Theoretical Considerations in the Adaptation of Animal Communication Systems

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Abstract:
Using concepts drawn from semiotic, the general theory of signs, and from the mathematical theory of communication, a theoretical framework is developed within which the problems relating to communication system adaptation may be defined and models of such adaptation constructed. The relationship between the semiotical notions of qualisign and legisign is used to define a concept of tolerance space that permits the statistical concept of equivocation to take on physical dimensions in the analysis of natural communication systems. For each of three central properties of the communication system (entropy, equivocation and semantic-pragmatic relations) the components of the system that determine the property are identified and the ways in which these components might adapt to environmental changes are discussed.

Article:

1. Introduction

The unquestionably central position of the communication system in the structure of animal societies leads readily to the expectation that it will experience strong selective pressure under changing environmental conditions that impair the efficiency of its functioning. Since behaviour patterns do not fossilize our knowledge of their evolution must come from indirect evidence; in the case of communication patterns virtually the only evidence comes from comparative observations of related species (see, for example, Alexander, 1962; Baerends & Van der Cingel, 1962; Kruijt, 1962; Guthrie, 1971; Morton, 1970). As Tinbergen (1962) has pointed out, this approach is by and large limited to making inferences about the *course* of evolution in particular groups of species and in itself cannot provide information about the mechanism whereby the postulated changes might have occurred.

Although a number of attempts have been made to construct models of some of the mechanisms involved (e.g. Daanje, 1951; Tinbergen, 1952. Morris, 1957; Huxley, 1966; Moynihan, 1970) there is a lack of a general theoretical framework that can serve to define the problems with which particular models will have to deal. The aim of this paper is to supply at least the beginnings of such a framework and, hopefully, to stimulate further discussion that will continue its development.

2. Theory of Communication Systems

There is fairly widespread agreement among behavioural biologists on the need for a rigorous theoretical foundation upon which to base studies of animal communication. Such a foundation would provide a framework for the development of theoretical models dealing with specific aspects of communication and for guiding the course of analysis of observational and experimental data. Stephenson (1973b) has discussed in detail its use in the latter case in his analysis of social communication among Japanese macaques *(Macaca fuscata).* There is however, little agreement as to what form this theoretical foundation should take; various approaches have been proposed by Morris (1938, 1946), Hockett (1960), Marler (1961), Sebeck (1965), Smith (1965, 1968, 1969) and Stephenson *(1973a, b,* in preparation).

In this section I shall develop a theoretical terminology that will provide the basis for subsequent discussion. This development owes much to the published and unpublished work of G. R. Stephenson (op. cit.) and is based upon semiotic, the general theory of signs set forth by C. S. Peirce (see the collected papers of Peirce, edited by Hartshorne & Weiss 1931-1935), and on the mathematical theory of communication developed by Wiener (1948), and by Shannon (Shannon & Weaver, 1949).

(A) SEMIOTIC: THE GENERAL THEORY OF SIGNS

(i) The semiotical triad

Semiotic was developed as a general theory of signs by the pragmatic philosopher Charles S. Peirce (see Hartshorne & Weiss, 1931-1935, especially Volume 8, & Lieb, 1953). The central axiom of this essentially formal theory is the *semiotical triad,* whose members are identified in any semiotical analysis of *semiosis* or sign-functioning. The three members of the triad are the *sign*, its *object* and its *interpretant.* A sign is defined as "something which stands to somebody for something in some respect or capacity" (Collected Papers Volume 2, paragraph 228). It is thus defined by its participation in a certain kind of relationship, rather than by its being a certain kind of thing. The something for which the sign stands is its object; the somebody to whom it stands is its *interpreter;* and the effect of the sign in the interpreter is the interpretant. The members of the triad are defined solely by their relation to one another and cannot be defined in isolation.

From this definition, it is clear that any particular thing can serve, simultaneously or successively, as object, sign or interpretant, depending on the interpreter with respect to which the analysis is carried out. Wycoff (1970) has pointed out that one essential characteristic of semiotic processes is their ability to form infinite series. That is, the interpretant of one instance of semiosis can serve as a sign in a subsequent instance, having its own interpretant, which in turn can serve as a sign, and so on. The concept of semiotic series will be of importance in later parts of this discussion where it will be applied particularly to the operation of signs within the central nervous system of an individual: within-brain series of semioses (cf. Stephenson, 1973b, p. 18ff).

