Chapter 26

Language and Speech

Overview

One of the most remarkable cortical functions in humans is the ability to associate arbitrary symbols with specific meanings to express thoughts and emotions to ourselves and others by means of written and spoken language. Indeed, the achievements of human culture rest largely upon this kind of communication, and a person who for one reason or another fails to develop a facility for language as a child is severely incapacitated. Studies of patients with damage to specific cortical regions and normal subjects studied by functional brain imaging indicate that linguistic abilities of humans depend on the integrity of several specialized areas of the association cortices in the temporal and frontal lobes. In the vast majority of people, these primary language functions are located in the left hemisphere: the linkages between speech sounds and their meanings are mainly represented in the left temporal cortex, and the circuitry for the motor commands that organize the production of meaningful speech is mainly found in the left frontal cortex. Despite this left-sided predominance for the "lexical" aspects of language, the emotional (affective) content of speech is governed largely by the right hemisphere. Studies of congenitally deaf individuals have shown further that the cortical areas devoted to sign language are the same as those that organize spoken and heard communication. The regions of the brain devoted to language are therefore specialized for symbolic representation and communication, rather than for heard and spoken language as such. Understanding functional localization and hemispheric lateralization of language is especially important in clinical practice. The loss of language is such a devastating blow that neurologists and neurosurgeons make every effort to identify and preserve those cortical areas involved in its comprehension and production. The need to map language functions in patients for the purpose of sparing these regions of the brain has provided another rich source of information about the neural organization of this critical human attribute.

Language Is Both Localized and Lateralized

It has been known for more than a century that two regions in the frontal and temporal association cortices of the left cerebral hemisphere are especially important for normal human language. That language abilities are both localized and lateralized is not surprising; ample evidence of the localization and lateralization of other cognitive functions was reviewed in Chapter 25. The unequal representation of language functions in the two cerebral hemispheres provides an especially compelling example of this phenomenon.

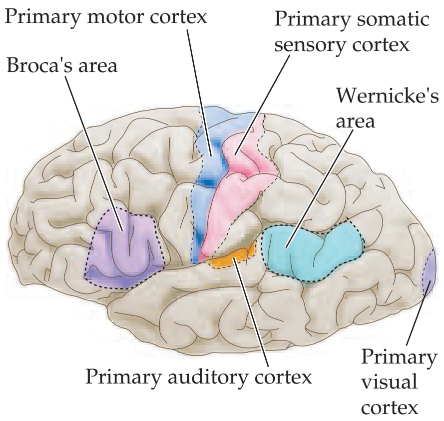

Figure 26.1 Diagram of the major brain areas involved in the comprehension and production of language. The primary sensory, auditory, visual, and motor cortices are indicated to show the relation of Broca's and Wernicke's language areas to these other areas that are necessarily involved in the comprehension and production of speech, albeit in a less specialized way.

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Although the concept of lateralization has already been introduced in describing the unequal functions of the parietal lobes in attention and of the temporal lobes in recognizing different categories of objects, it is in language that this idea has been most thoroughly documented. Because language is so important to human beings, its lateralization has given rise to the misleading idea that one hemisphere in humans is actually "dominant" over the other—namely, the hemisphere in which the major capacity for language resides. The true significance of lateralization for language or any other cognitive ability, however, lies in the efficient subdivision of complex functions between the hemispheres, rather than in any superiority of one hemisphere over the other. Indeed, pop psychological dogmas about cortical redundancy notwithstanding, it is a safe presumption is that every region of the brain is doing *something* important.

A first step in the proper consideration of these issues is recognizing that the cortical representation of language is distinct from the circuitry concerned with the motor control of the larynx, pharynx, mouth, and tongue—the structures that produce speech sounds (Box A). Cortical representation is also distinct from, although clearly related to, the circuits underlying the auditory perception of spoken words and the visual perception of written words in the primary auditory and visual cortices, respectively (Figure 26.1). Whereas the neural substrates for language as such depend on these essential motor and sensory functions, the regions of the brain that are specifically devoted to language transcend these more basic elements. The main concern of the areas of cortex that represent language is using of a system of symbols for purposes of communication—spoken and heard, written and read, or, in the case of sign language, gestured and seen. Thus, the essential function of the cortical language areas, and indeed of language, is symbolic representation. Obedience to a set of rules for using these symbols (called grammar), ordering them to generate useful meanings (called syntax), and giving utterances the appropriate emotional valence (called prosody), are all important and readily recognized regardless of the particular mode of representation and expression.

Given the profound biological and social importance of communication among the members of a species, it is not surprising that other animals communicate in ways that, while grossly impoverished compared to human language, nonetheless suggest the sorts of communicative skills and interactions from which human language evolved in the brains of our prehominid ancestors (Box B).

Aphasias

The distinction between language and the related sensory and motor capacities on which it depends was first apparent in patients with damage to specific brain regions. Clinical evidence of this sort showed that the ability to move the muscles of the larynx, pharynx, mouth, and tongue can be compromised without abolishing the ability to use spoken language to communicate (even though a motor deficit may make communication difficult). Similarly, damage to the auditory pathways can impede the ability to hear without interfering with language functions per se (as is obvious in individuals who have become partially or wholly deaf later in life). Damage to specific brain regions, however, can compromise essential language functions while leaving the sensory and motor infrastructure of verbal communication intact. These syndromes, collectively referred to as **aphasias**, diminish or abolish the ability to comprehend and/or to produce *language*, while sparing

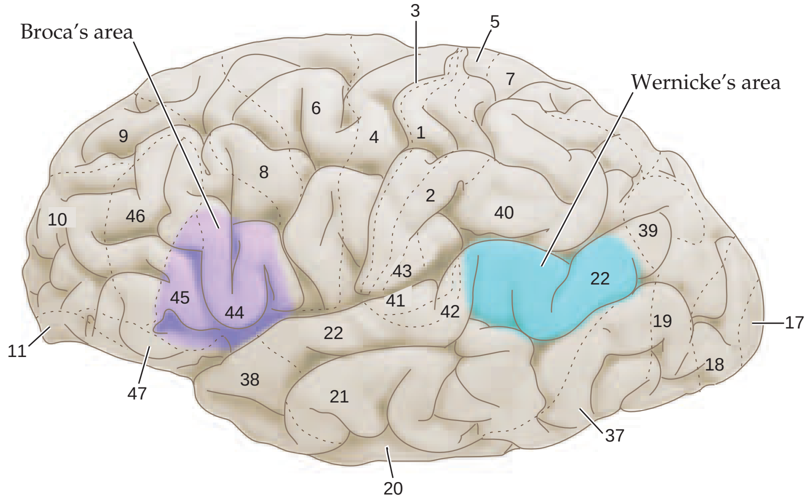

Figure 26.2 The relationship of the major language areas to the classical cytoarchitectonic map of the cerebral cortex. As discussed in Chapter 25, about 50 histologically distinct regions (cytoarchitectonic areas) have been described in the human cerebral cortex. Whereas primary sensory and motor functions are sometimes coextensive with these areas, more general cognitive functions like attention, identification, and planning typically encompass a number of different cytoarchitectonic areas in one or more cortical lobes. The language functions described by Broca and Wernicke are associated with at least three of the cytoarchitectonic areas defined by Brodmann (area 22, at the junction of the parietal and temporal lobes [Wernicke's area]; and areas 44 and 45, in the ventral and posterior region of the frontal lobe [Broca's area]), and are not coextensive with any of them.

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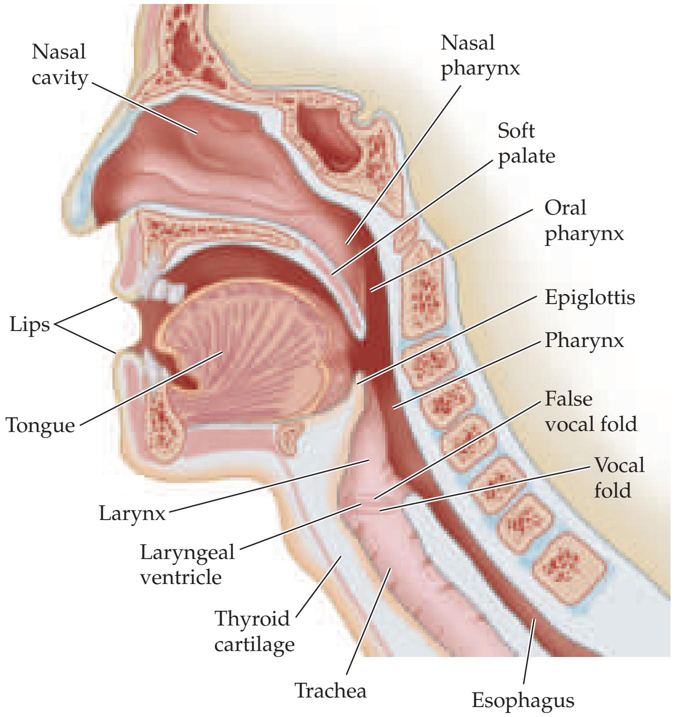
the ability to perceive the relevant stimuli and to produce intelligible words. Missing in these patients is the capacity to recognize or employ the symbolic value of words, thus depriving such individuals of the linguistic understanding, grammatical and syntactical organization, and appropriate intonation that distinguishes language from nonsense (Box C).

