I read Dr. Lockard's very interesting comment on comparative psychology, and was impressed not only with the scholarship he showed in it, but also by the fact that he feels comparative psychology has produced mostly what in comparative anatomy and comparative physiology we call analogy, rather than homology. I agree, and have therefore developed an aversion to comparative psychology as it is generally practiced. I am by choice a physiological psychologist, because I believe that only through the study of mechanism can we achieve insight into homology. In the language of genetics, only through an analysis of mechanism can we penetrate through the phenotypical to the genotype. Pure description of animal behavior, though fascinating, is not enough. I used to go out with Danny Lehrman and others to watch birds, and I find watching primates even more interesting. Watching people can of course be the epitome of fascination. But for me these observational techniques have no real chewiness to them, no earthiness. I have to participate, to know about mechanisms, before I can be really satisfied. Most comparative psychologists use Darwinism as an excuse to make their observations a science. To quote Sigmund Freud, this "has ... a dubious appearance of arbitrariness, even though it would be possible, pursuing a Darwinian line of thought to claim that ... [these mechanisms] are indispensable and consequently bound to survive." Now I don't mean by this that genetic population pressure studies or the pursuit of the machinery of evolution is to be regarded as trivial. What I am talking about is the oft-repeated, simple assertion that observations can be explained "by recourse to the principles of random variation and special selection," without spelling out the mechanism by which those principles come to apply to the particular behavior observed. Some have, of course, done the job properly. Danny Lehrman, Thorpe, Hinde, and the whole Cambridge group: these are people who have combined evolutionary principles with the search for mechanisms. So, in the tradition of these pioneers, let me illustrate how I apply the comparative method. I will address myself to the problem of grammar and meaning. I have deliberately chosen this difficult topic; there is no reason why our science should so utterly disregard cognitive processes as it has to date. Konrad Lorenz has said, showing great insight, "Life is a knowledge process."

In his address of acceptance of the chair at Edinburgh in 1970 and also elsewhere, Vowles suggested that perhaps phylogeny could be characterized by the development of a grammar of behavior. Invertebrates show finite-state Markov-type constructions; vertebrates show phrase-structure hierarchies; and
man is distinguished by transformational capacities. Though perhaps in error in points of detail, this sweeping statement grasps the essence of what I want to discuss. Since my competence is limited to primates and their brains, however, I will focus on the structure of grammar and meaning in these mammals and will leave the comparative problem to students of a greater variety of species.

Let me begin with some definitions. Information measurement theory is based on the ability of one communication to resolve the uncertainty produced by two disparate prior communications. The amount of reduction of uncertainty is measured in bits of information. If one is given that communication repeatedly, it is the same information, so there is no reduction of uncertainty. Yet a good deal of communication is of this sort. These repetitive communications are called redundancy. Redundant communication can, of course, be very dull. If I merely repeated the word “Yes, yes, yes, yes, yes,” you would soon be asleep (in fact, you may already be so). There are other forms of redundancy that are much more highly structured. Every novel, for instance, is a form of structured redundancy. For the most part, the plots are not informative or really novel. What makes a novel interesting is its grammatical elegance and its evocative meaning. These properties deal with the structure of redundancy, not with information and the reduction of uncertainty per se.

The problem of information and redundancy can be stated in another way. A communication can have a referent. Ordinarily, referent communication conveys information. But philosophers have for many years distinguished between reference and meaning. Meaning goes beyond reference into use, the use that the information conveyed can have to the conveyor or to the person to whom it may be conveyed. For example, Peirce makes the statement, “We are too apt to think that what one means to do and the meaning of a word are quite unrelated. He points out that meaning is always related to doing, the pragmatic, in some way. As we shall see in a moment, meanings can be of two kinds: significant and symbolic.