Thus, for example, a particular pattern of receptor cell activity (here considered as a sign of some external event) occurring in the retina of a cat, may produce a particular pattern of activity (here considered as an interpretant in the fibers of the optic nerve. At some higher level of the nervous system this pattern of activity (here considered as a sign, having the pattern of retinal activity as its object) may produce an impulse (here considered an interpretant) in a single interneuron, which impulse may in turn serve as a sign, having the pattern of activity in the optic nerve as its object, in a subsequent semiosis. Considered from the points of view of successive semiosis, the various phenomena referred to here occupy different axiomatic positions in the semiotical analysis, as illustrated in Fig. 1.

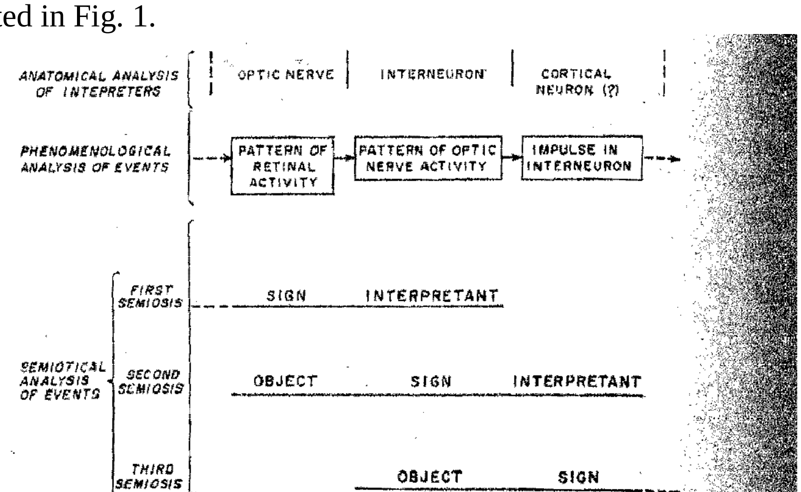

FIG. 1. The infinite regressiveness of semiosis. In a semiotical consideration of within-brain occurrences, any particular phenomenological event may be considered simultaneously as a sign, object and interpretant by virtue of its participation in three successive instances of semiosis. Thus any two events, say the initial perception of some external happening and the generation of some signal that stands for that happening to other conspecifics, may be linked by an indeterminantly large number of intervening semioses.

The three classes of signs

One direction in which Peirce carried his analysis of semiotic was to recognize the existence of three classes of signs: *qualisigns*, *sinsigns* and legisigns. The distinction between them is subtle and rooted in the complexities of Peirce's phenomenology. It can perhaps best be made clear by means of an example, rather than by trying to give formal definitions.

The word "the", in all of its occurrences on a page, is the same word indicating the same relationship, in the sense of indicating an established rule of correspondence between the sign and its objects It is recognized as such by appropriate interpreters despite variations in the precise shape of the letters that make it up; this is the sense in which it is a legisign. We recognise each occurrence as "the" and do not confuse it with "this" because it has a particular spatial patterning of ink that more or less closely corresponds to a learned normal configuration (the legisign), this is the sense in which it is a qualisign. The fact that each of its occurrences has a particular existence or factness, that it is "ineluctably before us, an actuality, *hic et nunc*"(Goudge, 1950, p. 88) establishes the sense, in which they are each sinsigns. The interested reader will find a more complete discussion of this trichotomy, and of related matters, in Goudge (1950, p. 139ff), Lieb (1953), Stephenson (1973b, p. 11ff) and Johnston (1974, p. 8ff).

(iii) *Sign, sign-vehicle and signal*

In his discussion of semiotic, Peirce did not allow room for the existence of an observer to the instance of semiosis. This step was taken by Morris (1938) who, in order to bring Peirce's system closer to the physical world and so allow the existence of an observer, gave each member of the semiotical triad a sensible representation. Thus that physical thing which is, semiotically the sign, he called the *sign-vehicle;* that thing for which it stands, semiotically the object, he called the *referent;* the behavioral response to the interpretant (i.e. a final interpretant in a series of within-brain semioses), which Morris let stand for the interpretant, is the *response.* Morris also pointed out three dimensions of semiotic analysis : the semantic, pragmatic and syntactic dimensions. These he characterized, respectively, as "the relations of signs to their objects… the relations of signs to interpretants… [and] the formal relations of signs to one another" *(ibid.*, p. 6).

Stephenson (1973b) has carried this synthesis further by pointing out that as observers, all we can monitor are signals (i.e. disturbances of the environment) some aspect(s) of which may serve as sign-vehicles. He also argues that the closest we can come to identifying the referent is to describe a cluster of contextual data points, invariant between instances of signal usage, which we presume to include the referent.

