

Differentiation and Syntax in the Evolution of Behavioral Flexibility²

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It has become something of a truism in anthropology that humans may be distinguished from other animals by the extreme flexibility of their behavior. Many students of human behavior assume that this flexibility is made possible by (and is indicative of) a lack of genetic control over the behavioral repertoire. Dobzhansky and Montagu (1962[1947]) point out, however, that the alternative to the concept of "genetically controlled fixity of traits" is that of "genetically controlled plasticity of behavioral traits," not the abandonment of all conception of a relationship between genes and behavior. They argue that plasticity itself is a type of biological adaptation with its own structural (and ultimately, therefore, its own genetic) underpinnings. They do not, however, suggest the nature of the biological structures which permit behavioral flexibility, nor do they seek the evolutionary sequence by which such structures are derived. Instead, they present plasticity as a binary alternative to fixity and talk of the "appearance" or "emergence" of the "characteristic human plasticity" (p. 151) as if flexible behavior replaced fixed behavior in a kind of saltatory leap.

There is, I will attempt to show, an alternative way of conceptualizing behavior and behavioral evolution which requires neither an abandonment of Darwinian gradualism (or its contemporary equivalent) nor a strict dichotomization of behavior into fixed and flexible kinds. It may be usefully applied to an understanding of the evolution of human behavioral flexibility, but it may also have more general application. True to a hal- lowed tradition among behavioral and social scientists, this conceptualization relies heavily on a linguistic "analogy."

The ubiquity and the continuing usefulness of linguistically inspired models should itself alert us to the possibility that the language ability of humans may be based on operating principles of much greater generality than communication via an oral-aural channel and much earlier derivation than the hominid grade of behavioral complexity. If it can be shown, as I will suggest here, that all motor behavior is characterized by the same structural organizing principles that are evident in speech, then we may be one step closer to understanding the biological preadaptations which permitted the evolution of speech. More important, however, for our present discussion, the application of linguistically derived principles to the analysis of motor behavior may prove to be a useful way to conceptualize and compare the varied degrees of behavioral complexity and flexibility characterizing different taxa.

The principles which linguists have used with great success to understand and compare languages include the isolation from the stream of speech of discrete component units (phonemes, morphemes) which can be combined and recombined

into a seemingly infinite variety of new wholes; the organization of units on at least two distinguishable hierarchical levels simultaneously (duality of patterning), vastly increasing the possible number of new combinations; the existence of rules for combination (grammar) which group component units into categories and channel (limit) innovative combinations. It is at least plausible that homologues of all these features of language may be operating, and may have had their origin, in prelinguistic behavioral systems, perhaps of the most primitive kind. Paralleling, therefore, the propositions which have proved so useful in the analysis and understanding of language, it is possible to construct the following series of hypotheses about motor behavior:

1. The behavior of all organisms shows repetition. That is, from the flow of movement repetitious units can be distinguished.

2. These units, if examined carefully, are themselves composed of repetitious units. That is, a hierarchy of behavioral units exists.

3. At each level, at least some recombination of units is possible. Recombinations of units at different hierarchical levels take place simultaneously.

4. At each level, these combinations are not (or are not always) random, but follow rules which are finite in number. That is, at least some behavior may be said to be organized by syntactic principles.

That a finite set of constituent units and syntactic rules can generate a seeming "infinity" of behavioral products has been demonstrated for language by Chomsky (1964[1957]) and may prove to be true for motor behavior as well. In fact, the number of possible products may be larger for human motor behavior than it is for language. Motor behavior may be characterized by many more levels of hierarchical arrangement, by more components at each level, and by more rules (and more complex rules) for the combining of component units.

The idea of a similarity between the organization of language and that of motor behavior has come to the attention of a number of observers. Lashley (1951:121-22) was perhaps the first to hint at it when he referred to the "syntax of movement" and the relevance of "hierarchies of organization" for helping to unravel the mystery of serial organization in "skilled action." A more explicit comparison is made by Kaimus (1969:613), who paraphrases Chomsky's description of the grammar of a language and defines the "behavioral competence" of an animal species as "a device (set of rules) that provides a complete specification of 'all permitted sequences of motor patterns, including their structural modifications.'" Bruner (1970:15) attempts to explain the language-like abilities of signing apes (a learning potentiality which seems to serve no function in the feral life-strategies of these animals) by suggesting that "higher primate skill . . . has about it certain language-like properties. . . . Constituent acts are put together in required serial order, yet permitting of substitution and modification better to conform to an intended outcome." He goes on to state that "the emergence of this form of more flexible skill (in contrast to fixed action patterns) made possible the emergence of language." Finally, the most concrete application of the syntactic idea to the actual behavior of a specific animal is that of Marshall (1965),³ who was able to construct a phrase-structure grammar which generated the reproductive behavior of the male pigeon on the basis of transition probabilities between component sequences of behavior worked out by Fabricius and Jansson (1963).