The localization of language function to a specific region (and to some degree a hemisphere) of the cerebrum is usually attributed to the French neurologist Paul Broca and the German neurologist Carl Wernicke, who made their seminal observations in the late 1800s. Both Broca and Wernicke examined the brains of individuals who had become aphasic and later died. Based on correlations of the clinical picture and the location of the brain damage, Broca suggested that language abilities were localized in the ventroposterior region of the frontal lobe (Figures 26.1 and 26.2). More importantly, he observed that the loss of the ability to produce meaningful language—as opposed to the ability to move the mouth and produce words—was usually associated with damage to the left hemisphere. "*On parle avec l'hemisphere gauche*," Broca concluded. The preponderance of aphasic syndromes associated with damage to the left hemisphere has supported his claim that one speaks with the left hemisphere, a conclusion amply confirmed by a variety of modern studies using functional imaging (albeit with some important caveats, discussed later in the chapter).

Although Broca was basically correct, he failed to grasp the limitations of thinking about language as a unitary function localized in a single cortical region. This issue was better appreciated by Wernicke, who distinguished between patients who had lost the ability to comprehend language and those who could no longer produce language. Wernicke recognized that some aphasic patients do not understand language but retain the ability to produce utterances with reasonable grammatical and emotional content. He concluded that lesions of the posterior and superior temporal lobe on the left side tend to result in a deficit of this sort. In contrast, other patients continue to comprehend language but lack the ability to organize or control the linguistic content of their response. Thus, they produce nonsense syllables, transposed words, and utter grammatically incomprehensible phrases. These deficits are associated with damage to the posterior and inferior region of the left frontal lobe, an area that Broca emphasized as an important substrate for language (see Figures 26.1 and 26.2).

Box A

Speech



The organs that produce speech include the lungs, which serve as a reservoir of air; the larynx, which is the source of the periodic stimulus quality of "voiced" sounds; and the pharynx, oral, and nasal cavities and their included structures (e.g., tongue, teeth, and lips), which modify (or filter) the speech sounds that eventually emanate from the speaker. The fundamentally correct idea that the larynx is the "source" of speech sounds and the rest of the vocal tract acts as a filter that modulates the sound energy of the source is an old one, having been proposed by Johannes Mueller in the nineteenth century.

Although the physiological details are complex, the general operation of the vocal apparatus is simple. Air expelled from the lungs accelerates as it passes through a constricted opening between the **vocal folds** ("vocal cords") called the glottis, thus decreasing the pressure in the air stream (according Bernoulli's principle). As a result, the vocal folds come together until the pressure buildup in the lungs forces them open again. The ongoing repetition of this process results in an oscillation of sound wave pressure, the frequency of which is determined primarily by the muscles that control the tension on the vocal cords. The frequencies of these oscillations—which are the basis of voiced speech sounds—range from about 100 to about 400 Hz, depending on the gender, size, and age of the speaker.

The larynx has many other consequential effects on the speech signal that create additional speech sounds. For instance, the vocal folds can open suddenly to produce what is called a *glottal stop* (as in the beginning of the exclamation "Idiot!"). Alternatively, the vocal folds can hold an intermediate position for the production of consonants such as *h*, or they can be completely open for "unvoiced" consonants such as *s* or *f* (i.e., speech sounds that don't have the periodic quality derived from vocal fold oscillations). In short, the larynx is important in the production of virtually all vocal sounds.

The vocal system can be thought of as a sort of musical instrument capable of extraordinary subtlety and exquisite modulation. As in the sound produced by a musical instrument, however, the primary source of oscillation (e.g., the reed of a clarinet or the vocal folds in speech) is hardly the whole story. The entire pathway between the vocal folds and the lips (and nostrils) is equally critical in determining speech sounds, as is the structure of a musical instrument. The key determinants of the sound that emanates from an instrument are its natural resonances, which shape or filter the sound pressure oscillation. For the vocal tract, the resonances that modulate the air stream generated by the larynx are called **formants**. The resonance fre-

As a consequence of these early observations, two rules about the localization of language have been taught ever since. The first is that lesions of the left frontal lobe in a region referred to as **Broca's area** affect the ability to *produce* language efficiently. This deficiency is called **motor** or **expressive** quency of the major formant arises from the fact that the approximate length of the vocal tract is 17 cm, which is the quarter wavelength of a 68-cm sound wave; quarter wavelengths determine the resonances of pipes open at one end, which is essentially what the vocal tract is. Since the speed of sound is about 33,500 cm/sec, the lowest resonance frequency of an open tube or pipe of this length will be 33,500/68 or about 500 Hz; additional resonant frequencies will occur at the odd harmonics of this major formant (e.g., 1500 Hz, 2500 Hz, etc.). The result of these physical facts about the vocal tract is that any power in the laryngeal source at these formant frequencies will be reinforced, and any other power will, in varying degrees, be filtered out. Of course, this general statement is complicated by the further fact that the shape of the vocal tract changes to produce different speech sounds. Thus, in addition to the effects of the larynx, specific speech sounds are generated by dynamic effects imposed by the configuration of the rest of the vocal tract.

In any given language, the basic speech sounds are called **phonemes**. (The sound stimuli as such are referred to as **phones**.) Phonemes are used to make up syllables, which are used in turn to make up words, which are used to create sentences. There are about 40 phonemes in English, and these are about equally divided between vowel and consonant speech sounds. Vowel sounds are by and large the voiced (periodic) elements of speech (i.e., the elemental sounds in any language generated by the oscillation of the vocal cords). In contrast, consonant sounds involve rapid changes in the sound signal and are more complex. In English, consonants begin and/or end syllables, each of which entails a vowel sound. Consonant sounds are categorized according to the site in the vocal tract that determines them (the *place of articulation*), or the physical way they are generated (the *manner of articulation*). With respect to place, there are labial consonants (such as *p* and *b*), dental consonants (*f* and *v*), palatal consonants (*sh*), and glottal consonants (*h*) (among many others). With respect to manner, there are plosive, fricative, nasal, liquid, and semivowel consonants. Plosives are produced by blocking the flow of air somewhere in the vocal tract, fricatives by producing turbulence, nasals by directing the flow of air through the nose, and so on.

A further variation on the use of consonants is found in the "click languages" of southern Africa, of which about 30 survive today. Each of these languages has 4–5 different click sounds that are double consonants (the consonant equivalent of dipthongs) made by sucking the tongue down from the roof of the mouth.

It should be obvious then that speech stimuli are enormously complex (there are more than 200 phonemes in human languages). To make matters worse, Alvin Liberman, working at the Haskins Laboratory at Yale University, showed that there is no one-to-one correspondence between phonemes (as defined above) and phones (i.e., the specific acoustic elements in speech). Because speech sounds changes continuously, they cannot be split up into discrete segments, as the concept of phonemes implies. This fact is now recognized as a fundamental problem that undermines any strictly phonemic approach to language. Moreover, the phones for different vowels (or at least the formants) overlap in natural speech of men, women, and children. Evidence from studies of illiterates suggests that phonemes are probably more related to learning how to read and spell than to actually hearing speech, implying that syllables or words are much better candidates for the natural units of speech perception.

Given this complexity, it is remarkable that we can communicate so readily. A clue to the obvious success of humans in this task is computer-based speech recognition programs. These programs achieve the very substantial success they currently enjoy by virtue of prolonged empirical training rather than in the *a priori* application of any logical rules.

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aphasia, also known as **Broca's aphasia**. (Such aphasias must be specifically distinguished from *dysarthria*, which is the inability to move the muscles of the face and tongue that mediate speaking.) The deficient motor-planning aspects of expressive aphasias accord with the complex motor functions of

Box B

Do Other Animals Have Language?

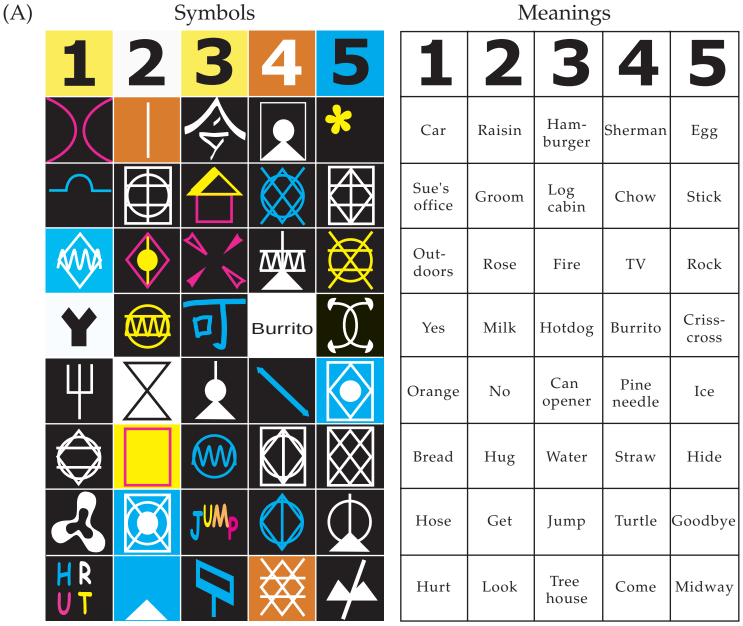
Over the centuries, theologians, natural philosophers, and a good many modern neuroscientists have argued that language is uniquely human, this extraordinary behavior being seen as setting us qualitatively apart from our fellow animals. However, the gradual accumulation of evidence during the last 75 years demonstrating highly sophisticated systems of communication in species as diverse as bees, birds, monkeys, and whales has made this point of view increasingly untenable, at least in a broad sense (see Box B in Chapter 23). Until recently, however, human language *has* appeared unique in the ability to associate specific meanings with arbitrary symbols, ad infinitum. In the dance of the honeybee described so beautifully by Karl von Frisch, for example, each symbolic movement made by a foraging bee that returns to the hive encodes only a single meaning, whose expression and appreciation has been hardwired into the nervous systems of the actor and the respondents.