The distinction between the signal and the sign-vehicle is important to the present discussion. We may know that a flashing light serves as a signal, but be unable to decide whether it is the light or the flashing that acts as a sign-vehicle and is hence a sign in that it stands to someone for something. This problem is being faced by students of bird song who are trying to discover the parameters of the song responsible for species recognition, individual recognition and so on (Weedon & Falls, 1959; Falls, 1963; Emlen, 1972). They have identified the signal (the song) but are unable to decide which of the many parameters of the song (mean frequency, inter-phrase spacing, frequency shifts, etc.) act as sign-vehicles by standing for such things as species and individual. The importance of the foregoing discussion to the arguments to be presented is that while we are initially limited, when investigating communication behavior, to an analysis of signals, what we are really interested in is a description of their operation as sign-vehicles. When the problem is one of deciding how a signal preserves its information-carrying capacity under changed conditions affecting transmission, the importance of the signal/sign-vehicle dichotomy becomes evident. What is of interest here is the effect of the changed circumstances on the sign-vehicles, not on the signals as a whole.

(iv) *The legisign and qualisign*

With the sign given physical dimensions by Morris and Stephenson, it is possible to extend our discussion of the qualisign, for it is with respect to this aspect of the sign that the sign-vehicle and the signal approximate to the semiotical notion of the sign (Stephenson, 1973b p. 15). Peirce noted that the qualisign "cannot differ much without being called quite another qualisign" (letter to Lady Welby, 12 October 1904; see Lieb, 1953). My interpretation of this statement is that each legisign may have associated with it a set of configurations of stimuli, which display a certain diversity. One that falls outside of this range will not be considered (by the interpreter) as embodying an appropriate qualisign and hence will not be recognized as an instance of legisign. Defining the range of acceptable stimuli may be quite difficult in any one case, for it is not variation in all aspects of the stimulus that count as qualisign-related differences but only variations in those aspect(s) of the stimulus (i.e. signal) that serve as sign-vehicles and are hence signs in that they stand to someone for something.

Consider, for example, the various configurations presented in Fig. 2. If we take each of these stimuli and test its acceptability as an instance of the legisign "the", say by presenting it to a native speaker and reader of English and assessing his or her readiness to assent to the question "The?" (cf. Quine's discussion of "stimulus meaning"; Quine, 1960; p. 32ff), we would achieve quite a different set of results for each of the three series A, B and C shown. Despite considerable differences in their configurations, all of the stimuli series A would elicit prompt positive responses to the question "The?" and those in series C, also different, would elicit equally prompt negative responses. Those in series B, however, would probably elicit a gradually decreasing readiness to assent, rather than a prompt negative or positive response in each case.

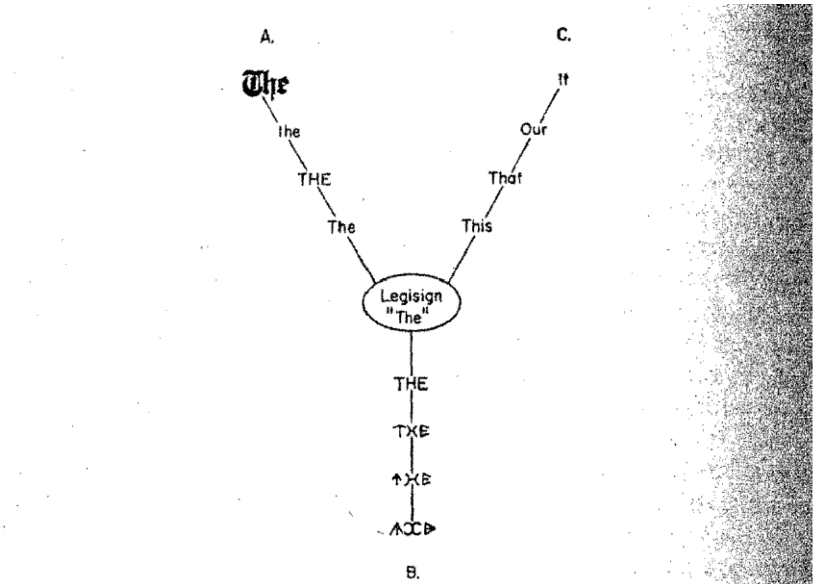

FIG. 2. The relationship of the legisign to the qualisign. All of the sinsigns represented in series A are accepted as instances of the legisign "the", whereas none of those in series C are. In series B there is a gradually decreasing tendency on the part of the interpreter to admit the sinsigns as instances of the legisign, because of a quantitative change in the qualisigns associated with them.

