

Evolution of Primate Vocal-Auditory Communication Systems¹

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One way of tracing the evolution of language is to (1) reduce language to its structural components or design-features, (2) discover to what extent these design-features are present in the communication of nonhuman primates, and (3) attempt to establish the brain structures that mediate linguistic behavior in man and the extent to which such structures can mediate similar behavior in nonhuman primates. It is also important to delineate those anatomical mechanisms that are prerequisites for language from those that are later adaptations. Human peculiarities of the auditory system, vocal tract, and motor system are better explained as the result of feedback from an evolving linguistic code than as necessary prerequisites for language. The abilities to engage in sequential behavior and to form nonlimbic, cross-modal associations are more likely to be linguistic preadaptations. The faculty of immediate memory also influences communication systems by setting constraints on sequential codes. The structure of the communicative code and the behavioral capacities of the mediating organism together determine the semantic characteristics of the code. Sign systems, when classified by their semantic properties, can be closed, semioopen, open, nominal open, subject-predicate open, and relational open. Given human limitations, a complex sequential code is necessary if the information load is to be increased.

THE reawakening of interest in the origin of language in recent years has been primarily due to the steady accumulation of data in a number of fields pertinent to language origin theory. The traditional speculations about language origin (summarized by Révész 1956) have been superseded by theories of more scientific interest.

Eric Lenneberg (1960, 1962, 1964a, 1964b, 1966a, 1966b, 1967) presents evidence for the thesis that the ability to use language demands a genetic predisposition unique to man. While it is obvious that language is a species-specific characteristic of man and that man has genetic predispositions that are unique, we learn nothing about language by postulating a language mechanism. What we wish to do is explain language, and one type of explanation is the reconstruction of its phylogeny. In this endeavor we would be better served by an investigation of the necessary prerequisites for language than in attributing the phenomenon to mutation, as has been suggested. Since almost all evolutionary changes have their basis in mutation, the language origin theorist must strive for greater specificity if his answers are to be more than truisms. To unravel the evolution of language it is necessary to reduce language to its components and explain the components. This does not give a complete explanation, any more than mammalian hearing is completely explained by tracing two of the

auditory ossicles to the jaw articulation bones of reptiles. It is nonetheless a satisfactory historical account, and the requisite gene changes, growth gradient shifts, and so forth can be presumed to have occurred. Similarly, we can trace the complex behavioral system of language by discovering its historical antecedents. Phylogenetic reconstruction is hampered by the absence of fossils, but some conclusions can be drawn from an examination of comparative material alone.

Hockett (1960a, 1960b) has used the term *design-feature* for a distinguishable characteristic of a communication system. The linguistic design-features discussed here retain only the essential characteristics of the design-features of contemporary languages, and may be more historically accurate for that reason. Similarly, anatomical structures are discussed in relation to a simplified linguistic code. It is important to distinguish between those anatomical changes that are *necessary prerequisites* for a simple linguistic code and those that occurred as *adaptations* to a *complexifying* linguistic system. These distinctions should be borne in mind in reading the following pages. There are three design-features considered in detail here: sequential ordering, semantic openness, and displacement.

VOCAL-AUDITORY CAPACITY

One aspect of sequential ordering is phonematization. While the importance of phonematization has long been recognized by linguists,

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language origin theory has tended to neglect it for discussion of phonetic capability. Since language employs the vocal-auditory channel, and did so exclusively until quite recently in human history, many authors have hoped to explain language or the lack of it by comparative studies of the vocal abilities of animals. The uniqueness of language is not likely to be explained by a capacity that man shares with nearly all other mammals. Nor is man unique in regards to the auditory component of the channel. One index of auditory capacity is the auditory threshold study.³ Man and the rhesus monkey manifest about the same auditory acuity in the 50 hertz to 8 kHz range, while the rhesus surpasses man in acuity for high frequencies, responding to sounds up to 3 kHz, which was the upper limit of the testing apparatus (Behar et al. 1965). Similarly the upper limit of the chimpanzee is above that of man, ranging from 26 to 33.3 kHz (Elder 1935). The upper threshold for an adult man is about 16 kHz, with the optimum range between 0.5 and 4.0 kHz when the intensity is about 50 db above the minimum intensity (Miller 1963). The frequencies of speech fall between 100 and 10,000 hertz (Denes and Pinson 1963) and are thus well within the primate ranges. Additional support for the communicative adequacy of the auditory mechanism in infrahuman primates is furnished by the animals' actual use of this channel in communication. While there are doubtlessly unique auditory decoding capacities in man, they must be looked for in the central nervous system rather than in peripheral sensory mechanisms. But it is unlikely that auditory decoding changes were a necessary prerequisite for language; they can be better explained as having evolved under the selection pressure of an already elaborate auditory code.