A series of controversial studies in great apes, however, have indicated that the rudiments of the human symbolic communication are evident in the behavior of our closest relatives. Although early efforts were sometimes patently misguided (initial attempts to teach chimpanzees to speak were without merit simply because these animals lack the necessary vocal apparatus), modern work on this issue has shown that if chimpanzees are given the means to communicate symbolically, they demonstrate some surprising talents. While techniques have varied, most psychologists who study chimps have used some form of manipulable symbols that can be arranged to express ideas in an interpretable manner.

For example, chimps can be trained to manipulate tiles or other symbols (such as the gestures of sign language) to represent words and syntactical constructs, allowing them to communicate simple demands, questions, and even spontaneous expressions. The most remarkable results have come from increasingly sophisticated work with chimps using keyboards with a variety of symbols (Figure A). With appropriate training, chimps can choose from as many as 400 different symbols to construct expressions, allowing the researchers to have something resembling a rudimentary conversation with their charges. The more accomplished of these animals are alleged to have "vocabularies" of several thousand words or phrases, equivalent to a child 3 or 4 years of age (how they use these words compared to a child, however, is much less impressive).

Given the challenge this work presents to some long-held beliefs about the uniqueness of human language, it is not surprising that these claims continue to stir up debate and are not universally accepted. Nonetheless, the issues raised certainly deserve careful consideration by anyone interested in human language abilities and how our remarkable symbolic skills may have evolved from the communicative capabilities of our ancestors. The pressure for the evolution of some form of symbolic communication in great apes seems clear enough. Ethologists studying chimpanzees in the wild have described extensive social communication based on gestures, the manipulation of objects, and facial expressions. This intricate social intercourse is likely to be the antecedent of human language; one need only think of the importance of gestures and facial expressions as ancillary aspects of our own speech to appreciate this point. (The sign language studies described later in the chapter are also pertinent here.)

Whether the regions of the temporal, parietal, and frontal cortices that support human language also serve these sym-



1	2	3	4	5
Car	Raisin	Hamburger	Sherman	Egg
Sue's office	Groom	Log cabin	Chow	Stick
Outdoors	Rose	Fire	TV	Rock
Yes	Milk	Hotdog	Burrito	Criss-cross
Orange	No	Can opener	Pine needle	Ice
Bread	Hug	Water	Straw	Hide
Hose	Get	Jump	Turtle	Goodbye
Hurt	Look	Tree house	Come	Midway

Section of keyboard showing lexical symbols used to study symbolic communication in great apes. (From Savage-Rumbaugh et al., 1998.)

(B)

The brains of great apes are remarkably similar to those of humans, including regions that, in humans, support language. The areas comparable to Broca's area and Wernicke's area are indicated.

bolic functions in the brains of great apes (Figure B) is an important question that remains to be tackled. In addition, field studies of vervets and other monkey species have shown that the alarm calls of these animals differ according to the nature of the threat. Thus, ethologists Dorothy Cheney and Robert Seyfarth found that a specific alarm call uttered when a vervet monkey spotted a leopard caused nearby vervets to take to the trees; in contrast, the alarm call given when a monkey saw an eagle caused other monkeys to look skyward. More recent studies of monkey calls by Marc Hauser and his collaborators have greatly extended this sort of work.

Although much uncertainty remains, in light of this evidence only someone given to extraordinary anthropocentrism would continue to argue that symbolic communication is a uniquely human attribute. In the end, it may turn out to be that human language, for all its seeming complexity, is based on the same general scheme of inherent and acquired neural associations that appears to be the basis of any animal communication.

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the posterior frontal lobe and its proximity to the primary motor cortex already discussed (see Chapters 15 and 25).

The second rule is that damage to the left temporal lobe causes difficulty *understanding* spoken language, a deficiency referred to as **sensory** or **receptive aphasia**, also known as **Wernicke's aphasia**. (Deficits of reading and writing—*alexias* and *agraphias*—are separate disorders that can arise from damage to related but different brain areas; most aphasics, however, also have difficulty with these closely linked abilities as well.) Receptive aphasia generally reflects damage to the auditory association cortices in the posterior temporal lobe, a region referred to as **Wernicke's area**.

A final broad category of language deficiency syndromes is **conduction aphasia**. These disorders arise from lesions to the pathways connecting the relevant temporal and frontal regions, such as the arcuate fasciculus in the subcortical white matter that links Broca's and Wernicke's areas. Interruption of this pathway may result in an inability to produce appropriate responses to heard communication, even though the communication is understood.

In a classic Broca's aphasia, the patient cannot express himself appropriately because the organizational aspects of language (its grammar and syntax) have been disrupted, as shown in the following example reported by Howard Gardner (who is the interlocutor). The patient was a 39-year-old Coast Guard radio operator named Ford who had suffered a stroke that affected his left posterior frontal lobe.

> ‘I am a sig…no…man…uh, well,…again.’ These words were emitted slowly, and with great effort. The sounds were not clearly articulated; each syllable as uttered harshly, explosively, in a throaty voice. With practice, it was possible to understand him, but at first I encountered considerable difficulty in this. ‘Let me help you,’ I interjected. ‘You were a signal…’ ‘A sig-nal man…right,’ Ford completed my phrase triumphantly. ‘Were you in the Coast Guard?’ ‘No, er, yes, yes, …ship…Massachu…chusetts…Coastguard …years.’ He raised his hands twice, indicating the number nineteen. ‘Oh, you were in the Coast Guard for nineteen years.’ ‘Oh…boy…right…right,’ he replied. ‘Why are you in the hospital, Mr. Ford?’ Ford looked at me strangely, as if to say, Isn’t it patently obvious? He pointed to his paralyzed arm and said, ‘Arm no good,’ then to his mouth and said, ‘Speech…can’t say…talk, you see.’
>
> Howard Gardner, 1974.
> (*The Shattered Mind: The Person after Brain Damage*, pp. 60–61.)

In contrast, the major difficulty in Wernicke’s aphasia is putting together objects or ideas and the words that signify them. Thus, in a Wernicke’s aphasia, speech is fluent and well structured, but makes little or no sense because words and meanings are not correctly linked, as is apparent in the following example (again from Gardner). The patient in this case was a 72-year-old retired butcher who had suffered a stroke affecting his left posterior temporal lobe.

> Boy, I’m sweating, I’m awful nervous, you know, once in a while I get caught up, I can’t get caught up, I can’t mention the tarripoi, a month ago, quite a little, I’ve done a lot well, I impose a lot, while, on the other hand, you know what I mean, I have to run around, look it over, trebbin and all that sort of stuff. Oh sure, go ahead, any old think you want. If I could I would. Oh, I’m taking the word the wrong way to say, all of the barbers here whenever they stop you it’s going around and around, if you know what I mean, that is tying and tying for repucer, repuceration, well, we were trying the best that we could while another time it was with the beds over there the same thing…
>
> Ibid., p. 68.

The major differences between these two classical aphasias are summarized in Table 26.1.

Despite the validity of Broca’s and Wernicke’s original observations, the classification of language disorders is considerably more complex. An effort to refine the nineteenth-century categorization of aphasias was undertaken

TABLE 26.1

Characteristics of Broca’s and Wernicke’s Aphasias

Broca’s aphasia[a]	*Wernicke’s aphasia*[b]
Halting speech	Fluent speech
Tendency to repeat phrases or words (perseveration)	Little spontaneous repetition
Disordered syntax	Syntax adequate
Disordered grammar	Grammar adequate
Disordered structure of individual words	Contrived or inappropriate words
Comprehension intact	Comprehension not intact

[a] Also called motor, expressive, or production aphasia
[b] Also called sensory or receptive aphasia

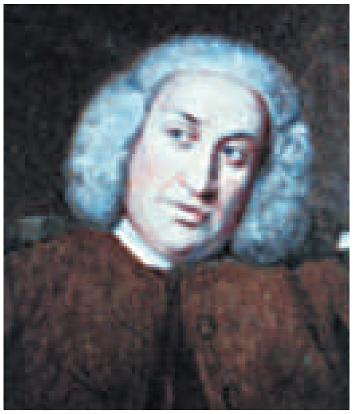
Box C
Words and Meaning

When Samuel Johnson (Figure A) compiled his *Dictionary of English Language* in 1755 under the sponsorship of Oxford University, he defined only 43,500 entries. The current *Oxford English Dictionary*, a lineal descendant of Johnson's seminal work and most recently revised in the 1980s, contains over 500,000 definitions! This quantitative difference is not the result of an increase in the number of English words since the eighteenth century, but rather is an indication of the difficulty collecting the enormous number of words we use in daily communication; the average college-educated speaker of English is said to have a working vocabulary of more than 100,000 words.

