Ann. Rev. Anthropol. 1977. 6:509–61

BIOLOGY, SPEECH, AND LANGUAGE

❖9604

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> *When the primeval matter had congealed but breath and form had not yet appeared, there were no names and no action.* The opening sentence in Kojiki, the oldest book in Japanese, completed A.D. 712. (264).

INTRODUCTION: THE IMPORTANCE OF LANGUAGE

The problems of symbolic language and of mind are the great problems in the evolutionary transit through three billion years from the first genes to man. Some interpret mind, and the ability to symbol, as an intrusion of complete novelty unique to the human species (44, 171, 172, 348). They emphasize the radical mental gap between man and other animals.

Others, including the philosopher Bergson and the geneticist Sewall Wright (359), suggest that if we are consistent in the criteria we use to attribute mind to other members of our species (especially those whose language we understand, although we cannot enter into their stream of consciousness) then we must ascribe minds to chimpanzees, other primates, and the higher vertebrates. If vertebrates have minds, why not all animals? Plants? Viruses? Individual cells? Genes? Nucleotides? Hydrogen atoms? Subatomic particles? They view mind as an aspect of all reality, they see the world as a multiplicity of minds, each with two aspects: (*a*) as it *is* to itself (mind), and (*b*) as it *seems,* as an incursion into the mind of another (matter). By stressing the evolutionary continuity of mental experience, Griffin (105) has reopened the question of animal awareness and discussed possible windows on the minds of animals. If most scientists accept biological evolution in animals and man, why do some shy away from the concept of continuity in mental experiences including language?

New studies on the brain and language, especially the split brain findings, help to resolve this major dichotomy in the theory of mind and communication—that consciousness is or is not a universal property of all things. Because the balance of the neurophysiological evidence favors the conclusion that consciousness is selectively localized within human and other mammalian brains and that some functionally important neural systems (cerebellum, etc) lack the property of conscious experience, Sperry (304) argues that it is not necessary to assume consciousness in brainless things such as plants or hydrogen atoms. Because the stream of consciousness in a human individual can be divided into right and left realms by cutting a set of forebrain fiber systems at the neocortical level, he concludes that "consciousness is an operational derivative of activity in particular cerebral circuit systems designed expressly to produce their own specific conscious effects . . . with action *upon* as well as *from* neural events" (304, p. 429). The evolutionary continuity of mental experience may embrace man, chimpanzees, dogs, horses, and octopuses, but not oak trees nor photons.

There are three great realms of evolution: cosmic, organic, and cultural (including linguistic) (191, 205, 206, 285). The evolutionary theory of language transformation is accepted by all who have mastered the empirical evidence, a process that requires some years of individual study. Some, like Chomsky, while accepting the general notion of linguistic evolution, are sceptical that we can discover anything verifiable and interesting about the actual past evolutionary linguistic events. Greenberg (102, p. 110) contends that the theory of evolution as transformation (as opposed to special creation) applies with relatively minor detailed alteration both to linguistic and biological change. In the *Descent of Man* (61, p. 40) Darwin remarked that "the formation of different languages and of distinct species and the proofs that both have been developed through a gradual process are curiously parallel." Descartes took biology and language apart; Darwin put them back together. In fact, as Greenberg (102) shows, scientific theories of linguistic evolution predate those on organic evolution. Among others, Hill (119, 120) urges the development of continuity theories of the evolution of human language.

White (347) distinguished four stages in the evolution of minding—simple reflex, conditioned reflex, insight, and symbol defined by yes or no answers on two criteria: dependence on intrinsic properties, and dominant role of organism. White restricted symbolling, mostly manifest in language, to man alone. Such classifications are useful in looking at major steps in the evolution of language, but it is doubtful that pure examples of even the "simple reflex" exist in nature (8, 220). In the classical monograph *Behavior of the Lower Organisms,* Jennings (143) showed that protozoans have in some degree all of the Aristotelian sensory modalities of man (hearing, sight, smell, taste, touch) and that they learn from individual experience to modify their behavior adaptively. The offspring of female insects that "instinctively" lay their eggs only on one species of plant (e.g. the silkworm, *Bombyx moti,* on mulberry leaves), "learn" a new instinct if the experimenter removes the eggs to a different species of leaf that is suitably nutritious (8).

The genesis of a new symbol is not as arbitrary and capricious as Leslie White claims. It is always based on a link to the past. There is a new association of stimuli, a new meeting of actors, or some new circumstance where the new symbol grows out of and emerges from old symbols, not completely new, but remodeled and redefined and still an arbitrary symbol. We know symbols mostly through words. And new words are variations of old words; the variation is arbitrary but not without linkage, phonetic or other, to old expressions.

We cannot talk intelligibly about the "square root of minus one"—a new symbol $\sqrt{-1}$ in 1637 A.D.—unless we know something about several different mathematical ideas, starting with numbers, negative numbers, roots, square roots, and so on. As Hoijer wrote, "meanings . . . are not in actual fact separable from structure" (130, pp. 92–104).

White is correct in emphasizing that the important cultural transmission of symbols is not by genes and that the important biological transmission of simple reflexes is by genes. But nongenic transformation of information in nonhuman animals is well known. For instance, Denenberg & Rosenberg (64) observed that the effects of handling experimental rats in infancy can be transmitted over at least two generations; presumably the maternal physiology and behavior of handled rats is altered, and this effects the experience of their offspring whose maternal behavior is, in turn, changed with results still detectable in their own young (220, p. 24).

Cooper (52) reports that insect eumenid (*Rygchium foraminatum*) and sphecid (*Trypoxylon clavatum*) females lay 1–10 provisioned eggs in a linear set of cells in a burrow 4–6 mm in diameter and 150 mm long. Early pupae can turn around but mature ones cannot. The mature pupae regularly face the sole exit of the burrow. The female makes the burrow walls asymmetric in relation to the exit, the mortar of the burrow wall serving as a communication channel from mother to offspring stored in an artifact in digital form.

Sapir (288) emphasized that language is an overlaid physiological function that uses diaphragm, lungs, vocal tract, tongue, teeth, lips, ears, and brain centers originally evolved for different purposes. The emphasis is proper but misleading if we assume that when language arrived it moved into a structure designed and built for other occupants and yet this language, different in degree if not in kind from anything that existed before, found the old structure so perfect in meeting the new function, that no alteration nor rebuilding was necessary. This is as unlikely a happening in historical biology as in real estate.

It is true that language uses structures originally used for other purposes, but it is also true that considerable modification, redesigning, and rebuilding is involved in the evolutionary acquisition of language (33, 184). The overlaying of function, such as the use of reptilian jaw bones to make mammalian inner ear bones, is an important process of evolutionary change. Overlaying of function is part of the reason that complex structures such as the vertebrate eye, or the blow hole of the whale, which, as the antievolutionists say, had to be perfect before they could function, came into being phylogenetically by gradual change (281, 300).

A wide variety of scholars including philosophers (171, 172), biologists (301), and psychologists (86) make language the most important result of the evolutionary developments that distinguish human beings from other species. As Sapir said (288, p. 235):

> "Language is the most significant and colossal work that the human spirit has evolved —nothing short of a finished form of expression for all communicable experience. This form may be endlessly varied by the individual without thereby losing its distinctive contours; and it is constantly reshaping itself as is all art. Language is the most massive and inclusive art we know, a mountainous and anonymous work of unconscious generations."

If propositional, spoken language is the most distinctive part of human cultural behavior, the brain is the most distinctive part of human anatomy and physiology (48, 144, 184).

It is possible and proper to study language and the brain together (186, 271). A new quarterly journal devoted entirely to neurolinguistics, *Brain and Language,* started publication in 1974, edited by Harry A. Whitaker. The biological foundations of language is one of seven announced "interests" of the new (1971) quarterly *Journal of Psycholinguistics,* edited by R. W. Rieber. R. Hoops and Y. Lebrun are editors of the recently founded international monographic series called *Neurolinguistics.* Harry A. Whitaker is editor of a new series on *Perspectives in Neurolinguistics and Psycholinguistics,* of which the first two volumes, *Studies in Neurolinguistics,* edited by Haiganoosh Whitaker and Harry A. Whitaker, appeared in 1976 and volume 3 is announced for 1977.

It is also possible and proper to study human language (15, 288), society (256), or culture (348) without consideration of biological variables except those of universal generic man. Human propositional language is a biological, a psychological, a cultural, and an individual process. Most biologists recognize the importance of psychological and cultural variables in speech and language; some anthropologists (e.g. 18, 19) deny any important explanatory power to biological variables in normal linguistic variation. Fifteen years ago, study of the interconnections of biology and language was virtually taboo among many anthropologists and most linguists. Today, observing, experimenting, speculating, and model-building in neurolinguistics, psycholinguistics, and glottogenesis is widely considered interesting, important, respectable, and sometimes verifiable [for details see many of the 75 papers in the 1976 *Origins and Evolution of Language and Speech* (111)].

The molecular geneticist Luria (214) pointed out that recent attempts to biologize language differ fundamentally from some recent attempts to biologize (human) aggression, ethnic differences in measured intelligence, or the ecological crisis [for a recent critical review see Reynolds (273)]. A biology of language could be a truly humane science that considers qualities common to all human beings and not to supposed genetic differences between peoples. Luria's biology of language would include a biology of the thinking process including logical structures, a priori ideas, artistic creation, and even connecting to ethical principles, but with full realization that nearly all of the socially important contents of language is of environmental origin, controlled not by genes but by upbringing. He speculates that this language-and-biology research may generate an applied science by discovering better ways to teach, to learn, and to make use of what we learn. It is important to note that Luria's main justification for treating language as a biological phenomenon (but not to deny that it is also a sociological, cultural, or genuine linguistic phenomena) comes from

Chomskian linguistics, specifically the conclusion that human language universally is based on innate grammatical and syntactic structures common to all normal human beings, that languages are functional manifestations of a species-wide genetically determined system of neural connections in the cerebral cortex and other parts of the brain.

Most of the works reviewed here were published after Lenneberg's *Biological Foundations of Language* (184), the baseline reference for the present article, but some earlier works are noted that have special human biological interest in relation to speech and language. Also, in general, works mentioned in the 1974 *Annual Review of Anthropology* article by Dingwall & Whitaker (66) on neurolinguistic aspects of brain localization of language function, linguistic and neurological analyses of aphasia, and manipulative studies of brain and language function are not included here unless they have special importance to the topic being considered. At least 1000 titles relevant to biology, speech, and language published in the last 10 years are not included in this review: titles of most of them may be found in *Bibliographie Linguistic de l'Année; Biological Abstracts; Current Citations on Communicative Disorders: Language, Speech, Voice;* and *Psychological Abstracts.* The massive *Origins and Evolution of Language and Speech* (111) and the recent two-volume *Studies in Neurolinguistics* (336) arrived barely in time for inclusion of several papers.

Details of four recent scientific developments that account for much of the current interest in biology and language—Chomskian universal deep-structure linguistics (41–46, 111), physiologically oriented psycholinguistics (111, 231, 232), and the related topics of pongid "language" and "ethology and language"—are not covered in this review. Since the innovative work of Gardner & Gardner (86) in teaching American Sign Language to a chimpanzee, all three living species of great apes have been involved in man-ape communicative studies (10, 170, 185, 186, 308). The results shatter excessive anthropocentrism and are widely discussed in the scientific and popular media. The papers by Fouts, Malmi, Miles, Premack, Rambaugh & Gill, and Terrace & Bever (111) provide an entry to the relevant sources. The work of Fouts and his associates (including the Norman chimpanzees) on direct chimp-to-chimp transmission of learned and shared sign language is of special importance.

There is a rich, recent literature from ethologists, primatologists, and comparative psychologists on behavioral parallels and possible continuities in linguistic (sensu lato) evolution, especially via birds and mammals (111, 245). Among anthropological linguists, Sebeok's compilations and comments (294–296) are particulary useful.

SPEECH AND LANGUAGE

Just as biology progresses splendidly without a widely accepted definition of life, and psychology with little agreement on the definition of mind or intelligence, linguistics has become perhaps the most sophisticated discipline in the human behavioral sciences without full agreement on *the* definition of language. There is no exhaustive compendium of language definitions to match Kroeber & Kluckhohn's (166) catalogue of culture definitions, although many of the latter include the former as a major part. Laguna (169) discusses several widely used definitions of language. The definitions listed in *Webster's Third* make speech and language sometimes synonymous, othertimes not. Premack (269) points out that a comparative psychological theory of language requires a functional definition, but that most definitions of language by linguists are structural. Toulmin (321) advocates a "functionalist" alternative to Chomsky's "nativist" account of language. Sampson (286) counters Toulmin by arguing that language cannot be explained functionally. The animal psychologists Gardner & Gardner (86) chide linguists for continually changing their definition of language so as to exclude new findings on chimpanzee and other nonhuman animal communication. Hockett, a linguist, devised design features universal in human language with the plan to discover how many of them are present in animal "languages" (122–125, 127). A definition of the linguist Lieberman (194) that says "language is a system of communication that permits exchange of new information" grants language to some insects (98). As Hirsh (121) points out, definitions like that of Lieberman and Mattingly (see 151)—"linguistic communication requires that a string of phones [e.g. insect stridulation, bird song] be transmitted from one individual to another"—eliminates the problems of whether language communication must involve speech or must be uniquely human to disappear.

Some behavioral scientists interested in man use "speech" and "language" almost interchangeably (91), some draw no clear distinction between "speech" and "language" (288), some make the distinction a nonradical difference in kind (85), and others a radical difference in kind (289, 348). As a human biologist, I will relate *speech* to the behavior of individuals; *language* to the behavior of populations.

Some behavioral scientists interested in man argue that they are concerned only in empirically observable behavior (15), some claim that we cannot ignore mental events in talking scientifically about speech and language (85, 265). Some say that our scientific business is to *describe* animal, primate, and human communication (194, 269, 295, 296); others make the prime test of behavioral science the ability to *control* what animals and people do (232). As a human biologist, in this particular review, I will be interested in skin-out observed behavior, skin-in mental events including the possibility of animal awareness (105), descriptions of what primates do as organisms, and with brains and speech apparatuses, and I fully acknowledge that in some instances the special kinds of animal communication called human speech and language "are excellent examples of man's ability to control the behavior of some other people" (231).