The vocal aspect of the channel has attracted far more interest and controversy than its auditory counterpart. The examination of vocal anatomy is considered relevant by many to an understanding of language origins. However, the ability to produce sounds phonetically akin to human speech sounds has in actuality little importance for language. Sound spectrographs show that mynah birds are capable of almost exactly duplicating human speech sounds (Sebeok 1965). That this can be done without even the benefit of a sound-producing larynx should lead us to question the utility of examining fossil mandibles for evidence of speech. In addition, human speech

can be produced by an atypical vocal anatomy: a man whose larynx has been removed can learn to talk with his esophagus. Andrew (1965) presents a spectrograph of a column of air being modulated by the tongue of a baboon, producing a feature quite like a formant. This last fact indicates that a study of vocal anatomy can tell us what sounds the organism is capable of producing; it tells us nothing about language. Nor is there any reason to suppose that language could not work if the evolution of vocal anatomy had been different and man produced sounds different from the ones he now produces. Of greater interest than the peripheral vocal anatomy itself is the degree of motor control exercised over the sound producing mechanism.

When a motor homunculus is drawn for the cortex of a monkey and a man (as in Washburn 1960), it can be seen that a relatively greater area of motor cortex is devoted to the mouth in man than in the monkey. Secondly, there has been a general increase in the precision of motor control in the primate line, as indicated by two anatomical observations. First, there is both a relative and an absolute increase in the number of stellate cells in the cortex as we ascend from ape to man (Noback and Moskowitz 1963), and stellate cells are linked to motor precision (Sholl 1956).⁴ Moreover, in man and to a lesser extent in apes, many a pyramidal tract fiber synapses directly with the motor neuron that innervates a muscle rather than first synapsing with an internuncial (i.e., intermediate) neuron (Noback and Moskowitz 1963). In the primates, then, there is a trend toward greater motor refinement. In the hominids it is reasonable to suppose that this trend interacted in a feedback fashion with a developing vocal-auditory communication system. The great vocal precision manifested by contemporary speakers is the end product of linguistic-neural evolution, not a necessary prerequisite for language.

VOCAL COMMUNICATION OF NONHUMAN PRIMATES

The vocal-auditory communication of non-human primates becomes increasingly less relevant to linguistic evolution as data on non-human primates accumulate. Human speech is a sign system that has *sequential* relations between signs (in contrast to a visual communication system which may have a simultaneity relation between signs). A sign system⁵ with a sequential relation is termed a *sequential*

sign system, and such a system can generate *strings* of signs. Speech has both strings of meaningless signs (phonemes) and strings of meaningful signs. Sign systems that combine both meaningful and meaningless signs exhibit the design-feature of *duality of patterning* (Hockett 1960a, 1960b). The vocal communication of nonhuman primates does not have duality of patterning, and there is no evidence that sequential relations between signs are used at all. Itani (1963) asserts that some of the sounds uttered by Japanese macaques (*Macaca fuscata*) in series had different meanings than the same sounds uttered singly. Since he does not give an example, the assertion remains to be proven. A certain amount of equivocal data can be found in the descriptions of vocal communication of other species as well. The difficulty of interpretation arises from the fact that sound spectrographs of the vocalizations of nonhuman primates show many intergradations of sounds. In the absence of systematic experimentation, it is impossible to conclusively demonstrate that vocalizations uttered in series are repetitions of the same call rather than two or more vocalizations with a sequential relation between them. Intergradations also make it difficult to establish the extent to which the vocal communication of nonhuman primates is analogical or digital. These problems are discussed further by Altmann (1967). If there are sequential relations in nonhuman primate vocal communication, they are clearly the exception rather than the rule.

Semantically, also, the vocal communication of nonhuman primates bears little relation to language. It has been suggested in the past (Bastian 1965) that the calls of nonhuman primates are largely expressions of the animal's emotional state and fall under what linguists have termed the expressive rather than the referential aspect of communication. Neurophysiological research has since given more precise definition to Bastian's characterization. Bryan Robinson (1967), using electrostimulation techniques, stimulated 5,880 loci in the brains of unanesthetized rhesus monkeys and evoked vocalizations from 479 of these sites. All vocalization sites were located in the limbic system—a system long known to be important in the mediation of emotional behavior (Smythies 1966). No vocalizations could be elicited from neocortical structures. Since similar emotional vocalizations, such as moans and screams, also occur in man, it is concluded that language did not evolve from vocal communi-

cation similar to that of contemporary nonhuman primates. Language is a new system demanding new structures. As such, the blending hypothesis of Hockett and Ascher (1964) is most unlikely.