Using words appropriately is made even more difficult by the fact that word meanings are continually changing, and by the enormous ambiguity of the words we do use. There is far more to a lexicon—be it a dictionary or a region of the left temporal cortex—than simply attaching meanings to words. Even when the meaning of a word is known, it must be understood in a particular context (Figure B) and used according to the rules of grammar and syntax in order to produce effective communication.

From the points of view of both neuroscience and linguistics, two related questions about words and grammar (i.e., the rules for putting words together to form sentences) are especially germane in relation to this chapter. First, what is the nature of the neural machinery that allows us to learn language? And second, why do humans have such a profound drive to learn language? The major twentieth-century figure who has grappled with these questions is linguist Noam Chomsky, working at the Massachusetts Institute of Technology. Chomsky, while not interested in brain structure has argued that the complexity of language is such that it cannot simply be learned. He therefore proposed that language must be predicated on a "universal grammar" laid down in the evolution of our species. Although this argument is undoubtedly correct (the basic neural machinery for language, like all aspects of brain circuitry that support adult behavior, is indeed constructed during the normal development of each individual, primarily as a result of inheritance; see Chapters 22 and 23), Chomsky's eschewing of neurobiology avoids the central question of how, in evolutionary or developmental terms, this machinery comes to be and how it encodes words and strings them together into meaningful sentences. Whatever the mechanisms eventually prove to be, much of the language we use is obviously learned by making neuronal associations between arbitrary symbols and the objects, concepts, and interrelationships they signify in the real world. As such, human language provides a rich source for understanding how the relevant parts of the human cortex and their constituent neurons work to produce the enormous facility for making associations, which appears to be a fundamental (perhaps *the* fundamental) aspect of all cortical functions.

(A)



Samuel Johnson

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(B)

The importance of context. When a person says "I'm going to our house on the lake," the meaning of the expression obviously depends on usage and context, rather than on the literal structure of the sentence uttered. This example indicates the enormous complexity of the task we all accomplish routinely. How this is done, even in principle, remains a central puzzle in language. (From Miller, 1991.)

by the American neurologist Norman Geschwind during the 1950s and early 1960s. Based on clinical and anatomical data from a large number of patients and on the better understanding of cortical connectivity gleaned by that time from animal studies, Geschwind concluded correctly that several other regions of the parietal, temporal, and frontal cortices are critically involved in human linguistic capacities. Basically, he showed that damage to these additional areas results in identifiable, if more subtle, language deficits. His clarification of the definitions of language disorders has been largely confirmed by functional brain imaging in normal subjects, and remains the basis for much contemporary clinical work on language and aphasias.

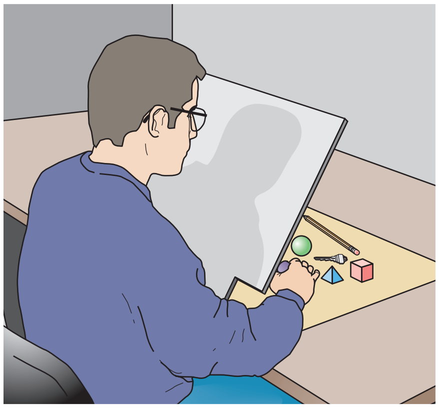
A Dramatic Confirmation of Language Lateralization

Until the 1960s, observations about language localization and lateralization were based primarily on patients with brain lesions of varying severity, location, and etiology. The inevitable uncertainties of clinical findings allowed skeptics to argue that language function (or other complex cognitive functions) might not be lateralized (or even localized) in the brain. Definitive evidence supporting the inferences from neurological observations came from studies of patients whose corpus callosum and anterior commissure had been severed as a treatment for medically intractable epileptic seizures. (Recall that a certain fraction of severe epileptics are refractory to medical treatment, and that interrupting the connection between the two hemispheres remains an effective way of treating epilepsy in highly selected patients; see Box C in Chapter 24). In such patients, investigators could assess the function of the two cerebral hemispheres *independently*, since the major axon tracts that connect them had been interrupted. The first studies of these so-called **split-brain patients** were carried out by Roger Sperry and his colleagues at the California Institute of Technology in the 1960s and 1970s, and established the hemispheric lateralization of language beyond any doubt; this work also demonstrated many other functional differences between the left and right hemispheres (Figure 26.3) and continues to stand as an extraordinary contribution to the understanding of brain organization.

Figure 26.3 Confirmation of hemispheric specialization for language obtained by studying individuals in whom the connections between the right and left hemispheres have been surgically divided. (A) Single-handed, vision-independent stereognosis can be used to evaluate the language capabilities of each hemisphere in split-brain patients. Objects held in the right hand, which provides somatic sensory information to the left hemisphere, are easily named; objects held in the left hand, however, are not readily named by these patients. (B) Visual stimuli or simple instructions can be given independently to the right or left hemisphere in normal and split-brain individuals. Since the left visual field is perceived by the right hemisphere (and vice versa; see Chapter 11), a briefly presented (*tachistoscopic*) instruction in the left visual field is appreciated only by the right brain (assuming that the individual maintains fixation on a mark in the center of the viewing screen). In normal subjects, activation of the right visual cortex leads to hemispheric transfer of visual information via the corpus callosum to the left hemisphere. In split-brain patients, information presented to the left visual field cannot reach the left hemisphere, and patients are unable to produce a verbal report regarding the stimuli. However, such patients *are* able to provide a verbal report of stimuli presented to the right visual field. A wide range of hemispheric functions can be evaluated using this tachistoscopic method, even in normal subjects. The list (above right) enumerates some of the different functional abilities of the left and right hemispheres, as deduced from a variety of behavioral tests in split-brain patients. ▶

To evaluate the functional capacity of each hemisphere in split-brain patients, it is essential to provide information to one side of the brain only. Sperry, Michael Gazzaniga (a key collaborator in this work), and others devised several simple ways to do this, the most straightforward of which was to ask the subject to use each hand independently to identify objects without any visual assistance (Figure 26.3A). Recall from Chapter 8 that somatic sensory information from the right hand is processed by the left hemisphere, and vice versa. By asking the subject to describe an item being manipulated by one hand or the other, the language capacity of the relevant hemisphere could be examined. Such testing showed clearly that the two hemispheres differ in their language ability (as expected from the postmortem correlations described earlier).

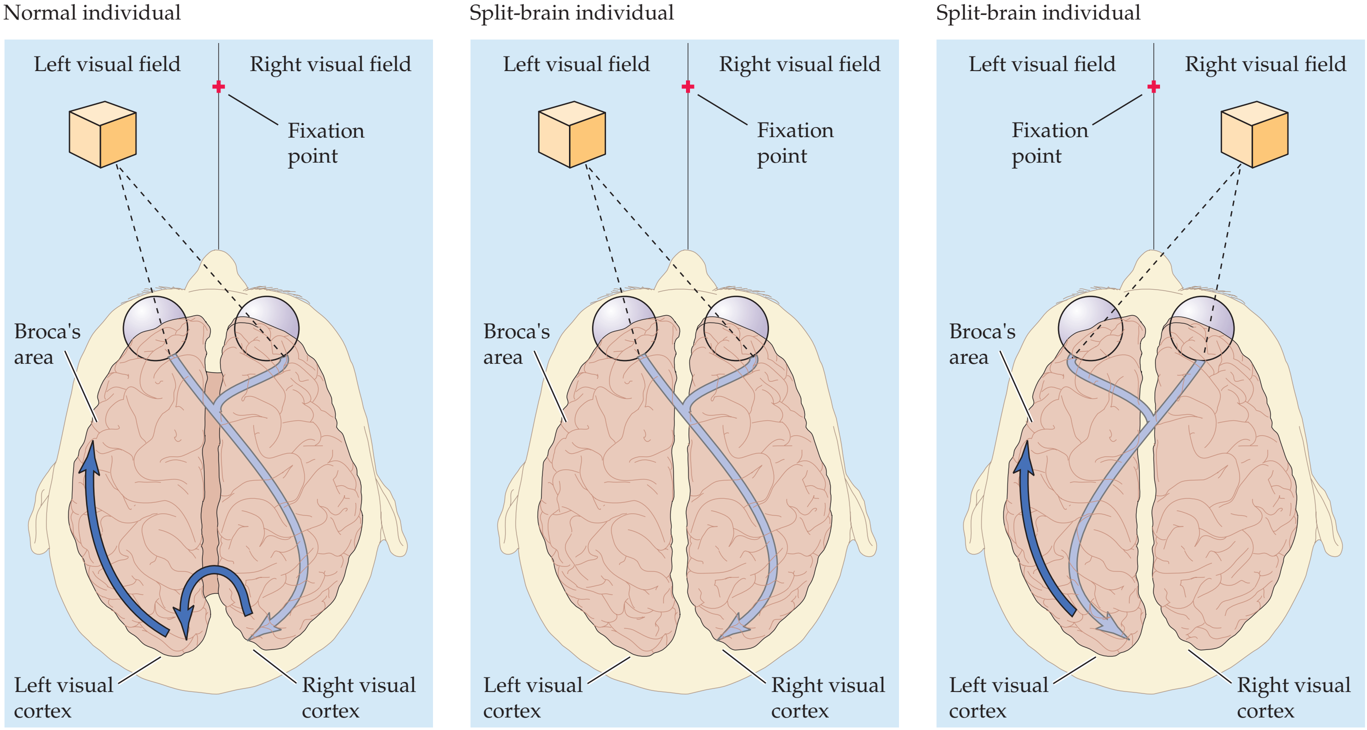
(A)