Four decades ago, in making distance and direction of movement in a total goal-oriented act known by objective observation the fundamental concept of animal behavior, Tolman (320), founder of purposive behaviorism and pioneer in animal behavioral genetics, excluded human behavior involving language and society from that formulation.

In a book completed just before his death, Leslie White (348, pp. xi-xii) wrote "Language(s) could not exist without man. But language, as a distinct order of phenomena—with its structure and processes of lexicon, grammar, syntax, phonetics, phonemics—is not to be explained in terms of man as a human animal; man is not an explanatory device in the science of linguistics." White emphatically does not deny the relevance of psychology in the realm of language and "man and culture": symbolates may be interpreted meaningfully in both psychological (including physiological) and culturological contexts; a treatise on grammar with no reference to biology does not invalidate or oppose a biologist's interest in the nerve-muscle-hard tissue actions, or conceptual and emotional factors involved in speech and language. "*The human behavior of peoples is determined by their respective cultures.* (I say *peoples* because the human behavior of individuals is affected, but not determined, by their biological makeup)" (p. 8). "It was the emergence of symbolling in the course of neurological evolution that transformed prehuman primate society into human cultural systems" (p. 21). "The 'institutions,' habits, and knowledge that the first human beings took over from their prehuman antecedents were important, but they were crude, simple, and meager. And, without articulate speech, the possibility of progress on a merely primate level seems to have been extremely limited if, indeed, it existed at all. It was symbolling—particularly articulate speech—that changed all this: it created cultural systems and launched them upon a course of development. In the Word was the Beginning." For White, symbolling and articulate speech are not synonymous; articulate speech is a particular form of symbolling, the most important characteristic expression of this ability (pp. 22–23).

Part of the difficulty with theories that make biology important for speech but irrelevant for language is the restriction of "biology" to the study of individuals. Human biology and biological anthropology include both individual and population biology (112, 316a). The individual man or woman who speaks, respires, feeds, excretes, and so on, is not *the* individual unit of enduring biology because he or she can maintain the species characteristics only for a limited time. The system that endures, that makes survival in sexually reproduced species nearly permanent, is not that of any single person or creature, but is embodied in two or more sexes (six in *Euplotes,* eight in *Paramecium*), and in the members of the local breeding population, and ultimately in the whole species (361). Language cannot be reduced to the biology of individuals; it can be related to the biology of populations.

Kroeber (165), most linguists (15, 41–45, 85, 102, 122, 127, 194, 265, 288, 289) and many anthropologists (19, 33, 114, 273, 348) insist that language is a system.

> Systems differ from congeries in that the first are meaningfully integrated; the latter have their elements associated fortuitously. The principal pure systems in culture are Language, Science, Fine Arts, Religion, and Ethics. Being integrated, each of these has a "self-directing unity"—something immanent—with a "margin of autonomy" against forces outside. Language is the most autonomous. . . . There is of course no novelty in recognizing these divisions or parts or segments of culture. . . . Similarly, whole cultures, be they little primitive ones or great civilizations, certainly exist and have a history; but languages, philosophies, economies, and so on, though they occur universally in all cultures, occur only *in* them, and never occur independently in the world, any more than nervous systems float free and detached (165, pp. 176–77).

The statements in this paragraph on the relations between speech and language are paraphrased or directly quoted from de Saussure (289) or from Gardiner (85):

Language is the general term including all those known items that enable a speaker to make effective use of words. Much of this knowledge was learned in childhood, most goes back to the child's family, community, group-tribe-nation, and to the species biology. The lexicon is continually enlarged, and areas of word meaning widened or narrowed. Every utterance has a double aspect that gives linguistics two of its most fundamental distinctions, that between speech and language, and that between the sentence and the word (85). The sentence is the unit of speech (some sentences use only one word). Words are one unit of language; syntactic rules and specific types of intonation in speaking words are other less tangible units. Words, as such, are not units of speech, for they lack the vivifying breath and willpower of a speaker requisite to call speech into being. The child learns language in order to exercise it as speech. The ultimate basis of speech is the fact that individual thoughts and feelings are, as such, entirely private and inalienable. Words are psychical entities and not objects of sense. In de Saussure's terminology, words are diachronic, sentences are synchronic. Of course, several-word sentences have sequence and duration in time, but the time occupied by a spoken sentence is short compared to a human life-span. Speech is triggered by an external or internal stimulus that later forms the thing-meant. Speech uses words to communicate; articulation translates words into sound waves which the listener translates back into words of the dictionary common to listener and speaker. Instances of speech (and spoken language) have four aspects: speaker, listener, spoken words, and thing-or-things meant. Speech is an abstract term, but it applies concretely to a particular speaker's act, firstly, that is relevant to a particular occasion, listener, and thing-meant, and secondly, that is due to the volition of the speaker, whose articulate utterance projects into reality the word-signs used, and endows them with a vitality absent from them at other times. Language enters into speech, but speech is the sole generator of language. Speech is the skill of shaping the muscles in and around the mouth and in the voice box in such a way to produce speech sounds. Language is the capacity to understand what is said and to construct sentences. Both speech and language depend on physiological mechanisms in the central nervous system. Either may become nonfunctional, interfering selectively with one or the other skill. In verbal communication, language is more basic than speech; many adult aphasics who cannot speak continue to have language, to read, write, and fully understand (142).

Mánczak (219), an admirer of de Saussure, questions on theoretical grounds the reality of the distinction between *langue* and *parole*.

Lenneberg (184) studied several children with minor brain damage before or shortly after birth that interfered with speech so that they never babbled and never were able to produce understandable speech. Such children may develop the capacity for language if they grow up in a family or institutional environment where they hear usual conversation and are spoken to frequently and normally. Fourcin (80a) describes a case of superior language development in the complete absence of expressive speech in an adult male congenital quadriplegic spastic with severe athetosis and bilateral high-frequency hearing loss. Some individuals are observed to have language without speech.

A striking example of speech without language or cognition comes from the case report of Geschwind, Quadfasel & Segarra (95) on a patient who had received extensive cerebral damage from carbon monoxide poisoning, resulting in essential isolation of the language areas of the dominant hemisphere from the rest of the cerebrum. The patient became a "talking machine" that repeated everything spoken to it and thus retained the capability of decoding auditory speech input, at least briefly retaining and encoding speech, without any contact with the rest of the brain and hence isolated from other cognitive functions and language. A case of isolation of the language function in a 59-year-old female suffering from presenile dementia is reported by H. Whitaker (335) along with a review of the literature and a neurolinguistic interpretation of echolalia. Some individuals are observed to have speech without language.

The possibility of inventing a private language is proposed by Ayer (5) and rebutted by Rhees (274). In a reprinted version, (6) Ayer adds one crucially important footnote, doubting that it is possible to construct a language all of whose words refer to nothing but private things in Wittgenstein's sense (see Cook 50): "I am now inclined to think that in any language which allows reference to individuals there must be criteria of identity which make it possible for different speakers to refer to the same individual. This would not prevent the language from containing private sectors, but it would mean that my idea that these private sectors could be made to absorb the public sectors was not tenable" (6, p. 263, fn. 10).

Speech is private in the sense that recordings of individual voices can be identified (322). Language is something that is spoken and listened to socially. Language is a population phenomenon, speech a phenomenon that involves two or more individuals belonging to the same language population.

BRAIN, SPEECH, AND LANGUAGE

The volume of a contemporary, normal, adult human brain is approximately 1.4 dm^3, the weight is around 1.2 kg, and its power about 2.5 W. Making up about 1/50 of the adult total body mass, the brain consumes about 1/5 of the total daily oxygen requirement (9, 173). Most recent attempts to define man in zoological terms stress the relatively large brain (48, 301), and most students of human paleontology point to man's recent spectacular phyletic increase in brain volume (48, 144, 299) and brain organization (132–134, 257–259).

In wide taxonomic comparisons, say between genera or families, the structure and function of the brain often show a strong correlation with behavioral differences. Probably the most remarkable case of physiological selfwise development is that reported by Giersberg (cited in 240, p. 348), who exchanged by transplantation at an early stage the brains of different species of toads (*Pelobates fuscus*) and frogs (*Rana arvalis*): an adult animal possessing a *Pelobates* brain in a *Rana* body performed the strong digging instinct characteristic of *Pelobates* and lacking in *Rana.* Evans (75) showed that members of two families of flat-fish, the sole (Soleidae) and the plaice (Pleuronectidae), have widely different hunting methods and that their brain structure and sense receptors reflect the difference: the sole hunts by smell and touch, has small eyes and a large olfactory lobe; the plaice hunts by sight and taste, has large, prominent, and movable eyes, and a small olfactory lobe.

During ontogeny the growth of the human brain contrasts with the growth of body weight in man in that the brain grows in the pattern characteristic of body weight in subprimate mammals and birds. Curvilinear growth of the human brain starts immediately at birth and continues in a rectilinear course to about puberty, without the adolescent spurt shown in the growth of human body weight. For this reason, man, and to a lesser extent the higher primates, spends a considerable part of the growth period with a nearly full-size brain housed in a body smaller than full size (314), an adaptation facilitating the long period of acquisition of language and culture distinctive of our species.

Luria (212), with the higher mental functions in view, describes three basic trends in the evolution of the brain in the primate lineages leading to the apes and man: (*a*) diminished specificity of cortical areas, with the primary sensory-projection areas occupying a smaller portion of the cortex; (*b*) lateralization of function, leading to a linguistically dominant hemisphere; (*c*) particular enlargement of two areas of the cortex: the anterior frontal areas and the inferior parietal areas.

For Rozen, a specialist on memory (283), the development of language has undoubtedly been a major factor in the evolution of the brain. Later in this section we consider the possible role of tools in this context.

Jerison (144) reviewed and synthesized the massive literature on brain evolution with special reference to allometric studies on brain size, using power equations of the sort

$$\text{Brain weight} = b(\text{body weight})^a$$

where a is the slope and b the Y-intercept of a log-log regression plot. Gould (99) gives a general review of the literature on allometry and size in ontogeny and phylogeny in a wide variety of animals.

In interspecific plots for mammals ranging in size from mice to elephants where each point represents an average adult of each species, the slope is 0.66, implying that between species brain weight increases slower than body weight but in step with body surface area, thus conforming to the theoretical power of 2/3 relating increase in brain weight and external body surface area suggested by dimensional analysis (144).

In intraspecific plots where each point represents an adult within one species, or the means of a population (including a race) belonging to a species, or samples from closely related species (for instance, the macaques), slopes range from 0.2 to 0.4, close to the universal theoretical slope of 5/18 or 0.28 proposed in 1898 by Lapicqué for brains of related adults that develop by enlarging old neurons without adding new ones.

Pilbeam & Gould (266) marshal the evidence that these two allometric relations support criteria to distinguish intraspecific functional equivalence in cephalization among related forms at the same evolutionary grade ($0.2 < a < 0.4$) from phyletic increases in cephalization independent of body size (a $> 2/3$). If related species differing in body size show a brain-body allometry with $a = 5/18$, they are of the same evolutionary grade; if related species in a time sequence evolve to larger body size with endocranial volume scaling $a > 2/3$, we must conclude that a phylogenetic increase in cephalization has taken place (266).

Using the available 3 points for plots within African pongids, Pilbeam & Gould (266) found that $a = 0.34$ for pygmy chimpanzee, chimpanzee, and gorilla. They found that the 3 points plotted for australopithecines produced a linear regression of the same slope ($a = 0.33$), indicating that the large *Australopithecus boisei* has the brain size expected in an australopithecine 1.5 times the body weight but otherwise similar in genetical design to the smaller *A. africanus.*

They obtained a much different regression by plotting 4 points representing a hominid lineage; use of *A. africanus* → *Homo habilis* → *H. erectus* → *H. sapiens* yields the slope $a = 1.73$ showing that the brain volume increased with marked positive allometry during the past two or three million years. Clearly the distinctive evolution of the hominid brain since the late Pliocene is a special adaptation unrelated to the mere physical requirements of increasing body size (133, 266). The critical factors in the phyletic volume increase, and, judging partly from the fossils but mostly from living forms, in brain organization advance, are often identified as the evolution of tools, of language, of general cognitive ability, or of some combination of these (see below).

The cumulated net evolutionary increase in hominid brain volume in the last few million years, and especially during the last one-half million years, is spectacular and well known (22, 48, 132–134, 144, 257–259, 281, 299) but the estimated increase *per generation* is commonplace and within the lower range of rates observed for some domestic and experimental animals under artificial selection (76). Cavalli-Sforza & Bodmer (37) considered the rate of evolutionary change in endocranial volume from *Homo erectus* to *H. sapiens* in terms of selection differentials operating during the past 500,000 years. The selection differential (S) is the difference between the mean phenotypic value of individuals selected as parents and the mean of all individuals in the parental generation before selection was made. The response to selection (R) is the difference between the mean phenotypic value of the offspring of the selected parents and that of the parental generation before selection. Under specific conditions, the ratio of response to selection differential is equal to the heritability (h^2), that is, the proportion of phenotypic variance due to additive genetic variance, and $S = R/h^2$. Using a standard deviation (σ) of 100 g for brain weight, the observed change of 500 g over the last 500,000 years, taken to occupy 25,000 generations, gives a rate of change in σ units per generation of $500/(100 \times 25{,}000) = 0.0002$. Assuming a heritability of 0.5 gives an average selection differential of 0.0004 per generation—very much smaller than selection differentials commonly achieved under artificial selection in chickens, swine, sheep, and cows (76). The same conclusion holds if the heritability is lower, say 0.1–0.2.

