Language and Communication

Language is one of the pillars of human intellect. It is the principal way we formulate thoughts and convey them to others. It plays a role in how we analyze the world, reason, solve problems, and plan actions. It lets us convey memories of the past and beliefs about the future, engage others in thinking about events that have not taken place, and express the relationships we perceive between items and events in the world.

Language is also an indispensable part of human culture. Without it, our systems of jurisprudence, commerce, science, art, and other human endeavors could not exist in the forms we know them, if at all. Language is itself an esthetic object, and many people find that linguistic renderings can capture the essence of profound emotions such as love and grief. Without language, each person’s discoveries would die with him or her; language makes it possible for the achievements of one individual to be transmitted to the rest of the human species. Language skills are therefore vital to the success of societies and of individuals within societies.

The way the human brain represents and processes language has been approached in many ways. Studies of the communication systems of other species give some hints about neural mechanisms that might support language. More direct evidence comes from the effects of diseases that affect language and from observations of brain activity that occurs while individuals are performing language tasks.

This chapter discusses aspects of language and the relationship of language to the brain. It begins with a discussion of animal communication, from which human language evolved and which provides a guide to the basic neural elements and processes that underlie our own system of communication. The next section of the chapter provides a brief summary of what human language is and how it is processed. The third section looks at how human language is related to the brain, relying on studies of patients with various types of neurological diseases and on brain imaging in normal subjects.

ANIMAL COMMUNICATION

Communication Is Important for Individual Survival

The ultimate goal of most animal communication, like that of behavior in general, is reproduction. Thus, signals that indicate the sender’s species, gender, and degree of reproductive readiness account for the vast majority of natural communication. These are the messages being broadcast by chirping crickets, flashing fireflies, pheromone-releasing moths, and singing birds. Frequently, the mate-attraction call is also used to warn off potential rivals; e.g., bird and cricket songs are also used to identify the boundaries of territories or personal space. Differences in signal quality are the usual basis of mate choice in species for which some degree of discrimination is evident. This competition for the attention of members of the opposite sex has led to the development of more conspicuous signals and, in many cases, to the evolution of displays, signaling morphology (i.e., sounds vs shapes vs color vs movement vs odors), and messages that go far beyond the basic needs of species and sexual identification (Gould and Gould, 1996).

Most animals are solitary except when mating; they abandon their eggs or larvae before the offspring are born. However, a number of species engage in some
degree of parental care. For them, signals between parent and offspring are often very important. Most birds, for instance, have about two dozen innate calls that communicate mundane messages such as the need to eat, defecate, take cover, and so on. In cases in which both parents tend the young—the usual circumstance in birds, for instance—additional signals are required to agree on a nest site, synchronize brooding shifts, and guard the nestlings. Most primes also come equipped with two to three dozen innate signals.

The minority of species that are highly social have the most elaborate communication systems of all. They need messages for a variety of elements of social coordination, including, in many cases, group hunting or foraging, defense, and working out of a social hierarchy.

Animal Communication Strategies and Mechanisms

Attracting a mate is vital to species survival. To ensure species specificity in mating, most organisms rely on more than one cue to identify a sexual partner. (Exceptions include some of the species that rely on pheromones.) Thus, multiple signals are sent, and a choice must be made between sending simultaneous messages and sending sequential messages (or a combination of the two). The sequential strategy has the advantage that the individual signals must be correct and the order must be appropriate. A female stickleback, for instance, requires the male to have a red ventral stripe, perform a zig-zag dance, poke his nose in a nest, and then vibrate her abdomen; the odds of this concatenation of signals occurring together in this order by chance are remote. However, sequential signaling is time-consuming. A faster strategy is to provide all the cues in parallel, an approach that accepts the larger chance that these cues can occur together by chance. For example, when a parent herring gull waves its bill in front of chicks to see if they need to be fed, the young simultaneously see a vertical beak, a red spot, and a horizontal motion, each of which is a discrete cue that combine in the mind of the chick to elicit pecking.

Nearly all animal communication is innate: the sender produces the appropriate signal in the correct context even without any opportunity for learning, and it can be recognized for what it is by equally naive conspecifics. The basis of innate recognition appears to lie with feature detectors in the nervous systems—the inborn circuits that automatically isolate iconic visual or acoustic elements. In the visual system the simplest elements include spots, lines, and movement. To the extent that the issue has been studied, innate recognition can usually be correlated with such feature detectors. In the case of European toads, the signals unwittingly emitted by prey (e.g., a line moving along its long axis, which corresponds to a worm crawling) and the behavior of the predator correlate perfectly with neural responses recorded simultaneously from the nervous system (i.e., when the prey-detector neurons fire, the toad snaps at the prey). In the jargon of ethology, innately recognized features with special salience for an organism are known as “sign stimuli”; the roughly equivalent term in psychology is “unconditioned stimuli” (Gould, 1982).

The availability of many visual, auditory, tactile, and olfactory feature detectors, which can, in theory, be used in any specific combination or order, accounts for most of the diversity of animal communication, and reliance on these single feature detectors, rather than pattern detection, accounts for its limitations. For instance, female crickets initially approach male conspecifics on the basis of a calling song. The carrier frequency and time intervals within the song are important, but the actual pattern of the song, so memorable to our ears, is lost on the females: the call is equally attractive played forward and backward. This makes sense because pattern detectors are rare in the nervous system. So, too, young gull chicks find a hand-held knitting needle with several “spots” more stimulating than an adult gull; the ability to recognize a gull head and beak as a holistic unit, although it might be adaptive, is absent, reflecting the rarity of complex innate pattern recognition.

Innate Communication Mechanisms

A common misapprehension is that complex behaviors must be learned. In fact, complex behavior in relatively short-lived species is usually innate, reflecting the reality that intricate activities are very difficult to learn and may require more time and risk of errors than an animal can afford (Gould and Gould, 1999). Thus, so far as is known, all bird nests are built on the basis of innate instructions, although some improvement with experience is also evident. Therefore, looking at just how complex innate communication can be is a useful calibration for the oft-made assumption that something as intricate as human speech must be largely learned.

In terms of its ability to communicate information, the most complex system of nonhuman communication known at present is the dance of honeybees (Gould and Gould, 1995). The system has some properties that are reminiscent of human language: it uses
FIGURE 52.1 The waggle dance of honeybees follows a figure eight; the two intersecting straight runs are emphasized by wagging of the body and the production of sound.

arbitrary conventions to describe objects distant in both space and time; i.e., it does not reflect a real-time emotive readout, as might be the case when a primate gives an alarm call or grunts at a banana. The dance simultaneously specifies the distance, direction, and quality of a food source, water supply, or potential nest site. The dance consists of a figure eight pattern of movement on the part of the signaling forager, with a simultaneous wagging of the body (at about 13 Hz) and buzzing (consisting of 280-Hz bursts occurring at 30 Hz) during the central parts—the waggle runs—of the dance (Fig. 52.1). The dance normally takes place on the vertical surface of the comb within the darkness of the hive cavity.

Direction is indicated by the orientation of the waggle runs: straight up is taken to be the direction of the sun, so that a dance whose average waggle-run angle is 80° to the left of vertical is indicating a site 80° to the left of the sun’s current azimuth (Fig. 52.2). Because the sun moves from east to west over the course of the day, dances indicating a specific site precess counterclockwise to compensate. This compensation is evident in the extended dances of foragers that have had no opportunity to see the sun for minutes or even hours: as time passes, the dance angle shifts counterclockwise at just the rate the sun’s azimuth shifts clockwise. That “up” should mean “the direction of the sun” seems arbitrary, as “down” would work equally well so long as encoder and decoder agreed on the convention; the dance direction could also be referenced to some other cue—magnetic north or the direction the hive entrance faces.

Distance is indicated by the duration of the waggle run or one of the several factors that correlate with it—duration of sound production, number of sound bursts, and so on. The conversion of meters flown to waggle duration differs among subspecies: for the Egyptian honeybee, a waggle is equivalent to less than 10 m, whereas Italian honeybees value a waggle at about 20 m, and German honeybees peg the exchange rate closer to 50 m (Fig. 52.3). These dialects are innate.
between this sensitive period and the process of overt song development; i.e., that is, practice and perfection of the adult song are based on the bird's memory of what it heard during its sensitive period (Gould and Marler, 1987).