(C)

Left hemisphere functions	Right hemisphere functions
Analysis of right visual field	Analysis of left visual field
Stereognosis (right hand)	Stereognosis (left hand)
Lexical and syntactic language	Emotional coloring of language
Writing	Spatial abilities
Speech	Rudimentary speech

(B)



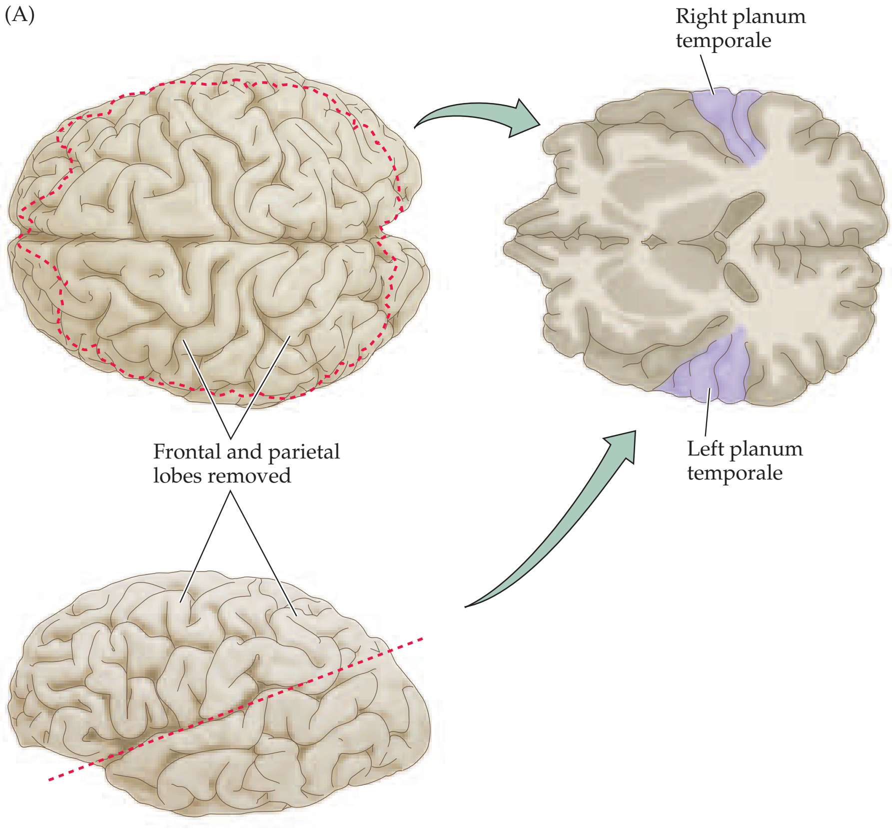
Using the left hemisphere, split-brain patients were able to name objects held in the right hand without difficulty. In contrast, and quite remarkably, an object held in the left hand could not be named! Using the right hemisphere, subjects could produce only an indirect description of the object that relied on rudimentary words and phrases rather than the precise lexical symbol for the object (for instance, "a round thing" instead of "a ball"), and some could not provide any verbal account of what they held in their left hand. Observations using special techniques to present visual information to the hemispheres independently (a method called *tachistoscopic presentation*; Figure 26.3B) showed further that the left hemisphere can respond to written commands, whereas the right hemisphere can typically respond only to nonverbal stimuli (e.g., pictorial instructions, or, in some cases, rudimentary written commands). These distinctions reflect broader hemispheric differences summarized by the statement that the left hemisphere in most humans is specialized for (among other things) the verbal and symbolic processing important in communication, whereas the right hemisphere is specialized for (among other things) visuospatial and emotional processing (see Figure 26.3).

The ingenious work of Sperry and his colleagues on split-brain patients put an end to the century-long controversy about language lateralization; in most individuals, the left hemisphere is unequivocally the seat of the major language functions (although see Box D). It would be wrong to suppose, however, that the right hemisphere has no language capacity. As noted, in some individuals the right hemisphere can produce rudimentary words and phrases, and it is normally the source of emotional coloring of language (see below and Chapter 28). Moreover, the right hemisphere in many split-brain patients understands language to a modest degree, since these patients can respond to simple visual commands presented tachistoscopically in the left visual field. Consequently, Broca's conclusion that we speak with our left brain is not strictly correct; it would be more accurate to say that we understand language and speak very much better with the left hemisphere than with the right, and thus that the contributions of the two hemispheres to the overall goals of communication are different.

Anatomical Differences between the Right and Left Hemispheres

The differences in language function between the left and right hemispheres have naturally inspired neurologists and neuropsychologists to find a structural correlate of this behavioral lateralization. One hemispheric difference that has received much attention over the years was identified in the late 1960s by Norman Geschwind and his colleagues at Harvard Medical School, who found an asymmetry in the superior aspect of the temporal lobe known as the **planum temporale** (Figure 26.4). This area was significantly larger on the left side in about two-thirds of human subjects studied postmortem, a difference that has also been found in higher apes, but not in other primates.

Because the planum temporale is near (although certainly not congruent with) the regions of the temporal lobe that contain cortical areas essential to language (i.e., Wernicke's area and other auditory association areas), it was initially suggested that this leftward asymmetry reflected the greater involvement of the left hemisphere in language. Nonetheless, these anatomical differences in the two hemispheres of the brain, which are recognizable at birth, are unlikely to be an anatomical correlate of the lateralization of language functions. The fact that a detectable planum asymmetry is present in only 67% of human brains, whereas the preeminence of language in the left



(B)

Planum temporale measurements of 100 adult and 100 infant brains		
	Left hemisphere	Right hemisphere
Infant	20.7	11.7
Adult	37.0	18.4

(C)

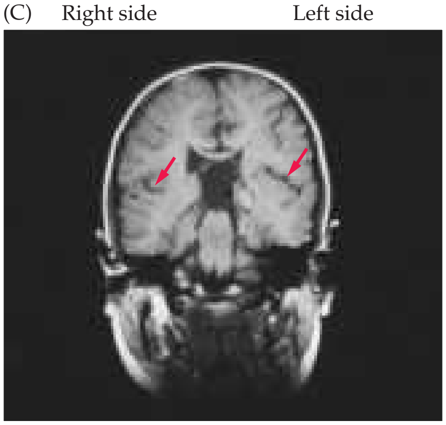


Figure 26.4 Asymmetry of the right and left human temporal lobes. (A) The superior portion of the brain has been removed as indicated to reveal the dorsal surface of the temporal lobes in the right-hand diagram (which presents a dorsal view of the horizontal plane). A region of the surface of the temporal lobe called the planum temporale is significantly larger in the left hemisphere of most (but far from all) individuals. (B) Measurements of the planum temporale in adult and infant brains. The mean size of the planum temporale is expressed in arbitrary planimetric units to get around the difficulty of measuring the curvature of the gyri within the planum. The asymmetry is evident at birth and persists in adults at roughly the same magnitude (on average, the left planum is about 50% larger than the right). (C) A magnetic resonance image in the frontal plane, showing this asymmetry (arrows) in a normal adult subject.

hemisphere is evident in 97% of the population, argues that this association has some other cause. The structural correlate of the functional left–right differences in hemispheric language abilities, if indeed there is one at a gross anatomical level, is simply not clear, as is the case for the lateralized hemispheric functions described in Chapter 25.

Mapping Language Functions

The pioneering work of Broca and Wernicke, and later Geschwind and Sperry, clearly established differences in hemispheric function. Several techniques have since been developed that allow hemispheric attributes to be assessed in neurological patients with an intact corpus callosum, and in normal subjects.

One method that has long been used for the clinical assessment of language lateralization was devised in the 1960s by Juhn Wada at the Montreal Neurological Institute. In the so-called Wada test, a short-acting anesthetic (e.g., sodium amytal) is injected into the left carotid artery; this procedure transiently “anesthetizes” the left hemisphere and thus tests the functional capabilities of the affected half of the brain. If the left hemisphere is indeed “dominant” for language, then the patient becomes transiently aphasic while carrying out an ongoing verbal task like counting. The anesthetic is rapidly diluted by the circulation, but not before its local effects on the hemisphere on the side of the injection can be observed. Since this test is potentially dangerous, its use is limited to neurological and neurosurgical patients.