Figure 1 identifies the anatomical terms used below to discuss some aspects of brain structure of interest to students of biology and language. Until 1968, despite

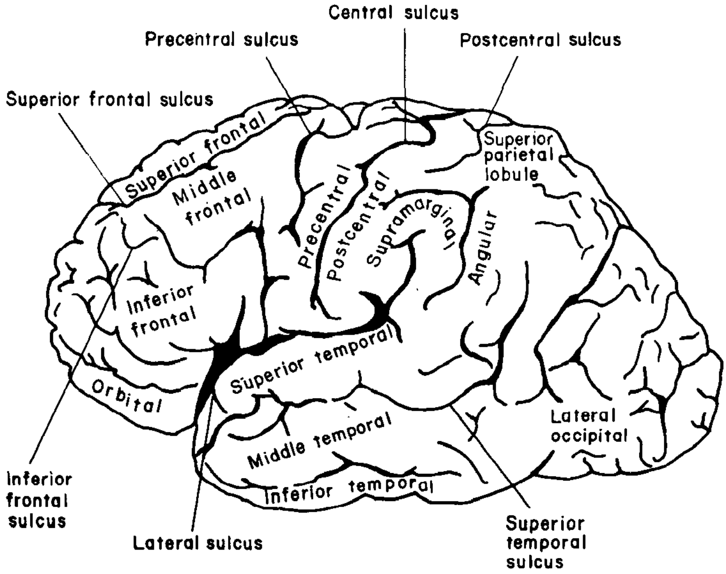


Figure 1 Outline sketch of the lateral surface of the left cerebral hemisphere of an adult human brain showing the main gyri and sulci.

several earlier reports to the contrary, it was generally accepted that the usual lateralization of the left hemisphere for speech and language was not associated with significant structural differences between the two sides of the brain (21, 22). In that year Geschwind & Levitsky (94) examined 100 adult human brains free of significant pathology obtained at postmortem. They demonstrated an anatomical asymmetry (often marked) between the upper surfaces of the right and left temporal lobes. The planum temporale (the area behind Heschl's gyrus and in front of the posterior end of the lateral sulcus on the superior surface of the temporal lobe) is larger on the left in 65% and larger on the right in only 11% of brains. The mean length of the outer border of the planum temporale was 3.6 ± 1.0 cm on the left and 2.7 ± 1.2 cm on the right (the difference being significant at the 0.001 level), that is, the planum averaged 0.9 cm or one-third longer on the left than on the right temporal lobe. The planum temporale is a part of Wernicke's speech center.

Figure 2 is a schematic drawing of the brain viewed from above with parts of the frontal and parietal lobes lying over the upper surface of the temporal lobe cut away to expose the transverse temporal gyri (of Heschl) and the planum temporale (of von Economo) which cannot be observed from outside the intact brain because they are located within the deep infold of the lateral sulci. A horizontal cut has removed the upper surface of the insula and other parts of the upper surface of the temporal lobe medial to the transverse gyri and planum temporale. The degree of bilateral difference shown in the size of the planum is within the observed human range but is larger than average.

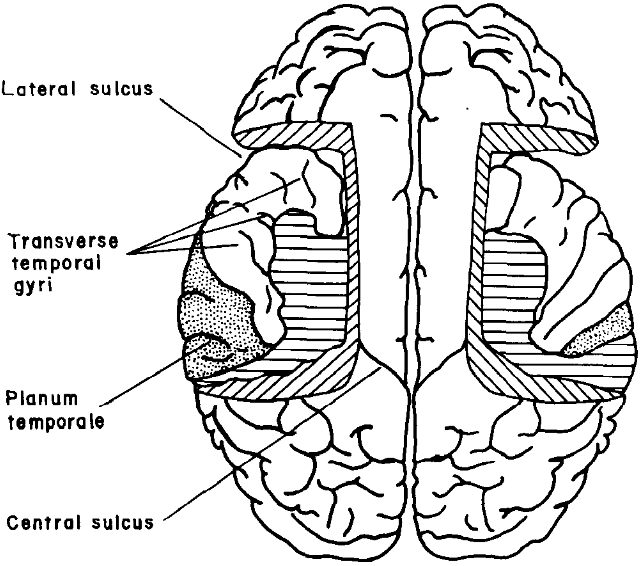


Figure 2 Hemispherical differences in the anatomy of the posterior speech area (of Wernicke). Parts of the brain lying above the upper surface of the temporal lobe have been cut away to expose the transverse temporal gyri (of Heschl) and the planum temporale which cannot be seen in the intact brain because they lie within the lateral sulcus. A horizontal cut has removed other parts of the temporal lobe's upper surface. The planum is considerably larger in the left hemisphere.

Probably the earlier observations by Flechsig 1908, Pfiefer 1936, and von Economo & Horn 1936 (cited in 94) of this left-right asymmetry of the planum were not generally accepted because the authors did not publish measurements or based their observations on small samples.

In 1969 Wada (cited in 91; see also 325) showed that the asymmetry of the planum is present at birth. In later studies the anatomical asymmetry of this major part of Wernicke's center has been confirmed on adequate samples by Astakhova & Karacheva (4), LeMay & Culebras (181a), and Witelson & Pallie (354). LeMay & Geschwind (182) report on hemispheric differences in the brain of the great apes.

Many aspects of neurophysiology applicable to man, say at the molecular and cellular level, are best studied in nonhuman primates and other experimental animals (361). Direct investigation of the problem of the organization of language in the brain cannot be carried out on experimental animals because none of them have language in the full human sense, although rudimentary forerunners of this ability may exist (86, 120, 128, 170, 269). Speech and language disorders observed following localizable brain damage provide the best evidence on the neural basis of linguistic behavior. Geschwind (91) gives an excellent compact account of the major ideas and procedures in this branch of neurolinguistics, a subject to be considered in more detail in the later section on Whitaker's model on the representation of language in the human brain. Welker (333) presents a review of some guiding concepts used during the past century of inquiry into localization of brain functions.

Some years ago several distinguished linguists, including Bloomfield (15) and Sapir (288), scoffed at the search for "speech centers," not so much from considerations of the biological evidence for or against localization but from full recognition of the social transmission of language content. Bloomfield's argument in 1933 (15, pp. 36–37) is worth quoting at length:

> Now, speech is a very complex activity, in which stimulation of every kind leads to highly specific movements of the throat and mouth; these last, moreover, are not, in a physiologic sense, "organs of speech," for they serve biologically earlier uses in man and in speechless animals. Many injuries to the nervous system, accordingly, will interfere with speech, and different injuries will result in different kinds of difficulty, but the points of the cortex are surely not correlated with specific socially significant features of speech, such as words or syntax; these appear plainly from the fluctuating and contradictory results of the search for various kinds of "speech centers." We may expect the physiologist to get better results when he looks for correlations between points of the cortex and specific physiologic activities concerned in speech, such as movement of special muscles or the transmission of kinesthetic stimuli from larynx and tongue. The error of seeking correlation between anatomically defined parts of the nervous system and socially defined activities appears clearly when we see some physiologists looking for a "visual word-center" which is to control reading and writing: one might as well look for a specific brain center for telegraphy or automobile driving or the use of any modern invention. Physiologically, language is not a unit of function, but consists of a great many activities, whose union into a single far-reaching complex of habits results from repeated stimulation during the individual's early life.

That speech has a population (social) component is fully recognized by all biologists concerned with the study of language. Nearly four decades ago Bloomfield or Sapir could not have foreseen the development of an integrated, or at least correlative, human biology of individuals *and* breeding populations nor foretold the marked extent of genetic variation within local breeding populations (37, 112), nor realized the rich data supporting localization (in a specific neurophysiological sense) of Exner's writing center. The old sociological dictum of "one human species biology—many human societies and cultures" must be rejected flatly at most fundamental levels.

Exner's center is localized at the posterior end of the second frontal convolution just anterior to the hand area of the precentral motor cortex (57, 66). Lesions in this area disrupt writing output as do lesions in some other cortical areas. Do we conclude therefore that writing is not localized in the cortex? Not so, because the specific kind of writing error *is* localized. A subject with damage to Wernicke's area cannot write dictated speech but can copy writing visually. One with a lesion in Exner's area shows change in the form of written output (91, 210, 284, 342).

The question of localization depends on what aspect of language one is interested in. Some aspects are local in the cortex, some are diffuse. For nearly every possible aspect, nearly everyone would put more localization in the cerebrum than in the foot. Penfield (262) showed that electrical stimulation of a point in Wernicke's area can disrupt speech output of a *noun* (e.g. "comb" when shown a picture of a comb) but not the *verb* "to comb" (e.g. when shown a picture of a comb the patient does not identify "comb" but may say "I comb my hair." Or when shown a picture of a foot, the patient says not "foot" but "that is what I put in my shoe.")

Part of the current difficulty in communication between biologists and linguists about speech and language is that the biological notions of "function" and "localization" are composite. Some biological things and events called "functions" are highly specific and sharply localized in some sense; others are unspecific and spread through the whole body, or even into the skin-out environment. Insulin functions in carbohydrate metabolism (and perhaps in other intracellular roles); the production of insulin in the body is localized in the β-cells lying near the center of the Islets of Langerhans in the pancreas. The function of gametes in bisexual organisms is to bring together two haploid sets of genetic material to form a diploid zygote; production of sperms and eggs in higher animals is localized in specific tissues in the gonads. Metabolism, reproduction, and mutation are three global functions basic to the operation of natural selection and the evolution and maintenance of species. The global function of locomotion is also clearly important in metabolism and reproduction. The global functions are located in all or much of the whole body. Most physiologists would localize language in the brain and not in the heart or liver, nor even in the "organs of speech." Yet one of the few known major genes with a specific effect on language production involves an enzyme mostly active in the liver (histidine α-deaminase, see below); thus at least one specific aspect of speech/language is localized in the liver. In one or more meaningful sense there are demonstrable biological speech and language centers. Many modern linguists point out that language has an important biological function. According to Hockett (127):

> The major biological function of talking is to *redistribute information* among members of a community. The kind of talking with which we do this may be called *consultative prose*. It is different from, usually duller than, some other kinds of talking, but it is the germ from which all other kinds derive. It is consultative prose that gets information shared and gets joint plans made.

Whitaker & Selnes (345) review individual and bilateral anatomical variation in the human cerebral cortex and conclude that lack of strict correspondence between lesion sites and behavioral deficits is expected.

Authorities disagree whether Broca's area is unique to the human brain [compare (22) with (342)]. Cytoarchitectural studies support the presence of a cell structure typical of the human Broca's area in apes and some Old World monkeys (164). For a review of the structure of the cerebral cortex in nonhuman primates see (260). Bogen & Bogen (20) proposed that mapping Wernicke's area with a probability distribution giving the likelihood at any locus of a language defect from a lesion at that locus would be a major step toward resolution of the long-standing controversy between topism and holism. Brain weight in normal adults varies from 680 to 1939 g. Cerebral cortical surface area varies by 310 cm^2. Amount of striate (visual) cortex on the outer cerebral surface varies threefold, 359 to 1308 cm^2. The central fissure, one of the striking landmarks on the lateral surface of the brain, may be interpreted by a gyrus connecting the frontal and parietal lobes, as in some monkeys. The planum temporale and Heschl's gyrus (including Wernicke's language area) are the most variable regions of the brain in cytoarchitecture (72). Waddington (327) reports marked variation in number and pattern of branching of the major cerebral arteries so that occlusion of any single branch would result in damage to widely different amounts of brain tissue in the language areas. In otherwise neurologically normal individuals undergoing brain surgery, even the topography of the precentral motor and postcentral sensory cortices—generally considered to be innately wired-in—may show complete reversal of the standard localization for lip and jaw movements and tongue and cheek sensations [Ojemann, cited in (345)]. In general, cortical cytoarchitecture is more variable in the right than in the left hemisphere; on both sides gyral patterns are highly variable in Broca's area [Stengel in (345)] and in the auditory cortex [Campain & Minckler in (345)]. Dobelle & Mladejovsky (in 345) found that the phosphene map (sensations of light spots produced by electrical stimulation to the striate cortex through the skull) varied considerably in 15 individuals demonstrating concomitant physiological and anatomical individual differences in brain function. Patzig (261) illustrates lateral views of the brains of identical twins with marked variation in the cortical configuration, indicating that such individual variation is nongenetic.

Kimura (157, 158) studied the hemispherical localization of the capacity to interpret numbers, words, non-sense syllables, and melodies by the method of dichotic (two ear) listening. Two different sounds are presented simultaneously through earphones to each ear. Three pairs of sounds are presented in rapid succession. The subject repeats all he hears in any order he selects. Electrophysiology shows that the right ear usually has a richer nerve supply to the left auditory cortex than does the left ear. The same holds for the tracts from the left ear to the right auditory cortex. If speech is localized in the *right* hemisphere as determined by sodium amytal tests (326), recall of digits is 89% for the left ear and 78% for the right during dichotic testing. The ear on the side opposite the hemisphere dominant for speech is superior in dichotic listening regardless of handedness. Dichotic listening tests show that speech is hemispherically localized as early as age 4 years. Dichotic tests indicate that boys are slower to develop speech asymmetry than girls just as they are well known to be slower on the average in the onset of speech.

In dichotic listening to melodies the left ear is superior, showing that the area for singing is located in the right hemisphere. This finding offers an explanation of the observation that individuals with severe central speech impediments can sing beautifully and individuals with left hemisphere dominant for speech with Broca's aphasia can sing elegantly and easily. Kimura (157) suggests that speech is distinguished from nonspeech sounds by articulability rather than by conceptual content. Vowels show weaker right-ear effect than consonant + vowel syllables.

McAdam & Whitaker (224, 344) produced the first physiological evidence for the localization of speech production in a specified convolution in the intact human brain. The experimental subjects were eight right-handed young-adult females with normal speech. Bechman miniature biopotential electrodes were attached to the skin over the precentral gyri, Broca's area, the corresponding part of the third inferior frontal convolution on the right, the mastoid processes, and on the frontal bone to serve as a ground. The subjects, starting with the vocal apparatus in the neutral position, made four sets of responses: 1. spitting gestures, 2. words of three syllables with initial "k," 3. coughs, and 4. words of three syllables with initial "p." Slow negative electrical potentials were recorded at a maximum over Broca's area in the left hemisphere (but not the right) when the polysyllabic words with initial "k" or "p" were produced. When the nonspeech spit and cough occurred the electrical potentials recorded were bilaterally symmetrical.

Eimas and associates (73) studied the discrimination of synthetic speech sounds in 1- and 4-month-old infants. The experimental stimuli were synthetic speech sounds recorded by a parallel resonance synthesizer with three variations of /b/ and three of /p/, the six stimuli having voiced onset time values of –20, 0, +20, +40, +60, and +80 msec where the minus sign indicates that the voicing occurs before, and the plus sign after, the release burst. Discrimination was measured by an increase in conditioned sucking response rate on an artificial nipple. The results show that infants 1 month old not only respond to and discriminate speech sounds but also show categorical perception of speech sounds along the voicing continuum in approximately the same manner in which adults perceive these phonemes. This is done with relatively limited exposure to speech, with practically no experience in producing speech, and with little or no differential reinforcement for speech behavior. Seemingly categorical discrimination of voiceless and voiced stops is a part of the biological makeup of the human species and this makeup is operative within the first month after birth long before the infant has learned a language.