Given a range of possible song models during isolated rearing, a chick selects an example from its own species and memorizes it. If it hears only songs of other species, the mature song is the unmodified innate song (Fig. 52.4). Thus there is an innate bias in the initial learning. Where this bias has been studied, it appears to depend on acoustic sign stimuli (i.e., species-specific "syllables"). Indeed, chicks are able to extract syllables of their species embedded in foreign songs, or scored in a way never found in their species (e.g., a syllable that is repeated at an accelerating rate presented to a species that sings syllables at a constant rate, or vice versa will be extracted and used in the species-typical manner).

Practice is essential in the normal development of birdsong, and part of this practice occurs in a babbling phase known as subsong, which begins at a species-typical age. A bird deafened after its sensitive period, but before it begins producing notes in preparation for singing (subsong), is unable to produce even an innate song (Fig. 52.4). During the earliest parts of subsong, birds try out a number of notes. These notes are typical of the species, but most are absent from the song they eventually sing. The learning process may involve producing each member of an innate repertoire of notes, listening to them, checking to see if they match any element in the memorized song, discarding the unnecessary ones, and rearranging, scoring, and modifying the others to produce a reasonable copy of the original song heard during the sensitive period.

There is some flexibility in song development. For example, when the chick has heard two very different specimens of its own species’ song, it will often incorporate elements from each. Similarly, when the chick has been exposed to the sight of a singing conspecific and simultaneously the sound of a heterospecific song, it may pick out elements of the abnormal song and adapt them as best it can into its own species-specific organization.

Birdsong, therefore, depends on two processes that involve an interaction between innate capacities and learning: imprinting the song in memory and then learning to perform it. This system is flexible, but only within clear limits.

Communication Systems in Primates

Primates are the species with the closest evolutionary links to humans, and therefore the communica-
tion systems found in these animals are important to study for clues regarding the neural basis of human language.

Vervets, a species of monkey, provide a good case study. Vervets, like all social primates, have a large repertoire of innate calls used for social communication. Among these approximately three dozen signals are four alarm calls (Cheney and Seyfarth, 1990). In some parts of their range, one of the calls is specific for martial eagles; in another the same call is used for certain hawks. In either case, the call causes monkeys to look up; those at the tops of trees drop to the interior, whereas those on the ground move into bushes or under trees. A second call, specific to leopards in one region and to other solitary hunters elsewhere, sends the warned individuals up to the tree tops. A third, specific for snakes, induces the other members of the troop to stand up and look around in the grass. A fourth call is heard in the presence of humans or group-hunting predators.

The development of calling is revealing. Young vervets appear to understand the class of animals each call refers to, but not the particular species that are dangerous. Thus, infants will give the eagle call to harmless vultures, storks, and even falling leaves, but not to snakes or leopards. Consequently, adults generally respond to the alarm calls of infants with a casual look around, followed by their own alarm if there is a
genuine danger. Juveniles make fewer mistakes, and adult errors are confined to calls produced when the potential threat is so far away that human observers require binoculars to identify the species. In short, young vervets seem to learn the details of how to apply an innate categorical vocabulary.

Neural Structures for Animal Communication Systems

The neural mechanisms that underlie animal communication may give clues as to those that allow for human language. These systems of course differ in different phyla and species. This section briefly reviews aspects of the neural basis for birdsong and primate communication. It would be of great interest to report on the neural basis for the dance of the bees, but nothing is known about this subject.

Birdsong

Birdsong appears to be produced by a small number of nuclei (collections of nerve cells). In the canary, four important nuclei are involved: HVC, RA, DM and nXIIIts. Lesions in any of these nuclei destroy or seriously impair song production. These nuclei also respond when song is presented, and some neurons in some nuclei in some species (e.g., neurons in nXIIIts in the zebra finch and the white-crowned sparrow) respond specifically to particular aspects of song. This indicates an overlap in the neural mechanisms involved in song perception and production, a feature that may carry over to humans as well.

Birdsong is produced by a structure between the trachea and the bronchi called the syrinx. There is one syrinx on each side of the trachea. In some species, song is entirely, or mainly, produced by one of these two structures; in other species, both syrinxes participate in song, with each producing different parts of the song. Each syrinx is controlled by structures in its corresponding side of the brain and, when one syrinx is responsible for song, these structures are larger on that side. The perceptual system is also duplicated on both sides of the brain, and, in some species, the two sides of the brain respond to different aspects of song.

In species in which only male birds sing (most species), song nuclei are much larger in males than in females (“sexual dimorphism”). This is not true in those species in which males and females perform duets. In general, there is a correlation between song nucleus size and song complexity in individual birds. Furthermore, song nuclei grow by a factor of almost 100% during the spring mating season (when birds sing) compared to the fall and winter (when they do not).

Changes in the size of song nuclei are related to testosterone production (they can be induced in females by testosterone injection in some circumstances) and by other factors usually related to daylength—part of the birds’ innate calendar. They are due to many changes in nerve cells: increase in the number of dendrites, increase in cell size, and, most interestingly, increase in the number of cells. Studies using labeled thymidine, which is taken up by dividing DNA, have shown neurogenesis in neurons in the HVC nucleus in relationship to periods of increased song, indicating that new nerve cells are formed. These neurons project to the RA nucleus, strongly suggesting that they play a role in song.

Primates

The neural basis for primate vocalizations is beginning to be charted. Unlike humans, vocalizations in primates do not appear to begin in a lateral cortical region but rather in the medial portion of the brain (the cingulate), a region involved in connecting basic instinctual to more advanced cognitive functions. Actual motor planning appears to involve mainly brain stem nuclei. On the perception side, there are neurons in the auditory cortex of some species of macaque monkeys that selectively respond to conspecific calls. These regions show some degree of functional asymmetry in some species, with responses from cells in the left hemisphere and not the right.

Possible Lessons from Nonhuman Species Regarding Language and Its Neural Basis

It is dangerous to infer too much about human language, or about how the human brain may support language, from studies of species that are very distant, such as birds. However, these species provide evidence for the possibility of certain aspects of language and its neural basis that could have developed several times in evolution or that could date to a distant common ancestor.

At a behavioral level, human speech and language could have developed from the repertoire of two to three dozen innate calls typical of birds and primates. In that case, we would expect to find that language contains elements that are innately recognized and that may be distinguished by the sorts of acoustic features that provide the basis for the innate discrimination of sign stimuli in other species. In fact, babies have an innate ability to discriminate a small number of sounds found in human languages, which function as acoustic sign stimuli. The evolution of human speech could also have retained the sorts of sensitive periods and innate learning biases so evident in song.
birds and vervet monkeys. In this case, we might expect to see a species-typical babbling phase, and perhaps a sensitive period for easy learning of new languages. If the evolution of speech and language preserves the use of preexisting (innate) forms, we might expect there to be innate aspects of human language, which would presumably be found in all languages and which might surface in situations where we see a “default grammar,” not unlike the unlearned and impoverished songs of birds reared in isolation.

From the neurological perspective, several features of the neural organization for communication systems appear to be found in humans in a way that is relevant to language. These features are the fact that there are specialized neural nuclei for song production; that the neural basis for song production is often asymmetric, with one hemisphere producing most of song or the two hemispheres producing different aspects of song; that production and perception of song make use of same structures to some degree; and that there is a relationship of size to function. However, other important features of the neurobiology of birdsong, such as the neurogenesis that is important in the seasonal changes in song production, are not known to play a role in human speech and language. As for primates, the neural system responsible for call production is quite different from that in humans, being based in the cortex that is transitional from limbic to association regions (reflecting the limited semantic content and immediate biological relevance of most calls). Asymmetries in the neural basis for call perception, and the existence of neurons in the auditory association cortex that selectively respond to conspecific calls, may be quite direct evolutionary precursors of the human neural substrate for language.

**HUMAN LANGUAGE**

Although animal communication systems can be quite sophisticated and some of them share attributes with human language, human language is far more complex than animal communication. There are many features of human language that make it special.