In one respect nonhuman primate vocal communication may be a significant preadaptation for speech. Marler (1965) has suggested that the intergraded vocalizations of higher primates are more likely to preadapt for speech than the discrete vocalizations of the prosimians.⁶ Experiments with synthetic speech (reviewed briefly by Denes and Pinson 1963) indicate that phonemic segments are not paralleled by equally discrete acoustic signals. Rather, a continuous acoustic signal is segmented by a person fluent in the language into a string of discrete sounds. We would expect this ability to arise from a communication system that employed overlapping and continuous signals rather than from one whose signals were already discrete.

SEQUENTIAL SIGN SYSTEMS

A sequential sign system has consequences in the semantic sphere. Hockett (1960a, 1960b) notes that productivity is restricted to human vocal-auditory communication systems. Productivity is the ability to say something that was never said before and yet be understood by other speakers. A system without productivity is here called a *semantically closed system* and is defined as a semantic system in which the set of possible messages is equal to the set of actual messages. Not only is the set of messages in such a system finite, but there are no new messages. Hockett has used Paul Revere to explicate certain linguistic principles, and Paul can be of assistance here.

Trusting Longfellow as a source, Paul Revere's system was as follows: In Code C_1 there is one sign L (lantern). There are two formation rules: (1) L is a sentence in C_1 ; (2) LL is a sentence in C_1 . It was fortunate for the United States and Longfellow's poem that the British did not send half their army overland and the other half by ship, for " L and LL " is not a sentence in C_1 . This system can talk about the land or sea but not both. Similarly, in primate evolution, we must distinguish between an organism's capacity to encode certain information and the presence of a system into which it can be encoded. We can distinguish, in other words, between semantically open minds and semantically open systems. A brain with the capability of generating new messages will be said to exhibit *produc-*

tivity. A semantic system that allows new messages to be generated exhibits various kinds of *semantic openness*.

A *productive* brain is a brain that can generate new messages with the communication code. It follows that even a brain with the neural potential of productivity can be limited by the structure of the communicative code itself. If the prelinguistic code of the hominids was nonsequential, such a code when coupled with a productive brain could only achieve a state of semantic semiopenness. A *semioopen semantic system* is a semantic system in which the set of all possible messages is finite but in which some new messages can be encoded. In a code where each meaningful expression is composed of a single sign, there are only two possible ways of encoding new messages. In the first case, more than one meaning can be given to a single sign. While homonymy can increase the information capacity of the system, the technique is limited by the small number of unambiguous contexts. In the second case, the number of signs in the system can be increased. This technique is limited by the finite number of distinctions that the ear can make. Contemporary results of auditory-ambiguity limits on natural languages are the small number of phonemes (Miller 1963) and the measure of phonetic efficiency, which averages about 50 percent (Greenberg et al. 1966). It is apparent that a truly *semantically open* system—a semantic system in which the set of all possible messages is infinite—can only be achieved through sequential ordering.

Presumably, productivity has a neurological basis, as do other behavioral capacities. The phylogeny of productivity can be approached through the ability to name objects. Norman Geschwind (1964, 1965) has suggested that object-naming is an example of a process with a distinguishable neural basis. It is discussed here because object-naming involves the design-feature of openness and often displacement. When object-naming is coupled with a sequential system, an infinite set of object names can be generated. Since this is a semantically open system by definition, it is apparent that there are different types of semantic openness. A system in which an infinite set of object names can be generated is a *nominally open* system. It should be noted that "object"-naming is property-naming as well, since what are named in both cases are sensory inputs or memories of sensory inputs.

In Geschwind's theory, object-naming is based on the ability to make cross-modal, non-

limbic associations. Discussion of the Geschwind theory presupposes a knowledge of some neuropsychological terms: limbic, modality, and sensory. The limbic system is part of the phylogenetically older brain and forms the neurological mechanism for emotional responses, such as sex, fear, and aggression (Smythies 1966), although it mediates other behavior as well. It is anatomically distinct from a phylogenetically more recent structure, the neocortex. The neocortex can be divided into sensory areas that in turn can be subdivided on the basis of fiber inputs from the various receptors into visual, auditory, and somesthetic cortex. These are sensory projection areas. Stimuli mediated by the sensory projections Geschwind terms nonlimbic stimuli.