In recent years knowledge of the circulation of blood in the brain has increased greatly, mainly due to development of quantitative measures of both global cerebral blood flow (CBF) and regional cerebral blood flow (rCBF) summarized by Ingvar & Lassen (138, 139). It is now firmly established that normal variation in CBF is determined by the activity of the cerebral neurons and that rCBF variations not only reflect the anatomical connections of blood vessels in the regions of the brain, but also can be used for indirect measurements of brain activity and its distribution in specific parts of the two hemispheres (138).

Voluntary rhythmic hand movements are accompanied by a highly localized contralateral increase in rCBF in the rolandic hand area (252), especially along the central fissure and in the postcentral areas (139). Speech and reading provoke increased rCBF in superior, anterior, and posterior language cortices (140). The amount of increase in CBF during voluntary muscle activity depends upon the effort of the subject, while localized rCBF distribution (at least in the dominant hemisphere) reflects aspects of the specific physiological events underlying the way the brain handles symbols and abstractions (138, 277).

Normal human adults readily coordinate and integrate information perceived via different sensory modalities, and much of everyday adaptive human social behavior, including language, depends on the capacity for cross-modal perceptions. Freides (81) surveys recent experimental work on cross-modal perception with human subjects (including the blind, deaf, brain damaged, as well as normal children and adults). The equivalence in visual and tactile modes is now established in preverbal children below 1 year of age without specific language training, thus ruling out verbal mediation as a basic mechanism.

Postulated relationships between cross-modal integration and specifically human language are based on a wide variety of observations on man and other animals (62, 170): (*a*) the early failures to demonstrate clear cross-modal perception in nonhuman primates (63, 90); (*b*) neuroanatomical evidence for the relative independence of auditory, visual, somesthetic association areas in nonhuman primates in contrast with their neural connectivity in man (88, 91); (*c*) the apparent improvement of cross-modal perception in children in step with the acquisition of language; and (*d*) language deficiencies in children congenitally deprived of one or more sensory modes, especially the deaf-mute and the deaf. These observations appear to support the assumption that cross-modal perception is a uniquely human capacity and is necessarily mediated by language (62).

Since 1969 Davenport and associates have demonstrated in several papers (reviewed in 62) that apes have the capacity for haptic-visual cross-modal perception of objects and multidimensional representations of those objects without previous learning involving those objects. Davenport uses "haptic" in place of "touch" to denote active manual exploration. Cowey & Weiskrantz (53) used a well-designed experiment to demonstrate cross-modal perception in rhesus macaques. Over several days they presented variously shaped objects overnight to the macaques in darkness. Some of the objects were edible and some inedible. In the dark the monkeys ate the edible objects after haptic examination. In later tests *using vision alone* the macaques routinely chose the edible objects in discrete trials composed of one edible and one inedible object, thereby demonstrating haptic-visual cross-modal perceptual equivalence in a primate phyletically divergent from man by some 30 million years. Ettlinger (74) concluded that neural connections in the cerebral cortex of man, apes, and presumably some monkeys, that are absent in prosimians and nonprimates, enable the observed greater degree of cross-modal perception in the higher primates. The recent experiments on cross-modal perception support a high degree of continuity rather than discontinuity in the neurological evolution of language capacity from apes to man—an important difference in degree rather than a radical difference in kind evolved over several millions of years, a conclusion supported by an increasing number of topics in human behavioral evolution.

Most of the concepts and methods used to examine the representation of language in the living human brain cannot be applied to fossil specimens no matter how well preserved (134, 145). Natural (144) or reconstructed (133) endocranial casts provide reliable and important data on the phylogeny of brain volume, but quite restricted evidence of highly controversial interpretation on the neural changes important for the evolution of language (133, 134). Some living people with brains smaller than those of hominids existing two or more million years ago [e.g. KNMER 1470 (see 258)] have full propositional language (184).

Figure 3 illustrates the difficulties in getting information even on the boundaries of the major lobes of the primate brain from endocranial casts. In the higher primates the detailed topography of gyri and sulci are not recorded on the surface

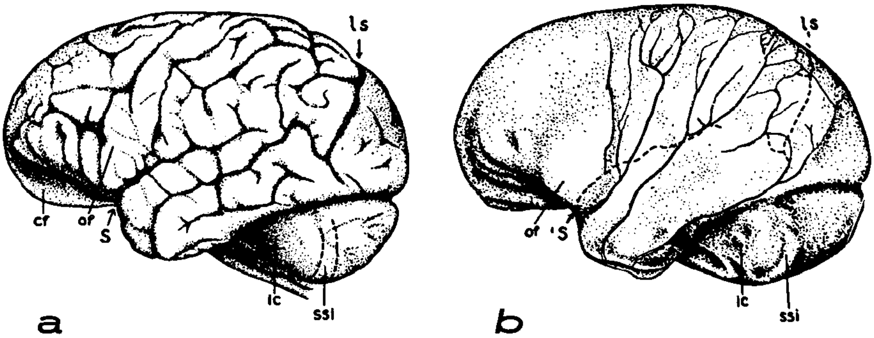


Figure 3 (a) Left lateral view of the brain of an adult male chimpanzee, X ½. The brain was hardened by injection before removal from the cranial cavity. (b) Left lateral view of the endocranial cast of the same chimpanzee to indicate how poorly the surface topography of the brain is preserved in an endocranial cast. From Weidenreich (331a).

of the endocast. The arrangement of the meningeal arteries is well preserved, but variation in these blood vessel patterns has yet to be related to language. A comparison of the brains and endocasts of chimpanzees by Le Gros Clark, Cooper & Zuckerman (49) in 1936 has long made primate paleoneurologists sceptical about the prospects of accurate identification of the functionally important small cytoarchitectural areas in fossil higher-primate specimens. But because such specimens provide the only data with geological time depth, their careful study is essential. Holloway in the US (132–134) and Kotchetkova in the USSR (161a–g) have published the most reliable studies.

The new information on brain asymmetries (181, 181a) and the open possibility that these bilateral variations can be specified with reasonable accuracy on endocranial casts provide some hope for a rich harvest of new information on the phyletic history of language in the near future.

GENETICS, SPEECH, AND LANGUAGE

In 1967 Lenneberg (184) wrote: "Pedigrees and twin studies suggest that genetic transmission is relevant to language facilitation. However, there is no need to assume 'genes for language.' " Likewise genetical investigation shows that genetic transmission is relevant to breathing and to precise manipulation using precision and power grips. And, likewise, there is no need to assume specific "genes for breathing" or "genes for manipulation." In the laboratory mouse, a mutant form of a single major gene prevents the development of the notochord and vertebral column (107). In one sense this is a "gene for breathing," and a "gene for nest building," or for all other general or specific activities including vocalization (349) of a mouse that survives with a normal vertebral column.

McKusick (225) catalogued the numerical status of known human genetic nosology in 1975: 1218 autosomal dominant, 947 autosomal recessive, and 171

X-linked gene loci, a total of 2336. Of these, hundreds of genes are known to be "relevant to language facilitation." As expected, more major genes are known to affect the four peripheral language modalities than the central language system, but many major genes do have fundamental importance for the structure and function of the central language system, starting, for instance, with those for anencephaly, or (by probable homology with a major gene known in the house mouse) for congenital absence of the corpus callosium (107), the largest single fiber tract in the human brain. Over 100 major gene loci are known to affect each of the visual, verbal, and auditory production and recognition systems, fewer are known that are specifically relevant to the tactile system. Given that all cases of severe mental retardation are relevant to language facilitation, well over 100 major gene loci are known to affect the central language system. These are catalogued in McKusick (225), many are representatively characterized in Bergsma (11), and some are discussed in more detail in Slater & Cowie (303), and in the many sources cited by the three works.

There is space here to mention only a few cases of major genes, polygenes, chromosomal abnormalities, and congenital defects of complex or unknown mode of inheritance that are of interest in the biological study of spoken or written language. Lenneberg (184) reviews sources up to 1966 (for additional surveys see 3, 233).

Histidinemia is the best known case in which a major gene has a specific, pinpointed effect on speech. This metabolic error, first described in 1961 by Ghadimi, Partington & Hunter (96), is inherited as an autosomal recessive genotype resulting in a defect in the enzyme histidine α-deaminase necessary for the normal metabolism of histidine to urocanic acid. The enzyme is active in the liver and the stratum cornium of the skin. The clinical findings in histidinemia are variable (11, 303). Subjects with the recessive genotype have increased concentrations of histidine in the blood plasma, generally above 6 mg/100 ml, and urinary output of histidine exceeds twice that normal for comparable age. Other laboratory findings include persistently low glutamic acid and high α-alanine in body fluids, and excretion of imidazolepyruvic, imidazolelactic, and imidazoleacetic acids in the urine. The sex ratio in the affected is one boy to two girls; this departure from the common sex ratio of about 1.05:1 is unexplained. Crome & Stern (56) suggest that the speech defect can be prevented, if treated early, by a diet low in histidine. As histidine is an essential amino acid required for normal growth, it cannot be eliminated from the diet while the child is growing, but it is not necessary for nitrogen balance in adults. About three-fourths of patients have specific speech difficulties, less than one-half show growth retardation, over one-third are mentally retarded, but about one-fourth are completely free from such symptoms (303). Woody, Snyder & Harris (356) suggest that inherited reduction in histidine α-deaminase activity can be expressed to a different degree in different tissues. Although most patients with histidinemia lack histadase activity in the skin, biopsies demonstrate that others have such activity, which may compensate for defective enzyme activity in the liver. A peculiar EEG pattern is found in some sibships with histidinemia (356).

Of the 10 cases of histidinemia surveyed by Witkop & Henry (355), 9 show defective speech articulation and language organization. Mispronunciations ("less" for "yes") are accompanied by a right deviation of the tongue tip and obicularis oris muscle and lateral movement of the mandible during elevation and descent in speech. The children have an auditory scramble manifested as an inability to repeat words in sequences added one at a time, a marked inability to link words together into a sentence. They have normal audiograms and normal response to sequential visual signals. Teachers characterize these children as visual learners who cannot learn by auditory means because of short auditory-memory span. The tongue is unable to perform movements independent of the mandible—"la, la, la" becomes "/ja/, /ja/, /ja/." The tongue is not able to rise to palatal contact while the mandible lowers for vowel formation. Consonants requiring independent movement of tongue and mandible (especially/t/, /d/, /n/, and /l/ are misarticulated to a degree varying with syllabic position relative to preceding and following vowels and consonants. The oral space requisite for vowel formation is reduced sporadically when the mandible assists or follows the tongue tip toward palatal contact in forming consonants. Errors occur in both syntax and noun usage.

The biochemical path(s) relating the enzyme deficiency to the auditory and speech production difficulties is (are) unknown. It is not known whether the defects result from accumulation of metabolic products such as imidazolelactic acid and imidazolepyruvic acid or the absence of metabolites like formiminoglutamic acid. Although the primary ahistidasia continues throughout life, the deleterious effects probably are restricted to the period of prenatal and infantile development.

Sex controlled or sex modified genic expression occurs when a genotype is expressed in both sexes but in a different manner in each. Bernstein (12) considered that the singing voice in adult Europeans is a sex-controlled trait with the low bass voice in males and the high soprano in females controlled by the same genotype, A^1A^1, the high tenor in males and the low alto in females by A^2A^2, and the baritone in males and mezzo-soprano in females by the heterozygote A^1A^2. Later studies showed that a single pair of alleles with simple expression in the two sexes is not sufficient to explain the facts, which await detailed analysis (307). The development of the voice box in the divergent male and female direction takes place at puberty under the influence of a testosterone-induced multiplication of cells in the thyroid and cricoid cartilages in boys at about the same time as the spurt in trunk length (314). Twin, family line, and population studies indicate that a polygenic mode of inheritance with many independently varying factors determines variation in voice types. The proportion of men with basso and women with soprano voices decreases from northern to southern Europe. Under Bernstein's single locus model the frequency of the basso-soprano allele (A^1) has a maximum of 61% along the northern coast of Germany and a minimum of about 12% in Sicily (13). Although the single locus model is now abandoned, there is good evidence that differences in multiple gene frequencies must account for the different frequencies of voice types in different populations (307).

Luchsinger (207) found that the voices of 28 pairs of monozygotic twins were very similar, the greatest difference being four half-tones in male identical twins 41 years old. A study of Japanese children analyzed by Schull & Neel (293) is the most elaborate attempt to measure the behavioral consequences of inbreeding in a human population. The study observed children in Hiroshima and Nagasaki. None of the parents of the children had received irradiation from the atomic bombs. The inbred children reported here are the offspring of single first cousins and the controls were children of parents whose relation was more remote than that of third cousins. "Age when walked" and "age when talked" are two behavioral criteria commonly used in pediatric and parental appraisals of child development. They are, of course, subject to errors of parental recall and may be biased by cultural norms. The mean age when talked was 11.81 months in the control boys, 12.60 in the offspring of first cousins, giving an inbreeding effect of 0.79 and a change with inbreeding of 6.7%. The mean age when talked for the control girls was 10.38, and 10.82 in the offspring of first cousins, giving an inbreeding effect of 0.44 and a change with inbreeding of 4.2%. As in 16 other behavior measurements, the mean of the inbred children is significantly depressed (at the 1% level for age when talked) compared with the mean of the control children. The inbred children as a whole come from families of lower socioeconomic status than the controls as measured by parental occupation and education, density of persons in the household, and food expenditures per person per month. However, none of the apparent inbreeding depression for age when talked could be attributed significantly to socioeconomic variation.

Lewitter, DeFries & Singer (190) performed a path analysis on 64 families with sons having a diagnosed reading disability. In general, educational level and occupational class of parents were found to have relatively little influence on their son's reading recognition, reading comprehension, spelling, perceptual speed, or perceived spatial relations, but the magnitude of the direct path between parent's and son's test scores suggested that the heritability of performance on these tests may be moderately high (0.3 to 0.7).