These results suggest that in each of the signals in series A, the respective sign-vehicle's are such that the qualisign retains its "great similarity" in each instance. What this similarity may consist of is difficult to say, but it probably has to do with the relative sizes and spatial positions of the elements that go to make up the signal. The prompt negative responses elicited by the signals in series C, however, suggest that their sign-vehicles show qualitative differences that disqualify the sinsigns as instances of the legisign "the" because their attendant qualisigns lie outside the range of acceptable variation. The graded series of responses to series B suggests a quantitative shift in the sign-vehicle, such that the qualisign gradually exceeds the acceptable limits of variation to become, potentially at least, another qualisign. A number of experiments of this kind would eventually define the limits of acceptable variation in the qualisign.

(B) MATHEMATICAL COMMUNICATION THEORY

An alternative framework within which communication can be discussed, and one that provides a different kind of insight into the communication process, is that of the mathematical theory of communication (Wiener, 1948;

Shannon & Weaver, 1949). In the light of this theory the process of social communication among animals may be seen as the maintenance of a channel of communication between the individuals of the social group. Schematically, the channel may be represented as shown in Fig. 3.

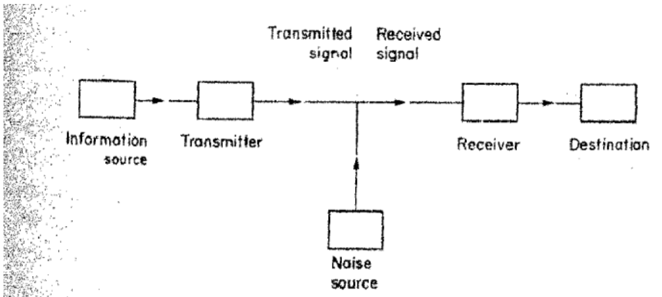

FIG. 3. The communication channel. After Shannon & Weaver (1949).

The message that is to be sent is chosen from a set of messages, which constitutes the information source, and is encoded in some physical form as a signal that is transmitted by the sender. The receiver senses the signal and decodes the message, by reference to the same set of messages from which the original signal was chosen; for communication to succeed it is necessary for sender and receiver to share a common alphabet of messages (Cherry, 1966).

Within this framework, communication between animals may be seen as one animal, acting as the sender, setting up a disturbance of the environment (the signal) via a communicatory behaviour pattern and the subsequent receipt of this signal by another animal, the receiver. The effect of communication is to transmit information, in the sense of reducing uncertainty about the environment or the sender's future behaviour. The information *H,* associated with a set of *n* messages, the i^{th} of which has probability p_i of being transmitted, is given by the equation:

$$H = -\sum_{i=1}^{n} p_i \log p_i.$$

Thus the greater the number of messages and the more nearly equal are the probabilities of their being sent, the more information is associated with the source. A channel that can transmit *N* messages per second is said to have a capacity of $C = HN$ bits per second, where the logarithm in the equation above is to the base two. This holds true so long as the transmitted signal is identical to the received signal, or, more generally, so long as each received signal uniquely specifies the transmitted signal from which it has come. For instance, a particular signal *x* may always result in a particular (different) received signal *x*'. In this case we may define a single-valued function, *f*, such that $x' = f(x)$ and so, in principle, the transmitted signal may recovered by applying the inverse function to *x'*. In practice, the received signal may be treated as the transmitted signal. In such cases signal distortion may be said to have occurred, but there will be no problem of communication since the *x*' will be isomorphic with the *x*, and each *x*' will uniquely specify the *x* from which it is derived.

Insofar as the difference between *x* and *x*' is random rather than consistent, there is said to be noise in the channel of communication. The effect of noise is to reduce the information carrying capacity of the channel by increasing the entropy or uncertainty associated with the receipt of any particular signal with regard to determining what signal was sent. This is know n as the conditional entropy of the input to the communication channel; i.e., the uncertainty of the input (transmitted signal *x*) when the output (received signal *x*') is known.

Thus the rate of transmission of information, R, in a noisy channel is given by:

$$R = H(x) - H(x|x') \quad \text{bits},$$

where

$$H(x|x') = \sum_{i=1}^{n} 1 - p_i(x|x').$$

$p_i(x|x')$ being the probability that x_i was transmitted if x_i' is received. The conditional entropy $H(x|x')$ will be called the equivocation, following Shannon & Weaver (1949, p. 67).

