

# 3

## THE NEUROPHYSIOLOGICAL CONTEXT

**The entire doctrine of [phrenology] is contained in two fundamental propositions, of which the first is, that understanding resides exclusively in the brain, and the second, that each particular faculty of the understanding is provided in the brain with an organ proper to itself.**

**Now, of these two propositions, there is certainly nothing new in the first one, and perhaps nothing true in the second one.**

*Pierre Flourens, 1846*

### Preview

Partitioning the philosophical antecedents to psychology and the neurophysiological background into two chapters implies the presence of two nonoverlapping paths that eventually merged to form the new psychology of the late nineteenth century. There is a grain of truth to this—the British empiricists did not spend their time cutting into spinal cords or stimulating nerves connected to frogs legs, and the scientists to be encountered in this chapter did not write long philosophical treatises on “human understanding.” But the distinction between philosophical and physiological antecedents to psychology is somewhat artificial, brought about by the decisions made when structuring a textbook. In fact, developments in philosophy and in the natural sciences proceeded apace, especially in the eighteenth and nineteenth centuries. The physiologists and other natural scientists were deeply concerned with philosophical issues, especially the epistemological questions about human understanding and the problem of the relationship between mental and physical reality (the mind-body problem). In turn, philosophers were well aware of, and in some instances contributed to, developments in physiology (e.g., Berkeley’s work on vision), and they proposed theories that led naturally to physiological research.

This chapter will focus on nineteenth- and early twentieth-century studies of the nature and functioning of the nervous system. In particular, we will examine research that explored (a) the

physiology of basic sensory-motor processes and reflexes, (b) the issue of whether specific functions could be “localized” in different areas of the brain, and (c) the nature of the basic unit of the nervous system, the neuron. The chapter closes with a description of Karl Lashley’s research on the role of the cortex in learning. Lashley was the twentieth century’s first prominent physiological psychologist. The Original Source Excerpt is from Broca’s famous case history of “Tan.” This case helped establish the clinical method of determining brain function.

## HEROIC SCIENCE IN THE AGE OF ENLIGHTENMENT

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As discussed in the last chapter, the years marking the end of the Renaissance were characterized by a gradual change from a reliance on authority as the source of truth to a reliance on scientific methodology and human reasoning powers. Bacon, Galileo, Harvey, and Descartes exemplified this shift in the beginning of the seventeenth century. Sir Isaac Newton solidified the change in the second half of the century. With the publication of his *Principia Mathematica* in 1687, serious thinkers began to take for granted the idea that objective truth could be gained through the methods of science and the unbiased use of reason. Because science and reason came to be seen as the only sure way to shed light on the darkness of ignorance, this period became known as the **Enlightenment** (Appleby, Hunt, & Jacob, 1994). Scientists like Newton became heroic figures, searching impersonally for objective truth about the universe by applying scientific methodology to its study. Newton’s influence on the philosophers was mentioned in the last chapter—Newton’s analysis of light into basic components and his theory of gravitation influenced the British empiricists, who tried to produce a similar analysis of the mind and thought of association as a force analogous to gravity.

Enlightenment thinking even spread into the political arena. America’s founding fathers were passionate and knowledgeable about science, and Benjamin Franklin made substantial contributions to the theory of electricity,

including the invention of the lightning rod. The Constitution itself borrowed from the Newtonian concept of equilibrium when developing the concept of a balance of powers among the executive, legislative, and judicial elements of government (Cohen, 1995).

The Enlightenment reached its height of influence in the second half of the eighteenth century, but its ideals remained strong throughout the nineteenth century, and well into the twentieth. By the early nineteenth century, the faith in science seemed to be paying dividends in the form of the kinds of technological innovations that eventually produced the Industrial Revolution. Thus, science seemed to lead inevitably to progress and scientists were viewed as being totally objective, simply looking for the truth without imposing their values in any way, and improving society through the inventions that derived from their science. It wasn’t until such technological innovations as the poison gas that “efficiently” reduced the populations of concentration camps and the atom bomb that serious questions began to be raised about whether science could possibly be totally objective and value-free and whether scientific discoveries necessarily meant progress. Nonetheless, during the period when the idea of a scientific approach to psychology began to take shape in the minds of such philosophers as the British empiricists, the model of scientist as hero held sway. If scientific thinking and human reason could enlighten the world about physics and chemistry, why not biology? If biology, why not psychology?

In the middle of the nineteenth century, scientific psychology evolved out of the philo-

sophical questions examined in Chapter 2 and research on the nervous system to be described in this chapter. Physiologists trying to “shed light” on how the senses and the nervous system actually worked developed methods and made discoveries that were directly relevant to the epistemological questions about the nature and origins of human knowledge being raised by philosophers such as John Stuart Mill. This dynamic convergence of philosophy and physiological science created an atmosphere out of which a “scientific” psychology was perhaps inevitable.

## SENSORY PHYSIOLOGY

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From the time of Descartes, scientists had been intrigued by the nature of nervous system activity. Most of the advances resulted from the medical community trying to deal with the problem of brain and nervous system damage, which was quite common in the context of two European wars in the middle of the eighteenth century and both the American and French revolutions during the second half of that century. At a time long before the development of antiseptic surgical procedures and antibiotic drugs, the vast majority of those suffering head wounds died from infection. Many of those who lived, however, became case studies that increased our knowledge of the brain and nervous system.

One issue of interest was whether the brain was the center of consciousness and the controller of voluntary action. Decapitated soldiers who nonetheless showed arm and leg movements raised questions about how soon consciousness left the body after death and where consciousness was localized. The problem was directly investigated with reference to executions that used the invention of noted French physician Joseph Ignace Guillotin. The device, which now bears his name, was said to be a marvelous improvement over large hairy men

with axes, who sometimes required several tries before completing their gruesome task of separating head from body. Although the guillotine was clean and quick and therefore considered humane, bodies continued to twitch for a brief time after execution. Eye movements and quivering facial muscles could also be seen. Did some level of awareness remain after a beheading? If so, then perhaps the instrument was not so humane after all. The problem was investigated in the early nineteenth century by Theodor Bischoff, who arranged to conduct tests on the decapitated head of a criminal immediately after execution. If consciousness remained, Bischoff reasoned, then the head should react predictably to having fingers thrust toward its eyes, having smelling salts placed under its nose, and having the word “Pardon!” spoken in its ear. Bischoff tried all of these tests, but the unfortunate head showed no reaction (Fearing, 1930). He concluded that consciousness ended with the moment of execution, thereby reinforcing the theory that consciousness resides in the brain, while at the same time reassuring investors in guillotines. The muscle twitches that occurred after death were therefore involuntary actions unrelated to consciousness. The question of why they occurred at all still remained, however, resulting in intensive research into the nature of basic reflex action and the role of the spinal cord in these movements.

## REFLEX ACTION

Prior to the nineteenth century, the most significant contribution to the study of reflexes was made by Robert Whytt (1714–1766) (pronounced “White”) of Edinburgh, Scotland. The leading neurologist of his day, Whytt is known primarily by historians of psychology for his research into the physiology of the involuntary reflex, but he is also justly famous in the history of pediatric medicine for being the first person to adequately describe tuberculous meningitis (Radbill, 1972). With regard to reflexes, in

1751 Whytt published *The Vital and Other Involuntary Motions of Animals*,<sup>1</sup> the outcome of years of research on the role of the spinal cord in mediating reflex action. It was the first extensive treatment of reflexes to be based on experimental research (Fearing, 1930). Studying decapitated animals (mainly frogs) Whytt was able to show that leg muscles responded in predictable ways to physical stimulation. Pinching the leg of a headless frog produced a reliable muscle contraction. On the other hand, if the frog was deprived of its spinal cord, these “involuntary motions” failed to occur. Hence, Whytt demonstrated that the spinal cord played a vital role in reflexive behavior.

Whytt distinguished between voluntary and involuntary actions, the former under the control of the will, with the action originating in and requiring an intact brain, and the latter controlled through the spinal cord. In between voluntary and involuntary control, and serving to link them, was habit formation. Thus, actions that begin as voluntary, and under the deliberate control of the will, become similar to reflexes when they have been sufficiently practiced. As Whytt put it,

We not only acquire, through custom and habit, a faculty of performing certain motions with greater ease than we are wont to do them, but also, in proportion as this facility is increased, we become less sensible of any share or concern the mind has in them. (cited in Fearing, 1930, p. 79)

Whytt also pointed out that a consequence of the formation of habits was that the mere idea of a stimulus was sometimes sufficient to bring about a response. In a passage that will make you think of Ivan Pavlov (Chapter 10), Whytt illustrated the point with two everyday

examples of what would eventually come to be called conditioned reflexes: “Thus the sight, or even the recalled idea of grateful food, causes an uncommon flow of spittle into the mouth of a hungry person; and the seeing of a lemon cut produces the same effect in many people” (cited in Fearing, 1930, p. 80).

The existence of the kinds of reflexes documented by Whytt demands that a distinction be made between the sensory and motor components of a reaction, which in turn implies that some nerves may be for the purpose of conveying sensory information and others designed to pass messages along to the muscles, telling them to move. This distinction between sensory and motor nerves became established through the work of two scientists working at about the same time in different countries.

### THE BELL-MAGENDIE LAW

As you recall from Chapter 1, a “multiple” refers to a case in which two or more people make the same discovery during the same historical era, but do so independently of each other. E. G. Boring (1950) used the concept to support his idea that the zeitgeist helped to determine the activities and ways of thinking of scientists during a particular historical era. The Bell-Magendie law is sometimes used as an example of a multiple—two scientists, working in different laboratories (different countries in this case) at about the same time and neither aware of the other’s research, arrive at the same results. The situation was not quite that simple in the case of Bell and Magendie, however, and during the years following their codiscovery, there was a nasty fight over priority. The judgment of history is that Magendie should have been credited with the discovery;

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<sup>1</sup> Whytt was a contemporary of David Hartley and published his book just two years after Hartley’s *Observations of Man* appeared. You will recall that Hartley went beyond a philosophical treatment and attempted to explain the nervous system by appealing to “vibrations.” Whytt does not seem to have been directly influenced by Hartley, but the fact that both men were concerned with the nervous system indicates the importance of the topic to intellectuals of the day.

his research was more systematic and he published it in the public forum of a journal. Bell's research, while occurring a few years earlier than Magendie's, was not conclusive and he published it in a private pamphlet with limited distribution. That Bell's name became paired with Magendie's is more of a tribute to the public clamoring of the politically influential Bell and his equally vociferous friends than to the quality of his research.

François Magendie (1783–1855) grew up during the turbulent years of the French Revolution, the son of a surgeon who was a politically active “Republican” in the efforts to overthrow the French monarchy. Lacking much in the way of formal education, François used his father's influence to become an apprentice at a Paris hospital, where, at the tender age of 16, he was entrusted with the task of doing anatomical dissections (Grmek, 1972). After becoming a medical student and completing a degree in 1808, he quickly earned a reputation as a gifted scientist who distrusted theorizing in favor of inductively collecting “facts.” This Baconian attitude he once described in this way: “I compare myself to a ragpicker: with my spiked stick in my hand and my basket on my back, I traverse the field of science and gather what I find” (cited in Grmek, 1972, p. 7).