Moorhead, Mellman & Wenar (236) studied a family with an autosomal translocation involving chromosomes 13/22 and a total complement of 45 chromosomes in the mother and four of her six children. The father and the fifth child are karyotypically normal, and the youngest child has Down's syndrome with trisomy for chromosome 21 and does not possess the translocation. The father has normal intelligence and speech; the mother has normal intelligence and speech function except for a mild speech hesitation. Failure of speech is present in three of the four translocation-bearing children and does not seem to be causally related to intelligence level. The boy with IQ of 68 had not developed speech at 7 11/12 years of age. The 6-year-old girl has never developed intelligible speech and has an IQ of 38. The girl of 3 5/12 years spoke first words at 1 and spoke in sentences at 3 5/12 years; her IQ is 70. Her speech is the best developed of the children, but most of it is repetition of the sentences of others; she initiates simple but complete sentences. The youngest child with the translocation had not used words at age 2 1/12 years. The karyotype common to these four children and the mother is characterized by a hemizygous deletion for whatever genes occupied the eliminated minute element from chromosome 13. Seemingly, a double dose of genes at this locus is necessary for normal development of speech.

A syndrome involving deletion of about one-half of the short arm of chromosome 5 was discovered by Lejeune and associates (179) and named *cri du chat,* an unusual feature of the syndrome being a plaintive continual crying, particularly by younger children, which resembles the mewing of a cat. All patients with this chromosomal deletion have severe mental retardation but variable life span. Legros (178) published a phonogram of the cry of an infant with *cri du chat* syndrome.

Ward, Engle & Nance (327b) describe the laryngomalacia in 4 cases of *cri du chat* syndrome. The long, curved, flappy epiglottis, narrow diamond-shaped arrangement of the vocal cords during inspiration, and anterior approximation of the vocal cords during inspiration, and anterior approximation of the vocal cords with an abnormally large air space in the posterior commissure during phonation are responsible for the strident, cat-like cry.

Isochromosomes are formed if the centromere divides transversely, instead of longitudinally, in the second meiotic division; as a result the long arms of sister chromatids form one chromosome, and the short arms form another chromosome which in acrocentric autosomes is commonly lost (307). Wang et al (327b) reported two cases of isochromosomes 16, one with faulty speech characterized by spitting out words, the other mute.

Cleft uvula is a frequent cause of hypernasality of speech. The cleft is usually congenital, varies from a small notch to a complete cleft extending to the posterior border of the soft palate and is a result of the failure of complete fusion of the uvular portion of the lateral halves of the soft palate during embryogenesis. The mode of inheritance is unknown but probably is conditioned by minor gene(s) similar to those of cleft palate. The anatomical defect contributes to the palatal insufficiency syndrome involving incomplete closure of soft palate and pharynx during phonation and results in hypernasality. The trait is of special anthropological interest in that its prevalence is about 1 in 71 in European live births, less in African blacks, and greater in Asians, 1 in 10 to 1 in 5 (228–230).

Sankoff (287) presents several areas where historical linguistics (311a) and molecular and evolutionary genetics employ similar mathematical models and several where they are quantitatively different. Although the two fields are not perfect metaphors of one another, their attributes in common are sometimes so striking that many descriptive and analytical aspects are interchangeable. He suggests that models of gradual gene replacement seem a likely place to look for universals and variables of linguistic change. There is a striking parallel between the controversy surrounding chemical paleogenetics (362) and that in lexicostatistics. Cavalli-Sforza (36) and Cavalli-Sforza & Feldman (38, 39) discuss a number of similarities and dissimilarities in social-cultural-linguistic and biological evolution.

An identical capacity for language among all extant human races suggest that this capacity must have evolved before racial diversification (184). Conclusions about the existence of human races prior to historical records are usually based on skeletal, especially cranial evidence. With multivariate statistical methods and suitable samples of modern skulls of known race, racial identification may reach a reliability of 90% (167). Most anthropologists assume that the races of modern man date back no further than the formation of *Homo sapiens* as a species distinct from *H. erectus* (137). Campbell (34) divides *H. sapiens* into two sets of chronological subspecies with a 50,000 B.P. time-line separating the living geographical subspecies from the four fossil subspecies of Europe, Africa, western Asia, and eastern Asia, all of which are separated from the late subspecies of *H. erectus* by 300,000 B.P. If Le Gros Clark

(48) is correct in assigning Steinheim and Swanscombe skulls to *H. sapiens*, then our species has existed for at least 250,000 years. Coon (51), with minority support from other paleoanthropologists, claims that five contemporary major races may have existed for as long as 500,000 years.

Cavalli-Sforza & Bodmer (37) use a model of evolution based on a uniform rate of genetic drift, a measure of genetic distance based on gene frequencies, the observed gene frequencies for 16 blood group systems, and an assumed genetic isolation of the American Indians from Australian and Indonesian peoples 15,000 years ago, to estimate the times when the human population separated into three major races: Negroid/Mongoloid 41,000, Negro/Caucasoid 33,000, and Mongoloid/Caucasoid 21,000 years ago with large standard errors. Nei & Roychoudhury (243), using data on protein genetic polymorphisms and rather different theoretical assumptions, arrive at estimates of 120,000, 115,000, and 55,000 years for the three separations.

The plant cytogeneticist Darlington (58, 59) deduced a genetic component of language from an observed correspondence between ABO blood group isogenes (map lines showing equal gene frequencies) and θ and ð isophones in the south and west of Europe. Darlington concluded that evolutionary changes in grammar, etymology, and phonetics are independent in the long run, that only in phonetic evolution may we expect to find "a serious genetic component," and that "the genetic preference of the group rather than the genetic capacity of the individual is what determines phonetic evolution" (59). Mourant & Watkin (238) assembled additional data from Wales and the Western Countries in support of the correspondence. In an expansion of this hypothesis, Brosnahan (29) argues for the existence of both hereditary and environmental components of language operating at the individual and the breeding population levels. He does not identify specific linguistic phenotype-genotype correspondences nor does he estimate the relative importance of the genetic and nongenetic components for particular cases on linguistic change.

Darlington did not suggest that the ABO genotype determined whether a specific individual articulated the voiceless fricative in *thin* or the voiced fricative in *then* (θ and ð) but rather that the ABO gene frequencies reflect local population biological history and are associated with genes at other loci which influence via anatomical variation the production of those fricatives. Both θ and ð vary widely in North American Indian languages in regions where the blood group O gene is fixed (the genes for group A and B being absent) and the phonetic distinction is not correlated with the gene frequency cline centering in the area of the world's highest frequency of group A among the western Algonkian Blackfoot and Blood Indians.

Although for several years Darlington's blood group-language notions were a prominent part of the display on evolutionary biology in the British Museum (Natural History), generally they have been ignored by both linguists and geneticists —perhaps the best single exposé is that of Hogben (129), who is both expert geneticist and competent linguist.

Brosnahan (28), who argues that languages show different degrees of progressive evolution (29), assembled a large body of evidence he believed to support the

Darlington hypothesis. Both authors conclude that [th] has disappeared from central Europe because of gradual changes in the vocal tract and that the change is due to a slow diffusion of genes through the local breeding populations from east to west.

Roberts (278) concluded that the known distribution of local anatomical variation in the speech apparatus does not support Darlington's thesis, and Lenneberg (183) doubts that minimization of effort is indeed demonstratably responsible for sound shifts; the only evidence to the contrary I have found is Shohara's (298) study of physiological factors in Coptic sound changes.

Twins, on the average, are retarded in speech development compared with singletons of the same age, sex, and social class (30). Bulmer thinks that the retardation is probably due to the fact that mothers of twins have less time to spend with each child and that the twins may develop an idiosyncratic language of their own. He surveys the evidence that the development of speech is strongly affected by the amount of contact with adults, only children showing a striking superiority in language development compared with children reared with one or more siblings, and children from institutions often show a marked retardation although the latter set of children differ in ways other than degree of contact with adults (30). Several twin studies report that a concordant history of speech development is observed in about 90% of monozygous but only 40% of dizygous pairs (184).

In her review of the evidence for a genetic component in the determination of handedness, Levy (187) speculated that cerebral and manual dominance share an underlying genetic mechanism. 99% of right-handers have left language laterality, but only 53–65% of left-handers have left language lateralization. The evidence is clearly against the hypothesis that hand dominance itself induces contralateral language dominance. She points out strong evidence for individual variation in utilization of uncrossed pyramidal tracts and that cerebral dominance might be a perfect predictor of manual dominance given information on the ipsi- or contralaterality of motor control pathways (187). Luria (210) found that a family history of left-handedness was a better predictor of cerebral lateralization than was the actual handedness of the subjects themselves.

Levy & Nagylaki (189a) proposed genotypes for handedness and cerebral dominance that would account for the observed proportions of left- and right-handers among offspring of parents who are both left-handed, both right-handed, and of discordant handedness, as well as for aphasia resistance and recovery rates in right vs left handers (188). One pair of autosomal genes, *L*,*l*, are postulated to control hemispherical language dominance and a second pair, *C*,*c*, to control whether dominant control is contralateral or ipsilateral to cerebral dominance. The allele *L* is dominant for left hemisphere language and the allele *C* is dominant for contralateral hand control (188).

Now that techniques for studying cerebral asymmetry of function in intact, normal populations (157, 158, 181a) without injections are available, Levy's results give promise that new genetic studies in which cerebral and other lateralizations are specified on the same individuals in adequate samples of genetic relatives and foster children will produce interpretations of fundamental importance for understanding the interplay of environmental and genetic factors in speech and language.

WHITAKER'S MODEL OF PERIPHERAL AND CENTRAL LANGUAGE SYSTEMS

H. A. Whitaker (338, 340, 342) developed a functional anatomical model of how language is represented in the brain. His is the first model that attempts to correlate brain structure and function with contemporary linguistic theory. And his model incorporated all the well-tested features of the models based on neurophysiology without major regard to linguistics as developed in the USSR by Luria (208) and in the Boston Veterans Administration Hospital by Geschwind (88) and Green (101). In addition to incorporating linguistics, Whitaker's model is the first to include the extremely important relationships between central and peripheral mechanisms, as well as the role of thalamic and other subcortical nuclei (248, 249, 249a, 279) in the working of the central language system. This multidisciplinary model is one product of the new hybrid science of neurolinguistics. Until recently, the term neurolinguistics (341) was in more common use in Russia and Europe than in the United States (209, 222). Lebrun (176) gives a brief history of neurolinguistic models of language and speech. Green (101) discusses general problems in the construction of such models.

Neurolinguistics assumes that a proper and adequate understanding of language depends upon correlating information from the several fields concerned with the structure and function of both language and the brain (341). For most workers active in the field, the philosophical basis of neurolinguistics is a mild but reasonable form of materialism (80), a position incompatible with strict behaviorism but fully compatible with Chomskian views (126). Fromkin (83) summarizes performance error data from normal subjects and presents evidence for the psychological reality of phonetic, syntactic, and semantic features, for phonological sequential constraints, phonological rules, and underlying representations, arguing that speech errors are not random but are predictable constrained by linguistic organization. Watt (331) reviews recent literature on the psychological reality of linguistic constructs.

Whitaker's model is an extrapolation from a wide spectrum of data (summarized in Figure 4) relating to brain structures and aphasic symptomology (40, 87, 89, 91, 93, 100, 163, 189, 208–213, 217, 234, 244, 251, 262, 284, 292, 343). Just as single function theories that language is solely a product of the brain's ability to associate stimuli (302) are overly simple (42), so theories that all aphasic symptoms are due to disruption of the brain's ability to associate stimuli are likewise overly simple (342).

The model consists of peripheral and central language systems. The peripheral language system contains four structurally and functionally distinct subsystems: 1. speaking and 2. listening systems are present in all human languages and thus are termed primary production and recognition systems; 3. writing, and 4. reading systems are absent in many languages and thus termed secondary production and recognition systems. These systems are biologically distinct because they use distinct sense receptors (eye and ear) and distinct effector nerve-muscle-support tissues (the