Antecedent to and independent of the notion of parallels to linguistic structure in the organization of motor behavior is the repeated reference by psychologists and ethologists, in their

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³ Although Marshall's manuscript has not been formally published, discussion by Hutt and Hutt (1970), Vowles (1970), and Dawkins (1976) has brought this work to wider public attention.

attempts to analyze the structure and functioning of behavior, to the concept of hierarchical organization. Weiss (1941) distinguished six levels of motor organization, each containing components of the next higher level. Tinbergen (1951) outlined the component-behaviors of the reproductive instinct (fighting, building, mating, care of offspring) and suggested that each of these has component behaviors (e.g., fighting may take the form of chasing, biting, threatening). However, because this model describes behavior in terms of consequence or function rather than in terms of the form or structure of motor movement (cf. Hinde 1970:10-11), it does not easily accommodate an idea which is central to the argument being developed here, that of recombining component units into *different* configurative wholes on the next higher level of organization.

Discussions of the concept of "instinct" invariably describe behaviors which fall under this rubric in functional terms (e.g., the reproductive instinct describes the consequence of the behaviors involved). A much more useful analysis of the innate basis of behavior (and one which emphasizes *form* as well as function) has developed with the concept of "fixed action pattern" (Schleidt 1974). Fixed action patterns have been described as "movements whose form seems to be independent of environmental stimuli even though they may be elicited by such stimuli in the first instance" (Hinde 1970:17). To the degree that fixed action patterns represent repeated and isolable units of behavior, we can begin to ask if they can be combined in variable patterns to form variable behavioral wholes at a higher level of abstraction. In discussing the work of von Holst on fin movements in the spinal lip fish, Eibl-Eibesfeldt (1970:42) has pointed to the "hierarchical organization of . . . fixed action patterns" and expressed the view that "all complex fixed action patterns . . . can be subdivided into elements which in turn are fixed action patterns." Although he does not explicitly develop the idea that component fixed action patterns may be combinable in *variable* ways to form variable complex fixed action patterns, we might add this as a corollary hypothesis. That is, it may be useful to begin to consider if the same component action patterns are involved in different higher-level behavioral wholes.

Looking at behavioral phenomena in this way may help us better to explain the sequence of events in behavioral evolution. To refute the suggestion by Bruner quoted above (that flexible behavior *contrasts* with fixed action patterns), it may be that behavior became more "flexible" when more permutation of the component action patterns became possible. Inflexible behavior may be compared to a sentence which, once started, must be completed in an unvarying way, while flexible behavior allows for a rearrangement and substitution of the parts to form "new" sentences. If we consider complex fixed action patterns as being themselves composed of fixed action patterns (as Eibl-Eibesfeldt has suggested) and flexible behavior as the ability to isolate behavioral units and then rearrange them, then we can begin to define a sense in which even flexible behavior is composed of "fixed" behavioral sequences. Thus, Bruner may not be completely correct in contrasting flexible behavior with fixed action patterns as if they were completely different in kind. Instead, we can begin to see how flexible behavior may have been *derived* from fixed behavior in a kind of evolutionary sequence in which the fixed action patterns of earlier and simpler organisms are differentiated into component units which can then be recombined in variable ways in descendant, more complex organisms. Such a conceptualization would enable us to explain how the fixed behavior patterns of earlier organisms can provide the substratum for complex behavior in descendant organisms.