One is what messages human language can convey. As we have seen, most animal communication systems serve the purposes of identifying members of a species. These systems do sometimes designate items of immediate biological significance, such as designation of predators by monkeys or food sources by bees. Human language differs from these systems with respect to the number of items that can be designated and the relationship of these items to present biological necessity. Human language allows us to designate an infinitely large number of items, actions, and properties of items and actions, and to do so with respect to items that are not immediately biologically compelling.

Human language also allows us to relate items, actions, and properties to one another. This propositional level of semantic content is beyond the scope of any known animal communication system. At a yet higher level, human language allows us to express relationships between events and states of affairs in the world, such as temporal order and causation. Again, this level of meaning is far beyond anything available to other species as far as we know.

The power of language to express so many aspects of meaning is due to the fact that language has many types of representations. It consists of words, words made from other words, groupings of words into phrases and sentences, and groupings of sentences into a discourse. Each of these levels of linguistic representation consists of specific forms that are related to specific aspects of meaning. The forms at each level are intricately structured, and there are an infinite number of different structures that can be built at each level of the system. This leads to a situation in which items can be elaborated on in infinitely many ways. The result is a powerful and complex system of representation.

Human language develops naturally in the auditory-oral modality. However, humans who are deaf can develop language in the visual and gestural modalities, and the structures of these language are essentially the same as those of spoken language, once allowances are made for the fact that they are signed instead of spoken. Languages can also be represented orthographically. Orthographies range from alphabetical scripts such as English, to syllabic, consonantal, and ideographic orthographies. Orthography is not acquired in the way spoken and signed language is; reading and writing require instruction to master. This chapters deal only with spoken language. For an introduction to signed language and its neurology, see Bellugi et al. (1990); for a discussion of orthographic representational systems, see Henderson (1982).

**Words**

Simple words are defined and distinguished from each other primarily by their phonemes. A phoneme is a single distinct sound that contrasts with another (see Fig. 52.5) and makes it possible to determine the existence of a word in a language. For instance, in English /p/ and /b/ are different phonemes because they determine the separate existence of the members
of word pairs such as pat-bat, pale-bale, pull-bull, lap-lab. A major distinction between different types of phonemes is the difference between vowels and consonants. Consonants involve some degree of constriction of the vocal tract; vowels are produced with a relatively open vocal tract. Each language "selects" its inventory of phonemes from a relatively small set of phonemes found across languages. American English phonemes have 25 consonants and 17 vowels, as listed in Tables 52.1 and 52.2.

At the semantic level, put in very simple terms, words designate concrete objects, abstract concepts,

<table>
<thead>
<tr>
<th>Consonants</th>
<th>Vowels</th>
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<tbody>
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<td>Symbol</td>
<td>Example</td>
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<td>/w/</td>
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<td>/r/</td>
<td>you</td>
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<td>/ŋ/</td>
<td>charm</td>
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*Phonemic symbols corresponding to the consonants are shown on the left along with an example of a typical word that includes each sound as indicated by the underlined letter or letters in each word. Right-hand columns present a similar list of vowel sounds and words that include these.*

<table>
<thead>
<tr>
<th>Place of articulation</th>
<th>Glide</th>
<th>Nasal</th>
<th>Stop</th>
<th>Fricative</th>
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<td>p</td>
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<td>Labiodental</td>
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<td>Middle</td>
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<td>Dental</td>
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<td>Back</td>
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<td>Velar</td>
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<td>g</td>
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<td>Pharyngeal</td>
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*The articular features of manner, place, and voicing classify the consonant sounds according to similarities and differences that exist in the way in which each sound is produced. Note that the voicing distinction is relevant only for stops and fricatives in English.*
actions, properties, and logical connectives. Many philosophers and psychologists, and most neurologists who have considered the subject, have thought that the meaning of a word consists of a set of features of objects and actions that are associated with the word's sound through one's experience. However, the meaning of a word also includes unobserved properties of the item that the word designates, such as our knowledge that cats can swim even if we have never observed one swimming. This knowledge may be based on inductive generalizations, logical inferences, or innate concepts regarding the structure of items. Tulving (1972), who called the complex set of properties that make up word meaning "semantic memory," emphasized that the hallmark of this type of knowledge is the relations that items have to one another.

Words Formed from Other Words

The word-formation level of language allows words to be formed from other words. Language uses many devices to accomplish this—compounding, affixation, agglutination, and others. English affixation provides a useful illustration. There are two main types of affixes in English: inflection and derivation. Inflection is related to the syntactic structure of a sentence, as in agreement between subjects and objects (I see; he sees). English is relatively poor in overt inflectional features; languages such as Dutch and German have more complete and complex agreement systems that affect adjective–noun agreement, verb inflections, and the case markers on nouns. Derivational processes are those that create new syntactic categories of words (e.g., destroy → destruction; happy → happiness). Derivation allows the meaning associated with a simple lexical item to be used as a different syntactic category without coining a large number of new lexical forms that would have to be learned.

Affixation has semantic consequences. Agreement features convey the semantic features inherent in the agreement. For example, the third-person present tense marker s conveys the information that an action is being accomplished (or is habitually accomplished) by an individual (or a set of individuals considered as a whole) who is neither the speaker nor the listener. Derivational morphology also has effects on semantics. For instance, the thematic roles assigned by a verb (information about who is doing what to whom) are reassigned to different nouns when certain adjective-formation suffixes are added (a noun is understood as the theme of the action of hugging when it is modified by the adjective huggable, as in "The boy is huggable," as opposed to being understood as being the agent of the action of hugging, as when it is the subject of the verb hugging, as in "The boy is hugging ... ").

Sentences

The sentential level of language consists of syntactic structures (Chomsky, 1965, 1981, 1986) into which words are inserted. Individual words are marked for syntactic category [e.g., cat is a noun (N); read is a verb (V); of is a preposition (P)]. These categories combine in a hierarchy to create nonlexical nodes (or phrasal categories), such as noun phrase (NP), verb phrase (VP) and sentence (S). The way words are inserted into these higher order phrasal categories determines a number of different aspects of sentence meaning. For instance, in the sentence "The dog that scratched the cat killed the mouse," there is a sequence of words—the cat killed the mouse—that would, in isolation, mean that the cat killed the mouse. However, "The dog that scratched the cat killed the mouse" does not assert that the cat killed the mouse, but rather that the dog did. This is because the cat is not the subject of killed and does not play a thematic role around killed. The cat is the object of the verb scratched in the relative clause—that scratched the cat—and is the theme of scratched. The dog is the subject of the verb killed and is the agent of that verb. The syntactic structure of "The dog that scratched the cat killed the mouse" is shown in Fig. 52.6, which demonstrates these relationships.

At the sentence level the set of semantic values that language can express expands greatly (Pinker, 1994). Sentences convey aspects of the structure of events.

FIGURE 52.6 Syntactic structure of the sentence "The dog that scratched the cat killed the mouse" indicating the hierarchical structure responsible for its meaning.
and states in the world. These semantic values are collectively known as the propositional content of a sentence. These values include thematic roles (information about who did what to whom), attribution of modification (information about which adjectives go with which nouns, such as the fact that in the sentence “The big boy chased the little girl,” the boy is big and girl is little), scope of quantification (information about what items are included in the scope of quantifiers, such as the fact that in the sentence, “None of the boys wearing hats was cold,” the quantifier “none” applies to the boys wearing hats, not just to the boys), the reference of pronouns and other anaphoric elements (information about which words in a set of sentences refer to the same items or actions, such as the fact that in the sentence “The brother of the visitor shaved himself,” “himself” refers to “brother” and not to “visitor”), and so on.

Sentences are a crucial level of the language code because the propositions they express make assertions about the world. These assertions can be added to an individual’s knowledge of the world. Because they can be true or false (something that is not possible with words), they can be entered into logical systems. They can serve to add information to semantic memory, they can serve to plan actions, and they can serve other purposes. While the number of words that are available distinguishes human language from animal communication systems, as we have seen, the ability to refer to items is present in a rudimentary form in some nonhuman species. The combinatorial mechanism that produces an infinite number of propositions, however, is distinctly human.