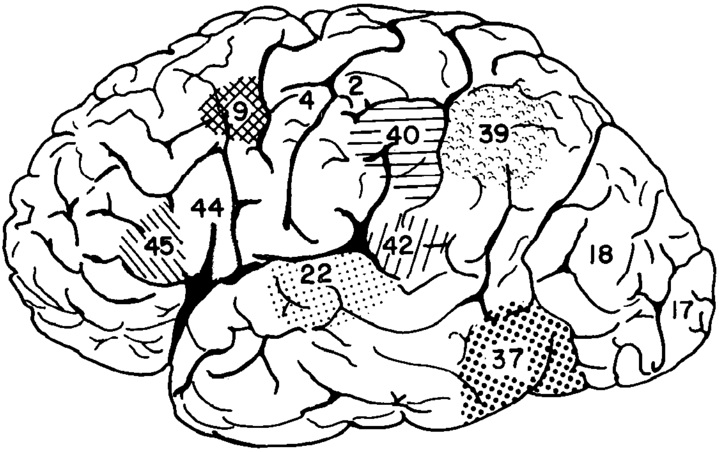
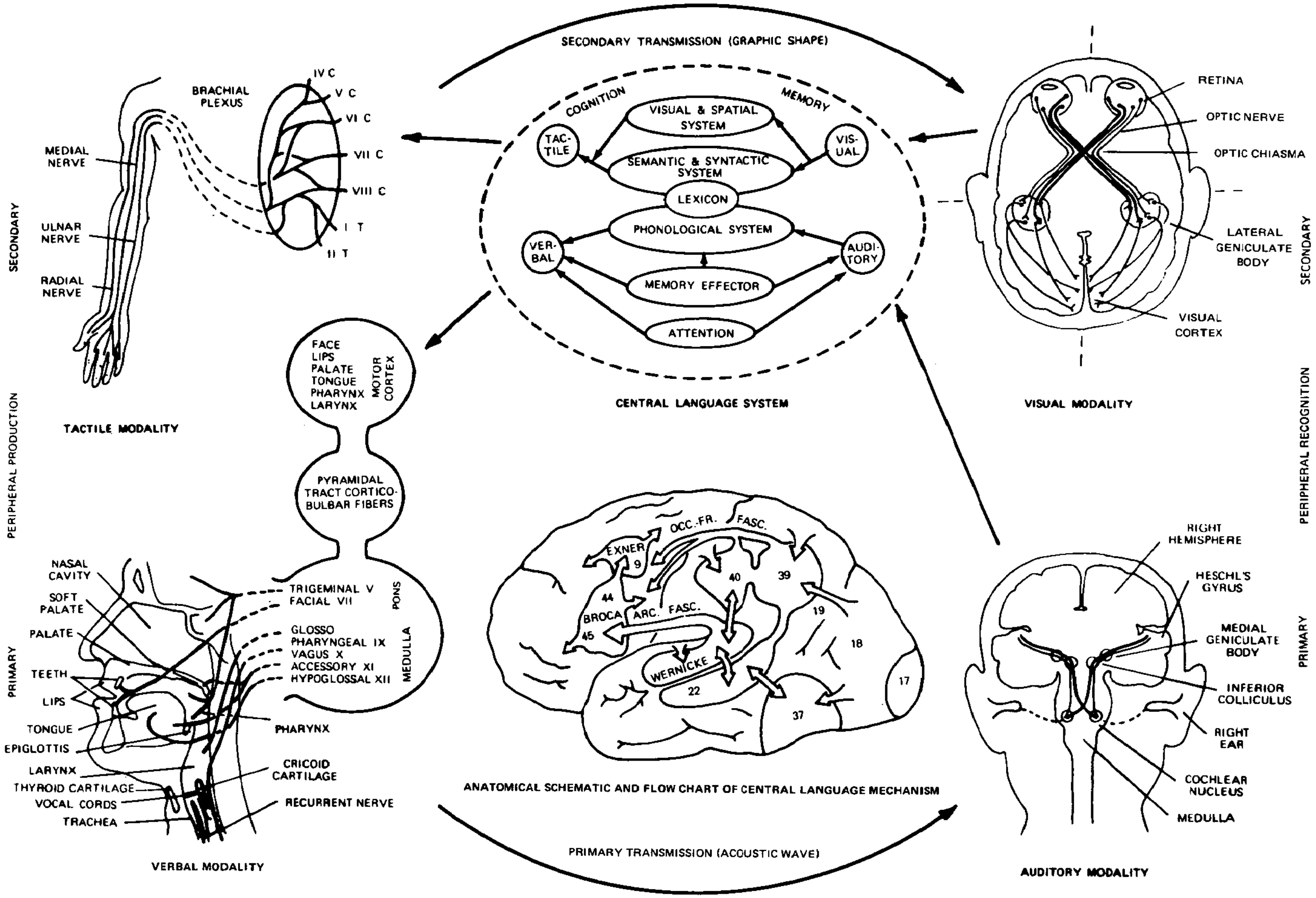


Figure 4 A more detailed sketch of the same brain shown in Figure 1, showing the surface location of some of the areas related to speech and language. The numbers refer to Broadmann's cytoarchitectural areas; see the text for more details. The cross-hatched part of area 9 is Exner's writing center; area 22 is the auditory association cortex and is a part of Wernicke's speech center; area 37 is the visual-auditory association cortex; area 39 occupies the angular gyrus; area 40 is in the supramarginal gyrus; and area 44 with the adjacent part of area 45 is Broca's speech center. Drawn from photograph reproduced from Crosby, Humphrey & Lauer (57).

arm/hand and the vocal tract) but the effectors may be generalized to other motor systems in man. Both primary and secondary systems link production and reception by high level feedback compatible with the meaning or semantics of the intended production (174). These mechanisms coordinate the speaking and hearing modalities with one another where the feedback is by way of the eighth cranial (acoustic) nerve, proprioceptors being absent from the muscles of the voice box (22). Two types of feedback are proposed, one being peripheral and system-specific (216) and the other general to the central language system.

The speaking-hearing system is the primary production and recognition system in the sense that it is difficult to imagine speaking with an organ other than the vocal tract or hearing with an organ other than the ear, whereas one can easily substitute the foot for the dominant hand in writing in the sand, or substitute the finger for the eye in reading braille (342). The primary system transmits by acoustic wave and the secondary system by conventional graphic patterns received visually or tactically. In a given individual all four peripheral systems, although of separate evolutionary history, converge in being a part of the same language system. The four peripheral modalities are shown in Figure 5.

The central language system contains three or (on a different view) four linguistically distinct components collectively called the grammar: 1. semantic, 2. syntactic


SECONDARY TRANSMISSION (GRAPHIC SHAPE)
COGNITION
MEMORY
VISUAL & SPATIAL SYSTEM
SEMANTIC & SYNTACTIC SYSTEM
LEXICON
PHONOLOGICAL SYSTEM
MEMORY EFFECTOR
ATTENTION
TAC-TILE
VIS-UAL
VER-BAL
AUDI-TORY
CENTRAL LANGUAGE SYSTEM
RETINA
OPTIC NERVE
OPTIC CHIASMA
LATERAL GENICULATE BODY
VISUAL CORTEX
VISUAL MODALITY
SECONDARY
PERIPHERAL RECOGNITION
PRIMARY
RIGHT HEMISPHERE
HESCHL'S GYRUS
MEDIAL GENICULATE BODY
INFERIOR COLLICULUS
RIGHT EAR
COCHLEAR NUCLEUS
MEDULLA
AUDITORY MODALITY
BRACHIAL PLEXUS
IV C
V C
VI C
VII C
VIII C
I T
II T
MEDIAL NERVE
ULNAR NERVE
RADIAL NERVE
TACTILE MODALITY
SECONDARY
PERIPHERAL PRODUCTION
PRIMARY
FACE
LIPS
PALATE
TONGUE
PHARYNX
LARYNX
MOTOR CORTEX
PYRAMIDAL TRACT CORTICO-BULBAR FIBERS
TRIGEMINAL V
FACIAL VII
PONS
GLOSSO PHARYNGEAL IX
VAGUS X
ACCESSORY XI
HYPOGLOSSAL XII
MEDULLA
NASAL CAVITY
SOFT PALATE
PALATE
TEETH
LIPS
TONGUE
EPIGLOTTIS
LARYNX
THYROID CARTILAGE
VOCAL CORDS
TRACHEA
PHARYNX
CRICOID CARTILAGE
RECURRENT NERVE
VERBAL MODALITY
OCC.-FR.
FASC.
EXNER
9
44
BROCA
45
ARC.
FASC.
40
39
19
18
17
WERNICKE
22
37
ANATOMICAL SCHEMATIC AND FLOW CHART OF CENTRAL LANGUAGE MECHANISM
PRIMARY TRANSMISSION (ACOUSTIC WAVE)

(or semantic/syntactic), 3. phonological, and 4. lexical. The central language system uses an appropriate set of semantic, syntactic, and phonological rules to define words (morphemes) and sentences.

Chomsky's (43) distinction between *competence* (the grammar of the language, what one must know to know the language) and *performance* (what one actually says and hears) is of obvious heuristic value in allowing grammarians who control linguistic input to ignore "extraneous" features of output such as slips of the tongue, accents, stammers, and the like. Chomsky holds that the theory of performance is different from and irrelevant to the theory of competence, which he makes the central concern of linguistics (126). Other students of language, whether attracted to biology or avoiding it, find some applications of the distinction difficult. Lenneberg (184) and Weigl & Bierwisch (332) present examples of the theoretical confusion resulting from attempts to apply the competence/performance distinction to aphasia. These authors suggest that competence remains intact in aphasia while performance is changed, and that if brain damage cannot affect competence, then competence is not a property of the brain. In a 1968 paper, Whitaker (337) attempted redefinition of the two terms in order to meet difficulties in their application to aphasiology; in later papers (339, 341, 342) he recommends abandoning the distinction altogether. Bever (14) questions the domain of a science of linguistics that does not investigate actual language behavior. McNeill (226) and Palmer (254) find the distinction hard to apply in grammatical studies where the investigator does not control input, and Rodrigues (280) was unable to use the distinction satisfactorily in a study of English speaking and writing in children bilingual in Spanish and English.

Whitaker (342) concludes that present evidence from aphasia is equivocal on the problem of anatomical separation of deep and surface linguistic structures, although the data tend to support a model with separate surface and deep components. With reservations, he provisionally avoids modeling deep and surface components of grammar. Rather grammar is modeled to contain three components: the syntactic/semantic system, the phonological system, and the lexicon. The grammar integrates input and output of the four peripheral language systems by employing four tracking systems (see Figure 5). See Hockett (126) for a criticism of Chomsky's views and Postal (267) for a fuller description of general grammatical properties. Parkinson (255) gives a critique of Chomsky's views on linguistic infinity.

Most neurolinguists are more comfortable with the concept of language universals than with the competence/performance dichotomy (341, 342), despite the fact that at the level of individual neuronal and glial cells the representation of language in the brain cannot be identical in all members of the species. Individuals with full language capacity vary up to a factor of two in the number of cerebral neurons (22, 184, 317, 318); the rate of production of new brain neurons slows markedly after 18 weeks of gestation and effectively stops after 18 months of age (67); in adults some

◄

Figure 5 Peripheral and central language systems as modeled by H. A. Whitaker. Redrawn with modifications from (341).

10,000 neurons die at random each day in each brain (9, 361). But at the tissue level the language areas of the cortex and their interconnections together with their connections to subcortical nuclei may be assumed to represent a universal biological basis for speech and language in all normal, intact, developed members of *Homo sapiens* (342).

A language model for the brain must provide for convergence or complete transfer between the modalities. This is done by what Whitaker calls the central language system (enclosed in the dashed ellipse of Figure 5), a system that corresponds to the grammar, and which, as mentioned above, has a minimum of semantic/syntactic, phonological, and lexical components. Tatham (316), MacKay (215), Whitaker (339), and Denes & Pinson (64a) discuss the tracking mechanism (represented in Figure 5 by the four ellipses labeled Verbal, Auditory, Tactile, and Visual) which convert linguistically motivated units into units which represent motor commands to the articulatory muscles.

The major pathways (Figure 5) for the transfer of symbols in the central language system are well established although the detailed mechanism of the transfer is unknown (87–93, 341, 342): the angular gyrus connects with the visual association cortex [area 19; see (27)]; the supramarginal gyrus connects with the somatic afferent association cortex (areas 7 and 40); the posterior part of Wernicke's area and the auditory association area connects with the association cortex surrounding Heschl's gyrus (area 42); the long fibers of the arcuate fasciculus connects parts of Wernicke's area with parts of Broca's and Exner's centers; the long fibers of the occipitofrontal fasciculus connect the angular and supramarginal gyri with the precentral motor cortex (area 4).

Whitaker (341, 342) postulates that the regions of the cortex representing the semantic/syntactic component and the lexicon are localized in the posterior part of Wernicke's area, the auditory association area, the supramarginal and angular gyri. The numerous cortical interconnections of the inferior parietal lobe and the superior temporal lobe, and the lack of subcortical connections to these parts, led Geschwind (91–93) to suggest that evolutionary reorganization of this area was a prerequisite for the capacity of language in man. Paleoanthropologists have long recognized that the inferior parietal and superior temporal lobes show the greatest quantitative change in the evolution of the hominid brain (22, 48, 132, 144, 161e-f).

The cytoarchitecture of the cortical language areas is clearly distinct in the different composition of the six cell layers with differing kinds of neurons and arrangements of dendrites and axons (27, 106, 184, 361). Bailey & von Bonin (7) and Schaltenbrand (289a) provide a critical account of Brodmann's *Lokalisationslehre.* Whitaker (341, 342) calls attention to the remarkable correspondence of the different Broadmann areas with the "areas" classically identified with the central language system: Broadmann's area 44 with Broca's, a part of area 9 with Exner's, the primary motor and sensory areas with 4 and 2 respectively, the supramarginal gyrus with parts 40 and 42, the angular gyrus with 39, Wernicke's with 42 and parts of 22, Heschl's gyrus with 41, and the auditory association area with the main part of 22. Because the architectonic areas of Broadmann show less variation between individuals than the surface topography of the cortex mapped by major ridges and grooves—which show considerable variation between individuals, including within pairs of monozygotic twins (261), it is claimed that these cytoarchitectonic areas are the anatomical correlates of the central language system (341, 342). Richman et al (275) present a mechanical model of convolutional development in the cerebral cortex. However, it seems likely that the more classical names for the speech and language centers based on the superficial landmarks of sulci and gyri will continue to be used.

Memory is a complex of at least short- and long-term varieties (283). The type of memory that is part of the central language system may be called verbal memory and is a topic we will return to later. The lexicon is a component of the central language system whether localized at the tissue level or not (313, 341, 342).

The fact that retrograde and anterograde amnesia do not affect current language shows that there is a memory system quite independent from language, which in Figure 5 is simply labeled "memory." The anatomical locus at the tissue level for this kind of memory, if any, is also unknown although the system which stores experiences in memory, the memory effector system, is located in large part in the hippocampal gyri and adjacent limbic structures (250). Disruption of the short-term memory system, as in Wernicke-Korsakoff's syndrome, with the result that the patient cannot remember things or events for more than 15–20 minutes, affects the central language system only to the extent that such patients cannot learn new words (342). Details of the physiological and molecular basis of all memory systems are still unknown (283), and, as mentioned above, the extent of anatomical localization, if any, beyond that of diffuse large biomolecules, is uncertain. The various forms of aphasia strongly indicate that the memory system is functionally separate from the language system regardless of localization. Some recent review papers on the possible biochemical storage of the lexicon include Kimble (155, 156), Pribram (270), and Rozin (283).

The requirement that long-term memory of the lexicon must be "content-addressable" in recall and not merely "location-addressable" presents both theoretical and experimental difficulties in supposing that long-term memory operates according to purely local storage principles. Julesz & Pennington (149) suggested that certain types of composite stimulus may be stored in memory in a holographic rather than a photographic manner. Longuet-Higgins (204) expounds the hypothesis that time-varying patterns can be stored in an analogous manner, and proposed the term "holophone" for such a system. If memorization of short sequences does involve holophonic as opposed to gramophonic principles, the problem of content-addressing is immediately solved and the parts of the brain storing the memories in question should exhibit periodic response characteristics which may be directly accessible to neurophysiological study.

Whitaker's model requires minor modification to include separate boxes for short- and long-term memories, especially as linguistic input and output to and from short-term memory may underlie man's unusual abilities for sustained minding in prolonged situations with everchanging makeup, as in group hunting or manufacture of complex implements (141, 144).