Box D

Language and Handedness

Approximately 9 out of 10 people are right-handed, a proportion that appears to have been stable over thousands of years and across all cultures in which handedness has been examined. Handedness is usually assessed by having individuals answer a series of questions about preferred manual behaviors, such as "Which hand do you use to write?"; "Which hand do you use to throw a ball?"; or "Which hand do you use to brush your teeth?" Each answer is given a value, depending on the preference indicated, providing a quantitative measure of the inclination toward right- or left-handedness. Anthropologists have determined the incidence of handedness in ancient cultures by examining artifacts; the shape of a flint ax, for example, can indicate whether it was made by a right- or left-handed individual. Handedness in antiquity has also been assessed by examining the incidence of figures in artistic representations who are using one hand or the other. Based on this evidence, the human species appears always to have been a right-handed one. Handedness, or its equivalent, is not peculiar to humans; many studies have demonstrated paw preference in animals ranging from mice to monkeys that is, at least in some ways, similar to human handedness.

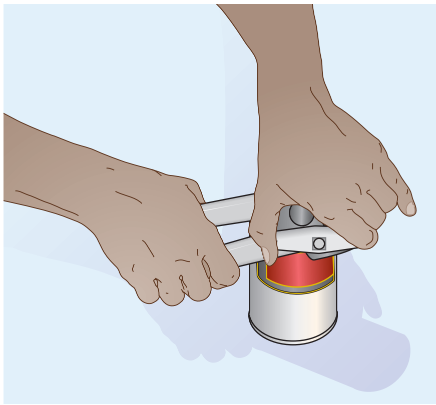
Whether an individual is right- or left-handed has a number of interesting consequences. As will be obvious to left-handers, the world of human artifacts is in many respects a right-handed one (Figure A). Implements such as scissors, knives, coffee pots, and power tools are constructed for the right-handed majority. Books and magazines are also designed for right-handers (compare turning this page with your left and right hands), as are golf clubs and guitars. By the same token, the challenge of penmanship is different for left- and right-handers by virtue of writing from left to right (Figure B). Perhaps as a consequence of such biases, the accident rate for left-handers in all categories (work, home, sports) is higher than for right-handers, including the rate of traffic fatalities. However, there are also some advantages to being left-handed. For example, an inordinate number of international fencing champions have been left-handed. The reason for this fact is simply that the majority of any individual's opponents will be right-handed; therefore, the average fencer, whether right- or left-handed, is less practiced at parrying thrusts from left-handers.

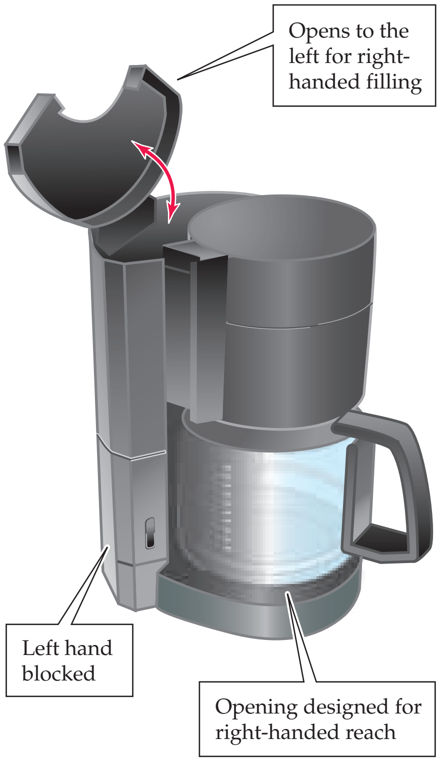
Hotly debated in recent years have been the related questions of whether being left-handed is in any sense "pathological," and whether being left-handed entails a diminished life expectancy. No one disputes the fact that there is currently a surprisingly small number of left-handers among the elderly (Figure C). These data have come from studies of the

(A)

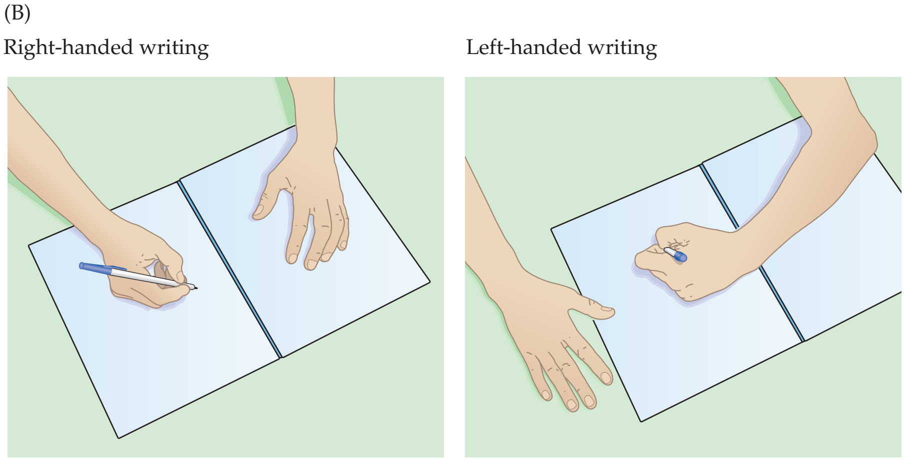
Right-handed

Left-handed





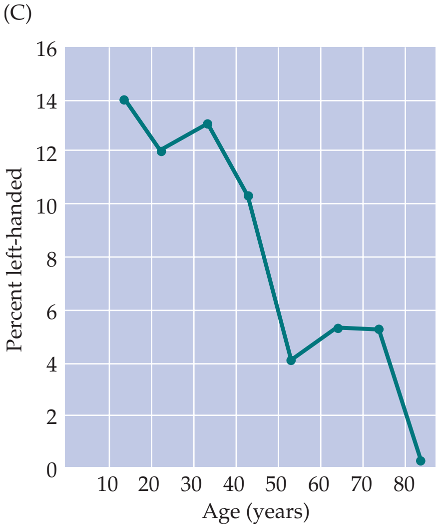
Examples of common objects designed for use by the right-handed majority.



Right-handed writing

Left-handed writing

Writing techniques for right- and left-handed individuals.



The percentage of left-handers in the normal population as a function of age (based on more than 5000 individuals). Taken at face value, these data indicate that right-handers live longer than left-handers. Another possibility, however, is that the paucity of elderly left-handers at present may simply reflect changes over the decades in the social pressures on children to become right-handed. (From Coren, 1992.)

general population and have been supported by information gleaned from *The Baseball Encyclopedia* (in which longevity and other characteristics of a large number of healthy left- and right-handers have been recorded because of interest in the U.S. national pastime).

Two explanations of this peculiar finding have been put forward. Stanley Coren and his collaborators at the University of British Columbia have argued that these statistics reflect a higher mortality rate among left-handers partly as a result of increased accidents, but also because of other data that show left-handedness to be associated with a variety of pathologies (there is, for instance, a higher incidence of left-handedness among individuals classified as mentally retarded). Coren and others have suggested that left-handedness may arise because of developmental problems in the pre- and/or perinatal period. If true, then a rationale for decreased longevity would have been identified that might combine with greater proclivity to accidents in a right-hander's world.

An alternative explanation, however, is that the diminished number of left-handers among the elderly is primarily a reflection of sociological factors—namely, a greater acceptance of left-handed children today compared to the first half of the twentieth century. In this view, there are fewer older left-handers now because in earlier generations parents, teachers, and other authority figures encouraged (and sometimes insisted on) right-handedness. The weight of the evidence favors the sociological explanation.

The relationship between handedness and other lateralized functions—language in particular—has long been a source of confusion. It is unlikely that there is any direct relationship between language and handedness, despite much speculation to the contrary. The most straightforward evidence on this point comes from the results of the Wada test described in the text. The large number of such tests carried out for clinical purposes indicate that about 97% of humans, including the majority of left-handers, have their major language functions in the left hemisphere (although it should be noted that right hemispheric dominance for language is much more common among left-handers). Since most left-handers have language function on the side of the brain opposite the control of their preferred hand, it is hard to argue for any strict relationship between these two lateralized functions. In all likelihood, handedness, like language, is first and foremost an example of the advantage of having any specialized function on one side of the brain or the other to make maximum use of the available neural circuitry in a brain of limited size.

