIPLES

Neural impulses and transduction

Information in the nervous system is conveyed by trains 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 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), increasing the probability that the receiving neuron will generate an impulse, or inhibitory (e.g. gamma amino butyric acid, GABA), decreasing the probability that the receiving neuron will fire an impulse.

Environmental energy takes a number of forms, as Table 1.1 showed. Each sense requires specialised 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 1.9). 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 hairlike outgrowths (cilia). Vibrations initiated by sound pressure waves arriving at the outer ear deflect the cilia and trigger an electrical change in the receptor.

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.