Universal Features of Linguistic Representations

By some counts, there are over 6500 languages in the world. These languages differ in many ways from one another: they have different vocabularies, use different sounds, and have different ways of forming words and different syntactic rules. However, beyond these surface level differences, there are features that are common to all human language. For instance, the sound systems of all human languages consist of alternations of consonants and vowels; no language forms different words by varying features of sound such as its loudness or whether a word is whispered. These “linguistic universals” form a framework within which the features of individual languages occur.

Linguistic universals can arise because of universal features of motor or sensory systems or, possibly, because of constraints on cognitive computational capacities. Linguistic research on language universals investigates those that may reflect abstract aspects of linguistic structure itself. Chomsky’s work in the area of syntax is the best known and most controversial example of such analyses.

The syntactic structures of different languages appear to differ enormously. Some languages use agreement to express relationships between lexical items, others use morphology, and others use word order. Languages that use word order differ in the order of words they require (verb-medial, such as English; verb-last, such as Japanese). Despite these differences, Chomsky and his colleagues and students have argued that basic features of syntax are common to all languages. A famous example of his work in this area is the study of constraints on how items at a distance can be related to one another. For instance, in sentence 1, the boat is related to painted.

1. The boat that you believe John painted is red.
There are limitations on these long-distance relationships. For instance, sentence 2 is ungrammatical.

2. The boat that you believe the claim John painted is red.

What makes sentence 2 unacceptable? It cannot be its meaning because it means the same thing as sentence 1. It must be some aspect of its form. What seems to be the problem is that the presence of the words “the claim” makes the distance between the boat and painted too great for this relationship to be established. Chomsky’s insight was that the notion of “distance” is not defined in terms of the number of words between the boat and painted. Sentence 3 is perfectly acceptable, even though it has many more words between these phrases.

Discourse

The propositional meanings conveyed by sentences are entered into higher order structures that constitute the discourse level of linguistic structure. Discourse includes information about the general topic under discussion, the focus of a speaker’s attention, the novelty of the information in a given sentence, the temporal order of events, causation, and so on. Information conveyed by the discourse level of language also serves as a basis for updating an individual’s knowledge of the world and for reasoning and planning action.

The structure of discourse involves relationships between propositions, and it also includes information about the syntactic role of words in sentences, intonation, and nonlinguistic items such as the intentions of a speaker and listener and their attentional foci. The discourse level of language is therefore not a purely linguistic structure but integrates several types of representations.
3. The boat that you believe the workman told Mary John painted is red.

What makes sentence 2 unacceptable is the nature of the syntactic boundaries that occur between the boat and painted. Chomsky and other have developed theories of what kinds of syntactic boundaries can and cannot occur between nouns and the verbs they are related to. These “constraints” differ in different languages, but all languages have restrictions on the syntactic categories that can intervene between elements that are related in certain ways, and these restrictions are always expressed in quite similar terms.

The theoretical issue that makes this analysis important is that Chomsky has argued that universal features of language such as the constraints on the relationship of items are innate. They must be innate, he argues, because it is impossible that a child would ever learn such constraints on the basis of the fragmented and limited exposure he or she has to language. Not only must they be innate, he argues, but the evidence suggests that these universal features of syntax are very abstract and specific to language. Indeed, the exact constraints on the relationship of items as just reviewed are only defined over syntactic structures. Chomsky argues that the child comes to the task of learning a language with a great deal of highly abstract knowledge of what language is like; his or her task is to set a few parameters of these models (such as how many and what types of nodes constrain the connections between particular types of items) to generate the language he or she is exposed to.

Other models of language make very different claims about the nature of innate features of language and the balance between innate knowledge and learning in the development of language abilities. In the past few years, some theorists have argued that the bulk of language acquisition is the result of a massive pattern-association process, supported by mechanisms that can be simulated in “connectionist” (or “neural net”) models (Seidenberg, 1997). While such models have had important successes in simulating a few isolated domains of language processing (see, e.g., Seidenberg and MacClelland’s (1988) model of learning to read), they have not begun to account for the vast majority of features of language that linguists have described. However, these models tend to be more realistic from a neurological point of view, whereas the neural mechanisms that underlie the representation of the abstract categorical features of language proposed by Chomsky and many linguists remain quite mysterious.

Creoles Suggest That Language May Have a “Default” Grammar

If certain aspects of language are universal and innate, and languages preferentially contain the most elementary structures consistent with these universal features of language, perhaps these features can be seen in some situations in which a language does not become fully developed. Bickerton (1990) has proposed that this is the case for spontaneously created languages. These include the sign languages created by untutored deaf children to allow them to communicate with one another and the many creoles that have developed across the globe. Of the two, creoles are the easiest to study.

Creoles are languages with simple syntactic structures that develop when speakers of several different languages are forced to communicate with one another. This can occur through immigration and invasion or when individuals are brought together from different cultures to work. The adults in such situations develop a crude pidgin, an impoverished communication system in which a limited number of nouns, verbs, and modifiers are combined with extensive gesturing. Children of the pidgin speakers learn their parents’ language, but not the pidgin; instead, in addition to using their parents’ language, they also create a creole for communication with one another that is based on the pidgin. All creoles share a set of common features, which can contrast with those in fully developed languages.

1. The grammar is based on word order; in contrast, most human languages rely largely on inflection (agreement and derivation—see earlier discussion).
2. There are seven parts of speech: nouns, pronouns, adjectives, verbs, adverbs, articles, and conjunctions; many human languages omit one or more of these categories or add new ones.
3. Nouns are distinguished as singular, plural, or indefinite in number; many languages lack the latter category.
4. There are three particles used as auxiliary verbs to indicate whether an action is successful, unsuccessful, or repeated; many languages lack these distinctions.
5. There is a single verb conjugation system; most languages have a general rule for most verbs, but special-case rules for most of the commonly used (irregular) verbs.
6. Questions are based on intonation rather than word order; many languages use both.

Bickerton points out that, in many cases, these universal features of creoles are not present in the
languages spoken by the parents of the children who created the creole. Therefore, creoles are very likely to be related to innately specified features of language.

However, even creoles do not illustrate such features directly. If all the features of creoles just listed were innate, it would be impossible to explain how any languages have any other features. Innate properties of language must be more abstract than the features found in creoles and must allow all the different forms of language that are currently found to develop. Instead of thinking of creoles as demonstrating universal features of language directly, we might better think of them as showing us what features of language develop most easily. It is possible that these features characterized human languages at an early stage of their development. If they did, our

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**FIGURE 52.7** A model of the major psycholinguistic operations involved in processing simple words.
goal must be to understand these properties of early human languages and also the processes that drove the diversification of the original human languages into the thousands of distinct tongues that exist today.

**Language Processing**

Every time a speaker produces an utterance and a listener recovers the meaning of that utterance, all the complex structures of a language must be activated. How is this done?

Current models of language processing subdivide functions such as reading, speaking, auditory comprehension, and writing into many different, semi-independent components, which are sometimes called "modules" or "processors." These components can be further divided into variable numbers of highly specialized operations, such as those involved in mapping features of the acoustic signal onto phonemes or in constructing syntactic structures from words. Each operation accepts only particular types of representations as input and produces only specific types of representations as output.

Models of language processing are often expressed as flow diagrams (or "functional architectures") that indicate the sequence of operations of the different components that perform a language-related task. Fig. 52.7 presents a model indicating the sequence of activation of components of the lexical processing system. Fig. 52.7 simplifies information flow in four ways. First, it does not specify the nature of the operations in each of the major components of the system. Second, it does not fully convey the extent to which the components of the system operate in parallel. Third, it does not convey the extent of feedback among the components of the system. Lastly, not all components are represented. Despite these simplifications, the model captures enough aspects of information processing in the language system to give an idea of what functional architectures of language processing look like.

Beyond specifying the flow of information through the language processing system, researchers have begun to understand the operating characteristics of its components. Several important features of language processing operations have been demonstrated in experimental laboratories or in studies of patients.