In 1822, Magendie published a three-page article that summarized the results of a study on the posterior and anterior roots of the spinal cord. From his earlier dissections he knew that nerve fibers exited the spinal cord in pairs before joining together, with one type of fiber, the posterior root, closer to the surface of the skin, and the other (anterior root) closer to the interior of the body. Different structures suggest different functions, and Magendie's research aimed at identifying these functions.

Using a six-week old dog as the subject, Magendie exposed its spinal cord and cut the posterior fibers (i.e., those closer to the surface) while leaving the spinal cord intact. He sutured up the wound and observed the animal after it recovered. As he described it,

...I did not know what would result from this operation.... At first I believed the limb corresponding to the cut nerves to be completely paralyzed; it was insensitive to pricking and the hardest pressures and, further, it seemed immobile; but soon, to my very great surprise, I clearly saw it move, although sensibility remained completely absent. (Magendie, 1822/1965, p. 20)

Hence, the posterior roots controlled sensation. When destroyed, the animal could still move the limb, but had no sensation in it. Next, Magendie severed the anterior root in another animal, a task that required all of his considerable surgical skills. Because the anterior root lies below the posterior one, it is difficult to get to the former without damaging the latter. Nonetheless, Magendie worked out a successful procedure and managed to sever an anterior root cleanly (Bell, on the other hand, was never able to accomplish this). The results were clear: “there could be no doubt whatsoever; the limb was completely immobile and flaccid, although it retained an unequivocal sensibility” (Magendie, 1822/1965, p. 20). In summary, then, Magendie's finding, now known as the **Bell-Magendie law**, was that the posterior roots of the spinal cord controlled sensation, while anterior roots controlled motor responses. This was a major discovery, for it provided anatomical foundation for further study of the two sides of the reflex: sensation and movement. Furthermore, the distinction implied that nerves send messages in a single direction and there were different sensory and motor tracts within the spinal cord and perhaps different sensory and motor regions within the brain.

As for Sir Charles Bell (1774–1842), his *Idea of a New Anatomy of the Brain: Submitted for the Observation of His Friends* had been written 11 years prior to the publication of Magendie's work, but it had been sent privately to no more than 100 colleagues. Bell was a prominent English anatomist with influential friends, however, and together they launched a campaign against Magendie when the latter's work was published, accusing the Frenchman of

everything from unnecessary replication of Bell's original finding to animal cruelty. Bell went as far as to alter the wording of some of his earlier work and republish it to make it appear that he had anticipated Magendie by a decade (Gallistel, 1981). Yet Magendie was unaware of Bell's work with "stunned rabbits," which was not nearly as decisive as Magendie's research. Bell had severed the more accessible posterior root and observed a paralysis of a muscle in the rabbit's back; he then found that touching the anterior root with his knife produced a convulsion in that same muscle.

Magendie, personally affronted by the attacks from across the English Channel, recognized the value of Bell's research once he learned of it, but refused to concede priority for discovering the critical distinction between sensory and motor functions. In particular, while acknowledging Bell's priority concerning the strategy of segregating the spinal roots and the discovery that the anterior root influenced "muscular contractility" more than the posterior root did, Magendie vigorously asserted that "as for having established that these roots have distinct properties, distinct functions, that the anterior ones control movement, and posterior ones sensation, *this discovery belongs to me*" (cited in Grmek, 1972, italics added).

### THE SPECIFIC ENERGIES OF NERVES

Another feature of Bell's 1811 pamphlet was his argument that different sensory nerves have different "qualities." Thus, "an impression made on two different nerves of sense, though with the same instrument, will produce two distinct sensations" (Bell, 1811/1965, p. 24). As an example, Bell pointed to the "papillae" on the tongue, some of which convey the sense of

taste, others the sense of touch. When touching these latter papillae with a sharp steel pin, the resulting sensation is one of "sharpness." When touching one of the taste papillae with the same pin, however, the resulting sensation is one of a "metallic taste." Similarly, if two different types of stimuli affect a single type of nerve, then the sensation experienced will be determined by the type of sensory nerve stimulated. Thus, light waves stimulate the optic nerve to produce a visual sensation, but pressing on the side of the eyeball also results in the sensation of a flash of light and, according to Bell, cataract patients often reported seeing a "spark of fire" when the surgeon's needle pierced their eye.

This idea of Bell's eventually developed into the **doctrine of the specific energies of nerves**, and although Bell's 1811 paper once again had chronological priority, credit went elsewhere, this time to the leading German physiologist of the first half of the nineteenth century, Johannes Müller (1801–1858). Müller, whose frenetic pace of work alternated with several long periods of severe depression,<sup>2</sup> was the first person ever named a professor of "physiology" at the University of Berlin, Germany's premier university. Müller elaborated on the specific energies doctrine and developed it more fully than Bell. In addition to making the point about different sensory qualities, Müller argued that in perception, we are not directly aware of the external world; rather we are only aware of the action of our nervous system, which conveys information of the world to us. Thus, our knowledge of the world is filtered through the physiology of the nervous system.

The doctrine of specific energies of nerves eventually became associated more with Müller than with Bell, mainly because Müller named it as such and presented it as a series of

<sup>2</sup> Müller believed that his status had declined after his famous *Handbook* was published and by the mid-1850s, he was convinced that his years as a productive scientist were over. This plunged him into his final depression, and few of his friends believed that his death in 1858 was anything but a deliberate overdose of morphine (Studel, 1972).

10 related principles in his massive (eight books totaling more than 1600 pages) *Handbook of Human Physiology*, which first appeared in 1840. This was the authoritative physiology text of the mid-nineteenth century, and its stature guaranteed that Müller's name, not Bell's, would become attached to the doctrine (Boring, 1950).

### HELMHOLTZ: THE PHYSIOLOGIST'S PHYSIOLOGIST

If Müller was the leading German physiologist of the first half of the nineteenth century, the honor for the second half goes to one of his followers, Hermann von Helmholtz (1821–1894). Shortly after he died, Helmholtz was eulogized by Carl Stumpf, another well-known German physiologist, as the person most responsible for building the “bridge between physiology and psychology that thousands of workers today go back and forth upon” (cited in Turner, 1972). Helmholtz became *the* nineteenth-century authority on the sensory systems for vision and audition, developing theories still considered to be at least partly correct. He also provided a simple demonstration of nerve impulse speed that paved the way for one of psychology's most enduring methods, reaction time. And despite accomplishing more than any other nineteenth-century physiologist, his true love actually was physics, to which he also made original contributions!

Helmholtz was born in 1821 into a family of modest means (his father was a teacher) in Potsdam, Germany. He quickly emerged as an academic star at the local gymnasium (high school), where he developed his lifelong love for physics, but financial straits prevented him from attending a University. The government was offering full scholarships for students to attend the medical school in Berlin, however, and Helmholtz jumped at the opportunity, even though it meant committing himself to eight years of service in the army's medical corps (after completing five years of schooling).

He left for Berlin in 1838, where he completed the five-year program in four years. While enrolled at the medical institute, he also studied informally at the University of Berlin with the great Johannes Müller. Helmholtz quickly moved into Müller's inner circle and developed lifelong friendships with three other students destined to become leaders in the world of German science: Ernst Brücke, Emil du Bois Reymond, and Karl Ludwig.

Although he was the leading physiologist of his day, Müller was already being challenged by his students in the 1840s, especially on the issue of **vitalism** versus **materialism**. Müller believed that in addition to the physical and chemical components that made up physiological systems, there also existed a “vital force,” or a life force that could not be reduced further. It was an idea with deep roots and obvious theological connotations. Opposed to vitalism was a position that also had a long history but was becoming especially prominent in the nineteenth century—materialism (see Chapter 2, pp. 39–41). According to this view, the vital force was a myth: physical matter was the only reality and all living organisms could be reduced to physical, mechanical, and chemical processes that would eventually be understood by applying scientific methods. The movement was naturally congenial to the advances in science that occurred during this time. Müller's students, joined by Helmholtz, were committed materialists with all the enthusiasm and confidence of youth (all were under 30), and all made important contributions to physiology that supported the materialist position.

After finishing his medical degree in 1842, Helmholtz began his stint as an army surgeon, while at the same time maintaining his Berlin connections. It was during this time that he made the first of his lasting contributions, one that simultaneously reflected his love of physics and his desire to support a materialist physiology. It was a paper on the mathematical basis for a law of **conservation of energy**, first read to a scientific society in Berlin in 1847, then

published privately after being rejected for publication by a leading journal (Warren, 1984). Helmholtz is today considered one of the originators of this important principle in physics, which states that the total energy within a system remains constant, even if changes occur within the system. For Helmholtz, the principle was an important weapon in the fight against vitalism. Thus, he argued that body heat and muscle force could be explained by chemical energy accumulated during the oxidation process that accompanied digestion—there was no need to propose a special life force that could create its own energy. He supported his argument by showing that muscle contractions generated measurable amounts of heat (Turner, 1972).

### ***Measuring the Speed of Neural Impulses***

After being released early from his army commitment, Helmholtz was hired by the University of Königsberg in 1849, where he stayed for six years.<sup>3</sup> It was during this time that he completed a series of studies that had important implications for the study of the reflex and that laid the groundwork for the reaction time methodology that would become a key feature of every laboratory of experimental psychology.

When Helmholtz began studying the problem of nerve impulse speed in the early 1850s, it was already known that the impulse had electrical properties. A theory of electricity had arisen in the eighteenth century, and several scientists, including Helmholtz's materialist friend du Bois Reymond, had demonstrated that nerves could conduct electricity in order to make muscles twitch. Authorities such as Müller believed that the nerve impulse might be instantaneous or at the very least that it occurred too rapidly to be measured, but a study by du Bois Reymond in 1850 suggested

that the impulse was propagated along the nerve by an electrochemical process that would be slower than a pure electrical transmission. If so, then perhaps impulse speed could be measured. Helmholtz succeeded in doing so by isolating a motor nerve and a connected muscle from the leg of a frog. He then stimulated the nerve electrically at several different distances from the muscle and recorded the time from stimulus to response. Knowing distance and time, the calculation of rate was easy (rate = distance/time). It averaged about 90 feet per second (or just over 60 miles per hour), quite sluggish compared with estimates that placed it near the speed of light. Helmholtz also estimated impulse speed in sensory nerves by showing that human subjects took longer to respond to stimulation of their toe than their thigh.

For Helmholtz, the implications of the research were obvious. Here was more evidence that vitalism was wrong and materialism was right. Vitalists argued that the conscious decision to move an arm and the arm's movement were simultaneous, but Helmholtz had shown that the event took a measurable amount of time, a conclusion consistent with the idea that nervous action involved the movement of physical, material entities. For Helmholtz, this conclusion was enough: he was not interested in any further applications of the concept of reaction time. It would be for others to develop the idea into a technique for measuring the time of various mental activities. That story will be told in the next chapter.