Although Shannon & Weaver extend their discussion of noise and demonstrate methods whereby equivocation can be reduced by appropriate encoding, a consideration of their arguments would be inappropriate here, since, as Cherry (1966, p. 198) has pointed out, they are of a strictly mathematical nature and hence require a rigorous mathematical description of the communication system to which they are to be applied. Thus far such a description is only available for artificially constructed systems; in a consideration of natural communication systems it is the logical rather than the mathematical structure of the above equation that is of interest. This is that information carried in any channel of communication maintained among individuals of a social group depends on two things: the entropy, $H(x)$ of the source, in this case the set of messages corresponding to the signals utilized by the group; and the equivocation, $H(x|x')$, in this case a result of interference causing the received signal x' to be different from the transmitted signal x.

(C) BIOLOGICAL CONSIDERATIONS OF COMMUNICATION

The two theoretical systems of semiotic and communication theory have provided a basis from which to develop specifically biological arguments concerning some of the problems faced by an adapting social group. The most central of these problems with respect to communication is that of maintaining the information carrying capacity of the communication system despite changing environmental conditions. From the above discussion it appears that there are basically two ways to do this: by increasing the entropy of the source and by decreasing the equivocation in the channel. Although the equation for R given above implies that the entropy and the equivocation are effectively equivalent in determining the channel capacity, this is an inadequate characterization of the situation with regard to an adapting social group. The entropy of the information source at a particular time is determined by the selection pressures that have acted on the communication system in the past so as to alter its carrying capacity as the species' informational requirements demanded. It does not depend on the present state of the environment. Equivocation, on the other hand, is determined by the interactions between the physical form of the signals and the physical parameters of the transmission medium, i.e. it depends both on the past states of the environment, which have determined the present form of the signals, and on the present state of the environment, which, given a signal of particular physical form, determines the equivocation.

If the environment changes, the change may provide a source of selection pressure to change the entropy but this effect will be delayed, probably for some generations. Any effect that the change has on the equivocation, however, will be immediate; if the effect of the change is to increase equivocation, then it will also provide a source of selection pressure tending to reduce the equivocation.

Thus entropy and equivocation make contributions to determining the capacity of a biological communication channel that are importantly different in kind, when considered at the biological rather than at the mathematical or logical level.

A model of communication system adaptation (which will be a part of biological, not mathematical, theory) appears to have at least two sets of questions with which to concern itself: those relating to the factors concerning entropy and those relating to the factors concerning equivocation. A third set may be added (stemming from a semiotical rather than from a communication theoretic consideration of the problem); namely those that concern the semantic and pragmatic relationships of the sign-vehicles involved. Before considering in detail the nature of the biological problems involved in these three areas, I wish to examine a little more closely the logical features of signal equivocation, in the light of the concepts we have been discussing.

The concept of equivocation, as defined by communication theory, is a statistical one that makes no explicit reference to the physical interaction, between the signal and its environment, that determine it. The nature of these interactions can be made explicit and hence more amenable to biological argument by a consideration of equivocation from a semiotical point of view. The question to be addressed here is what might constitute an adequate, characterization of the operation of environmental sources of equivocation, regardless of the specific modality in which they operate, or the specific nature of their effects.

(D) EQUIVOCATION AND TOLERANCE SPACE

In considering this question, it is important to recall the distinction made previously between the signal and the sign-vehicle, and the relationship between the physical properties of the sign-vehicle and the legisign. In the light of this discussion it is apparent that we may describe a set of qualisigns (sensible qualities) that, when combined in a sign-vehicle, allow it to act as a sinsign of a particular legisign that is a part of the alphabet of signs that the society uses to communicate. From the point of view of equivocation, we may describe the legisign as a point in *n*-dimensional space, where *n* the number of parameters needed to completely describe the legisign. We noted above that more or less small variations in the nature of the qualisign are permitted without its ceasing to function as a representative of its legisign. I shall refer to this permissible variation in the qualisign as the *tolerance* of the corresponding legisign. Tolerance is specific to a particular parameter for a particular legisign.

In the case of a blue circle standing in a pragmatic relation to some interpreter, three of the parameters needed to completely describe the legisign represented by that particular instance of a blue circle standing for something are blueness, size and circularity. Depending on how the rule of correspondence was set up, a range of frequencies of reflected or transmitted light may be admissible as candidates for "blueness", part of the legisign involved in this example. Similarly, more or less variation in the size and circularity of the stimulus may be acceptable, the more-or-less depending on the exact definition of the legisign.