1. They are specialized for language. For instance, recognition of phonemes is probably accomplished by mechanisms that separate very early in the processing stream from those that recognize other auditory stimuli.

2. They are obligatorily activated when their inputs are presented to them. For instance, if we attend to a sound that happens to be the word "elephant," we must hear and understand that word; we cannot hear this sound as just a noise.

3. They generally operate unconsciously. We usually have the subjective impression that we are extracting another person's meaning and producing linguistic forms without being aware of the details of the sounds of words, sentence structure, and so on.

4. They operate quickly and accurately. For instance, it has been estimated on the basis of many different psycholinguistic experimental techniques that spoken words are usually recognized less than 125 ms after their onset, i.e., while they are still being uttered. The speed of the language processing system as a whole occurs because of the speed of each of its components, but also is achieved because of the massively parallel functional architecture of the system, which leads to many components of the system being simultaneously active.

5. They require processing resources. Although we do not appreciate it consciously, language processing demands some effort. It is unclear whether there are separate pools of processing resources for each language processing component or for language processing as a whole or whether language processing can "borrow" resources from other systems if it needs to.

The operations of the language processing system are regulated by a variety of control mechanisms. These control mechanisms include both ones internal to the language processor itself and those that are involved in other aspects of cognition. The first category—language-internal control mechanisms—consists of a large number of operations that schedule psycholinguistic operations on the basis of the ongoing nature of a given psycholinguistic task. The second category of control mechanisms—those that are related to cognitive processing outside the language system—determine what combinations of processors become active in order to accomplish different tasks such as reading, repeating what one has heard and taking notes on a lecture. Functional communication involving the language code occurs when people use these processors to inform others, to ask for information, to get things done, and so on. The use of language is thus one type of intentional action. There are conventions (or rules) that regulate the use of language for these purposes. However, it is a mistake to think that language is only used, or even mainly used, for functional communication and that language is, at its core, a communication system. The heart of human language is a system of representa-
Neural Organization for Language

Sources of Evidence Regarding Language and the Brain

This last part of this chapter reviews the functional neuroanatomy of language. The major techniques used to study the neural basis of language are listed. These techniques have also been used to study other human cognitive functions.

1. Correlating lesions with deficits. This is the approach that first gave insights into how language is organized in the brain. It originally consisted of studying a patient’s language and performing an autopsy on the patient after death to determine what part of the brain was affected by a disease. By looking at many patients, a picture of what deficits occurred after damage in particular brain regions can emerge. Today, instead of autopsy data, neuroscientists can obtain images of the living brain. Areas of both structural and metabolic damage can be identified using magnetic resonance imaging (MRI) and positron emission tomography (PET), and these areas can be analyzed by computer to identify the size and location of lesions quite accurately. Although autopsies remain the “gold standard” for determining where a lesion is located and what type of disease caused it, there are advantages to the use of radiological images compared to the use of autopsy material. Many more patients can be studied radiologically than can be studied via autopsy. Images can be obtained at the time the patient has a particular deficit, not years after the patient has been studied, so there is no chance that new diseases can affect the brain, confusing the correlation. The ability to reliably analyze these images is thus a great step forward in allowing deficit-lesion correlations to be studied.

2. Recording electrophysiological responses to language stimuli. The brain generates electrical charges and magnetic fields as it processes information. It is possible to record these charges and fields using event-related potentials (ERPs) and magnetoencephalography (MEG). By designing experiments in which participants process certain language structures while ERPs and MEG are measured, researchers can relate changes in ERPs and MEG to specific aspects of language processing. These changes in ERPs and MEG are rapid (they occur in milliseconds) and capture the time course of language processing. ERPs can be analyzed to indicate the general regions of the brain that are active during a particular process, and MEG can give much more detailed information about where these regions are.

3. Temporarily interrupting brain activity by local stimulation. Interestingly, stimulating the brain electrically usually results in interfering with language functioning, not producing it. Neurosurgeons first used this technique during operations in an effort to locate—and spare—the neural tissue involved in language. Now this approach is also used as part of looking for the location of tissue responsible for seizures in patients. In this approach, electrodes are temporarily placed above the brain (in the subdural space) for days to weeks, allowing a greater number of observations to be made. Some researchers have stimulated the brain across the skull, with no operation involved, using magnetic fields (transcranial magnetic stimulation or TMS). This approach also interferes with function and can be used to localize a language process.

4. Recording cell responses to language stimuli intraoperatively. A few neurosurgeons have recorded responses from cells during operations and related these responses to language functions. It is also possible to record from subdural electrodes (see earlier discussion); and this technique has been used to localize language.

5. Recording vascular responses to language stimuli using PET and functional magnetic resonance imaging (fMRI) (see Box 13.1). A rapidly expanding field is the recording of changes in blood flow and other responses of circulation to cognitive processes using PET and fMRI. As with ERPs and MEG, these approaches can be used in normal subjects, where they measure normal brain responses to language processing. They therefore provide a complementary type of information to the analysis of permanent or temporary lesions. PET and fMRI records can be analyzed to identify the location of increases and decreases in activity. The time scale of PET is somewhat slow (minutes), but adequate to study many language functions; the time scale of fMRI is faster (seconds). These techniques require careful experimental design to yield information about the neural tissue involved in supporting particular language functions.

The development of all of these techniques has been extremely rapid in the past decade. Neuroscience is in a period in which an enormous amount of data regarding brain and language is being collected. One result has been that our ideas about how the brain is organized to support language have changed considerably in the past decade or so. A second is that many new ques-
tions are being posed about the way the brain is organized to process language, and we do not have the answers to all of them yet. However, a fair amount is known about language-brain relationships.

Inventory of Brain Structures Related to Language

Human language depends on the integrity of the unimodal and multimodal association cortex in the lateral portion of both cerebral hemispheres. This cortex surrounds the sylvian fissure and runs from the pars triangularis and opercularis of the inferior frontal gyrus [Brodman’s areas (BA) 45, 44: Broca’s area] through the angular and supramarginal gyri (BA 39 and 40) into the superior temporal gyrus (BA22: Wernicke’s area) (Fig. 52.8). For the most part, the connections of these cortical areas are to one another and to the dorsolateral prefrontal cortex and lateral inferior temporal cortex. These regions have only indirect connections to limbic structures. These areas consist of many different types of association cortex, devoted not to sensation or motor function but to a more abstract type of analysis. The nature of this cortex and its patterns of connectivity are thought to combine to give language its enormous representational power and to allow its use to transcend biological immediacy.

![Figure 52.8](image1.png)  
**FIGURE 52.8** A depiction of the left hemisphere of the brain showing the main language areas. The area in the inferior frontal lobe is known as Broca’s area, and the area in the superior temporal lobe is known as Wernicke’s area, named after the 19th century physicians who first described their roles in language. Broca’s area is adjacent to the motor cortex and is involved in planning speech gestures. It also serves other language functions, such as assigning syntactic structure. Wernicke’s area is adjacent to the primary auditory cortex and is involved in representing and recognizing the sound patterns of words.

The evidence that language involves these cortical regions was originally derived from deficit-lesion correlations. Patients with lesions in parts of this cortex have been described who have had long-lasting impairments of language (“aphasia”). Disorders affecting language processing after perisylvian lesions

![Figure 52.9](image2.png)  
**FIGURE 52.9** Activation of parts of the language area by language tasks, as demonstrated by PET scanning.
have been described in many different types of
disease, in all languages that have been studied, in
patients of all ages and both sexes, and in both first
and subsequent tongues, indicating that this cortical
region is involved in language processing independent
of these factors. Functional neuroimaging
studies have documented increases in regional cere-
bral blood flow (rCBF) using PET or blood oxygena-
tion level-dependent (BOLD) signal using fMRI in
tasks associated with language processing in this
region (Fig. 52.9). Event related potentials whose
sources are likely to be in this region have been
described in relationship to a variety of language
processing operations. Stimulation of this cortex by
direct application of electrical current during neuro-
surgical procedures interrupts language processing.
These data all converge on the conclusion that lan-
guage processing is carried out in the perisylvian
cortex.