### ***Helmholtz on Vision and Audition***

During the Königsberg years, Helmholtz also began investigating the physiology of vision and audition and invented a tool that made him famous among eye doctors: the **ophthalmoscope**, a device for directly examining the

<sup>3</sup> Having well-connected friends never hurts. The position at Königsberg opened when Brücke, one of Helmholtz's Berlin friends, left a position there to take one at Vienna (where his prize student would be Sigmund Freud). The Königsberg job was first offered to du Bois Reymond, who turned it down but apparently recommended Helmholtz, who accepted (Turner, 1972).

retina. His research on vision culminated in a massive three-volume *Handbook of Physiological Optics*, published over an 11-year period, from 1856 to 1867. During this same time he moved twice, first to Bonn and then to Heidelberg, where he spent 13 of the most productive years of his life (1858–1871).

Helmholtz is perhaps best remembered for elaborating a theory of color vision first proposed by the English scientist Thomas Young at the beginning of the nineteenth century. Sometimes considered another example of a multiple, it has come to be called either the Young-Helmholtz theory or as Helmholtz called it, the **trichromatic theory**. It is based on the facts of color-matching experiments. If you shine a red spotlight against a wall and then shine a green light so that it overlaps the red, the colors in the area of overlap will “mix” and be seen as a new color, yellow. Both Young and Helmholtz demonstrated that by mixing various combinations of three colors together, red, green, and blue, the resulting color could be made to match any other single color. On this basis, they concluded that the eye must contain three different kinds of color receptors, one for each of these so-called primary colors, red, green, and blue (or violet). Incoming light of a particular wavelength was said to stimulate these receptors to different degrees, resulting in the perception of a certain color. In Helmholtz’s words,

...Suppose that the colors of the spectrum are plotted horizontally in Fig. [3.1] in their natural sequence, from red to violet, the three curves may be taken to indicate something like the degree of excitation of the three kinds of fibers, No. 1 for the red-sensitive fibres, No. 2 for the green-sensitive fibres, and No. 3 for the violet-sensitive fibres.

Pure *red* light stimulates the red-sensitive fibres strongly and the two other kinds of fibres feebly; giving the sensation red.

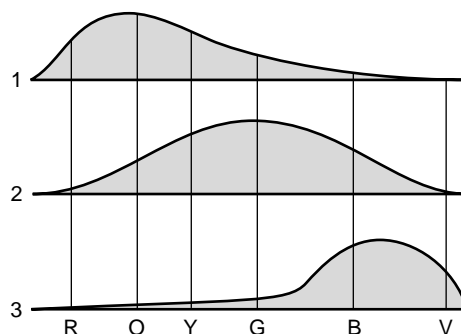
Pure *yellow* light stimulates the red-sensitive and green-sensitive fibres moderately

and the violet-sensitive fibres feebly; giving the sensation yellow.

Pure *green* light stimulates the green-sensitive fibres strongly and the two other kinds much more feebly; giving the sensation green.

...When all the fibres are stimulated about equally, the sensation is that of *white* or pale hues. (Helmholtz, 1860/1965, p. 42)

Although Helmholtz’s Figure 3.1 was hypothetical, it is quite similar to modern-day data plotted in what are called spectral sensitivity curves. Thus the trichromatic theory has held up over the years, at least in part. It failed to account for certain color phenomena that were better explained by other theories, however, most notably Ewald Hering’s **opponent process theory**. Hering proposed that color-sensitive cells were designed to respond to opposing pairs of colors (i.e., red-green, yellow-blue, black-white). When seeing red, for instance, Hering proposed a chemical breakdown in the receptor for red-green, what he called a “catabolic” process. Seeing green resulted in an “anabolic” or building-up process. If both red and green were mixed together, Hering believed the two processes would cancel each other, resulting in the perception of a neutral gray color. One of the trichromatic theory’s problems was its prediction that someone with



**Figure 3.1** Relative sensitivity of the three color receptors proposed by Helmholtz, from his *Handbook of Physiological Optics*.

severe red-green color blindness would not be able to see yellow properly either. Yellow, according to Helmholtz, relies on the stimulation of properly functioning red and green fibers, both of which would be defective for someone with red-green color blindness. Such persons do see yellow, however. Also, the phenomenon of color afterimages seemed to fit Hering's model better than the Helmholtz model. After staring at a red square for a minute or so, then shifting one's gaze to a white surface, an afterimage in the form of a green square appears briefly. Yellow and blue complement each other in a similar manner. Today, theories of color vision include elements of both theories. The Young-Helmholtz version applies well at the retinal level—there do seem to be three different kinds of cones, each maximally responsive to the three colors of trichromatic theory, red, green, and blue. As for the Hering theory, his notions of anabolic and catabolic processes within individual receptors have not held up, but there do seem to be opposing pairs of cells located in numerous sections of the visual pathway. For example, in the lateral geniculate nucleus, about midway between the retina and the visual cortex, there are cells that fire rapidly whenever red is presented to the retina, but are inhibited from firing when green is shown. In addition to these R+G- cells, the nucleus also holds a collection of R-G+, B+Y-, and B-Y+ cells (Goldstein, 1996).

Color vision was only a small portion of Helmholtz's work on the visual sense. His love of physics, for example, led him to examine the basic question of optics: How does light become focused on the retina? Thus, he provided a systematic analysis of how light rays are bent, both by the cornea and through the process of **accommodation**, in which the lens changes shape in order to alter the focus of objects at different distances. He also examined the perception of depth through the operation of **binocular vision**, and in the spirit of Bishop Berkeley, took a strong empiricist stance on the question of how we come to perceive objects in space.

Helmholtz would be justly famous even if he restricted his expertise to vision. In 1863, between the publication of volumes II and III of his *Optics*, however, he also published what quickly became the authoritative text on the sense of hearing, *The Theory of the Sensation of Tone as a Physiological Basis for the Theory of Music*. It is still in use today. In it Helmholtz presented his famous **resonance theory** of hearing, which proposed that different frequencies of sound were detected by receptors located in different places along the basilar membrane of the cochlea.

It is worth noting that both the trichromatic theory of color vision and the resonance theory of hearing were elaborations of Müller's doctrine of the specific energies of nerves. Whereas Müller proposed a single specific energy for each of the five basic senses, Helmholtz's theories amounted to proposing more than one specific energy for *each* sense: three for color vision and many for hearing.

### ***Helmholtz and the Problem of Perception***

As a physicist, Helmholtz was accustomed to look for precision in nature. Hence, he was perplexed by what could be called the **problem of perception**. On the one hand, it appears that the human sensory systems for seeing and for hearing are remarkably capable. On the other hand, the structures designed to deliver these senses seem to be terribly flawed. In vision, for example, Helmholtz noted that aberrations in the cornea often distorted light waves, that the fluids within the eye distorted the perceptions of shape, motion, and color, and worst of all, when light reached the retina, it had to pass through several layers of blood vessels and nerve fibers before reaching the receptors. Helmholtz once said that "...if an optician wanted to sell me an instrument which had all these defects, I should think myself quite justified in blaming his carelessness in the strongest terms, and giving him back his instrument" (cited in Warren, 1984, p. 257). Similar problems occurred with hearing.

Given such design flaws, Helmholtz asked, what accounts for the quality of our perception? The answer, he believed, could be found in the doctrine of the specific energies of nerves and in traditional empiricist philosophy. Thus, because our nervous system mediates between reality and the mind, we are only indirectly aware of the external world. As a result, the role of experience must be central to perception, he argued. The raw information processed by the sensory systems is meaningless in itself, then, but takes on meaning only when a particular combination of sensory events becomes associated with specific consequences. Consider, for example, the perception of objects located at different distances. According to Helmholtz, we make what he called an **unconscious inference** about distance, based on our past experiences of various cues that are associated with distance. As a person gets closer to us, for example, the retinal image enlarges, but we perceive the person getting closer, not bigger. Helmholtz would say that because we know through experience that people don't grow or shrink as they approach or recede, we conclude logically (i.e., unconsciously infer) that the person must be getting closer. All of this occurs quickly and without our awareness, hence the term "unconscious" inference.

Despite being sickly as a youth, Helmholtz was strong and energetic in his later years. His favorite hobby was mountain climbing, for example, and he could often be found hiking through the Alps (Wade, 1994). The experience gave him a metaphor that summed up his approach to science. The elegance of his final theorizing contrasted with the messy and unpredictable day-to-day process of doing research. To explain how he proceeded, he compared himself to

...an Alpine climber who, not knowing the way, ascends slowly and with toil, and is often compelled to retrace his steps because his progress is stopped; sometimes by reasoning, and sometimes by accident, he hits upon traces of a fresh path, which again leads him a little further; and finally, when

he has reached the goal, he finds to his annoyance a royal road on which he might have ridden up if he had been clever enough to find the right starting-point at the outset. In my memoirs I have, of course, not given the reader an account of my wanderings, but I have described the beaten path on which he can now reach the summit without trouble. (cited in Warren, 1984, p. 256)

In 1871, at age 50, Helmholtz left Heidelberg for Berlin when he was offered a prestigious professorship in physics. Thus, in the last stage of his career he returned to his first love, physics. He traveled widely, even visiting the United States in 1893 to represent German science at the World's Fair in Chicago. On the return voyage he suffered a severe concussion and prolonged double vision from a fall down a flight of stairs. He died of a cerebral hemorrhage the following year.

## LOCALIZATION OF BRAIN FUNCTION

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In addition to the advances in knowledge about sensory physiology, nineteenth-century scientists also explored the nature of the brain, and argued over the problem of localization. Even a superficial visual inspection of the brain reveals some obvious structural differences. There are clearly two hemispheres, the cortex subdivides further into a number of ridges (convolutions), the cerebellum is separate from the cerebrum, and the lower brain areas, an extension of the spinal cord, have their own distinct shapes and features. It is only natural to suppose that there are functional differences corresponding to these structures, and this raises the question of **localization of function**. To what extent do the different locations in the brain correspond to different physiological and psychological attributes? That is, just how precise can localization be delineated? The answers range from

very much to very little to it depends on the area of the brain being studied.

### THE PHRENOLOGY OF GALL AND SPURZHEIM

The phrenologists proposed the first major theory of localization and their answer to the question just raised was “very much.” According to advocates of **phrenology**, human “faculties” could be identified and located in precisely defined areas of the brain. Phrenology began as a legitimate scientific attempt to study brain function, but it gradually degenerated into the nineteenth century’s best example of pseudoscience. When portrayed in today’s introductory psychology texts, it is usually caricatured as a bizarre scientific dead end in which charlatans read character by looking at the bumps on someone’s head. Actually, the story is considerably more complicated and much that is characteristic of American psychology has its roots in the phrenological movement.