The model separates the system that executes memory storage from the storage itself (283, 312). In addition to nonverbal memory, several human faculties (emotions, probably general cognition, problem solving, visual-spatial pattern processing) are independent of the major parts of the central language system but are related to or make use of language. Aside from providing a box for "attention," for reasons discussed in (340) Whitaker does not model the effect of emotion on the operation of the central language system because intuitively emotion is less closely related than other included systems in terms of rules, units, and components. See Grossman (106) for details on the problem of emotion and language.

Penfield & Roberts (262) were first to suggest that parts of the thalamus must be included in the central language system, based mostly on the observation that electrical stimulation of the left pulvinar (but not the right in individuals with left hemispherical dominance) causes anomia, and damage to other left-sided thalamic nuclei may cause aphasia. Ojemann, Fedio & Van Buren (249), Ojemann & Ward (249a), and Riklan & Levita (276) review the role of the thalamus in the central language system. The pulvinar is phylogenetically late in evolution of the thalamus and is more specialized in man than in other primates (48). Emotions influence the central language system through the frontal lobes or the thalamus (57). The reticular activitating system controls attention (217).

The special box for the visual and spatial systems is supported by studies on brain lesions showing that a neuronal pathway between peripheral tactile and visual systems must exist independently of the central language system, because a meaningless sequence of letters can be copied without invoking any part of that system (342). Problem solving abilities and general cognitive functions are combined in the model as a general cognitive system labeled simply "cognition." See Rosenzweig & Bennett (282) and Worden, Swazey & Adelman (357) for reviews of the neurological aspects of these topics.

Current knowledge on impairment of the phonological component is surveyed by Blumstein (16, 17), Johns & Darley (146), Kinsbourne (159), Lecours & Lhermitte (177), and Luria (210). Schnitzer (290) presents evidence for specific losses of phonological rules including laxing and velar softening; his research supports the generative phonological model developed by Chomsky & Halle (46).

Additional information on the structure and function of the peripheral language production and recognitions systems are in a wide variety of handbooks [including (57, 150, 160, 184, 289a)]; several references are of interest to the neurolinguistics of the auditory modality (40, 223), tactile modality (110), verbal modality (147, 291, 315, 322), and visual modality (9, 106).

TOOLS AND LANGUAGE

The manufacture of tools has long been regarded as a sign of human status [Benjamin Franklin in (346), see also (246)]. It is supposed that (*a*) tool-making involves foresight as to the use of the tool, and (*b*) that tools are made by techniques learned from others and involve symbolic communication, presumably by language. Young (361) points out that all organisms show "foresight" or prediction in much of their behavior, and that the manufacture of tools is observed in chimpanzees (97) and other animals (108, 246); for example, birds make nests with the standard techniques that are not learned from others, but tits learn by imitation and share a tradition of opening milk bottles (220). It cannot be assumed dogmatically that all hominoids that make tools following a standard technique have language (361).

Washburn (328, 330) showed that much of what we consider anatomically characteristic of modern man, for example, the reduction of the face and jaws relative to the neurocranium, evolved long after the use of tools made by standardized techniques.

Hall (108) points out the important distinction between the occasional use of implements in agonistic behavior, grooming, courtship, and nest building which are special adaptations with no particular significance in the evolution of "intelligent" tool use, and the daily use of implements in hominid food getting, which was basic in the early evolution of material culture.

The neural delay required when some extraorganic tool is interposed between stimulus and response probably has much to do with the further development of cognitive behavior in hominids and perhaps with the first ability to symbol and the start of language (305, 306).

Tool use (but not standardized manufacture) has been postulated by Leakey for *Ramapithecus* in East Africa 14 million years ago (175) on the basis of an ungulate humerus that shows signs of use as a club. Mamak (218) has speculated that *Ramapithecus* in southern Asia must have had tools because the canines are reduced and the creatures could not have survived without some substitute means of defense.

The earliest evidence for stone tool manufacture after a fixed and set pattern now goes back 2.5 to 3 million years ago in East Africa (141). These pebble tools were made with a few simple acts of a single chipping operation. Isaac (141) assumes they could have been manufactured by a primate of pongid status. Although pongids in the wild have not been observed to make stone tools, they have learned to do so in captivity (358). Montagu (235) is less cautious in extending language back 1.75 million years on the basis of "the grammatical precision of toolmaking" on the living floors of Bed I in Olduvai Gorge.

Bordes (24) discusses the parallelism between the increasing complexity of the brain from australopithecines to Upper Paleolithic man and the increasing complexity of the techniques used to work stone by Paleolithic peoples. Tobias (317) gives the cranial capacity of eight adult samples of *Australopithecus* (sensu lato) as ranging from 435 to 540 cc, and that of three specimens assigned to *Homo habilis* from 633 to 684 cc. These small-brained hominids reached a first level of abstract thought in comprehending that there is a cutting edge inside suitable rocks which can be released by some blows with another stone. Variations on the technique (by facial working, pointing a chopping tool to make a proto-handax) lasted over a million years from 3.6 million years up to the hominids at the bottom of Bed II in Olduvai, which some classify as small pithecanthropines.

The second level of abstraction achieved in the lower Acheulean by true pithecanthropines with medium size brains [the range in endocranial volume for 13 *Homo erectus* is 750 to 1225 cc, with a mean of 935 cc (317)], and perhaps by other unknown hominids, involved the idea that not only a cutting edge, but also a standard shape can be obtained at will from a suitable rock. The manufacture of hand-axes was facilitated by the observation that working with soft bones or wood produced a cutting edge less sinuous, straighter, and sharper than working with a stone hammer.

A third level of abstraction was reached by middle Acheulean hominids of Swanscombe and Steinheim levels. Coon (51) gives the cranial capacity of the incomplete Swanscombe skull as falling in the range 1275–1325 cc and the estimated capacity of the Steinheim skull as 1145 cc. This third level is marked by the invention of Levallois flaking techniques. By mastery of several different flaking techniques—flat vs steep flaking vs striking off the flake from the shaped core—the tool maker now predetermines the shape of the tool before striking it out of the stone. There were probably several independent discoveries of Levallois technique in Africa and in Europe, where the method seems to appear in the lower part of Middle Acheulean about 300,000 years ago (23). The skillfully made Upper Paleolithic and Chalcolithic blades are an elaboration of the Levallois technique.

A fourth level of abstraction invented by large-brained *Homo sapiens* in the Upper Paleolithic involved representative art based on the ability to separate the shape from the object shaped. Drawing or engraving lines on bone or stone is older than true representative art, dating from the Acheulean Pech de l'Azè. Accurate representation in three dimensions was achieved in Aurignacian I at Vogelherd, when two-dimensional drawings were still crude in other Aurignacian I sites (221).

The concept of transmission of force by the punch technique may date from the Mousterian, and the abstraction of the multiplication of force by first and second order levers was made at the Swanscombe level, and by third order levers, which are used in spear throwers, at least by Solutrean times.

Multiple tools go back at least to the Acheulean. Composite tools were quite exceptional in the Mousterian, but common in the Upper Paleolithic. Lieberman (196) points out that the Olduwan and other Lower Paleolithic pebble tools could be made using a phrase structure grammar but that Levallois toolmaking presupposes a transformational grammar which formally incorporates a memory. The makers of pebble tools had to keep only two things in mind: (*a*) the last chip made, and (*b*) the final form of the tool being made. A memory of the operations involved in intermediate stages is not necessary. The makers of Levalloisian tools must keep in memory a particular functional attribute of the striking platform and the intermediate operations that change the upper surface of the core (23). As phrase structure grammars cannot formally account for the syntax of human language (41, 43), so by analogy they cannot account for the Levalloisian techniques of tool manufacture (see also 117).

Semenov (297), by reconstructing the probable process of working, concluded that a majority of Mousterian stone tools were made by Neanderthalers with dominant right hands. From a multivariate analysis of the small sample of recovered hand bones representing both sides, Musgrave (239) judged that Neanderthal man was not as strongly right-handed as modern man. LeMay (180) considers that the left-right differences in the angle of the lateral fissure observed on the endocranial cast indicates that the La Chapelle-aux-Saints Neanderthal man had the anatomical asymmetry association with functional differentiation of Wernicke's speech center in recent *Homo sapiens.* From an examination of the position of fractures made by blows with an implement on 42 baboon skulls collected from the Pleistocene sites of Taung, Sterkfontein, and Makapansgat, Dart (60) concluded that the South African australopithecines had apparently developed a preference for using the right hand, perhaps by 2 million years ago.

FOSSIL HOMINIDS AND ARTICULATE SPEECH

Although the larynx and the supralaryngeal vocal tract through the throat, mouth, and nose are homologous in all higher primates (68, 241, 242, 351, 352), the size and shape of the hard and soft tissues of the tract differ in modern *Homo sapiens* from that in the living pongids, dryopithecines, ramapithecines, australopithecines, *Homo habilis, Homo erectus,* and *Homo sapiens neanderthalensis.* The voice box of nonhuman primates is in slight to close contact with the soft palate and the base of the tongue, the airway flowing directly from the larynx into the mouth. This structure of the vocal tract is one reason why chimpanzees, for example, cannot make long resonant sounds (69, 79, 153, 154, 351, 352). As one consequence of man's upright posture and the bending of the cranio-facial axis, the voice box in man is moved down the throat away from contact with the soft palate, with the base of the tongue forming the anterior wall of an elongated pharynx, thus forming the lower part of an oral chamber that makes possible the human sort of vocal performance (192, 193, 201, 202). The reduction of the jaws and snout was important for the acoustics of man's articulate speech by the opening out and the broadening of the floor of the jaws and the transfer of the bony braces of the mandibular symphasis from inside to outside to give more room for tongue movement (150, 184).

The increased length and bending of the supralaryngeal voice tube is of no advantage in breathing or swallowing, and is a disadvantage in the greater probability of fatal choking on objects lodged in the pharynx (241) and in the higher probability of wet and dry drowning (350). Kirchner (160) estimates that the respiratory efficiency of the bent adult human supralaryngeal airways is about half that of the straight airway of the newborn. Lieberman (194) suggests that the disadvantages are outweighed by the selective advantage of a vocal apparatus capable of producing stable sapiens-like articulate speech. Bosma (25) points out that the principal sensory-cued motor performances and the lower supralaryngeal tract are those of position maintenance by the pharynx and the mouth, of pharyngeal participation in tidal respiration, and of pharyngeal swallowing, and because these activities are performed much more frequently than speech, infers that speech is of little significance as a mechanism effecting the muscular and skeletal form of the air and food tubes.

Lieberman (195) marks the final crucial stage in the evolution of *human* language by the development of the bent two-tube supralaryngeal vocal tract. The bending of the vocal tract consequent on the bending of the craniofacial axis permits modern man to generate supralaryngeal vocal tract configurations that involve abrupt discontinuities at the midpoint (tongue to palate) analogous to a pipe organ with two differently shaped tubes (194).

DuBrul (68) argued that the assumption of erect, bipedal posture and locomotion produced morphological changes in the cranium, larynx, pharynx, and oral cavity that were the prime factors in the evolution of human speech and language. Today most human biologists, including DuBrul (69), believe that the primary organ in the evolution of articulate speech is the brain, in particular the cerebral cortex, and that the peripheral structures of the oral cavity, pharynx, and larynx are secondary (184, 309). Therefore, most biological anthropologists today are sceptical that we can find "stigmata" of articulate speech in the hard or soft parts of the peripheral speech apparatus (70, 323, 324). Hooton (135, p. 169) reported that "The presence of well developed genial tubercles is the surest anatomical evidence of articulate speech that the skeleton affords. But a poor development of these bony spines to which the tongue muscles are attached is no evidence at all that the possessor is or was unable to speak." It follows that absence of genial tubercles in a neanderthal man does not make him dumb because they are known to be absent in some "excessively loquacious" persons.

Some earlier investigators suggest that the canine fossa is restricted to hominids and that it is diagnostic for articulate speech because the caninus muscle arises from the fossa and inserts into the angle of the mouth where, intermingling with the fibers of the zygomaticus, triangularis, and orbicularis oris muscles, its action is important for speech production. But the canine fossa is sometimes present in living apes and in fossil dryopithecines (299, p. 249) so that it is of no value either in distinguishing hominid from pongid affinity nor in diagnosing a capacity for articulate speech.

Mamak (218) suggests that canine teeth in the hominoid line were reduced in size when language replaced the selective advantage of large canines for aggressive display. This would place the origin of language at least at the australopithecine level 3 million or more years ago) if not at the ramapithecine level (up to 14 million years ago). Others explain canine reduction as a result of tool use (329), selection for reduced aggression without reference to language (181), or change to a small-seed diet (148).

The anatomist Crelin and his associates (198, 200) reconstructed the supralaryngeal vocal tract of the La Chapelle-aux-Saints skeletal remains, a classical Neanderthal man from the Upper Mousterian of France dated 35–45,000 years ago (247). The reconstruction is based on the morphology of the cranial base, especially the estimated intersection of the stylohyoid ligament and the geniohyoid muscle with the hyoid bone of the larynx. Casts of the fossil skull and mandible were used. Comparative materials included 6 skulls and 6 heads and necks of newborn humans completely divided in the midsagittal plane, 50 skulls and 6 divided heads and necks of adult humans, along with skulls of a chimpanzee and an adult female gorilla. Although the larynx was judged to be as high in position in the Neanderthal specimen as in newborn humans and adult apes, it was purposely dropped to a slightly lower position, but much higher than in adult modern man. It is of interest to note that Keith's reconstruction (241) of the larynx of a "Neanderthal" compounded from the Gibraltar skull (it does not show postmortem deformation of the critical region) and the Tabun mandible and spinal column, suggests that the distance between the planes of the soft palate and the vocal chord was 74% of that in modern man compared with 52% in Crelin's estimate from the deformed La Chapelle-aux-Saints specimen. After the vocal tract was reconstructed by building the laryngeal, pharyngeal, and oral cavities with modeling clay, a silicone-rubber cast was made from the clay mold of the air passages including those of the nasal cavity.