Regions outside the perisylvian association cortex
also appear to support language processing. Working
outward from the perisylvian region, evidence shows
that the modality of language use affects the location
of the neural tissue that supports language, with
written language involving the cortex closer to the
visual areas of the brain and sign language involving
brain regions closer to those involved in movements
of the hands than movements of the oral cavity. Some
ERP components related to processing improbable or
ill-formed language are maximal over high parietal
and central scalp electrodes, suggesting that these
regions may be involved in language processing. Both
lesion studies in stroke patients and functional neuro-
imaging studies suggest that the inferior and anterior
temporal lobe is involved in representing the meanings
of nouns. Activation studies also implicate the frontal
lobe just in front of Broca's area in word meaning.
Injury to the supplementary motor cortex along the
medial surface of the frontal lobe can lead to speech
initiation disturbances; this region may be important
in activating the language processing system, at least
in production tasks. Activation studies have shown
increased rCBF and BOLD signal in the cingulate
gyrus in association with many language tasks. This
activation, however, appears to be nonspecific, as it
occurs in many other, nonlinguistic, tasks as well. It
has been suggested that it is due to increased arousal
and deployment of attention associated with more
complex tasks.

Subcortical structures may also be involved in lan-
guage processing. Several studies report aphasic dis-
turbances following strokes in deep gray matter
nuclei (the caudate, putamen, and parts of the thala-
mus). It has been suggested that subcortical structures
involved in laying down procedural memories for
motor functions, in particular, the basal ganglia, are
involved in “rule-based” processing in language, such
as regular aspects of word formation, as opposed to
the long-term maintenance of information in memory,
as occurs with simple words and irregularly formed
words. The thalamus may play a role in processing
the meanings of words. In general, subcortical lesions
cause language impairments when the overlying
cortex is abnormal (often the abnormality can be seen
only with metabolic scanning techniques), and the
degree of language impairment is better correlated
with measures of cortical than subcortical hypometab-
olism. It may be that subcortical structures serve to
activate a cortically based language processing system
but do not themselves process language.

The cerebellum has also increased its rCBF in some
activation studies involving both language and other
cognitive functions. This may be a result of the role of
this part of the brain in processes involved in timing
and temporal ordering of events, or in being
directly involved in language and other cognitive
functions.

The other major component of the subcortical
region of the cerebral hemispheres is the white matter.
White matter tracts transmit representations from one
area to another. Lesions of white matter tracts discon-
nect regions of the brain from others and make the
operations performed in one region unavailable to
others. This can cause language disorders. The best
known such disturbance is pure alexia, in which a
patient can write but not read—not even read his/her
own writing. This can result from a lesion that
destroy the primary visual cortex in the left hemi-
sphere and extends forward in the white matter so
that visual information cannot get from the right to
the left hemisphere (Fig. 52.10). As discussed later,
because the left hemisphere is responsible for many
aspects of language (this is called “cerebral domi-
nance” for language), this lesion disconnects visual
input from language, resulting in the inability to read.
Because the language hemisphere still has access to
the motor system, the patient can write, however. In
addition to these “disconnection” syndromes, lan-
guage disturbances of all sorts occur with lesions
affecting many white matter tracts, while sparing of
language functions can follow lesions in the same
areas in different patients. The fact that multiple lan-
guage processing disturbances occur following sub-
cortical strokes that affect white matter is consistent
with the idea that a wide variety of information is
carried by white matter fibers. This also implies that
many of the areas of the cortex and/or subcortical
nuclei that carry out sequential language processing
operations are not contiguous. The fact that lesions in the same location can affect a particular function in one patient and spare it in another indicates that the areas in which functions are carried out are different in different individuals to some extent, or that white matter routes carry different information from one region to another in different individuals.

In summary, a large number of brain regions are involved in representing and processing language. Ultimately, they all interact with one another as well as with other brain areas involved in using the products of language processing to accomplish tasks. In this sense, all these regions are part of a "neural system," but this concept should not obscure the fact that many of these regions appear to compute specific linguistic representations in particular tasks. The most important of these regions is the dominant (usually left) perisylvian cortex. It is likely that if there are universal features of language structure that are innate, these features of language are related to features of this region of the brain. However, except for the macroscopic asymmetries between left and right hemispheres that appear to correlate grossly with lateralization (see later), these features are not yet understood.

**Lateralization**

Most language processing goes on in one hemisphere, called the "dominant" hemisphere. Which hemisphere is dominant shows considerable individual differences and bears a systematic relationship to handedness. In about 98% of right-handed individuals, the left hemisphere is dominant. The extent to which left hemisphere lesions cause language disorders is influenced by the degree to which an individual is right handed and by the number of nonright handers in his/her family. About 60–65% of nonright-handed individuals are left hemisphere dominant; about 15–20% are right hemisphere dominant; and the remainder appear to use both hemispheres for language processing. The relationship of dominance for language to handedness suggests a common determination of both, probably in large part genetic.
The neural basis for lateralization was first suggested by Geschwind and Levitsky (1968), who discovered that part of the language zone (the planum temporale—a portion of the superior temporal lobe; Fig. 52.11) was larger in the left than in the right hemisphere. Subsequent studies have confirmed this finding and identified specific cytoarchitectonically defined regions in this posterior language area that show this asymmetry. Several other asymmetries that may be related to lateralization have also been identified. The exact relationship between size and function is not known, as there are instances of individuals whose dominant hemisphere is not the one with the larger planum temporale. In general, however, relative size is a good predictor of lateralization. This is another example of the “bigger is better” principle that we saw applied to song nuclei in birds.

Although language was the first function known to be lateralized, and is still the best example of a lateralized function, it is not completely lateralized. Although not as important in language functioning as the dominant hemisphere, the nondominant hemisphere is involved in many language operations. Evidence from the effects of lesions and split brain studies, experiments using presentation of stimuli to one or the other hemisphere in normal subjects, and activation studies all indicates that the nondominant hemisphere understands many words, especially concrete nouns, and suggests that it is involved in other aspects of language processing as well (see later). Some language operations may be carried out primarily in the right hemisphere. The best candidates for these operations are ones that pertain to processing the discourse level of language, interpreting nonlinear language such as metaphors, and appreciating the tone of a discourse, e.g., the fact that it is humorous. Some scientists have developed models of the sorts of processing that the right hemisphere carries out. For instance, it has been suggested that the right hemisphere codes information in a more general way compared to the left, representing the overall structure of a stimulus as opposed to its details. This may be true for language as well as for other functions, such as visual perception. This and other suggestions provide the bases for ongoing research programs into the nature of language processing in the right hemisphere.

Organization of the Perisylvian Cortex for Language Processing

Because the perisylvian cortex is essential to the representation and processing of language, the way it is organized to support these functions has been the subject of much investigation. Two general classes of theories of the relationship of parts of the perisylvian association cortex to components of the language processing system have been developed. One is based on “holist” or distributed views of neural function and one on localizationist principles. The basic tenet of holist/distributed theories is that linguistic representations are distributed widely and that language processing components rely on broad areas of the association cortex. Localizationist theories
maintain that language processing components are localized in specific parts of the cortex.

**Holist Theories**

Lashley (1950) identified two functional features of holist/distributed models that determine the effects of lesions upon performance: equipotentiality (every portion of a particular brain region carries out a particular function in every individual) and mass action (the larger the neuronal pool that carries out a function, the more efficiently that function is accomplished). The features of equipotentiality and mass action jointly entail that (1) lesions of similar sizes anywhere in a specified brain region have equivalent effects on function and (2) the magnitude of any functional deficit is directly proportional to the size of a lesion in this specified area. Modern work with parallel distributed processing models provides formal models of holist concepts.

There is some evidence for holist theories. Lesions throughout the language area have been found in some studies to have similar effects on language functions, consistent with the principle of equipotentiality. There is an effect of lesion size on the overall severity of functional impairments in several language spheres, consistent with the principle of mass action. These results are consistent with a distributed, or holistic, neural basis for linguistic representations and processes. However, they do not necessarily show that these models are correct because they also could result from variability in the localization of language processing components across the population.