The origins of phrenology may be traced to the respected but eccentric Viennese physician and comparative anatomist Franz Josef Gall (1758–1828). Gall was born in Tiefenbronn, Germany, into an intensely devout Catholic family—his parents assumed that he would one day become a priest. Instead, his theory about the brain came to be considered antireligious, his books were banned by the Church, the best that could be said about his personal life was that it was morally unconventional, and upon his death in 1828 he was denied a religious burial (Young, 1972). Gall decided on a career in medicine early in life, and he earned an M.D. in Vienna in 1785. There he developed a successful practice and became a skilled anatomist, although he was criticized for charging admission to those who wished to observe him in surgery and his theory about brain function became controversial. After his public lectures and surgical demonstrations were banned for allegedly promoting immorality and atheism, he took the show on the road and lectured

throughout Europe before settling in Paris in 1807, where he remained until his death.

Gall secured a place in the history of medicine with his careful anatomical work. He identified the fibers connecting the two hemispheres and confirmed earlier speculation that some fibers crossed from one side of the brain to the opposite side of the spinal cord. Thus, Gall confirmed the concept of **contralateral function**, the notion that each side of the brain controls the opposite side of the body. Gall also compared the brain structures of different species and made a convincing argument that the mental abilities of different species correlated with the size and complexity of the brain, especially the cortex. He was also the first to argue that the brain’s convolutions formed the same pattern within a given species; hence, the surface of the brain was not a random jumble of ridges and valleys but had a reliable structure. His anatomical research was impeccable—the great French physiologist Pierre Flourens, phrenology’s harshest critic (below), nonetheless reported that when he saw Gall dissect a brain, it was like seeing the organ for the first time. Unlike most anatomists, including Flourens, who dissected brains by slicing off segments from the top down, Gall worked from the brain stem up, removing structures one by one and thereby tracing the interconnections between structures with a precision that was impossible when starting at the top (Temkin, 1947).

Despite these notable accomplishments, Gall is best known for originating phrenology, or what he called “cranioscopy.” The theory is historically significant as the first serious theory of the localization of brain function, and Gall is justly credited with being among the first to argue that the brain was the organ of both the intellectual and the emotional components of the mind. Unfortunately, though, Gall identified the wrong functions and put them in the wrong places in the brain. In addition, his logic and his methods were flawed.

Gall began developing his ideas about localization very early in his life—as a youth, he

thought he detected a relationship between the shape of a person’s head and certain behavioral characteristics of that person. He noticed, for example, that schoolmates with protruding eyes seemed to have better memories than he did. This early experience began a lifelong pursuit of anecdotal evidence to support his theories. Thus, he claimed that the impulse to steal resulted from an overdevelopment of the faculty of “Property” (later called “Acquisitiveness”), located in the temporal lobe of the cortex about an inch above and in front of the ear. According to Gall,

...[w]hen these cerebral parts are very much developed, they produce a prominence on the head and skull.... I have constantly found this prominence, in all inveterate thieves confined in prison, in all idiots with an irresistible propensity to steal, and in all those who, otherwise well endowed with intellect, take an inconceivable pleasure in stealing, and even feel incapable of resisting the passion which forces them to theft. (Gall, 1825/1965, p. 218)

Gall’s beliefs eventually developed into the theory that his followers came to call phrenology, a term that derives from the Greek words for the study of (“-ology”) the mind (“phrenos”). The term was coined by Joseph Spurzheim (1776–1832), who collaborated with Gall for a time, but later broke with him. Spurzheim is the person most responsible for popularizing the theory, both in Europe and in America. As described in his *Outlines of Phrenology* (1832/1978) and elsewhere, phrenology’s main principles reduced to five:

- a. The brain is the organ of the mind.
- b. The mind is composed of a large number (about three dozen) of abilities or attributes called “faculties”; some of these faculties are intellectual (cognitive) and some are affective (emotional).
- c. Each faculty is associated with a specific brain location.

- d. For a given faculty, some people have more than others, and those with more of a particular faculty will have more brain tissue in the corresponding location than those with less of that same faculty.
- e. Because the skull corresponds roughly to the shape of the brain, the strength of various faculties can be inferred from the shape of the skull.

This last point came to be known as the “doctrine of the skull” and for the phrenologists it was the key to measurement. If the size and shape of various brain locations reflected the strength of faculties and if brain shape affected skull shape, then measuring the skull would yield a measurement of faculties. In short, everything of importance about people could be known by examining the shapes of their skulls. Figure 3.2 shows a typical phrenological skull with its faculties labeled.

In the first two decades of the nineteenth century, craniology/phrenology was a legitimate

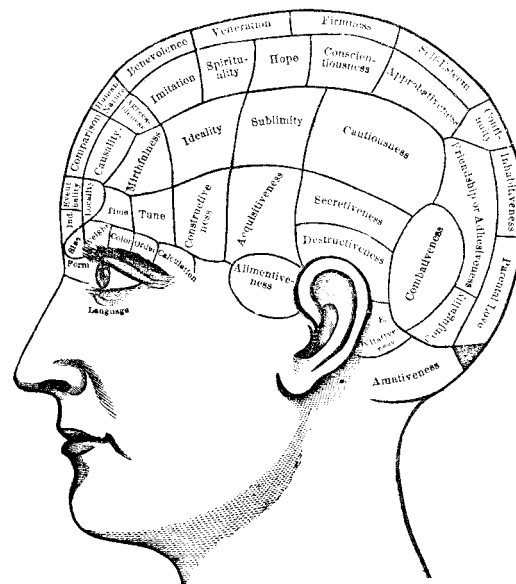


Figure 3.2 A phrenological skull, with faculties identified.

attempt to identify the localized functions of the brain. By the time Spurzheim produced his *Outlines of Phrenology*, in the year he died while on an American lecture tour (1832), thousands of skulls had been examined with an eye toward correlating skull shape with character. The *Outlines* includes detailed delineations of the faculties, with each description identifying the faculty's location in the brain and describing some of the supporting evidence for the faculty. On close examination, however, it is clear that there were serious weaknesses with the evidence. As indicated above in connection with the faculty of Property (Acquisitiveness), the phrenologists relied heavily on **anecdotal evidence**. That is, they looked for specific case examples to support their theory. This approach is not necessarily flawed—gathering lots of data and then looking for generalizations is a standard inductive strategy. The problem, however, is that the phrenologists were not interested in examples that did not support their case. Thus, their theory failed an important criterion of an authentic scientific theory: it must be stated precisely enough to be capable of disproof. But the phrenologists would not do this. A thief with a small area of Acquisitiveness would either be ignored, described as a potential thief (“he will start stealing any day now”) or explained away by referring to combinations of other faculties that would be said to offset the lack of Acquisitiveness. For instance, the thief might be described as having large faculties of Imitation and Self-Esteem, causing him to maintain his self-image by copying his pickpocket older brother, despite his lack of “natural” Acquisitiveness. Perhaps the ultimate example of phrenological refusal to consider disproof was a comment attributed to a phrenologist upon learning that Descartes’ skull was rather small in the areas related to some of the intellectual faculties. The phrenologist concluded that perhaps Descartes wasn’t so smart after all (Fancher, 1990)!

This failure of phrenology as a theory did not seem to bother the phrenologists, but it was quickly recognized as a fatal flaw by other sci-

entists, and phrenology was relegated to the status of pseudoscience by the mid-1830s. Unfortunately, it shared an important feature with other pseudosciences (e.g., biorhythms in the late twentieth century)—the general public loved it. Phrenology became enormously popular throughout the rest of the nineteenth century. Gall and Spurzheim spread the faith throughout Europe and Spurzheim and others exported it to the United States.

It was in America that phrenology reached its zenith of popularity. The version that was imported by Spurzheim and spread by him and others fit in perfectly with the American culture of the “common man,” especially during the middle and last half of the nineteenth century (Bakan, 1966). Although Gall believed the size of a person’s faculties was an indication of native traits, Spurzheim argued that faculties could be affected by nurture. To Spurzheim, the brain was analogous to a muscle—its faculties could be exercised and strengthened through education and self-help. Thus, phrenology provided a seemingly scientific basis for the traditional American belief that anyone, regardless of heritage, could “pull oneself up by one’s bootstraps” and accomplish virtually anything in life (e.g., go from a log cabin to the White House). The hopeful notion that children’s brains and therefore their futures could be shaped by controlling their environments and improving their educations resonated with Americans. That same optimism would make behaviorism just as fashionable with the public in the 1920s. Phrenology also was consistent with the American idea that everyone is a unique person, possessing his or her own special talents. In phrenological terms, this translated into everyone having his or her own distinctive configuration of faculties, to be measured with proper phrenological tools. Thus, phrenology was an important early example of a major theme of research in psychology that continues today: the search for ways to identify and gauge individual differences (Bakan, 1966). And if individual differences could be identified and

measured, then a person's strengths and weaknesses could be known and he or she could be counseled about careers, mate selection, and so on. A final reason for phrenology's appeal, then, was in its promise to deliver practical applications to improve daily living.

Phrenology's popularity with the masses was enhanced through the energetic marketing efforts of the New York firm of Fowler and Wells. Despite the fact that the scientific and more educated community rejected phrenology

rather quickly, the public never seemed to tire of it. After all, it appeared to provide simple answers to life's difficult problems. Fowler and Wells published thousands of "improve-your-life-through phrenology" pamphlets, a phrenological journal, and paraphernalia ranging from busts with the faculties clearly marked on them to charts to simple tools for measuring head shapes. As you can see from the Close-up, phrenology held the American public's interest into the early years of the twentieth century.

## c CLOSE-UP

### The Marketing of Phrenology

When Orson Fowler was a student at Amherst College in the early 1830s, he made pocket money by examining the heads of classmates for two cents per head (Joynt, 1973). Upon graduation, he joined with his brother Lorenzo and sister Charlotte in forming a museum of phrenology in New York City that featured a large collection of skulls, casts of heads, and other phrenological tools of the trade. Admission was free, but once the museum-goers were in the door, the Fowlers tempted them with a phrenological assessment that cost from one to three dollars. When Charlotte married a medical student named Samuel Welles, the firm of Fowler and Wells was born. Located at 753 Broadway, with branches in Boston and Philadelphia, it dominated the phrenology business from its inception in 1844 to the turn of the twentieth century.

Fowler and Wells, Inc., published a seemingly endless list of pamphlets designed to bring phrenological insights into every home. They also began the popular *Phrenological Journal*, trained and "certified" phrenologists, and during an era when the public lecture was a primary means of communication, maintained a list of accomplished public speakers ready to spread the phrenological faith. To give you some idea of the range of topics addressed by the firm, consider the following titles of pamphlets and books that could be ordered from Fowler and Wells, as advertised in the October 1881, issue of the *Phrenological Journal*:

*The Indications of Character*, as manifested in the general shape of the head and the form of the face. Illustrated. 15 cents.

*Wedlock*; or, The Right Relations of the Sexes. A Scientific Treatise disclosing the Laws of Conjugal Selection, Pre-natal Influences, and showing Who Ought and Who Ought Not to Marry. \$1.50; in fancy guilt, \$2.00.

*Amativeness*; or, Evils and Remedies of Excessive and Perverted Sexuality; including Warning and Advice to the Married and Single. 25 cents.

*Choice of Pursuits*; or, What to do and Why. Describing Seventy-five Trades and Professions, and the Temperaments and Talents required for each. 508 pp. \$1.75.