The length and shape of the supralaryngeal vocal tract determines the frequencies at which maximum energy will be transmitted by puffs of air from the laryngeal source to the air adjacent to the speaker's lips. These maximum frequencies are called formant frequencies. A speaker varies the formant frequencies by changing the length and shape of his supralaryngeal vocal tract. The formant frequencies are computed from the cross-sectional area of the reconstructed supralaryngeal vocal tract at 0.5 cm levels up to 10.5 cm above the larynx. The computer simulation program was written by Henke (113). The three formant frequencies computed by the program providing the best approximation to the human vowels [i], [a], [u] are tabulated and scaled to the average dimensions of the adult human vocal tract (200). The simulation is at the *phonetic* rather than the *phonemic* level. These three vowels are taken to delimit the universal human vowel space (78). The results were compared with the formant frequencies obtained by Peterson & Barney (263) of American English vowels spoken by a sample of 76 men, women, and children.

The properties of the laryngeal source and the degree of motor control in fossil specimens are unknown; therefore, this type of reconstruction-computer simulation analysis cannot determine the total range of phonetic variation (194). Lieberman and his associates conclude that the La Chapelle-aux-Saints individual could not produce vowels like [a], [i], [u], or [ɔ] as in *father, feet, boot,* and *brought,* nor could he produce consonants like [g] or [k]. However, this Neanderthal man had much more "speech" ability than the living pongids. He could produce vowels like [I] , [e], [U], [ae] as in *bit, bet, but,* and *bat,* in addition to a reduced schwa vowel, as the first vowel in *about.* Dental and labial consonants like [d], [b], [s], [z], [v], and [f] were possible (198). Boule & Vallois (26) also concluded, on other grounds, that neanderthal man "... had doubtless only the most rudimentary articulate language."

> If Neanderthal man were able to execute the rapid, controlled articulatory maneuvers that are necessary to produce these consonants and had the neural mechanisms that are necessary to perceive rapid formant transitions ... he would have been able to communicate by means of sound. Of course, we do not know whether Neanderthal man had these neural skills; however, even if he were able to make optimum use of his speech-producing apparatus, the constraints of his supralaryngeal vocal tract would make it impossible for him to produce "articulate" human speech, i.e., the full range of phonetic contrasts employed by modern man (198, p. 217).

Reconstructions of the supralaryngeal vocal tract of five additional fossil hominids were made by Crelin and his associates (54, 55, 194, 197, 199). The classical

Le Ferrassie Neanderthal, from the Mousterian of France more than 35,000 years ago (247), was judged to have the same limited capacity for articulate speech claimed for Le Chapelle-aux-Saints (199). The progressive Neanderthal man represented by Skhul V, from the Lower Levalloiso-Mousterian of Israel about 30,000 years ago (247), had a reconstructed vocal tract within the range of modern man (194). The neanderthaloid Broken Hill man, from the early Gambian of Zambia about 30,000 years ago (247), was judged to be intermediate between the classical neanderthals and modern man but within the range of the human vocal tract (194, 199). The reconstructed supralaryngeal vocal tract of the early neanderthaloid Steinheim man, from the late Hoxnian beds of Germany about 200,000 years ago (247), although showing some pongid features, was functionally equivalent to the modern supralaryngeal vocal tract and able to produce the full range of human articulate speech (54, 55, 194). Crelin's reconstruction (55, 194) of the supralaryngeal vocal tract of Sterkfontein 5, a gracile australopithecine dated about 2 million years ago (319), has the same phonetic limitations as present-day apes with greater similarity in size and shape of the tract to the orangutan than to the chimpanzee [for an independent claim of australopithecine-orangutan affinity see Oxnard (253)].

The methods and conclusions of Lieberman, Crelin, and their associates on the reconstructed phonetic limitations of fossil hominids, especially Neanderthal man, were met with wide criticism on both biological and linguistic grounds (31–33, 35, 71, 77, 162, 180, 237, 353). The criticisms include the use of inaccurate casts of post-mortem-deformed skulls, doubts that a correct model of the vocal tract of a fossil man can be constructed from the skull, fallacies in the comparison of human newborns with adult Neanderthals, inability to use data on parallel resonators (e.g. the maxillary sinuses) in the acoustic analyses (104), failure to recognize that speech is little impaired by tongue amputation (152) and that many morphological defects in the tongue (103) as well as limited tongue movement (84) produce only minor defects of speech, invalid assumptions about the relations between the tongue and the larynx, the possibilities of alaryngeal speech (65), and invalid conceptions about the posture of the old man from La Chapelle-aux-Saints (310).

LeMay (180) pointed out that the brain of Neanderthal man was as large as that of modern man, and that the endocranial cast of the La Chapelle-aux-Saints skull resembles that of modern man in areas important for speech and thereby suggests that Neanderthal man had the neural development necessary for articulate speech and language.

Abler (2) demonstrated that among living hominoids skull asymmetry tends to characterize only those species possessing lateralized brains and that the asymmetry in the skulls of Neanderthal man and *Homo erectus* suggest they had lateralized brains and, by implication, language [but see (47)].

Comprehensible English can be written with only one vowel: The Eneversete ef Bermenghem phesecest Fremlen (82), well knewn fer hes deleghtfel esse en the het deth ef er speces, cencleded thet whel the Ne'enderthels mey hev speken less well then ther sepeent secessers et es emprebebl thet ther demes wes beces thre vewels present en medern Ende-Eerepeen mey hev been leckeng te ther phenelegecel cepecete: "The kemplexete ef speech depends en the kensenents, net en the vewels, es ken be seen frem the generel kemprehensebelete ef thes letter," where the neetrel vewel threegheet es /e/ es en Englesh *her.*

While perhaps giving Fremlen his point, most linguists would object that the above paragraph is not an adequate phonetic representation of English, that it probably is not homologous with Neanderthalese, that it uses visual redundancy, that several vowels do add to the comprehensibility of English by doing work the consonants cannot accomplish alone, especially in comprehending sex, age, emotional state, and pragmatic as opposed to semantic meaning of the speaker.

Kuipers (168) concluded that the Kabardian language of the Caucasus has no vowels by defining [*a*] as a "feature of openness" instead of a "vowel" and [ə] as "the concomitant syllabic feature of the explosive variant of a consonant," but Halle (109) in a fresh analysis of Kuipers's data concludes that Kabardian has two vowels [*a*] and [ə] in agreement with Roman Jakobson's opinion (141a) that the minimal vowel system in all human languages must have at least a vertical ə-a axis. Either way, if we accept Lieberman and Curlin's reconstruction that La Chapelle and La Ferassie classical neanderthal men could articulate only five vowels, they could therefore articulate more than the number of vowels in at least one known human language and could have had at least 14–16 phonemes which is sufficient to articulate properly Hawaiian and other Polynesian languages (227, 272).

ORIGINS OF LANGUAGE

The origins of language remain unknown, but the problems of language origins has received serious attention during the last decade after a long period of relative neglect, indifference, or opposition. The 1976 symposium on *Origins and Evolution of Language and Speech* sponsored by the New York Academy of Sciences (111) is a massive indicator of the degree and scope of current interest.

Aarsleff (1) presents an outline of language-origins theory since the Renaissance. Hewes's (116) second revised and enlarged bibliography of *Language Origins* is a reliable guide to the extensive literature on the topic. The papers in Wescott (334) give an excellent, compact summary of the empirical evidence on glottogenesis, and Lieberman (195), Stross (311), and Swadesh (311a) illustrate different approaches to the problem.

Many linguists insist that questions on the origin(s) of language are now and will remain unanswerable. They support Chomsky's argument (in several works after 1968) that language is unique, discontinuous, species specific, and without evolutionary growth, as if due to the mutation of a supergene.

The linguist Hoijer (130) concluded that although there is no archaeological evidence on the early stages of glottogenesis, we must assume that language, like other aspects of culture, passed through a period of evolutionary development. The psychologist Miller (231, p. 72) considered it necessary to separate linguistic from cultural evolution: "with respect to biological change, evolution is an explanatory concept, with regard to cultural change, evolution is a descriptive concept, with regard to linguistic change, evolution is an unacceptable concept." In opposition, Greenberg (102), Hockett (127), and Sebeok (294–296), to mention only three anthropological linguists, support evolutionary studies as one part of general linguistics. Holloway (132–134), a biological anthropologist who is a main contributor to our knowledge of the evolutionary reorganization of the hominid brain since the Miocene, points out that hypotheses on language origins are essentially unprovable. Lenneberg, a linguist and biologist, after proposing in the late 1950s [references in (184)] that the human capacity for language can be explained only on the basis of the biological properties of man's brain and vocal tract, remained sceptical about prospects of gaining reliable evolutionary evidence on glottogenesis: in 1973 he wrote (186, pp. 59–60): "My own theory is that language is intimately related to human forms of cognition and perception. This means that the history of human language can only be told in connection with the history of the human forms of knowing the world. The biologist, however, can contribute very little to this historical research."

Hewes (115) classified theories on the origin of language into 12 categories: (*a*) Interjectional, or pooh-pooh, (*b*) Imitative, onomatopoetic, or bow-wow, (*c*) Imitative of sounds made by striking objects, or ding-dong, (*d*) Work-chant, or yo-he-ho, (*e*) Lip and tongue gesture, or ta-ta, (*f*) Infant babbling, or babbleluck, (*g*) Instinctivist, (*h*) Conventionalist, (*i*) Contract, (*j*) Divine, (*k*) Chance mutation, and (*l*) Gestural. He points out that some of these theories are tautologies, some are unfalsificable, some are incapable of operational formulation, some are plausible but not empirically tested. An example of the latter is Höpp's (136) proposal that human language began when a proper name was used to specify an individual. This *Einwortsprache* limited to one-word imperative utterances came before verbs and nouns, and thus grammar. One-word language was later dualized into verbs and nouns which then gave rise to grammar and full language. Höpp finds that one-word imperative utterances still exist in four languages, of which Eskimo is considered technologically the most primitive. The theory has received and deserves no further empirical testing.

Language may have no true origin (171, 172) or date of rank, unless we place it with the origin of life on earth. Speech and language evolved slowly through many phases and our placement of origins will vary with different criteria of language. The distinction between language and protolanguage is variously defined (127). If we argue for homologous language in *Pan* and *Homo,* the origin of language would be placed about 27 million years ago at the time many paleontologists (299) date the divergence of pongids and hominids. If we insist on historical records of known human languages Egyptian is recorded in hieroglyphics from about 3000 BC with comparable antiquity for Mesopotamia and about 2000 BC for China.

Several investigators conclude that increase in general cognitive abilities, rather than ease in verbal communication, was crucial in the origin of language (111, 141, 144, 171, 172).

Holloway (133, 134) interprets the evidence of paleoanthropology to place language origins 2–3 million years ago. Isaac (141) infers on archaeological grounds that "the milieu in which capabilities for language were first important" started before 1 million years ago but that the crucial developments in language took place about 30,000–40,000 years ago. Hewes (114) gives an explicit formulation of the relationship between tool-using, tool-making, and the emergence of language, and relates (115, 118) current studies on primate communication to the hypothesis of a gestural origin of language. If language required symboling, it is of interest that the earliest archaeological evidence for symbolic behavior dates from the Mousterian about 90,000 years ago (221).

Hockett (122–125) deduced that because his 13 design features are not all independent (e.g. semanticity must precede arbitrariness and duality of patterning) comparative study of living species may support a phylogenetic sequence for the evolution of design features in the hominid lineage. For instance, given that living gibbons have features 1 through 9 (125), we may assume that Miocene pongids had arbitrariness, interchangeability, and specialization. Four new properties are required for the evolution of human language—productivity, duality of patterning, displacement, and cultural transmission. Productivity could develop without duality, displacement, or cultural transmission, but it is hard to get these without productivity. Learning is necessary for a system which is arbitrary, productive, and cultural. Arbitrary signs might become productive through "blending." Displacement developed after arbitrariness and duality after displacement. Hockett (127) dates the transition from a closed call system (like those of gibbons and other apes) to "good prelanguage" about 2 million years ago, in or not far from eastern Africa.

Hockett (127) places the transition from prelanguage to language 150,000 to 50,000 years ago based on (*a*) archaeological evidence of complex technology at that time, (*b*) the supposition that such complexity could not be achieved and maintained without extremely effective communication, (*c*) the evidence that 4000 to 5000 known languages could not diverge in less than about 50,000 years, and (*d*) because true language is such a powerful instrument for technological and social change, the transition could not occur before about 150,000 years ago or modern cultures would be more complex than they are. On the basis of linguistic reconstruction and glottochronology, Wurm (360) suggests a temporal depth up to 60,000 years for the approximately 700 mutually unintelligible languages of New Guinea.

Among recent workers Lieberman (194, 195) has used the fullest range of biological and linguistic data to speculate on the origins of language. He concludes that speech communication played a strategic role in the survival and perpetuation of early hominid culture and that this role presupposes a *Homo sapiens*-like supraglottal vocal apparatus. Bosma (25) countered with the surmise that hominids having the social orientation and integrative competencies requisite to ethnographically known cultures could communicate with any approximately humanoid vocal apparatus.

The new evidence for hemispherical differences in the representation of language in the brain [some of which are demonstrable on skulls and endocranial casts (2, 132–134, 161d–f, 181)] gives promise of the early discovery of new, verifiable evidence in paleolinguistics. The neurological evidence that song and music are localized in the hemisphere not dominant for language (210, 244, 284) argues against the hypothesis that song was a major step in the evolution of language (171, 172, 203).

Levy (188, 189) finds a possible basis for the evolution of lateral specialization of the two hemispheres in the hominid brain in the consideration that, given partial hemispherical specialization for language, competition of that dominant hemisphere for control of the motor mechanism concerned with language production, would result in specialization of the mute hemisphere for gestalt perception and the ability to visualize spatial relations in three dimensions as a result of antagonism between the functions of language and nonverbal perception and cognition.

In 1971 Whitaker (341, p. 208) characterized the state of neurolinguistics as follows: "Suffice to say, we are not dramatically close to understanding brain function as complex as language but what we have is rather far from a black-box. In a modest way, it is possible to show empirical support for quite a number of linguistic constructs—some of which are quite predictable and others are perhaps a bit unusual."

There are no instantaneous jumps between peripheral recognition of a uniquely new external event and peripheral production of a uniquely new word and sentence across a linguistically void brain in which nothing biological happens pertinent to the study of language. Knowledge of exactly how language is represented in the brain probably must await discovery of the molecular basis of memory, the biochemistry of receiving, storing, and recalling the lexicon according to the principles of the central language system.

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