Even if we choose to argue that a particular behavior pattern could not have been derived from any subdivision of earlier fixed behavior, that it arose *de novo*, it still seems reasonable to argue that behavior patterns are composed of "fixed" components which became increasingly limited in spatiotemporal

coverage as complex, behaviorally flexible organisms evolved. Thus, it is not necessary for us to eliminate all conception of fixed behavior in order to explain the increasing plasticity of behavior as we go from simple to complex organisms, nor (as suggested earlier) is it useful to dichotomize behavioral plasticity and behavioral fixity as if they were mutually exclusive. Plasticity has often been attributed to humans and other higher animals without any attempt to explain how it evolved. If we are to understand the derivation of plasticity from a base of fixed behaviors, then the model proposed here becomes useful as an evolutionary explanation of this phenomenon. Plasticity is no more than fixed behaviors of increasingly limited scope making possible an increasing variety of combinations and providing the repertoire for more appropriate response to a stimulus situation. Seen in this light, behavioral plasticity should not be conceived of as a terminal adaptation or singular quality. Instead, it seems more useful to think of a continuum of increasing possibility for behavioral plasticity, with many aspects of human behavior representing an extreme development along a particular evolutionary path.

Not only "plasticity," but even the concept of learning takes on new meaning in the context of this model. "Learning" more often means putting together behavioral units which are already in the repertoire of the animal to form new behavioral wholes rather than the initiation of completely innovative behavior. Schiller (1957) emphasized this idea particularly as it applied to the insight learning of chimpanzees, but it may have even wider application. It may be that all learning involves the learning of combinations and/or the learning of rules for combining behavioral units. In the mature animal, these learned combinations may take on a rigidity of performance which rivals that of the long sequences of inherited fixed action patterns. It is the ability to add *learned* "fixities" of behavior to the genetically inherited fixities that makes an animal more rapidly adaptable to changing circumstances while keeping behavior socially predictable.

The inheritance of particular combinations of behavioral units or rules for combining units (or of predispositions to learn certain combinations or rules) suggests a new means by which the evolutionary relationship between taxa may be traced. Historical linguists dating back to Sir William Jones in the 18th century have suggested that relationships between languages can be more accurately established through similarity in grammatical structure than through similarity in vocabulary because the rules change more slowly than the lexicon (Waterman 1963:16). In the same way, ethologists can begin to ask to what degree a similarity in the rules for combining behavioral units (seen as a similarity in the structure of particular combinations observed, irrespective of the behavioral units involved) may indicate evolutionary relationship. Taxonomists already use homologues of behavior to aid in the classification of animals. The model proposed here would break down the search into one for both homologues of behavioral elements and homologues of rules for combining behavioral elements.

The controversy over whether humans possess innate behaviors may find some clarification when understood in terms of this model. Have humans really lost the inherited responses other animals possess (an anti-evolutionary view, as many ethologists have emphasized), or is their response set so varied that the large number of possible responses blinds us to the innate components of many of them? Eibl-Eibesfeldt (1970:462) has suggested that humans, being more complex than other animals, must have *more* rather than fewer inherited fixities of behavior. In an attempt to discredit the notion of the existence of innate behavior in humans, it has often been pointed out that the long sequences of unvarying behaviors which are exhibited by lower animals do not exist in humans. If this is true (and it is by no means beyond debate), it would still not prove that humans are without unlearned fixities, although it might be interpreted to suggest that the permuta-

tions of fixed elements (on several hierarchical levels) could vary without limit. In terms of this model, we could say that the elements were still inherited but the rules for combining them were not. However, rather than say that no rules have been inherited, it might be advisable (following the lead of Eibl-Eibesfeldt) to suggest that *more* rules for combining elements have been inherited by humans and/or that the rules are of a nature which allows for more permutation of the elements.⁴

Borrowing from the notational system of early transformational linguistics (Chomsky 1964[1957]), itself derived from that of mathematics and symbolic logic, we might represent this change in terms of phrase-structure rules. Where a less complex animal might inherit a rule such as $S \rightarrow A B C$, a more complex animal in the same evolutionary line might inherit a rule like $S \rightarrow A \{B^{(C)}\}$, where S represents a sequence of behavior, A , B , C , and D are constituent units of behavior, $\{ \}$ signifies choice, and $()$ signifies option.⁴ The second rule includes the behavioral sequence $S \rightarrow A B C$ as one of its possibilities, but it also includes, as other possible sequences, $S \rightarrow A B$, $S \rightarrow A D$, and $S \rightarrow A D C$. The number of elements which can be chosen for a behavioral sequence has increased only slightly, but the rule for combining elements allows for more possibilities, more "flexibility." Flexibility, therefore, may denote not an absence of inherited rules, but a difference in the generative capacity of those rules.