As for the journal itself, each issue contained brief phrenological sketches of well-known individuals, articles on other hot topics of the day (e.g., hypnotism, spiritualism)

## 70 Chapter 3 / The Neurophysiological Context

and short pieces covering just about anything (e.g., “Why Bees Work in Darkness”; “The Morality of Brakemen”). Although nothing quite like the *Phrenological Journal* exists today, the annual *Old Farmer’s Almanac*, with its down-east commonsense wisdom, bears some similarity.

A typical phrenological article in the journal featured some well-known person and showed how a phrenological assessment could “explain” that person’s character and behavior. For example, the September 1873, issue included a piece about a notorious triple murderer. Here’s how he was described by a phrenologist who interviewed him:

I found his head to be 22 inches in circumference, 13.5 inches from Individuality to the occipital spine, and 14 inches from Destructiveness to Destructiveness, over the top of the head at Firmness. The animal portion of the brain predominates over all others. Destructiveness is the largest organ in his brain, the head swelling out enormously over the ears. The organ of Conscientiousness is, I think, the smallest I ever saw.... All the spiritual organs are small and inactive, while Cautiousness and Secretiveness are both below the average.

The firm of Fowler and Wells had a long run, but interest in phrenology finally began to wane near the end of the nineteenth century, as the general public became more informed about the workings of the brain and as other approaches to measurement (e.g., IQ testing) began to be popularized. In 1911, the *Phrenological Journal* published its last issue.

### FLOURENS AND THE METHOD OF ABLATION

Phrenology might have seemed like good science to Main Street America, but the real scientists were not fooled. As mentioned earlier, the scientific community rejected the Gall/Spurzheim theory well before the middle of the nineteenth century. Phrenology’s worst enemy was the distinguished French physiologist and surgeon Pierre Flourens (1794–1867), who deliberately set out to show that the phrenologists were wrong. He reduced phrenology to two main points: the mind is centered in the brain, and the mind is composed of numerous faculties, each located in specific places in the brain. In his sharply worded *Examination of Phrenology*, first published in 1843, he sarcastically observed that “of these two propositions, there is certainly nothing new in the first one, and perhaps nothing true in the second one” (Flourens, 1846/1978, p. 18).

To falsify the phrenologists’ claims, Flourens took an experimental approach to the problem of localization, using the method of **ablation**. Although he did not create the procedure, he

raised it to such a level of refinement that it is now associated with his name. Rather than wait for natural experiments to occur, in the form of accidental brain damage, Flourens removed specific sections of the brain and observed the effects (“ablation” derives from the Latin words for “carry away” or “remove”). If the result of an ablation is an inability to see, then presumably the area of the removed portion has something to do with vision. Clearly, the method required animals as research subjects, and Flourens experimented on numerous species, ranging from dogs to pigeons.

Flourens’s attack on phrenology took the form of showing that specific areas of the brain that were alleged to serve function X in fact served function Y, and that the cerebral cortex operates as an integrated whole, rather than as a large collection of faculties located in specific places. One focus of his research was the cerebellum. To the phrenologists, this portion of the brain controlled sexual behavior and was the center of the faculty of “amativeness.” Flourens had little trouble disproving this and demonstrating instead that the cerebellum is the

center of motor coordination. Thus, pigeons deprived of the organ were unable to coordinate wing movements in order to fly, and dogs were unable to walk properly and would be observed staggering, falling down, and bumping into objects they could normally avoid. Also, the degree of abnormality in movement was directly proportional to the amount of cerebellum ablated.

As a result of removing varying amounts of the cerebral cortex, Flourens found a similar relationship between the amount removed and the seriousness of the ensuing problem. He could find no indication of distinct functions residing in specific areas of the cortex, however, so he concluded that it operated as a whole and served the general functions of perception, intelligence, and will. Thus, pigeons without a cortex or with most of it removed did seem to be able to perceive the world around them, but showed no indication of an ability to learn from their experiences, and did not seem to be able to do anything except to vegetate. The difference between a pigeon without a cerebellum and one without a cortex was that the first bird would attempt to fly but could not, while it would never occur to the second bird that flying was an option in life.

The general principles that the cortex acts as a whole and that the amount of disability is proportional to the extent of ablation were verified and extended by the discoveries of the great American physiological psychologist Karl Lashley, who referred to them as the principles of equipotentiality and mass action, respectively. (Lashley's work will be considered briefly at the end of the chapter.) Yet while Flourens was able to use these principles to attack phrenology in such a way that it never recovered, at

least in the eyes of scientists, he overstated his case. He argued against any degree of localization in the cortex, a position soon to be shown inadequate by other brain scientists using methods other than ablation.

## THE CLINICAL METHOD

The results of ablation studies are not always easy to interpret, mainly because destroying one portion of a brain also influences connections to that portion, producing outcomes that are not always predictable or consistent. Also, ablation studies are sometimes impossible to do, as in the case of human subjects. It is one thing to systematically ablate portions of a person's brain for certain beneficial medical reasons (e.g., severing the corpus callosum to treat epilepsy), but destroying human brain tissue simply for the purpose of observing what happens is obviously indefensible.<sup>4</sup> An alternative way to study human brain function is called the **clinical method**. This involves either (a) studying the behavioral and mental consequences of brain injury, events such as strokes, or illness, or (b) identifying people with some behavioral or mental disorder and examining their brains after death. The person generally credited with developing the clinical method is Paul Broca, whom we will meet shortly, but there are numerous examples of famous clinical cases in the mid-nineteenth century. One of the best-known concerned a well-respected Vermont railroad worker, Phineas Gage.

### *The Remarkable Phineas Gage*

While blasting rock in preparation for a new railway line near Cavendish, Vermont, in 1848, Gage survived an accident that seemed certain

<sup>4</sup> This rather obvious ethical point was lost on Dr. Roberts Bartholow of Cincinnati in 1874, who inserted electrodes into the cortex of an unwitting immigrant domestic worker (i.e., powerless) who had come to him for treatment of an ulcerous scalp wound that had exposed a portion of her brain. Mild stimulation produced some muscular contractions, but when the curious Bartholow inserted the electrodes deeper and increased the strength of the current, the unfortunate woman went into severe convulsions and soon died (Hothersall, 1995).



**Figure 3.3** Sketch of Gage's skull, showing position of tamping iron, from the original medical report by Harlow (1869).

to be fatal. After pouring some gunpowder and a fuse into a hole drilled into rock that was about to be blasted away, Gage used a "tamping iron" to compress the powder. Momentarily distracted, he scraped the edge of the rock hard enough to create a spark that ignited the gunpowder. This converted the tamping iron into a missile which flew into the air and landed 30 meters away. Unfortunately for Gage, his head was in the flight path. The missile entered just below his left eye and exited from the top left of his forehead, taking a healthy portion of his left frontal cortex with it (see Figure 3.3). Miraculously, Gage only lost consciousness for a brief time, and once he arrived back in town, was able to walk (assisted) to a doctor's office. There he sat and conversed with friends (!) until the doctor arrived, about 30 minutes after the accident. Within two months he was sufficiently recovered to live independently,<sup>5</sup> but he

was never able to work productively again and his personality changed dramatically. From a dependable, conscientious, respected community leader (he was foreman of the railroad crew), Gage degenerated into an obstinate, profane, irresponsible embarrassment to the community (MacMillan, 1986).

One of Gage's doctors, John Harlow, was amenable to phrenology and saw the case as providing support for the phrenologist's belief in cerebral localization. Harlow kept meticulous notes on the case and published accounts of it in 1848 and 1868, describing this case of frontal lobe damage as one in which

...[t]he equilibrium or balance...between his intellectual faculties and animal propensities seems to have been destroyed. He is fitful, irreverent, indulging at times in the grossest profanity (which was not previously his custom), manifesting but little deference for his fellows, impatient of restraint or advice when it conflicts with his desires, at times pertinaciously obstinate, yet capricious and vacillating, devising many plans of future operation, which are no sooner arranged than they are abandoned.... Previous to his injury, although untrained in the schools, he possessed a well-balanced mind, and was looked upon by those who knew him as a shrewd, smart businessman, very energetic and persistent in executing all his plans of operation. In this regard his mind was radically changed, so decidedly that his friends and acquaintances said he was "no longer Gage." (Harlow, 1868, cited in MacMillan, 1986, pp. 13–14)

Thus, while Gage survived the injury, he was radically altered by it—the brain damage resulted in irreversible changes to his personality and behavior. Within 12 years (at age 37) he

<sup>5</sup> That he survived at a time prior to the use of antibiotics to treat infection was nothing short of amazing, but his recovery was probably aided by fact that the entry wound provided a natural drainage area that prevented him from developing the kind of abscess that would almost certainly be fatal (MacMillan, 1986).

died, after experiencing a number of increasingly severe convulsions. The tamping iron and Gage's skull can be seen today at Harvard's Warren Anatomical Medical Museum.

## c ORIGINAL SOURCE EXCERPT:

### Broca Discovers the Speech Center

In the Gage case, it was possible for Harlow to trace events from the initial brain injury to the resulting psychological outcome. Another type of clinical case occurs when a patient manifests some specific mental or behavioral problem, but it cannot be correlated with brain damage until after death. Such was the situation facing the French neurologist Paul Broca (1824–1880) in April of 1861, when confronted with a very unusual patient, known to history as “Tan,” for reasons that will soon be apparent. This patient had been in the Bicêtre hospital in Paris for 21 years, and had been incapacitated and in bed for the seven years prior to 1861, when a severe case of gangrene brought him to Broca's attention. What follows is an excerpt from Broca's description of this remarkable case (Broca, 1861/1965), which eventually resulted in Broca's name being forever associated with a specific location on the cortex.

On 11 April 1861 there was brought to the surgery...a man named Leborgne, fifty-one years old, suffering from a diffused gangrenous cellulitis of his whole right side, extending from the foot to the buttocks. When questioned the next day as to the origin of his disease, he replied only with the monosyllable *tan*, repeated twice in succession and accompanied by a gesture of his left hand. I tried to find out more about the antecedents of this man,...and here is the result of this inquiry.

Since youth he had been subject to epileptic attacks, yet he was able to become a maker of lasts,<sup>6</sup> a trade at which he worked until he was thirty years old. It was then that he lost his ability to speak and that is why he was admitted to the hospice at Bicêtre....

...He was then quite healthy and intelligent and differed from a normal person only in his loss of articulate language. He came and went at the hospice, where he was known by the name of “Tan.” He understood all that was said to him. His hearing was actually very good, but whenever one questioned him he always answered, “Tan, tan,” accompanying his utterance with varied gestures by which he succeeded in expressing most of his ideas. If one did not understand his gestures, he was apt to get irate and added to his vocabulary a gross oath [“Sacré nom de Dieu!”]....

Ten years after he lost his speech a new symptom appeared. The muscles of his right arm began to get weak, and in the end they became completely paralyzed. Tan continued to walk without difficulty, but the paralysis gradually extended to his right leg; after having dragged the leg for some time, he resigned himself to staying in bed. About four years had elapsed from the beginning of the paralysis of the arm to the time when

<sup>6</sup> A “last” is a wooden block in the shape of a foot, used in the making or repairing of shoes.