What then of grammar? Grammar will here be considered as a form of logic, and I refer especially to the form of logic that orders sequential dependencies among communicative occurrences. When a communication reflects only the immediate state of the organism, then that communication can be thought of as determined by a Markov process, very much as a set of dice or the image produced in a kaleidoscope depends only on the configuration of the parts at the moment that they cease to be perturbed. On the other hand, when a communication becomes organized according to some rules that determine the order in which the communications take place, then, in the terminology of linguistic grammarians, a phrase-structure grammar is involved. It is quite obvious, however, that such phrase structures do not occur only in human linguistic communications. A good deal of the concatenation of egg-rolling behavior or of mating and maternal behavior in birds, for instance, depends on “phrases” of behavior that trigger some state in the communicant to whom the behavior is addressed; this state then gives rise to another set of behaviors, which in turn change the state of the original communicant. The important thing here is that it is not just one communicative act or one behavior that is triggered by the change of state; a
whole sequence is generated. The idea of a generative grammar, so popular in
current linguistics, is therefore applicable to certain forms of animal commu­
nication as well. What is believed to be unique to human communication is the
ability to transform these rules that determine sequence. When I write a paper or
present a lecture, I do it differently every time, even though the material covered
may be the same. In order to achieve this flexibility, transformational rules seem
to be imposed upon the more primitive phrase-structure rules.

A word about the relationship between grammar and meaning. My own
formulation is that grammar is to meaning as a partition is to the mathematical
set that it partitions. Thus grammar and meaning usually imply one another. In a
sense, the distinction between reference and meaning is similar to the distinction
between grammar of finite state and phrase-structure grammars. It is also
possible to distinguish a level of meaning that corresponds to transformational
grammar. This level of meaning comes about when the meaning of the
communication that is its use depends on the context in which it occurs. We can
therefore distinguish between meanings that are context-free and those that are
context-sensitive; and, as we shall see, there are specific brain mechanisms that
have been identified for each of these types.

Let me begin with context-free constructions: these we will call signs. The
operational paradigm for the construction of signs is a discrimination: a visual
discrimination, an auditory discrimination, a somatosensory discrimination, a
taste discrimination - in other words, various sensory discriminations. Discrimi­
nations allow one to identify events and objects and to name them in the
ultimate sense, irrespective of the environmental situation or even the subjective
situation in which they occur. A sign, therefore, is a context-free construction: a
rose is a rose is a rose is a rose, whether it appears on one's lapel, in a garbage
can, or in a vase on a table.

About 20 years ago, Harlow's group at Wisconsin and my group at the Yerkes
Laboratories and at Yale simultaneously discovered a part of the monkey brain
that dealt with context-free constructions - with signs, that is, with discrimina­
tive behavior. It is located in the inferior part of the temporal lobe. We had
known for many years that lesions of the temporal lobe give rise to visual
disturbances in man, but we had always thought that this was due to the
involvement of Henle's loop, a portion of the optic radiation that was assumed
to course around the anterior portion of the temporal horn of the lateral
ventricle. When neurosurgeons began to perform anterior-temporal lobectomies
without producing any visual field defects, the existence of Henle's loop was
called into question. In fact, the visual difficulties that occur in man, especially
from the subdominant hemisphere, arise from involvement of the temporal
cortex itself, just as they do in the monkey. Behavioral analysis of the
discrimination deficits in monkeys is therefore relevant to our problem. What
this analysis has shown is that the cortex that lies in the posterior part of the
hemisphere, in between all the projection areas, can be divided into zones, each of
which is associated with one of the primary sensory modalities: somesthesia,
taste, audition, and vision. The disturbance in the sensory discrimination is not
due to inability to tell the difference between two objects to be discriminated.
For instance, monkeys who have learned to make a visual discrimination between an ashtray and a tobacco tin in a simultaneous discrimination, albeit with a deficit as compared to their normal controls, cannot use this ability to discriminate in another situation, as in successive discrimination, in which the tobacco tin and ashtray are placed in a central location and the monkey has to go right whenever the ashtray is present and to go left whenever the tobacco tin is present. Many other tests have shown that it is the utilization of the differentiation that the monkey finds difficult. Neurological analysis of the mechanism involved in utilizing discriminative information shows that the pathways involved appear to be downward from the temporal cortex into the visual system, as far down as the retina itself. The temporal cortex may be thought of as a mechanism for generating rules that organize the input within a primary visual system. These rules allow invariances in the input to be identified. When the temporal cortex is removed and the environmental context is altered, these invariances can no longer be utilized to guide behavior. Context-free constructions are therefore dependent on the rules (phrase-structure rules) generated by the temporal cortex. The significance of differences in sensory input is a function of such rules of utilization. Significant meanings, or signs, are therefore due to context-free phrase-structure-type constructions, and the mechanism involved is the generation of such rules by the temporal cortex and their imposition through efferent control on sensory input.