These ranges of acceptable variation define the tolerance of that particular legisign for those particular parameters and supply an *n*-dimensional volume (the *tolerance space)* surrounding the point in *n*-dimensional space that defines the legisign. We may then say that any physical disturbance of the environment whose physical properties can be represented by a point within the tolerance space may act as a sign-vehicle for the sign. The sign-vehicle may be, and usually is, only one or a few aspects of a more extensive disturbance of the environment, the signal. In order for a sign-vehicle to be easily perceptible, it is necessary for the energy that makes it up to be perceptually distinct from the energy that makes up the rest of the signal. The fact that a sign-vehicle may be more effectively masked by attendant energy that is perceptually close to it than by energy that is perceptually distinct has been demonstrated in both the acoustical (Zwicker, Flottorp & Stevens, 1957) and visual (Pantle & Sekuler, 1968; Harmon, 1973) modalities. If, for example, one aspect of the sign-vehicle in an acoustical signal is a particular pattern of amplitude modulation of spectral energy between 8 and 8.1 kHz, a concentration of non-communicative energy between, say, 7.9 and 8 kHz may severely reduce the ability of that aspect of the sign-vehicle to full its communicative function. This problem may be overcome to some extent by appropriate processing of the signal but in general it will be advantageous if the sign-vehicle stands out as much as possible from the rest of the signal.

With the conceptualization of the relation between the sign-vehicle and the legisign in these terms, anything in the environment that tends to alter the physical properties of the signal so as to cause the co-ordinates of those aspects of the signal acting as a sign-vehicle to move outside of the tolerance space of the legisign may be identified as a potential source of equivocation.

So far we have been treating the tolerance space as an *n*-dimensional space with sharp edges. That is, it has been assumed that as the point corresponding to the physical description of the sign-vehicle moves towards the edge of the tolerance space, the probability of its effecting the appropriate interpretant in the interpreter remains 1 until it crosses the boundary of the space, where it drops instantaneously to 0. Although this may be an adequate characterization of the situation from the abstract point of view of semiotic, it requires modification if it is to be applied to any real interpreting system.

Consider the case where I am looking at a panel that emits light of a single wavelength and that initially it is emitting light at a wavelength of 700 nm. I am asked to look at the panel and comment frequently on the conformity of the stimulus to the legisign "red". As I do so, the wavelength of the emitted light is gradually changed. Although initially I readily admit the stimulus as an instance of "red", after a while my inclination to do so begins to decline, until there comes a point where I positively do not admit it as "red". Between my last definite positive response and my first definite negative response is a gradually declining inclination to admit the stimulus as "red", there is no abrupt shift in my behaviour. This suggests that the boundaries of the tolerance space are defined by a probability curve that is not a step function.

Depending on the resolution of the interpreting system, the sides of the curve will be more or less steep; the greater the resolution, the steeper the sides. Most biological interpreters are likely to show a considerable fuzzines at the edge of the legisign's tolerance space. The tolerance space thus defines a fuzzy set (Zadeh, 1965) whose members are the sinsigns that are instances of a particular legisign. This fuzziness is of great importance in the evolution of communication systems, as it allows the legisign associated with a particular semiosis to be gradually shifted one way or another, without a sudden breakdown in the coherence of the semiosis.

A further refinement in the concept of the tolerance space may be made at this points In the foregoing discussion it has been implied that the boundaries of the tolerance space are uncurved; that is that the acceptable variation in any one qualisign is independent of the values of the other qualisigns. However, it is reasonable to suppose that, in order to reduce equivocation, a different relationship may in general obtain between the qualisigns of a legisign in a natural communication system. Suppose a legisign is associated with a set of qualisigns which are susceptible to different sources of equivocation that, in the environment in which the signal is evolving, are not usually found together. Then a definition of the tolerance space in such a way that as its boundary is approached along any one axis, its dimensions along the other axes becomes smaller will tend to be favoured by natural selection. The selection of qualisigns associated with a particular legisign that are susceptible to different sources of equivocation offers the advantage that under conditions where one qualisign is maximally affected by a particular source of equivocation, at least some of the others will not be. The specificity in the operation of the legisign may then be preserved by requiring that when a stimulus lies very close to the boundary of the tolerance space as measured along one axis (qualisign) it must lie that much closer to the legisign as measured along other axes in order to be accepted as a sinsign. This is represented by a curving of the boundaries of the tolerance space as shown in Fig. 4. This reduces the possibility of the receiver's accepting as sinsigns stimuli that in fact are not, while also extending somewhat the range of environmental conditions under which communication is possible.