Geschwind theorizes that infrahuman animals readily form associations only between a limbic stimulus (e.g., pain) and a nonlimbic stimulus (e.g., a light flash). Only man has a ready facility for associating two nonlimbic stimuli, although monkeys can be trained to perform such tasks when the stimuli are in the same modality—if the stimuli are both visual or both auditory. Weinstein (1945) presented a rhesus monkey on each trial with a new pair of red and blue objects and one member of a single pair of colorless geometrical shapes. When an ellipse was present the blue object was correct, and when the triangle was present the red object was correct. The monkey learned to sort new objects by color on the basis of a shape cue. When nonlimbic stimuli are cross-modal (e.g., a sound and a light), the Geschwind theory predicts that nonhuman primates will be incapable of solving problems which demand associations between the two.

Theories such as these provide plausible mechanisms for the advent of semantically open systems. Given neural structures that permit the easy formation of cross-modal, nonlimbic associations, a sensory input could easily become associated with a simultaneous vocalization by another member of the hominid troop. Marler (1965) has drawn attention to the fact that the communication systems of infrahuman primates involve more than the auditory modality, and a given signal may be a composite of signs in several modalities. In our terminology, these are sign systems with simultaneity relations between the signs. Thus contemporary nonhuman primate communication systems already demand some facility at cross-modal associations, but the signs are largely limbic stimuli in Geschwind's termi-

nology. Nonetheless, the compositeness of signs may be the most significant preadaptation⁷ for language in nonhuman primates.

The importance of the Geschwind theory does not depend upon its ultimate veracity. It demonstrates that neurological theories that relate animal and human capacities can be integrated with communication theory to give evolutionary models that are amenable to experimental verification. Linguistic evolution becomes a phenomenon susceptible to scientific treatment.

The ability to associate the memories of prior sensory inputs is the neural equivalent of the linguistic design-feature of displacement. Displacement is the ability to talk about things for which no sensory input is present. It presupposes memory and may include what is frequently called "imagination" and "innovation." That is, we may talk about things for which we have never had a sensory input. Monkeys give the predator call long after the predator has vanished, so their communication manifests some degree of displacement. Psychological tests and behavioral observation indicate a far greater capacity for memory in nonhuman primates than is ever employed in the communication system. Once again, we must distinguish between neural potential and the limits of the communicative code. A brain capable of what is here termed *neuro-displacement*—the association of memories—must have a code to communicate this information. A semantic system more sophisticated than nominal openness is needed. In fact, to match the capacity of the human brain a semantic system must have subject-predicate openness and relational openness. We shall define such systems as we consider how they evolved.

Not only is a nominally open displacement system meager from the point of achievement, it is also unsatisfying for the evolutionist. The ability to say "dog" when no dog is present—the ability to cry wolf—has no obvious selective advantage. The selective advantage of language hinges upon its ability to transmit information relevant to group survival that cannot be transferred by imitative learning. How did a code with this information capacity come about? It will be shown that language employs structural principles common to many animals, that certain constraints are placed on sequential systems by immediate memory, and that language evolved in a cultural environment.

Morris (1938) has defined syntactics as the

study of the relations of signs to one another. We speak of syntax when signs occur together or in sequence and their order is not random. In a sequential sign system syntactics deals with sequential constraints. Lashley (1961) has recognized the similarities of language to other behavior and suggested that language is another example of the widespread phenomenon of serial order with a hierarchical ordering of units. It is here suggested that underlying language is the capacity to engage in sequential behavior.

SEQUENTIAL BEHAVIOR

Monkeys have demonstrated their ability in this area. In the course of investigating other phenomena, Stepien et al. (1960) gave to green monkeys (*Cercopithecus aethiops*) auditory discrimination tests of the following type. The test uses two different stimuli, X and Y . When two identical stimuli are presented in sequence, XX or YY , the monkey must give a certain response to be rewarded. When two nonidentical stimuli are given in sequence, XY or YX , the monkey must withhold the response. The tested monkeys learned this discrimination to criterion with a one to five second interval between stimuli, and they learned it with both auditory and visual stimuli.

The "syntactics" of this test can be written as a simple code, C_2 . The expressions XY , XY , YY , and YX are sentences in C_2 . The semantics of C_2 is given by the following:

- (1) XX and YY have the designation, D_1 , in which are the denotata d_1 : behavioral responses a ; and d_2 : pleasant sensory inputs a .
- (2) XY and YX have the designation, D_2 , in which are the denotata d_1 : behavioral responses b ; and d_2 : no reward a .