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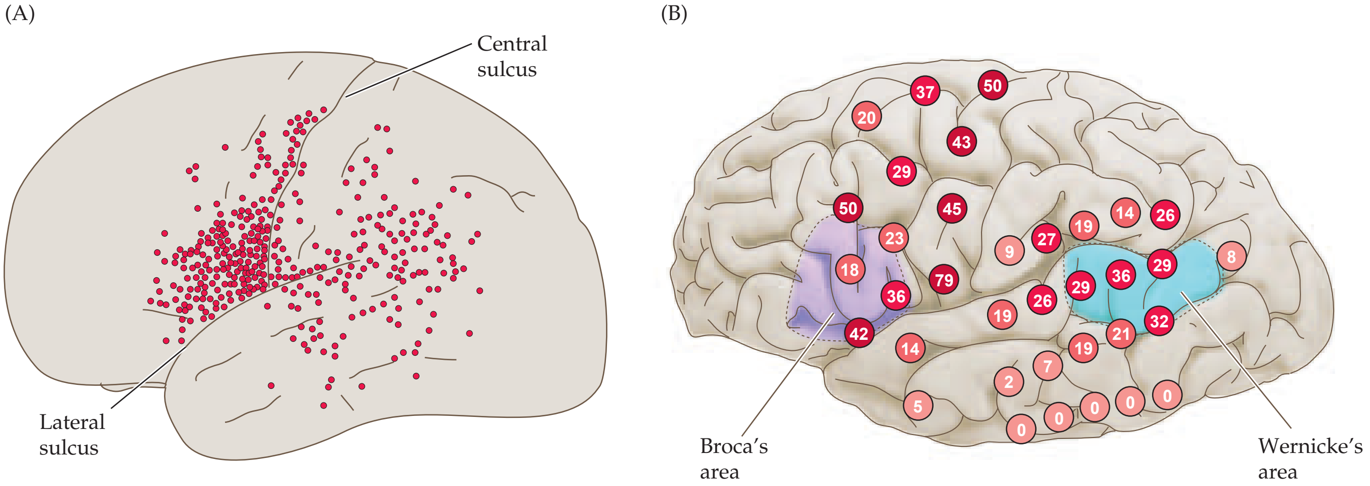
Less invasive (but less definitive) ways to test the cognitive abilities of the two hemispheres in normal subjects include positron emission tomography, functional magnetic resonance imaging (see Box C in Chapter 1), and the sort of tachistoscopic presentation used so effectively by Sperry and his colleagues (even when the hemispheres are normally connected, subjects show delayed verbal responses and other differences when the right hemisphere receives the instruction). Application of these various techniques, together with noninvasive brain imaging, has amply confirmed the hemispheric lateralization of language functions. More importantly, such studies have provided valuable diagnostic tools to determine, in preparation for neurosurgery, which hemisphere is "eloquent": although most individuals have the major language functions in the left hemisphere, a few—about 3% of the population—do not (the latter are much more often left-handed; see Box D).

Once the appropriate hemisphere is known by these means, neurosurgeons typically map language functions more precisely by electrical stimulation of the cortex during the surgery to further refine their approach to the problem at hand. By the 1930s, the neurosurgeon Wilder Penfield and his colleagues at the Montreal Neurological Institute had already carried out a detailed localization of cortical capacities in a large number of patients (see Chapter 8). Penfield used electrical mapping techniques adapted from neurophysiological work in animals to delineate the language areas of the cortex prior to removing brain tissue in the treatment of tumors or epilepsy. Such intraoperative mapping guaranteed that the cure would not be worse than the disease and has been widely used ever since, with increasingly sophisticated stimulation and recording methods. As a result, a wealth of more detailed information about language localization has emerged.

Penfield's observations, together with more recent studies performed by George Ojemann and his group at the University of Washington, have further advanced the conclusions inferred from postmortem correlations and other approaches. As expected, intraoperative studies using electrophysiological recording methods have shown that a large region of the perisylvian cortex of the left hemisphere is clearly involved in language production and comprehension (Figure 26.5). A surprise, however, has been the variability in language localization from patient to patient. Ojemann found that the brain regions involved in language are only approximately those indicated by older textbook treatments, and that their exact locations differ unpredictably among individuals. Equally unexpected, bilingual patients do not necessar-

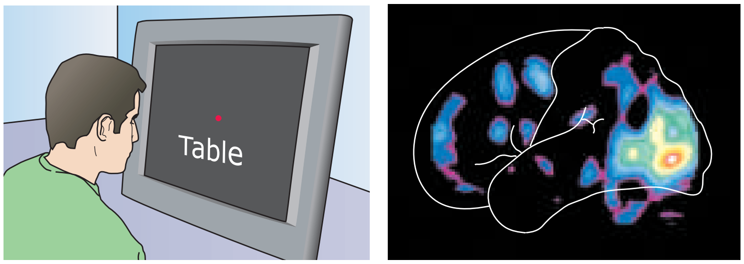
Figure 26.5 Evidence for the variability of language representation among individuals, determined by electrical stimulation during neurosurgery. (A) Diagram from Penfield's original study illustrating sites in the left hemisphere at which electrical stimulation interfered with speech. (B) Diagrams summarizing data from 117 patients whose language areas were mapped by electrical recording at the time of surgery. The number in each red circle indicates the (quite variable) percentage of patients who showed interference with language in response to stimulation at that site. Note also that many of the sites that elicited interference fall outside the classic language areas (Broca's area, shown in purple; Wernicke's area, shown in blue). (A after Penfield and Roberts, 1959; B after Ojemann et al., 1989.)



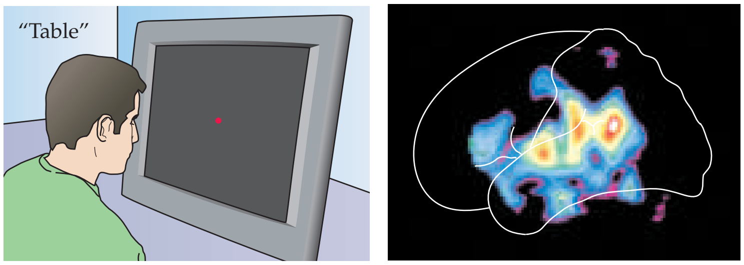
ily use the same bit of cortex for storing the names of the same objects in two different languages. Moreover, although single neurons in the temporal cortex in and around Wernicke’s area respond preferentially to spoken words, they do not show preferences for a particular word. Rather, a wide range of words can elicit a response in any given neuron.

Despite these advances, neurosurgical studies are complicated by their intrinsic difficulty and to some extent by the fact that the brains of the patients in whom they are carried out are not normal. The advent of positron emission tomography in the 1980s, and more recently functional magnetic resonance imaging, has allowed the investigation of the language regions in normal subjects by noninvasive brain imaging (Figure 26.6). Recall that these

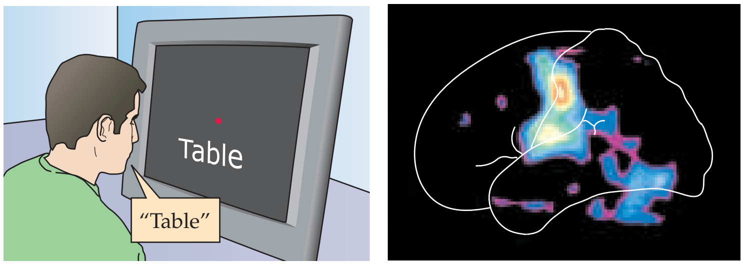
Passively viewing words



Listening to words



Speaking words



Generating word associations

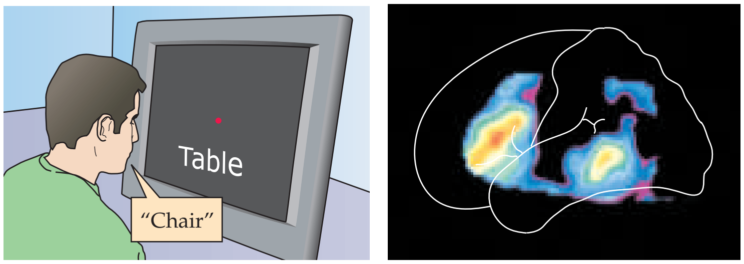


Figure 26.6 Language-related regions of the left hemisphere mapped by positron emission tomography (PET) in a normal human subject. Subjects reclined within the PET scanner and followed instructions on a special display (these details are not illustrated). The left panels indicate the task being practiced prior to scanning. The PET scan images are shown on the right. Language tasks such as listening to words and generating word associations elicit activity in Broca’s and Wernicke’s areas, as expected. However, there is also activity in primary and association sensory and motor areas for both active and passive language tasks. These observations indicate that language processing involves cortical regions in addition to the classic language areas. (From Posner and Raichle, 1994.)