Holost models may be better models of how individual areas of the brain work to support language. A behavioral finding supporting holist theories is the frequent observation of so-called “graceful degradation” of performance within specific language domains after brain damage. For instance, certain dyslexics patients read irregularly spelled words according to a regularization strategy (e.g., pint is read with a short i). Some of these patients are more likely to make these regularization errors in words that are less frequent. This observation implies that frequent exposure to an irregular word makes its pronunciation less susceptible to disruption; that is, the “degradation” of the connection between a whole word and its sound is related to an individual’s experience with that word. Modern work with parallel distributed processing models indicates that such patterns of performance can arise following lesions in systems in which information is represented and processed in massively parallel, distributed forms. A very reasonable view is that different neural areas support different language functions and that each of these areas works as a whole, as holist models claim. Holism may not be wrong; it just needs to be applied on the right scale. As has been said, the brain may be “globally local and locally global.”

**Localizationist Theories**

Evidence against any holist model is the finding that multiple individual language deficits arise in patients with small perisylvian lesions, often in complementary functional spheres. For instance, some patients have trouble producing the small grammatical function words of language (such as the, what, is, he), whereas others have trouble producing common nouns. The existence of these two disorders indicates that the tissue involved in producing function words is not involved in producing common nouns in the first set of patients, and vice versa in the second set. Strong evidence against holist models also comes from activation studies that demonstrate vascular responses to particular types of language stimuli in restricted cortical areas. How language is organized at this finer-grained level in the perisylvian association cortex is an ongoing topic of research.

**Classical Clinical Localizationist Models**

The first localizationist theories emerged from clinical observations in the mid- and late 19th century. The pioneers of aphasiology—Paul Broca, Karl Wernicke, John Hughlings Jackson, and other neurologists—described patients with lesions in the left inferior frontal lobe whose speech was hesitant and poorly articulated and other patients with lesions more posteriorly, in the superior temporal lobe, who had disturbances of comprehension and fluent speech with sound and word substitutions. These correlations led to the theory that language comprehension went on in the unimodal auditory association cortex (Wernicke’s area, Brodmann area 22) adjacent to the primary auditory cortex (Heschl’s gyrus, Brodmann areas 41) and that motor speech planning went on in the unimodal motor association cortex in Broca’s area (Brodmann areas 44 and 45) adjacent to the primary motor cortex (Brodmann area 4). These theories incorporated the idea that localization of a language operation depends on the way it is related to sensory and motor processes. According to this view, speech planning goes on in Broca’s area because Broca’s is immediately adjacent to the motor area responsible for movement of the articulators and Wernicke’s area is involved in comprehension because it is immediately adjacent to primary auditory cortex.

These ideas and models were extended by Norman Geschwind and colleagues in the 1960s and 1970s.
### Classical Aphasias

<table>
<thead>
<tr>
<th>Syndrome Location</th>
<th>Clinical Manifestations</th>
<th>Hypothetical Deficit</th>
<th>Classical Lesion Location</th>
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<tr>
<td>Broca’s aphasia</td>
<td>Major disturbance in speech production with sparse, halting speech, often misarticulated, frequently missing function words and bound morphemes</td>
<td>Disturbances in the speech planning and production mechanisms (Broca’s area)</td>
<td>Posterior aspects of the third frontal convolution</td>
</tr>
<tr>
<td>Wernicke’s aphasia</td>
<td>Major disturbance in auditory comprehension; fluent speech with disturbances of the sounds and structures of words (phonemic, morphological, and semantic paraphasias); poor repetition and naming</td>
<td>Disturbances of the permanent representations of the sound structures of words</td>
<td>Posterior half of the first temporal gyrus and possibly adjacent cortex (Wernicke’s area)</td>
</tr>
<tr>
<td>Pure motor speech disorder</td>
<td>Disturbance of articulation Apraxia of speech, dysarthria, anarchia, aphemia</td>
<td>Disturbance of articulatory mechanisms</td>
<td>Outflow tracts from motor cortex</td>
</tr>
<tr>
<td>Pure word deafness</td>
<td>Disturbance of spoken word comprehension repetition</td>
<td>Failure to access spoken words often impaired</td>
<td>Input tracts from auditory system to Wernicke’s area</td>
</tr>
<tr>
<td>Transcortical motor aphasia</td>
<td>Disturbance of spontaneous speech similar to Broca’s aphasia with relatively preserved repetition; comprehension relatively preserved</td>
<td>Disconnection between conceptual representations of words and sentences and the motor speech production system</td>
<td>White matter tracts deep to Broca’s area connecting it to parietal lobe</td>
</tr>
<tr>
<td>Transcortical sensory aphasia</td>
<td>Disturbance in single word comprehension with relatively intact repetition</td>
<td>Disturbance in activation of word meanings despite normal recognition of auditorily presented words</td>
<td>White matter tracts connecting parietal lobe to temporal lobe or portions of inferior parietal lobe</td>
</tr>
<tr>
<td>Conduction accurate aphasia</td>
<td>Disturbance of repetition and spontaneous speech (phonemic paraphasias); good comprehension</td>
<td>Disconnection between the sound patterns of words and the speech production mechanism</td>
<td>Lesion in the arcuate fasciculus and/or corticocortical connections between Wernicke’s and Broca’s areas</td>
</tr>
<tr>
<td>Anomic aphasia</td>
<td>Disturbance in the production of single words, most marked for common nouns. Intact comprehension and repetition</td>
<td>Disturbances of concepts, and/or the sound patterns of words</td>
<td>Inferior parietal lobe or connections between parietal lobe and temporal lobe; can follow many lesions</td>
</tr>
<tr>
<td>Global aphasia</td>
<td>Major disturbance in all language functions</td>
<td>Disruption of all language processing components</td>
<td>Large portion of the perisylvian association cortex</td>
</tr>
<tr>
<td>Isolation of the language zone</td>
<td>Disturbance of both spontaneous speech (spare, halting speech) and comprehension, with some preservation of repetition; echolalia common</td>
<td>Disconnection between concepts and both representations of word sounds and the speech production mechanism</td>
<td>Cortex just outside the perisylvian association cortex</td>
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Geschwind added the hypothesis that word meaning was localized in the inferior parietal lobe (Brodmann areas 39 and 40) because word meanings consist of associations between sounds and properties of objects, and the inferior parietal lobe is an area of multimodal association cortex to which fibers from the unimodal association cortex related to audition, vision, and somesthesia project. Geschwind’s model remains the best-known localizationist model of the functional neuroanatomy of language and is widely cited in clinical practice. The model is said to receive support from the existence of about 10 aphasic syndromes, described in Table 52.3, which serve the clinical purpose of helping to localize lesions.

However, despite its widespread use, this model has distinct limitations. It deals only with words, not with other levels of the language code. From a linguistic and psycholinguistic point of view, the syndromes are all composed of many processing deficits, which are different in different patients. The correlations between syndromes and lesions may reflect the fact that speech fluency is a critical dimension along which patients are classified, and nonfluent aphasias tend to be due to anterior lesions that affect motor structures whereas fluent aphasias tend to be due to posterior lesions that do not. The syndromes themselves do not provide a guide to the localization of more specific components of the language processing system. Ongoing work seeks to address this question.
The next sections review localizationist models in three areas: processing of phonemes, word meaning, and syntactic structures. These areas cover a spectrum with respect to abstractness of linguistic representations.

Localization of Phonemic Processing

A great deal of research on auditory perception indicates that complex auditory patterns provoke responses in cells in the auditory association cortex in the superior temporal lobe. It has long been theorized that phonemic perception, a quintessential example of complex auditory processing, takes place in this region. However, many lesion-deficit studies show that impairments in both discrimination and identification of phonemes follow strokes throughout the perisylvian cortex, with perhaps the greatest frequency following strokes in the inferior parietal lobe. Activation studies using PET, fMRI, and MEG have added to this picture. In many studies, contrasts between simply listening to speech and listening to a low-level auditory baseline (such as white noise) activate both left and right temporal lobes, whereas more complex tasks involving phonological representations, such as rehearsal, making rhyme judgments, and recognizing specific sequences of phonemes, have activated parts of a larger area that includes the left inferior parietal lobe and Broca's area.