## 74 Chapter 3 / The Neurophysiological Context

paralysis of the leg was sufficiently advanced to make standing absolutely impossible. Before he was brought to the infirmary, Tan had been in bed for almost seven years. (pp. 224–225, italics in the original)

During the seven years in bed, Tan was more or less forgotten, and little information was available about him, except that his vision began to deteriorate. Because he remained continent, his linen was not changed regularly; thus, the gangrene that brought him to Broca's attention was not discovered until it had advanced considerably, infecting the whole leg. Broca reported that he hesitated examining Tan, because his general state "was so grave that it would have been cruel" (p. 225). Nonetheless, Broca proceeded, both with a physical exam that confirmed the paralysis of the right arm and leg, and with an examination of Tan's mental capacities:

The state of Tan's intelligence could not be exactly determined. Certainly he understood all that was said to him, but, since he could express his ideas or desires only by movements of his left hand, this moribund patient could not make himself understood as well as he understood others. His numerical responses, made by opening or closing his fingers, were best. Several times I asked him for how many days had he been ill. Sometimes he answered five, sometimes six days. How many years had he been at Bicêtre? He opened his hand four times and then added one finger. That made 21 years, the correct answer. The next day I repeated the question and received the same answer, but, when I tried to come back to the question a third time, Tan realized that I wanted to make an exercise out of the questioning. He became irate and uttered the oath, which only this one time did I hear from him.... He could understand even quite complicated ideas. For instance, I asked him about the order in which his paralyzes had developed. First he made a short horizontal gesture with his left index finger, meaning that he had understood; then he showed successively his tongue, his right arm, and his right leg. That was perfectly correct, for quite naturally he attributed his loss of language to paralysis of his tongue. (p. 226)

Broca guessed that Tan had a cerebral lesion that for the first 10 years of the illness remained confined to a fairly limited area in the left side of the brain, but then had spread. He did not have long to wait in order to confirm the diagnosis:

The patient died on 17 April [1861]. The autopsy was performed as soon as possible—that is, after 24 hours. The weather was warm but the cadaver showed no signs of putrefaction. The brain was shown a few hours later to the Société d'Anthropologie and was then put immediately into alcohol. It was so altered that great care was necessary to preserve it. It was only after two months and several changes of the fluid that it began to harden. Today it is in perfect condition and has been deposited in the Musée Depuytren. (p. 227)

Remarkably, Tan's brain still resides in the Musée Depuytren, with the damage to the left frontal cortex clearly visible. As Broca summed up the case,

Anatomical inspection shows us that the lesion was still progressing when the patient died. The lesion was therefore progressive, but it progressed very slowly, taking twenty-one years to destroy a quite limited part of the brain. Thus it is reasonable to believe that at the beginning there was a considerable time during which degeneration did not go past the limits of the organ where it started. We have seen that the original focus of the disease was situated in the frontal lobe and very likely in its third frontal convolution. Thus we are compelled to say, from the point of view of pathological anatomy, that there were two periods, one in which only one frontal convolution, probably the third one, was attacked, and another period in which the disease gradually spread toward other convolutions, to the insula, or to the extraventricular nucleus of the corpus striatum.

When we now examine the succession of symptoms, we also find two periods, the first of which lasted ten years, during which the faculty of speech was destroyed while all other functions of the brain remained intact, and a second period of eleven years, during which paralysis of movement...successively involved the arm and the leg of the right side....

It follows that the first period of ten years, clinically characterized only by the symptom of aphemias, must correspond to the period during which the lesion was still limited to the frontal lobe. (pp. 228-229)

Broca's term for Tan's disorder was soon replaced with "aphasia" when it was pointed out that the Greek origin of "aphemia" refers to reputation or fame, while the root translation of "aphasia" is "without speech" (Ryalls, 1984). The disorder is now referred to as expressive or **motor aphasia**, and it is characterized by an inability to articulate ideas verbally, even though the vocal apparatus is intact and general intelligence is normal. Over the next few years, Broca encountered several other aphasic patients like Tan, found the same general pattern of left frontal lobe damage, and concluded that the ability to produce speech was localized in the left frontal lobe. In his honor, the area is now known as Broca's area.

Broca's research challenged Flourens's conclusions about the degree of localization to be found in the cortex. Additional evidence for localized language function came from clinical studies by the German neurologist Carl Wernicke (1848-1905). He studied a group of 10 patients who could produce articulate speech, but the speech tended to be nonsensical; they also had difficulty comprehending the speech of others. He named the disorder **sensory aphasia**, to distinguish it from motor aphasia, and discovered consistent brain damage to an area of the left temporal lobe of the brain, several centimeters behind Broca's area.

## MAPPING THE BRAIN: ELECTRICAL STIMULATION

We have seen that in the nineteenth century, discoveries about the nature of electricity were being applied to research on sensory physiology, and the idea was evolving that neural activity was electrochemical. In that context, two young German physiologists, both lecturers at the University of Berlin, asked whether the surface of the cortex would respond to mild electrical current. Although listed as second author in their famous paper, the primary investigator was lifelong brain researcher Edward Hitzig

**Key Date  
1861**

This year marked the year that Paul Broca discovered and studied the aphasic patient “Tan” and discovered the location of the brain’s speech center.

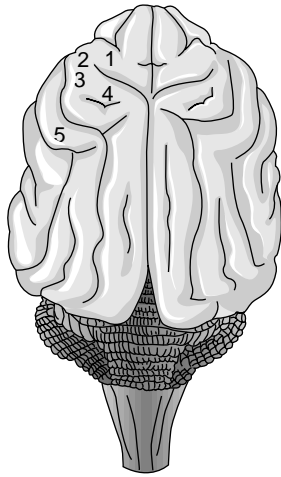
These events also occurred:

- Louis Pasteur proposed a germ theory of fermentation
- Daily weather forecasts began in Britain
- The skeleton of a link between reptile and bird (archaeopteryx) was discovered in Germany
- The United States introduced the passport system
- Russia emancipated its serfs
- The U.S. Civil War began with Confederate victories at Fort Sumter and Bull Run
- These people were born:
  - Alfred North Whitehead, English mathematician and philosopher
  - Nellie Melba, Australia operatic soprano
- These people died:
  - Elizabeth Barrett Browning, English poet
  - Frederick Wilhelm IV of Prussia

(1838–1907); he was assisted by Eduard Fritsch (1838–1927), who soon left physiology for the study of anthropology. Hitzig had observed muscle movements when the exposed brain of a wounded soldier had been mechanically stimulated, but it was generally believed that touching the surface of the brain did not produce reliable effects. Using dogs as their subjects, Hitzig and Fritsch exposed the cortex and probed different surfaces. The stimulus was an electric current of “an intensity that just barely evoked a sensation of feeling on the tongue” (Fritsch & Hitzig, 1870/1965, p. 230). It was delivered across two thin platinum wires that could be placed anywhere from 2 to 3 mm apart. Despite the relative crudeness of their procedures—the experiments were done in Fritsch’s home—they contributed evidence of localization by identifying several motor centers in the front half of the brain. Stimulation of the areas marked in Figure 3.4 produced consistent movements in the right side of the dog’s body, as follows:

- Area 1: neck
- Areas 2 and 3: anterior leg (extension and flexion, respectively)
- Area 4: posterior leg
- Area 5: face

The Fritsch and Hitzig research motivated a number of physiologists, who proceeded to map out motor areas in other species and with more precision. This activity became known as the “new” phrenology or “scientific phrenology”: localization was the goal, but now the brain’s functions would be identified scientifically, rather than through the selected anecdotes of Gall and Spurzheim. Just a few years after Fritsch and Hitzig published their work, for example, the Scottish neurologist David Ferrier (1843–1928) wrote *Functions of the Brain* (1876), which included the map of a monkey’s brain shown in Figure 3.5. Comparing this with Figure 3.4 makes it clear how rapidly brain sci-



**Figure 3.4** Motor centers of a dog's brain, identified via electrical stimulation by Fritsch and Hitzig (1870/1965).

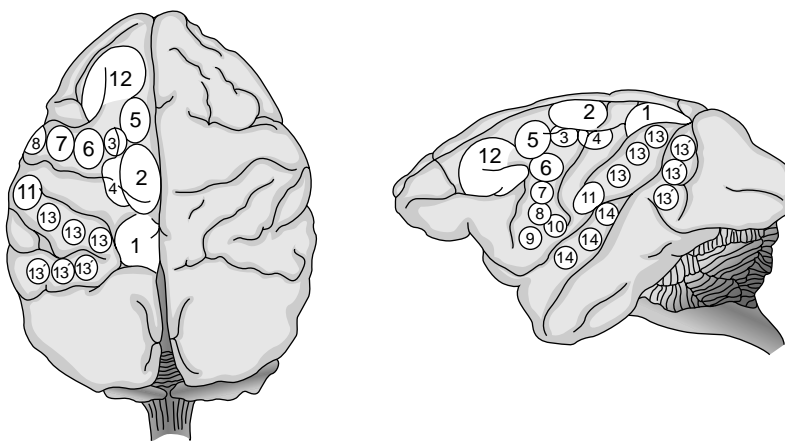
ence was advancing. Ferrier also extended the localization search beyond motor functions, identifying several sensory areas. Using both electrical stimulation and ablation, Ferrier was able to identify the occipital lobe as the primary sensory area for vision, and a portion of the temporal lobe as the center for hearing. It began to look like sensory nerves differed more in terms of their destinations in the cortex than in terms of "specific energies."

## EARLY TWENTIETH-CENTURY STUDIES OF THE NERVOUS SYSTEM AND BEHAVIOR

As the nineteenth century drew to a close, knowledge of the nervous system in general and of the brain in particular was increasing at a rapid pace. In addition to research on sensory physiology and the localization of brain function, however, another line of research developed toward the end of the century and spilled over into the twentieth. This concerned the nature of the basic unit of the nervous system itself, the neuron. This is a long and complicated history in itself, but a few of the highlights can be sketched here.

### NEURON THEORY

The discovery of the neuron as the basic element of the nervous system did not occur until the second half of the nineteenth century, when several important developments occurred in histology (the study of the microscopic structure of plant and animal tissue). Microscopes became more powerful, for instance, and techniques for hardening the brain were perfected. Before it was discovered that the brain could be solidified by soaking it in alcohol, precise dissection was impossible. Once it was known how to harden



**Figure 3.5** David Ferrier's map of the cortex of a monkey (from Boring, 1950).

the brain, however, its nerve pathways could be traced with some precision for the first time. For example, in 1857, Gratiolet was able to trace the optic nerve from the retina all the way to the back of the brain, where it radiated like a fan into the occipital cortex (Diamond, 1985).