In this simple code different sequences of signs have different semantic properties. In other kinds of psychological tests as well an animal must learn that sequential relations are important for the interpretation of a sign—that is, for its meaning. In the double alternation test (French 1965), an animal is presented with a right and left stimulus object, under one of which is a food well. The animal must learn that the correct choice alternates between R (right) and L (left), in which the sequence is $RRLLRR$, etc. Probably all mammals can do this test.⁸ Rhesus monkeys have also been taught to do sequential-order-

learning sets (Miles 1965). The animal is repeatedly presented with four stimulus objects. The objects are always presented one at a time (except on the test trial described below) and in a fixed sequence. The test trial consists of presenting two of the stimulus objects together. One member of the pair is in the correct sequential order and the other member of the pair is not. The animal is rewarded for choosing the member of the pair that is in the correct sequential order.

Of even more interest are the studies of rhesus social behavior by Altmann (1962, 1965). Given sequences of social interactions by rhesus monkeys, better and better predictions of subsequent acts can be made as more sequentially prior acts are included in the probabilistic sample. In theory, a point should be reached where sequentially prior interactions no longer increase predictive accuracy and these remote interactions can be excluded. However, as far as any individual rhesus monkey is concerned, all prior interactions engaged in by the monkey are relevant to the predictive accuracy, since the monkey's own behavior is based on just such prior interactions. Altmann has suggested that the interactions of primates in situations demanding the monitoring of complex sequential stimuli is one of the preadaptations for language. The data considered here attest to the utility of searching for the roots of syntax in general behavioral capacities that can be investigated in nonhuman animals. A similar conclusion has been reached by Premack and Schwartz (1966) who are attempting to determine the limits of concatenation in the chimpanzee by teaching these animals simple codes based on linguistic models.

A behavioral capacity such as sequential behavior makes possible combined behavioral and anatomical studies. If one restricts the study of language to language, it is clear that little can be said about its evolution, and only human data will be applicable to an investigation of its neural basis. This is unsatisfying not only to comparative communication but to the neural sciences as well, since only limited experimental work can be done on man. A broader conception is justified not only methodologically but for theoretical reasons as well. Milner (1967) has described striking deficits in the processing of verbal material by human patients with hippocampal and amygdala lesions. The hippocampus and amygdala are limbic system structures, found in all

primates; and as such they lend themselves to experimental investigation in animals. Moreover, evolutionary trends can be deduced on the basis of comparative neuroanatomical studies, and there is evidence of phylogenetic expansion of the amygdala (Crosby and Humphrey 1941) and hippocampus (Stephan and Andy 1964) in the order primates. Recent models of hippocampal function (Douglas 1967) have attempted to integrate both animal and human data in a unified theory. An understanding of brain mechanisms relevant to language and a reconstruction of phylogenetic trends through comparative neuroanatomy will eventually permit the formulation of testable theories of linguistic evolution.

BEYOND NOMINAL OPENNESS

While neurological structures make language possible, they also limit the variability of linguistic systems in various ways. The best available example is that of the limitations imposed by immediate memory. These limitations are discussed in relation to a simplified code:

Code C_3 is a sequential sign system with two elements, X and Y . Without repetition this code can encode no more than four messages: X , Y , XY , and YX . With repetition the number of possible messages is theoretically infinite, for we can have nX , nY , or an infinite number of X - Y combinations. Yet practically the sequences are severely limited. Miller (1956) has shown that the span of immediate memory—the ability to recall several stimuli after they have been presented in sequence—is limited to about seven plus or minus two units (about five in the case of monosyllabic English words presented randomly). In other words, given human limits on immediate memory, the concatenation of elements in code C_3 is limited to K elements where $K = 7 \pm 2$. However, we know that languages use more phonemes than this in sequence. How is this discrepancy to be explained? The answer is that phonemes become components of larger units. They are chunked together into words which are in turn concatenated. This procedure is possible because, as pointed out by Miller (1956), the span of immediate memory is limited by the number of units or chunks rather than the amount of information per chunk. The examination of code C_3 indicates that sequential sign systems, if they are to be mediated by the human brain, must become hierarchical if the string length is to be

increased. That is, sequential sign systems must expand in this way if the set of possible messages is not to remain restricted to the number of K unit strings that can be constructed out of a finite number of different signs.⁹ Vocalizations in animals are used to convey messages about food, escape, reproduction, and group movements (Collias 1960). Displaced messages about these same phenomena would demand a substantially greater channel capacity, as would an increased behavioral repertoire for coping with them. Linguistic codes can be seen as developing in conjunction with increasing demands on the channel capacity of the communication system. Language is as much a product of culture as its necessary prerequisite.