There has also been a good deal of work done on context-dependent constructions. Context-dependent communications have as their paradigm the delayed response or delayed alternation performance that has been used so extensively in physiological psychology. The meaning of a particular behavioral act, or of the stimulus, depends not on the situation of the moment in these tasks, but on what went before: on the context in which the performance occurs. In this instance, the context is a temporal one. Here again, the discovery was made some 20 years ago that the frontal part of the monkey's brain was involved in the performance of this type of task. Over the years, we have also shown that the limbic portion of the forebrain is involved in its proper performance. If these parts of the brain are removed, monkeys can no longer alternate. We know practically nothing about the details of the connectivity between the limbic systems and the frontal lobe that is specifically involved in this task. We do know that they are anatomically related. We know that there are connections, but we don't know how these connections operate to allow alternation and delayed response performances to occur. Many years ago the delayed response paradigm was modified, thus: instead of showing where a piece of food might be hidden and then asking the animal at some later time to find it, we placed a token in sight of the animal, then removed it, and the animal was asked to find food in the location where the token had appeared. In turn, this so-called indirect version of the delayed response problem was made more complex, until the animals were shown to be capable of working for tokens that could be used at a later occasion, depositing them in a chimpomat which would deliver food. Tokens whose meaning is very specific to the situation in which they occur are usually referred to as
symbols. Symbolic meaning differs from significant meaning in this very fact of context dependence. Significance is context-free; symbolism is highly context-sensitive.

There has been a shortcoming in the tests that we have used in our brain research to establish that primates are capable of significant and symbolic behavior and to trace the brain mechanisms that are involved in this behavior. This deficiency is that we have constructed the tests and have asked the animals to communicate with us only through some very simple instrumental act. This deficiency was overcome recently in two studies done with chimpanzees. The Gardners, at the University of Nevada, taught their chimpanzee, Washoe, to use American Sign Language and succeeded in constructing a vocabulary of approximately 150 words by which the chimpanzee could communicate with them. In another experiment, Premack, at the University of California at Santa Barbara, developed the token technique and showed that his chimpanzee, Sarah, could organize tokens in several orders of complexity to communicate with her trainer. As might be expected from the context sensitivity of tokens, Premack found that Sarah's behavior was highly sensitive to any change in the training personnel. The meaning of the tokens was too dependent on the specifics of the training situation. In short, subhuman primates have been taught to communicate with both signs and symbols, using both context-free and context-sensitive constructions.

I want now to address myself to the relationship between finite-state, significant, and symbolic processes. It is customary to think of them as being hierarchically organized, and perhaps this is so. But I have been set to pondering this problem by the fact that the limbic and frontal parts of the forebrain are so intimately related in delayed alternation and delayed response problems, while the posterior cortex seems to deal with discriminations of every sort. Could it be that instead of there being a trichotomy, as outlined in the initial parts of this paper, there are actually four fundamental processes that can be distinguished? The relationship between referent and sign seems to be a straightforward one. What I am wondering is whether there is a similar relationship between some finite-state-type process and the symbolic or transformational domain. One of the puzzles that has plagued us in brain research on the frontal lobes and the limbic system is that although delayed alternation is disrupted by lesions of any limbic or frontal system, delayed response is not. Delayed response behavior seems to be more specific to the frontal cortex than to the limbic forebrain. Could it be that delayed alternation behavior is a function of a finite-state-type process, just as is referent behavior? If so, what is the difference between them? As we have already noted, referent behavior addresses the invariant in the communication. It is tempting to suggest that alternation addresses some variances, but not all variances: only those that recur with some regularity. Recurrent regularities are ubiquitous in the internal environment of the organism. They lead to states of hunger, thirst, sexual and respiratory rhythms, and the like. Hence homeostatic rather than stochastic properties determine these states. We know altogether too little as yet to characterize the difference between a stochastic and a homeostatic process. The only lead I have obtained
has been from Sherrington's analysis of spinal cord mechanisms, in which he
talks about the difference between the organization of antagonistic and of allied
reflexes. I pursued this lead elsewhere some years ago, but it might be
worthwhile to look at this distinction once more in the light of more recent
knowledge.