It was also discovered that the brain could be immersed in paraffin, hardened, then cut into very thin slices, a procedure called sectioning. Furthermore, if these sections were stained with various dyes, identifiable structures could be observed in a microscope because the dyes would collect within these structures. When the Italian Camillo Golgi (1844–1926) began using what he called his “black stain,” for instance, the result was the first picture of an intact nerve cell, complete with elaborately branching dendrites, intact cell body, and main axon. Golgi’s discovery earned him a share of the 1906 Nobel Prize for medicine. He believed the nervous system to be composed of these neurons, but he also contended that the cells were physically connected to each other, a position that brought him into conflict with the other winner of the 1906 Nobel Prize for medicine.

Santiago Ramón y Cajal (1852–1934) was a gifted Spanish neuroanatomist with a love of art, whose research laid the foundation for the modern theory of the neuron (Taylor, 1972). Ramón y Cajal’s artistic side can be seen in his eloquent description of the neuron as the “aristocrat among the structures of the body, with its giant arms stretched out like the tentacles of an octopus to the provinces on the frontier of the outside world” (cited in Restak, 1984). Like Golgi, Ramón y Cajal believed the neuron to be the nervous system’s basic unit. In contrast with Golgi, however, he argued that each neuron was a separate unit that was not physically

connected with other units but merely in contact with them. Ironically, when he first proposed his neuron theory in 1889, he used Golgi’s own staining techniques to make his case. Thus, the two winners of the 1906 Nobel Prize for medicine were strongly opposed over the nature of their discovery, the neuron. To complicate matters further, Golgi the Italian and Ramón y Cajal the Spaniard were both fiercely patriotic and convinced of the inferiority of each other’s research. The 1906 Nobel Prize ceremony must have been interesting.

### SIR CHARLES SHERRINGTON: THE SYNAPSE

Direct photographic evidence supporting Ramón y Cajal’s neuron theory and refuting Golgi’s would have to await the discovery of the electron microscope, but empirical evidence supporting the existence of gaps between neurons was provided by a British contemporary of both men, Sir Charles Sherrington (1857–1952).<sup>7</sup> It was Sherrington who coined the term **synapse** (from the Greek word meaning “to join together”) for this proposed space between neurons. He did not observe its existence directly; rather he deduced it from a brilliant series of studies on spinal reflexes. The research was presented as part of a prestigious series of lectures at Yale University in 1904, then published as *The Integrative Action of the Nervous System* in 1906, the same year that Golgi and Ramón y Cajal shared the Nobel Prize. Sherrington would eventually win a Nobel Prize of his own in 1932 (Swazey, 1972).

In the tradition of Robert Whytt, but with the advantages of improved technology, Sherrington examined reflex action in “spinal

<sup>7</sup> Obituary accounts of Sherrington describe him as a genial and mild-mannered man. He was said to be “[g]entle in criticism, whole hearted in admiration and appreciation of the work of others, embod[ying] the intellectual and physical serenity which appears so characteristic of the Victorian era” (Denny-Brown, 1952, p. 477). Yet this “serenity” did not keep him from his favorite sport during his youth—while a lecturer in physiology at St. Thomas’s Hospital in London, he spent his Sunday mornings parachute jumping from the hospital’s tower (Swazey, 1972).

dogs,” dogs with spinal cords surgically severed from their brains. As all dog owners know, stimulating a dog’s side in the area of the rib cage will cause the dog’s hind leg to produce a rapid and repetitive scratching reflex. The fact that Sherrington found these reflexes in spinal dogs replicated Whytt’s basic finding about the role of the spinal cord in reflex action. Furthermore, the reflex was even more pronounced in spinal dogs than in intact dogs, which led Sherrington to conclude that the cortex has an inhibitory effect on reflex action.

Sherrington made several observations in his spinal dogs that led him to believe that synapses must exist. First, the reaction time of the reflexes he observed was much slower than predicted from what was known of the speed of neural transmission. Thus, something must have been slowing down the impulse. A second line of evidence came from the phenomena of temporal and spatial summation. Sherrington discovered that a single stimulation at a certain point on the skin might fail to elicit a scratch reflex, but if the point was stimulated many times in succession (at a rate of about 18 per second), the reflex occurred (Sherrington, 1906). This is **temporal summation**—stimuli separated in time combine to produce a response. **Spatial summation** occurred when two or more adjacent points on the skin were stimulated at the same time. Again, responses only occurred to the combined stimulation. Sherrington concluded that summation must occur at the points where the endpoints of neurons met each other, the synapse. Each sub-threshold stimulus caused some unspecified action at the end of neuron A that was by itself insufficient to fire neuron B, but the combined action of information coming many times from A (temporal) or from other locations (spatial) triggered the firing of B. That is, Sherrington anticipated the later discovery of neurotransmitters, chemicals that we now know cross the synapse to promote (or inhibit) neuron firing. After Golgi, Ramón y Cajal, and Sherrington, then, the neuron was established as the funda-

mental unit of the nervous system, interrelated with other neurons through synaptic activity.

### KARL LASHLEY: LEARNING AND THE CORTEX

A brief consideration of the life and work of Karl Spencer Lashley (1890–1958) is a fitting way to end this chapter. Like the nineteenth-century physiologists, neurologists, and physicists encountered thus far, his training was not in psychology. Unlike anyone else in the chapter, however, he eventually came to think of himself primarily as a psychologist. Thus, Lashley provides a transition between the physiologists of the nineteenth century and the physiological psychologists of the twentieth. You will encounter him again in Chapter 10, as a research colleague of behaviorism’s founder, John B. Watson, and again in Chapter 13, where his paper on “serial order” attacked simplistic S-R models of behavior and helped set the stage for the shift from behaviorism to cognitive psychology, and yet again in Chapter 14, as the mentor of Donald Hebb, a contender with Lashley for the title of the most important physiological psychologist of the twentieth century.

Karl Lashley was born in rural West Virginia and earned a bachelor’s degree in zoology from West Virginia University and a master’s degree in bacteriology from the University of Pittsburgh, before enrolling in a doctoral program in zoology at Johns Hopkins University in 1911. There he completed the Ph.D. under the tutelage of noted zoologist H. S. Jennings. More important for psychology’s history, Lashley also came under the influence of the behaviorist Watson and S. I. Franz, a psychologist at a psychiatric hospital (St. Elizabeth’s) in Washington, D.C., who was interested in the effects of brain damage on behavior. With Watson, Lashley conducted field studies of animal behavior, laboratory experiments on the sensory abilities of various species, and research on the conditioning of salivary and motor responses, adapting the procedures of two Russian physiologists who were

just beginning to be known to Americans: Vladimir Bekhterev and Ivan Pavlov. The conditioning research is especially noteworthy because it marked the point at which Lashley decided that his future would be not just in biology but in the intersection between biology and psychology (Bruce, 1986). This decision was cemented when he completed postdoctoral research on the effects of brain injury on behavior with Franz. By 1920, he knew he would be an experimental psychologist specializing in how learning and memory affect the brain.

Lashley's distinguished academic career included stops at the Universities of Minnesota and Chicago, and at Harvard University. In 1942, he became director of the Yerkes Laboratory of Primate Biology in Florida, where his research on animal behavior bridged the laboratory-based comparative psychology favored by American scientists and the field-based, naturalistic approach of European ethologists (Bruce, 1991). He died of heart failure in 1958, while on holiday in France. Among psychologists, Lashley is best known for the research he completed in the 1920s while at Chicago, a series of experiments that was characterized at the time of his death as being "without equal in recent experimental psychology" (Hebb, 1959).

### ***Equipotentiality and Mass Action***

The year 1929 was an important one for Lashley. His peers elected him president of the American Psychological Association, recognizing the value of the research he had been engaged in during the decade of the 1920s. That research was summarized in *Brain Mechanisms and Intelligence*, which also appeared in 1929. Lashley defined the term intelligence in an animal learning context, using it to cover the behavior of rats learning to negotiate mazes and solve simple discrimination and puzzle box

problems. He readily admitted that his choice of tests could be criticized: "They all deal with some aspect of the learning process, [but their] relation to the problem of intelligence is not yet clearly established" (Lashley, 1929, p. 14). Nonetheless, he argued that simple mechanical or reflexive explanations of learning, such as the ones proposed by Watson and Pavlov, were inadequate to capture the complexity of how animals went about solving the kinds of problems that enabled them to survive in their environments. Thus, he considered the tasks presented to his rats to be sufficiently intricate to bear at least some relation to the intelligent, adaptive behavior found in the animals' real-world environments.

Lashley's procedures were in the tradition of the great French physiologist Flourens—he observed the effects of brain ablations on behavior, systematically destroying different amounts of cortex and observing the effects on learning and retention. One of his procedures was maze learning and Figure 3.6 shows three of the four mazes he used. Maze I was a simple T-maze in which the animal had to make a single left-right choice. Maze II had three possible dead-ends, while Maze III had eight.<sup>8</sup> During training, each brain-damaged rat negotiated one of the mazes five times per day and learning was defined as 10 consecutive errorless runs through the maze. The relationship between the extent of cortical damage and performance for each of these mazes can be seen in Lashley's graph, Figure 3.7. For simple mazes such as Maze I, performance was quite good even after large amounts of cortical destruction. With maze II, the performance deteriorated slightly, but was still only marginally affected by the brain lesions. It is only with a more difficult problem, Maze III, that the rat's performance was dramatically affected by the extent of the damage. As the percent of destruction

<sup>8</sup> Maze IV had the same design as Maze III, but with the pattern reversed. In addition, while Mazes I–III were alley mazes (i.e., they had walls), Maze IV was an elevated maze, which required the rat to run on the edges of boards (only 3/16 of an inch wide) that were placed vertically on a table.

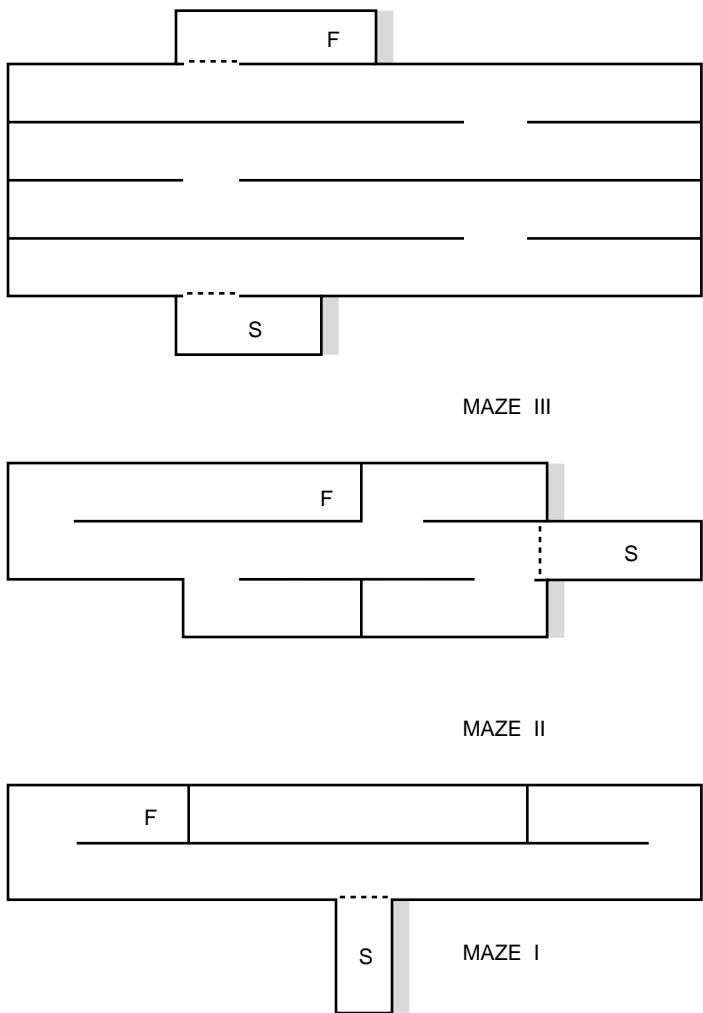


Figure 3.6 Mazes used by Lashley (1929) in his studies of equipotentiality and mass action (*S* = start box; *F* = food).