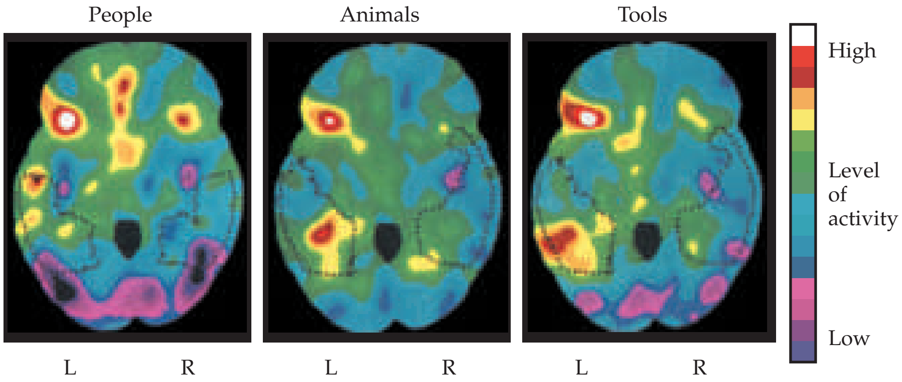


Figure 26.7 Different regions in the temporal lobe are activated by different word categories using PET imaging. Dotted lines show location of the relevant temporal regions in these horizontal views. Note the different patterns of activity in the temporal lobe in response to each stimulus catagory. (After Damasio et al., 1996.)

techniques reveal the areas of the brain that are active during a particular task because the related electrical activity increases local metabolic activity and therefore local blood flow (see Boxes B and C in Chapter 1). Much like Ojemann's studies in neurosurgical patients, the results of this approach, particularly in the hands of Marc Raichle, Steve Petersen, and their colleagues at Washington University in St. Louis, have challenged excessively rigid views of the localization and lateralization of linguistic function. Although high levels of activity occur in the expected regions, large areas of both hemispheres are activated in word recognition or production tasks.

Finally, Hanna Damasio and her colleagues at the University of Iowa have shown that distinct regions of the temporal cortex are activated by tasks in which subjects named particular people, animals, or tools (Figure 26.7). This arrangement helps explain the clinical finding that when a relatively limited region of the temporal lobe is damaged (usually by a stroke on the left side), language deficits are sometimes restricted to a particular category of objects. These studies are also consistent with Ojemann's electrophysiological studies, indicating that language is apparently organized according to categories of meaning rather than individual words. Taken together, such studies are rapidly augmenting the information available about how language is represented in the brain.

The Role of the Right Hemisphere in Language

Because exactly the same cytoarchitectonic areas exist in the cortex of both hemispheres, a puzzling issue remains. What do the comparable areas in the right hemisphere actually do? In fact, language deficits often *do* occur following damage to the right hemisphere. The most obvious effect of such lesions is an absence of the normal emotional and tonal components of language—called **prosodic elements**—that impart additional meaning to verbal communication. This "coloring" of speech is critical to the message conveyed, and in some languages (e.g., Mandarin Chinese) is even used to change the literal meaning of the word uttered. These deficiencies, referred to as **aprosodias**, are associated with right-hemisphere damage to the cortical regions that correspond to Broca's and Wernicke's areas and associated regions in the left hemisphere. The aprosodias emphasize that although the left hemisphere (or, better put, distinct cortical regions within that hemisphere) figures prominently in the comprehension and production of language for most humans, other regions, including areas in the right hemisphere, are needed to generate the full richness of everyday speech.

In summary, whereas the classically defined regions of the left hemisphere operate more or less as advertised, a variety of more recent studies have shown that other left- and right-hemisphere areas clearly make a significant contribution to generation and comprehension of language.

Sign Language

The implication of at least some aspects of the foregoing account is that the cortical organization of language does not simply reflect specializations for hearing and speaking; the language regions of the brain appear to be more broadly organized for processing symbols pertinent to social communication. Strong support for this conclusion has come from studies of sign language in individuals deaf from birth.

American Sign Language has all the components (e.g., grammar, syntax, and emotional tone) of spoken and heard language. Based on this knowledge, Ursula Bellugi and her colleagues at the Salk Institute examined the cortical localization of sign language abilities in patients who had suffered lesions of either the left or right hemisphere. All these deaf individuals never learned language, had been signing throughout their lives, had deaf spouses, were members of the deaf community, and were right-handed. The patients with left-hemisphere lesions, which in each case involved the language areas of the frontal and/or temporal lobes, had measurable deficits in sign production and comprehension when compared to normal signers of similar age (Figure 26.8). In contrast, the patients with lesions in approxi-

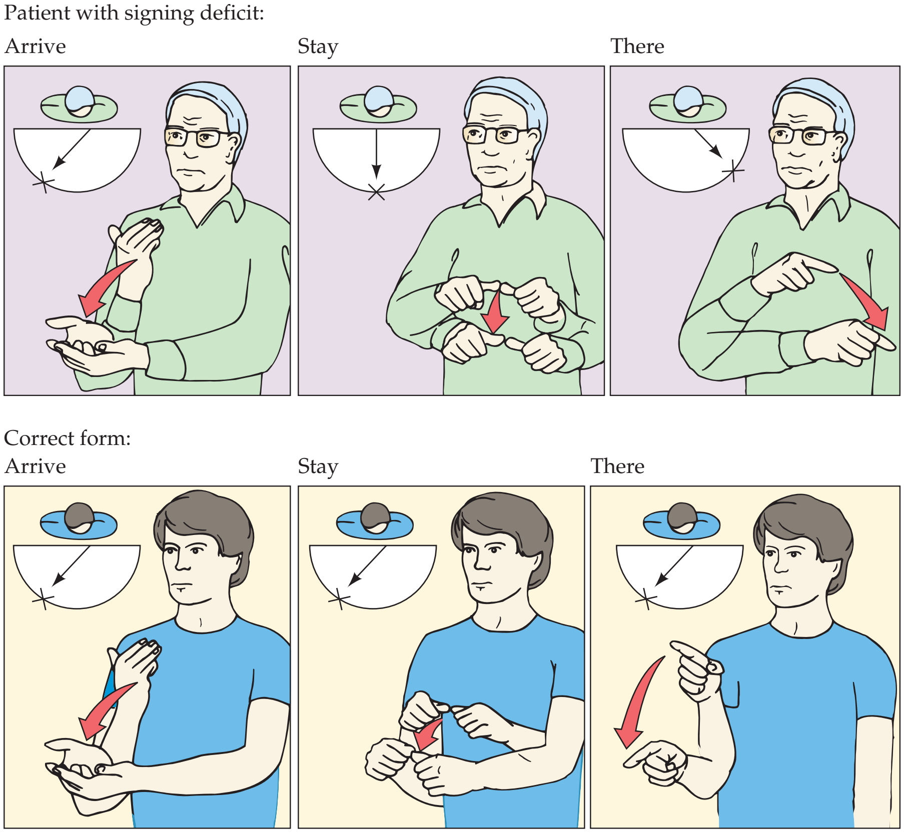


Figure 26.8 Signing deficits in congenitally deaf individuals who had learned sign language from birth and later suffered lesions of the language areas in the left hemisphere. Left hemisphere damage produced signing problems in these patients analogous to the aphasias seen after comparable lesions in hearing, speaking patients. In this example, the patient (upper panels) is expressing the sentence "We arrived in Jerusalem and stayed there." Compared to a normal control (lower panels), he cannot properly control the spatial orientation of the signs. The direction of the correct signs and the aberrant direction of the "aphasic" signs are indicated in the upper left-hand corner of each panel. (After Bellugi et al., 1989.)

mately the same areas in the right hemisphere did not have signing "aphasias." Instead, as predicted from other hearing patients with similar lesions, right hemisphere abilities such as visuospatial processing, emotional processing and the emotional tone evident in signing were impaired. Although the number of subjects studied was necessarily small (deaf signers with lesions of the language areas are understandably difficult to find), the capacity for signed and seen communication is evidently represented predominantly in the left hemisphere, in the same areas as spoken language. This evidence accords with the idea that the language regions of the brain are specialized for the representation of social communication by means of symbols, rather than for heard and spoken language per se.

The capacity for seen and signed communication, like its heard and spoken counterpart, emerges in early infancy. Careful observation of babbling in hearing (and, eventually, speaking) infants shows the production of a predictable pattern of sounds related to the ultimate acquisition of spoken language. Thus, babbling prefigures true language, and indicates that an innate capacity for language imitation is a key part of the process by which a full-blown language is ultimately acquired. The offspring of deaf, signing parents "babble" with their hands in gestures that are apparently the forerunners of signs (see Figure 23.1). Like verbal babbling, the amount of manual babbling increases with age until the child begins to form accurate, meaningful signs. These observations indicate that the strategy for acquiring the rudiments of symbolic communication from parental or other cues—regardless of the means of expression—is similar.

Summary

A variety of methods have all been used to understand the organization of language in the human brain. This effort began in the nineteenth century by correlating clinical signs and symptoms with the location of brain lesions determined postmortem. In the twentieth century, additional clinical observations together with studies of split-brain patients, mapping at neurosurgery, transient anesthesia of a single hemisphere, and noninvasive imaging techniques such as PET and *f*MRI have greatly extended knowledge about the neural substrates of language. Together, these various approaches show that the perisylvian cortices of the left hemisphere are especially important for normal language in the vast majority of humans. The right hemisphere also contributes importantly to language, most obviously by giving it emotional tone. The similarity of the deficits after comparable brain lesions in congenitally deaf individuals and their speaking counterparts have shown further that the cortical representation of language is independent of the means of its expression or perception (spoken and heard, versus gestured and seen). The specialized language areas that have been identified are evidently the major components of a widely distributed set of brain regions that allow humans to communicate effectively by means of symbols that can be attached to objects, concepts and feelings.

Additional Reading

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