To account for these results, it has been suggested that the superior temporal lobe of both hemispheres is involved in perceiving phonemes in an unconscious, automatic fashion as part of the process of recognizing words and that parietal and frontal areas, particularly in the left hemisphere, are involved in the conscious use of these representations (Hickok and Poeppel, 2000). Storage of these forms in short-term memory is thought to involve inferior parietal structures and rehearsal to involve Broca's area. Some researchers have gone further in localizing phonemic processing within the superior temporal lobe. Binder (2001) has argued that, contrary to a century-old belief, phoneme recognition involves the anterior, not the posterior, part of the auditory association cortex (Fig. 52.12). The area of the superior temporal sulcus, anterior to the primary auditory cortex, has been specifically identified as a possible site for this type of processing.

This recent work has made the case that phonemic processing involves several different functional operations and that each of them is localized in small parts of the language area. It retains the classical idea that phonemic recognition takes place in the auditory association cortex, but claims that this is the case only when the listener is recognizing words unconsciously and that this unconscious type of phonemic processing occurs bilaterally. Consciously controlled tasks that involve phonemes are thought to take place in other areas of the brain—the inferior parietal and inferior frontal cortex.

Localization of Word Meaning

As noted earlier, traditional neurological models of the neural basis for word meaning maintained that the meanings of words consist of representations of physical properties, which are associated with word sounds in the inferior parietal lobe. It is now known that most lesions in the inferior parietal lobe do not affect word meaning. Functional neuroimaging studies designed to require word meaning do not tend to activate this region. The idea that word meaning resides in this area therefore appears to be incorrect. Damasio (1989) developed a closely related model, suggesting that the meanings of words included "retroactivation" of neural patterns all the way back to the primary sensory cortex. In an extension of this model, Damasio proposed that these associations were more likely to reside in the frontal cortex for verbs and in the parietal and occipital
cortex for nouns because verbs refer to actions, memories for which would involve motor planning that had taken place in the primary and unimodal association motor cortex, and nouns refer to static items, memories for which would involve sensory processing that had taken place in the primary and unimodal sensory association cortex. As noted previously, the meaning of a word includes much more than its sensory and motor associations, so activating neural tissue in which such associations are stored would not account for all of word meaning.

Word meaning is affected by lesions in the inferior temporal lobe. This may be partly due to visual agnosia, which results from the disruption of high-level visual processing involved in object recognition that occurs in this location. However, this is not likely to be the entire reason for the effects of lesions in this region on word meanings. Patients with a condition known as semantic dementia, a degenerative disease that affects the anterior inferior temporal lobe, have major problems with many aspects of semantic memory and word meaning that extend beyond visual object recognition disorders. The important lesions in these patients are in the left hemisphere, corresponding to left hemispheric specialization or lateralization of semantic memory and lexical semantic representations and processing. Patients with lesions due to herpes encephalitis, which also affects the inferior and medial temporal lobe (in many cases, somewhat more posteriorly than in lesions in semantic dementia), also exhibit semantic deficits. Activation studies have implicated the inferior temporal cortex in representing word meanings. ERP studies have documented a robust wave—the N400—that arises when subjects are presented semantically anomalous sentences, such as I take my coffee with cream and cement. The N400 is also found in the unrelated trials in word priming experiments in which subjects are presented with sequences of related and unrelated words. The N400 has thus been interpreted as a wave that arises when semantically unexpected material occurs and, as such, a wave that reflects some aspect of semantic processing. Although the intracerebral sources of ERPs are hard to determine with certainty, there is some evidence that this wave originates in the inferior temporal lobe.

Activation studies using PET and fMRI have also shown increases in blood flow in semantic tasks in the inferior frontal lobe, just in front of what is usually taken to be Broca’s area. In the earliest PET studies on language, Petersen and colleagues (1988) found inferior frontal activation when subjects generated verbs associated with nouns compared to when they repeated the nouns. Petersen and colleagues interpreted this as evidence for involvement of this frontal cortex in processing word meaning. This interpretation has been controversial since it was first proposed, with alternative accounts being suggested, such as the possibility that the activation reflects the category-shifting aspect of the verb-generate task or the production of verbs (for the reasons outlined above). However, other studies support the interpretation that this frontal activity is due to semantic processing and is not restricted to verbs. For instance, one study found that making judgments about whether sentences contained synonyms or only closely semantically related words activated the left inferior frontal lobe, and decreased activation in the left inferior prefrontal cortex has been reported during repeated semantic processing of both words and pictures.

The picture that is currently emerging about lexical semantics is that it is represented multifocally. To explore this issue further will likely require making fine contrasts regarding the nature of the semantic representations that are being localized and the tasks that utilize these representations. In this respect, the picture that may emerge could be similar to that currently suggested in the domain of phonemic processing, where different uses of phonemic representations seem to involve different cortical regions.

Localization of Syntactic Operations

Syntactic comprehension deficits are typically established by showing that patients can understand sentences with simple syntactic structures (e.g., The boy chased the girl) and sentences with complex syntactic structures in which the relationships between nouns and verbs can be inferred from a knowledge of real-world events (e.g., The apple the boy ate was red), but not sentences with complex structures in which the relationships between nouns and verbs depend on a syntactic structure that needs to be constructed (e.g., The boy the girl pushed was tall). Deficits in syntactic processing in sentence comprehension occur in all aphasic syndromes and after lesions throughout the perisylvian cortex (Caplan et al., 1985, 1996). Conversely, patients of all types and with all lesion locations have been described with normal syntactic comprehension (Caplan et al., 1985). These data are most compatible with the idea that syntactic operations are localized, but in different locations in different individuals.

Functional neuroimaging sheds additional light on this topic. Using fMRI, Just et al. (1996) reported an increase in activity (BOLD signal) in both Broca’s area and in Wernicke’s area of the left hemisphere, as well as smaller but reliable increases in rCBF in the homologous regions of the right hemisphere when subjects
read and answered questions about sentences that contained syntactically complex relative clauses. In a different series of studies, PET activity associated with making plausibility judgments about syntactically simple sentences was subtracted from that associated with making judgments about sentences with the same words and propositions phrased in syntactically more complex forms. Broca’s area was activated in subjects who performed the task quickly and accurately (Fig. 52.13), whereas subjects who were much slower activated other structures. This may be because different areas support the same syntactic operation in high- and low-proficient subjects. Alternatively, the reason that subjects who are less proficient in performing syntactically based comprehension tasks activate other brain regions may be that they utilize supporting cognitive mechanisms, such as short-term memory or visual imagery, to help them perform the task.

Overall, these data are consistent with localization. They appear to suggest variation in the localization of syntactic processing within the language area across the adult population. Alternatively, at least some of the data can be understood by supposing that performing sentence comprehension tasks is a complex process that engages support mechanisms to different degrees in different individuals, in part as a reflection of how proficient they are at assigning syntactic structure and determining the meaning of sentences.

CONCLUSIONS

Human language is a unique representational system that relates aspects of meaning to many types of forms (e.g., phonemes, lexical items, syntax), each with its own complex structure. Animal communication systems are neither as complex nor as powerful as human language. Nonetheless, they have some similarities to language and provide clues as to the neural basis of human language. Perhaps the most important lessons learned from animal studies are that complex communication systems can be innate, that learning can shape an innately specified range of behavioral possibilities, and that communication systems can rely on specific nuclei within the brain. Assuming that there are important universal structural features of human languages, human language may have similar neural features. Animal studies also provide evidence for laterization and localization of the neural basis for communication systems, which are features of the functional neuroanatomy of human language. Other features of the neural basis for animal communication systems, such as seasonal variation in the size of birdsong nuclei and the mechanisms that underlie this phenomenon, are not obviously relevant to human language.

Deficit-lesion correlations and neuroimaging studies are beginning to provide data about the neural structures involved in human language. It
appears that one area of the brain—the left perisylvian association cortex—is especially important in representing and processing language (although other regions are involved as well), and that, within this area, particular language operations are localized in specific regions. The exact details of these localizations are just beginning to be understood, as the modern tools of cognitive neuroscience are applied to this problem.

References


Suggested Readings


David N. Caplan and James L. Gould