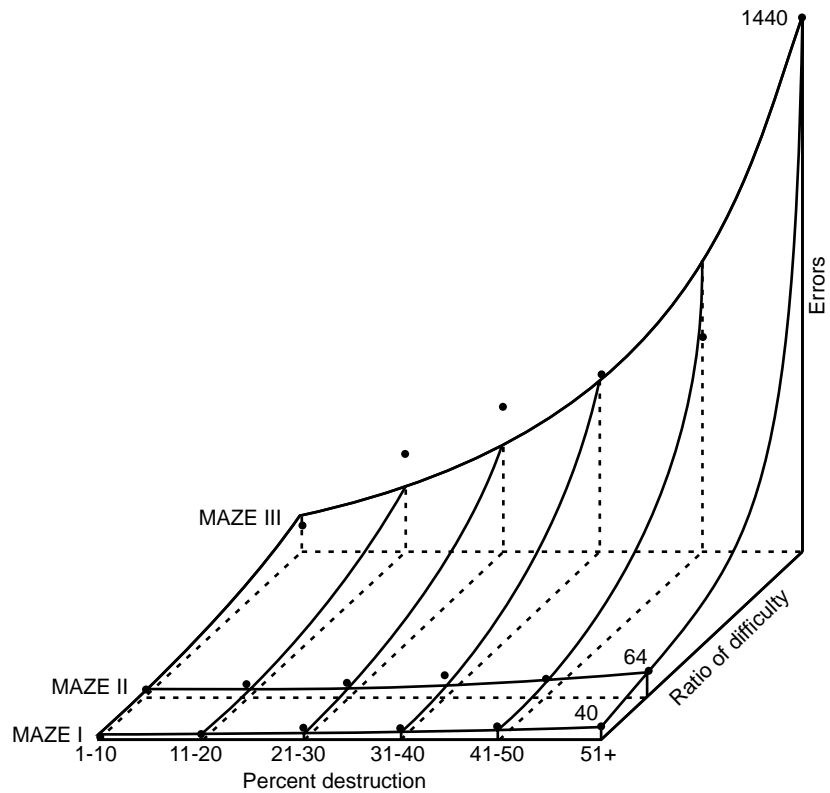
increased, performance declined precipitously. Hence, Lashley was reporting what amounted to an interaction between maze complexity and the degree of cortical lesioning. In simple tasks, the extent of destruction had little effect, while on difficult tasks, performance was directly related to the amount of destruction.

On the basis of the maze studies and similar experiments with his other procedures, Lashley reached two general conclusions very similar to the ones arrived at by Flourens nearly a century earlier. First was the principle that Lashley called **equipotentiality**, a term

...used to designate the apparent capacity of any intact part of a functional area to carry out, with or without reduction in efficiency, the functions which are lost by destruction of the whole. This capacity varies from one area to another and with the character of the functions involved. It probably holds only for the association areas and for functions more complex than simple sensitivity or motor coordination. (Lashley, 1929, p. 25)

Equipotentiality was a strong argument against cerebral localization of function, at least

**Figure 3.7** The effects of maze difficulty and degree of cortical destruction on maze learning, from Lashley (1929).



within the broad area of learning and in those cortical areas not known to govern specific sensory-motor functions. It was supplemented, however, by the law of **mass action**:

[E]quipotentiality is not absolute but is subject to a law of mass action whereby the efficiency of performance of an entire complex function may be reduced in proportion to the extent of brain injury within an area whose parts are not more specialized for one component of the function than for another. (Lashley, 1929, p. 25)

Thus, the process of learning does not seem to be localized in any specific area of the cortex, but learning efficiency is proportional to the amount of cortical destruction.

These principles of equipotentiality and mass action were Lashley's key findings, but he was

also interested in the general process of maze learning. He was well aware of the maze research of his former colleague John Watson, for example, and disagreed with Watson's belief that maze learning involved the kinesthetic sense and the conditioning of a chain of specific motor responses (see Chapter 10). Lashley argued that Watson's model could not account for the strange behavior of those animals with lesions affecting their motor movements. They could still make it through the maze, even if their motor movements were considerably altered:

One drags himself through with his forepaws; another falls at every step but gets through by a series of lunges; a third rolls over completely in making each turn, yet manages to avoid rolling into a cul-de-sac and makes an errorless run.... If the

customary sequence of movements employed in reaching the food is rendered impossible, another set, not previously used in the habit, and constituting an entirely different pattern, may be directly and efficiently substituted without any random activity. (Lashley, 1929, p. 136)

Lashley's conclusions about how the rat learned the maze were similar to those soon to be drawn by the neobehaviorist Edward Tolman (Chapter 11), who argued that rats developed an overall "cognitive map" of the maze and were thus aware of the general direction of the goal. When describing such maps, Tolman (1948, p. 203) referred specifically to Lashley's work for support. Although Lashley did not use the term "map," he clearly had the concept of directionality in mind when planning the following variation with Maze III. Removing the mesh cover normally on top of the maze, a few of his rats (5 out of 20 tested)

climbed on top of the maze and went straight across the top of it to the point where the goal was located. Lashley noted that "the behavior of the 5 that followed the direct course to the food suggested that they were perfectly oriented with respect to its direction, although they had never before reached it save by the indirect path of the maze" (Lashley, 1929, p. 137).

Lashley's research on the relationship between brain and behavior was a natural culmination of the developments in nervous system physiology that occurred in the nineteenth century and a link to the physiological psychology of the twentieth century. We are now a bit ahead of the story, however, and must return to the nineteenth century to examine how psychology emerged as a "new science" in Germany (Chapter 4) and how it was influenced by the theory of evolution, the nineteenth century's most important intellectual event (Chapter 5).

## SUMMARY

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### *Heroic Science in the Age of Enlightenment*

- The Enlightenment was a period during the eighteenth and nineteenth centuries when great faith existed in the ability of science and human reason to produce true knowledge about the world. Scientists were heroes, considered to be objective and value free, with Newton being the prime exemplar. Science was thought to lead inevitably to progress through technological innovation. In this context, the belief that psychology could become scientific began to take hold.

### *Sensory Physiology*

- From the time of Descartes, scientists have been interested in the nature of the simple reflex. In the eighteenth century, Whytt completed the first systematic studies, showing conclusively that the spinal cord was necessary in order for reflexes to occur. Anticipating the concept of conditioning, Whytt also pointed out that the stimulus-response connections could develop through habit.

- When Magendie severed the posterior root of a dog's spinal cord, the affected area could move but was insensitive to stimulation. When the anterior root was severed, no movement occurred. Magendie concluded that the posterior root controlled sensation, while the anterior root controlled motor movements. Bell made similar observations, and the distinction is now known as the Bell-Magendie Law.
- According to Müller's doctrine of the specific energies of nerves, (a) we are directly aware of our nervous systems, not the world, and (b) each of the five basic sensory systems has nerve fibers designed for that specific sense.
- Helmholtz was opposed to vitalism and fought it through his doctrine of conservation of energy and by measuring the finite speed of the neural impulse. He was without peer as an expert on visual and auditory perception, known for the trichromatic theory of color vision, the resonance theory of audition, and his empiricist approach to perception, which emphasized unconscious inference.

### Localization of Brain Function

- Phrenology, developed by Gall and promoted by Spurzheim, was the first serious theory of localization of brain function. Phrenologists believed that different parts of the brain served different faculties, that the portion of brain allocated to a faculty was proportional to the strength of the faculty, and that faculties and their strengths could be determined by measuring the skull.
- Because it relied too heavily on anecdotal evidence and faulty logic, phrenology lost scientific credibility quickly. It remained popular with the general public, however, being consistent with the American ideals of individuality and self-improvement.
- By developing the method of ablation, Flourens was able to falsify phrenological doctrine, while at the same time showing that the cortex operates as an integrated system.
- Evidence for localization came from clinical studies, in which those suffering from various forms of brain disease or damage were studied. The case of Phineas Gage illustrated the effects of severe frontal lobe damage on judgment and personality. Broca's study of "Tan," who suffered from motor aphasia, showed that the ability to produce artic-

ulate speech depended on a fairly circumscribed area of the left cortex.

- By developing the procedure of electrically stimulating the surface of the cortex, Fritsch and Hitzig in Germany and Ferrier in Great Britain began to map the functions of the surface of the brain with a "scientific phrenology."

### Early Twentieth-Century Studies of the Nervous System and Behavior

- The identification of neurons as the basic units of the nervous system was made by Golgi, who thought they were physically connected to each other, and Ramón y Cajal, who thought they were physically separate from each other.
- Ramón y Cajal's theory was verified by Sherrington, who is credited with discovering the synapse and demonstrating its existence in his research on reflexes and through the phenomena of temporal and spatial summation.
- Lashley's research on the brain and learning showed that maze learning was not localized in any particular area of the cortex. Rather, the cortex operated as a system and was characterized by equipotentiality and mass action.

### FOR FURTHER READING

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*A close analysis of the development of phrenology, its rejection by the scientific community, and its popularity with the American public; shows how phrenology fit in with the temperament of progressivism and was an early example of the approach to psychology that emphasizes individual differences.*

BRUCE, D. B. (1986). Lashley's shift from bacteriology to neuropsychology, 1910–1917, and the influence of Jennings, Watson, and Franz. *Journal of the History of the Behavioral Sciences*, 22, 27–44.

*A description of Lashley's formative years and how his eventual self-identification as a physiological psychologist was affected by his doctoral studies with Jennings, his collaboration with Watson, and his postdoctoral work with Franz.*

FEARING, F. (1930). *Reflex action: A study in the history of physiological psychology*. New York: Hafner Publishing Company.

*Not exactly a page-turner, but an excellent reference source for information on how the reflex has been studied from the Greeks until the date of publication; good example of an internal history, emphasizing research outcomes that gradually expanded knowledge about reflex action.*

MACMILLAN, M. B. (1986). A wonderful journey through skull and brain: The travels of Mr. Gage's tamping iron. *Brain and Cognition*, 5, 67–107.

*Despite the odd title, a scholarly and detailed account of the case of Phineas Gage, including a description of his medical treatment by Harlow, and an analysis of how the case bears on the localization issue.*