Given a code with names for objects and properties, it is possible to transmit the message, "X has the property Y." Such a code has a simple *subject-predicate openness*: the pairing of an object name with a property name. A code which can transmit information about the properties of objects has an obvious selective advantage, but it is far from a contemporary semantic system. A simple subject-predicate code cannot transmit information about relations between objects and properties. It cannot say, for example, "X is bigger than Y." The code lacks *relational openness*. Relational openness is made possible through linguistic devices called *markers* which correspond to the *formators* of symbolic logic. These are signs which function as quantifiers (such as *all, every*) and logical operators (such as *and, or*). Such signs are found in all languages (Weinreich 1963). While little can be said about such signs from a phylogenetic viewpoint, it is clear that the evolution of language must at some stage be discussed in conjunction with the evolution of logical processes.

The various types of semantic openness presuppose the psychological ability of innovation¹⁰ and the linguistic design-feature of traditional transmission. While no examples of vocal-auditory innovation are known from nonhuman primates, it is found in other spheres of behavior. Imanishi (1963) and Kawamura (1963) describe an innovation of sweet-potato washing by a female Japanese macaque and its diffusion to other members of the troop. Rowell and Hinde (1962) note that vocalizations of rhesus monkeys vary from troop to troop, indicating perhaps some traditional transmission of these calls. Traditional transmission of vocalizations is also

found in some species of birds (Marler 1963), although caution must be exercised in arguing from nonprimate animals. Traditional transmission of some nonvocal behavior has been described for nonhuman primates. Neither innovation nor traditional transmission are unique to man, and both can be postulated for the prelinguistic hominids.

It is common to consider language as a prerequisite of culture; while this is not tenable, it is reasonable to suppose that language is the prerequisite of some aspects of culture. Mark (1962) notes that a uniquely human situation occurs when problems are formulated by one brain and solved by another. Such a situation presupposes a complex communication system; and it is unlikely that science, for example, could exist without language. However, as Hymes (1964) points out, it remains to be determined just what cultural phenomena are dependent upon language for innovation and/or transmission. If the phylogenetic relations of various types of sign systems can be established, it may be possible to reconstruct cultural historical sequences by determining just what information can be transmitted by a particular type of sign system. Through such techniques language origin theory may prove useful to general anthropology.

NOTES

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³ Absolute threshold studies are not ideal measures of auditory capacity, but they must suffice in the absence of other comparative data.

⁴ There has been a wholesale de-emphasis in the neurological sciences of functional distinctions based on cell morphology. While this view of stellate cells has not been refuted, it should not be given too much weight.

⁵ This definition is modified from Greenberg's (1963) definition of a sign system. Since it is not useful for comparative purposes to restrict the term "sign system" to systems with sequential relations, I have distinguished between sequential and non-sequential sign systems.

⁶ It may be that systems with intergradations are more a function of diurnality than of phylogenetic

position. Moynihan (1966) has compared the vocalizations of the diurnal marmoset *Callithrix jacchus* with those of the phylogenetically more advanced but nocturnal *Aotus trivirgatus* and found the vocalizations of the latter to be more discrete.

⁷ The term "preadaptation" implies no teleological conceptions. A structure is a preadaptation if it permits a shift into a new adaptive niche (Mayr 1963).

⁸ Dethier and Stellar (1964) state that performance on this test increases with phylogenetic position. Warren (1965) has shown this result to be due to the small sample of animals tested.

⁹ While a hierarchical code explains how the limitations of immediate memory are circumvented, the value of K is not itself a sufficient explanation of why language is hierarchical. Where K is equal to the maximal length of the string and M is equal to the number of signs in the code, then the number of possible strings is equal to

$$\frac{M(M^K - 1)}{M - 1}$$

For a system of fifty phonemes, the number of different K (where $K=7$) unit strings is astronomically large. Other considerations of immediate memory effects on language can be found in Alverson (1963) and Yngve (1962).

¹⁰ Muriel Hammer (1966) has recently suggested that all natural systems, with the exception perhaps of the universe itself, are open systems. It is necessary to distinguish between innovation by rule or intent and innovation by error. The semantic system of a natural language can have innovation through intent or through error. Mutations in the genetic code, on the other hand, are innovations through error only.

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