A promising feature of the proposed model of behavioral organization is its capacity to accommodate what we now know about evolutionary and developmental trends in the structure and functioning of the nervous system. Holloway (1966) has pointed out, for example, that the difference in cranial capacity between humans and other hominoids is not just the result of an increase in the number of neurons, but principally the result of an increase in their structural complexity. Thus humans have an average of only 1.25 times the number of cortical neurons as chimpanzees even though they have 4 times the amount of cortex. The greater complexity of human neurons is manifest as a decrease in neuron density, an increase in the number of neuroglial cells per neuron, and an increase in neuron size and in the amount of dendritic branching. Taken together, these developments suggest the evolution of a system in which each neuron has both the structural and the metabolic potential to participate in frequent and varying firing patterns. This emphasis on increasing connectivity between existing neurons (rather than increasing number of neurons) is just what one would expect given our hypothesis that a change in the nature of the rules governing the combining of elements may be more important to the evolution of flexible behavior than a change in the number of elements. The proposed reconstruction of evolutionary events is consistent, therefore, with Holloway's suggestion that the evolution of the hominid grade may be most distinguishable by "neural reorganization" (p. 106).

Equally relevant to this argument is the volume of research which has developed around the discovery that rats whose early ontological development includes an experientially rich environment have higher cerebral cortex weights than paired animals raised in experientially impoverished environments. This difference is not attributable to any difference in the number of neurons per unit of cortical tissue, but seems to be the result of larger nerve cell bodies and nuclei and of an increase in the number of dendritic spines, the thickness of the post-synaptic membrane, and the number of neuroglial cells (Rosenzweig and Bennett 1977). A parallel between ontological acquisition and phylogenetic inheritance is suggested here. Ontological experience which requires or encourages flexible behavior pro-

duces neurobiological change which is in the same direction as change produced by natural selection. In both cases, it is the connectivity and the patterning potential of the neurons, not the number of neurons, which seem to have increased (or increased disproportionately).

Jerison (1973:81) has suggested that behavioral differences between the taxa *should* be reflected by differences in the nervous system:

It is likely that as we learn more about the wiring diagrams of various brains we will recognize more and more differences. These differences should impress us no more than the behavioral differences that are much more easily observed. . . . we should expect adaptation to various niches to be made possible by the evolution of appropriate structures and functions, and reorganizations of the brain would be no more than the neural equivalents of species-specific behavior patterns.

If we are able to organize our understanding of "species-specific behavior patterns" into behavioral grammars, then the "neural equivalents" (i.e., the "wiring diagrams") of these patterns may be easier to define. The syntactic model of behavioral organization may not only accommodate, but also contribute to our understanding of nervous organization and evolution.

In light of the perspective which has been developed in this paper, a reappraisal of the fixed action pattern concept may be in order. Fixed action patterns may be no more than a subset application of broad principles of behavioral organization which generate all animal behavior, both fixed and flexible. Extended sequences of unvarying behavior may be the result of a limiting, genetically coded grammatical heritage. There is little or no individual variation observable in the performance of certain behavioral sequences because the observed sequences are the only combination of behavioral elements connected (or connectable) in the central nervous system of the animal. Varying degrees of flexible behavior, on the other hand, may be the result of a genetic encoding of the nervous system which allows for varying combinations of behavioral elements. Perhaps the earlier enchantment of ethologists with describing fixed action patterns should now be replaced with the broader, though much more difficult, task of discerning how the behavioral repertoire of any species is syntactically organized to generate both inflexible *and* flexible patterns of behavior.

If the model proposed here should prove correct, it would provide an interesting example of what has been described as "throwing light both up and down the evolutionary scale" (Hinde 1974:191). It has generally been believed that the basic laws which govern behavior are more easily uncovered in the study of behaviorally simple animals. The present model, however, is derived from the study of the linguistic ability of that most behaviorally complex of animals, the human species. It could not have been as easily discovered in a simple organism because another concept, that of the fixed action pattern, has dominated efforts to describe behavior. The inadequacy of the fixed action pattern concept for explaining the complexities of human behavior in particular and the flexible behavior of other animals in general has provided impetus to the search for a more comprehensive theory. The model presented in this paper is a way of conceptualizing the total repertoire of both behaviorally simple and behaviorally complex animals and of specifying the evolutionary relationship between them.

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⁴ Following the distinction in usage initiated by Chomsky (1964 [1957]:110), parentheses are used to indicate that one and only one line *must* be chosen and brackets to indicate that the contents of the brackets may be either included *or* excluded in the rewriting.

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