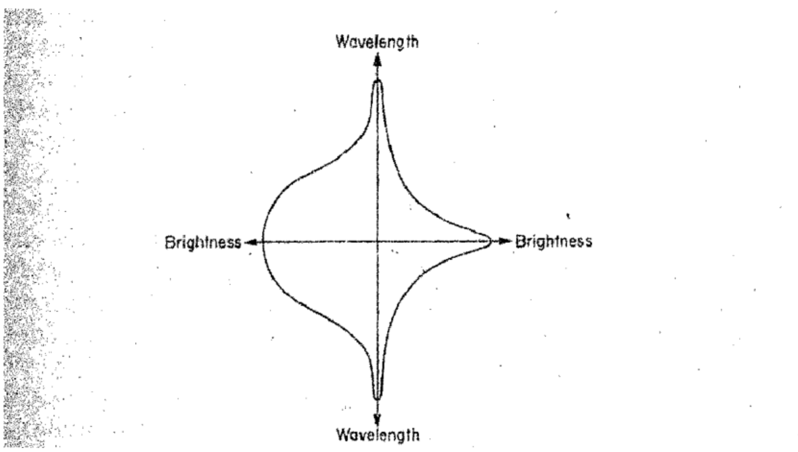

Fig. 4. ***The tolerance space with curved boundaries. A two-dimensional tolerance space as shown for clarity. As the brightness, for example, of a stimulus nears the edge of the tolerance space to the right of the diagram, its wavelength must lie closer to the value that defines the legisign for the stimulus to continue to be accepted as a sinsign.***

3. Mechanisms of Communication System Adaptation

In the preceding discussion, we have considered primarily formal arguments in setting up a conceptual and terminological framework within which to articulate specific theories of communication system adaptation. In this section we will consider more substantive problems within this formal framework, While maintaining the generality of the discussion; as far as possible we will avoid tying it to the particular problems posed by any particular species or sensory modality.

Any model of biological adaptation must obviously be firmly grounded in evolutionary theory at both the individual and population levels. It is the purpose of this discussion to present some further theoretical considerations that must form part of the basis for any model of communication system adaptation.

(A) BIOLOGICAL ADAPTATION

I wish first to draw attention to the fact that a consideration of problems of adaptation must recognize the many facetted nature of the adaptation of biological systems. The long term mechanisms of natural selection produce slow, relatively stable adaptations to slowly changing aspects of the environment. Developmental plasticity, physiological adaptation and learning provide the necessary "fine tuning" to short term fluctuations over the life span of an individual (Slobodkin & Rapaport, 1974; Mayr, 1974). Group learning in which the conservatism of older members of the society provides a stable basis for the incorporation of the innovations of younger members (Stephensson, 1968,1973c; Kummer, 1971, p. 126ff) provides an opportunity for responses to change on an intermediate time scale in socially complex species.

It is quite evident that adaptation is an integral process with close and essential dependencies among its various components; individual learning for example, can only become an important aspect of a species' adaptive capacity as the requisite neural plasticity evolves. However, it appears reasonable to consider these three facets as occupying different functional positions in the set of adaptive strategies that the species has available to it for coping with environmental changes (cf. Lewontin, 1961).

The process of adoption of appropriate strategies has been discussed within various theoretical frameworks by Lewontin (1961) and Warburton (1967), amongst others. An essential point that should be made concerning this process is that the population's role is entirely passive; a strategy is acquired by virtue of the survival of those variations that contribute to the organization of that particular strategy rather than of another. Thus the use of the term "adopted" in this discussion is not intended to imply a free choice by the population amongst a number of alternatives, but rather the imposition of a particular, successful, strategy by the action of selective forces.

(B) THE NATURE AND SOURCE OF VARIATION IN THE COMMUNICATION SYSTEM

In order for any natural system to adapt to changes in the environment, there must be some variation in those aspects of the system that are to change. The problems with respect to a communication system are threefold: first to identify those properties of the system that determine its effectiveness in mediating interactions among members of the society; second to determine how these properties might be influenced by environmental changes; and third to show how variation in those components of the communication system that determine the relevant properties can be supported in the population. The last problem is particularly acute, since a communication system functions by virtue of the predictability of its operation and thus we may suppose that variation will, in general, tend to be disadvantageous.

The properties of the system that will be considered here are the entropy of the source, the equivocation in the channel and the semantic and pragmatic relationships of the signs.

(i) Entropy

Signal number is a primary determinant of the entropy of the source. Although a large number of signals increases channel capacity, this advantage is offset by the disadvantage that a signal drawn from a large set of possibilities requires a longer time to recognize than the same signal drawn from a smaller set (Hick, 1952). Furthermore, a large number of signals increases the probability of a particular signal being misidentified because of similarity to others, and thus eliciting the wrong response. Since many of the signals used by animals are associated with situations in which it is essential that the correct response be given as rapidly as possible, there will be a relatively great adaptive advantage to keeping the signal set as small as possible and maximizing the likelihood of clear, equivocation-free transmission of those signals that are available. Such considerations set an upper bound on the number of signals to be expected (and see Moynihan, 1970).