I am encouraged by another set of observations to look for some
finite-state-type mechanism as a primitive context dependency. One of my few
forays into the behavior of nonfurry beasts was to study the octopus. My
reason for studying this animal was this: he changes color so well that one has a
fairly good idea of what is going on within the animal. He seems to turn livid
when he is angry, and when very, very angry he turns purple. On the other hand,
if he is scared, he turns white. And there are all kinds of shades in between. I
thought that perhaps I would find out whether these colors are specific
indicators of the octopus' "feelings," or whether they are context-dependent in
some way. It turned out that the color the octopus changes to is somewhat
context-dependent. For instance, if an octopus is approaching another octopus
and he is white and his tentacles are stretched out but the ends are flaccidly
hanging down, then it indicates that the approaching octopus is afraid and will
turn out to be submissive to the other one. On the other hand, if the octopus is
the same white color, but is just sort of sitting there in the presence of another
octopus with his tentacles waving loosely about, it means that he has had a good
meal, he is digesting and is probably very happy and satisfied, and he simply
wants to be alone to enjoy his postprandial state. The same thing applies to some
extent to the livid color. It can, for instance, mean that an octopus is in an
aroused, angry state, but again it is the tentacles that indicate whether in
approaching another octopus he is going to attack. If the tentacles are stretched
out and turned outward, he will. When they are turned inward and downward,
the chances are that he is playing. These are examples of rather primitive
context-dependent behaviors (or at least context-dependent indicators of
behavior) in an invertebrate that has also been shown to show excellent
discriminative behavior when the task is set for him. My question therefore is,
Can there be two types of finite-state process and perhaps two types of
phrase-structure-like process, just as there are context-free and context-
dependent mechanisms at a higher level?

Should this direction of my questioning be correct, then we must ask a
further question: What does human language actually consist of? According to
this direction of inquiry, transformational, symbolic processes are not sufficient
to characterize human language. It seems to imply that there is some still higher
form that combines both the significant and the symbolic mechanisms. In my
book Languages of the Brain, I deal with these problems rather extensively. I
pose them here only to show the direction in which research into the
comparative biology and psychology of cognitive processes can lead.

In summary, I have distinguished between context-sensitive and context-free
constructions that lead to significant and symbolic communication among
animals. I suggested that both are derived from some more primitive finite-state
process, one stochastic and the other homeostatic in nature. In the case of signs,
the development seems to be that of giving the communication a frame of
reference through the identification of its invariant properties. In the case of
symbols, the behavior appears to relate to recurrent variances. In both instances
the structure of redundancies is involved, and the resultant content of that
structure is that grammar performs the structuring and that meaning is the
resulting content. It seems to me that the pursuit of the comparative psychology
of cognitive processes is one of the most challenging tasks in this area of
investigation. For here we touch on man's most obvious difference from his
nonhuman relatives: communication by linguistic speech. To my mind it is here
that the most exciting avenues of research lie in the immediate future. They
touch on the question that confronts our age; as Heschel\(^2\) so beautifully put it,
"In an earlier period we asked the question, who is God? We today ask, who is
man?"

NOTE ADDED IN PROOF: Several months have intervened between the
composition of this manuscript and its coming to press. During this period I have
began to wonder whether the concept of entrainment might be the sought-for
primitive juxtaposed to "stochastic." Thus entrainment would be conceived as
leading to homeostatic and symbolic processes, just as stochastic Markov
mechanisms are conceived as developing into phrase structure hierarchies and
significant referents. In such a scheme, entrainment is the basis for dealing with
recurrent regularities, while stochastic mechanisms are the basis for processing
invariances. A good deal is becoming known about entrainment; the thesis put
forward here should therefore readily yield testable hypotheses in the immediate
future.

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