A lower bound may be set by the complexities of the informational relationships that the animal has with its environment. If it is adaptively advantageous for the animal to be able to signal differentially the existence of different situations, then presumably the ability to do so will be selected for. Since either of these determinants of signal number may change, we must consider here the problems of both acquisition and loss of signals.

The most obvious signals are displays (Tinbergen, 1952) and the processes whereby they are added to or deleted from the repertoire have been the subject of extensive discussion (Daanje, 1951; Tinbergen, 1952; Blest, 1961; Moynihan, 1970). Not all signals, however, are displays, which represent a high level of specialization to subserve a communicative function (Tavolga, 1970). Less specialized signals are involved in the process of social communication and we must also be able to account for their acquisition and loss. The problems involved in doing so are made explicit by a consideration of Tavolga's (1970) arguments for considering communication as a phenomenon that is related to a continuum rather than to a dichotomy between “communicative” and "non-communicative" acts. This is a view that meets with considerable sympathy from the semiotical analysis of communication being adopted here, because a sign is *anything* that stands in semiotical relationship, whether or not natural selection has operated to make it especially suited to this role. From this perspective, it is better to consider changes in the signal repertoire as involving the movement of acts that could serve as signs up and down this continuum of specialization. The point at which they enter or leave the repertoire depends on the arbitrary lower limit of specialization we choose to accept as the lower bound of the repertoire.

At the lowest level of specialization (called by Tavolga the vegetative) the particular phenomenological configuration that defines an organism as one type (species, sex, age, etc.) rather than another serves as a sign by virtue of its association with the particular type. The development of more specialized signals from this substrate involves the isolation of particular acts and their progressive specialization to a particular context and a particular form. Contextual specialization of a particular act occurs as a result of a process of selection that tends to increase the probability of that act being associated with the context.

For example, some act that incidentally but invariably precedes a particular pattern of copulation will come to be specialized into a precopulatory context as that particular pattern of copulation becomes selected for on the basis of the greater probability of insemination associated with it. This contextual specialization results in the formation of a semiosis having the incidental act as a sign, standing for impending copulation as its object and producing some appropriate anticipatory action, as the final interpretant, in the other sexual partner. Once this semiosis has been set up, the form of the act can come under pressure to change so as to be more efficient in the communication of this information. This process of contextual and structural refinement may continue, up to the level of a display. The ritualization, in this manner, of small "intention movements" associated with locomotory activity into signals has been discussed by Daanje (1951). Such specialization need not occur, however, as Moynihan (1970, p. 97) has pointed out. Increasing specialization of either context or structure beyond a certain point may be opposed by the difficulty of integrating the more highly specialized act into other activity that subserves essential functions, by increasing exposure to predators or by some other factor (see Moynihan loc. cit.).

Signals may move to lower as well as higher levels of the hierarchy via a process of despecialization. Contextually this may occur if the behavior with which the signal is associated alters so that it is somehow difficult or impossible for the signal to continue to be appropriately associated with it. In this case the signal may be replaced by the specialization of some other act that is not so constrained. Structurally, despecialization may occur by a relaxation of selection pressure on signal form, as communication of the particular information with which it was associated becomes of less importance to social co-ordination than before, or as the circumstances surrounding signal transmission change so that the specialized form is no longer necessary for effective communication. Moynihan (1970) has described various processes that may be involved in the loss of displays and his arguments are applicable to the case of non-ritualized signals as well.

The variation on which appropriate sources of selection pressure might act to increase the number of signals in the repertoire can thus be seen to include the whole range of activities that the population engages in and all of structures associated with these activities. Since a reduction in signal number is probably achieved via a relaxation of selection pressure, there is no source of variation to be accounted for in this case.

As well as the absolute number of signals in the repertoire, the relative numbers in each sensory modality should be considered. Signals in different modalities have different physical properties and are generally susceptible to different sources of equivocation. Thus it will frequently be advantageous for a species to utilize several sensory modalities for communication, so as to take full advantage of this diversity. The relative numbers of signals with these properties that it is desirable to have in the repertoire will be determined by such selection pressures as incidence of predation, hunting methods of predators, pattern of space utilization, size of the social group and the presence of sources of equivocation to which the signals are susceptible. The physical properties of signals in different modalities and the sources of selection that may be expected to act on them are discussed in detail in a forthcoming paper (Johnston, in preparation).

Syntactic relationships. The incorporation of syntactical rules into the communication system has the effect of increasing the entropy of the information source, by increasing the number of possible different signal sequences.

The importance of syntax in animal communication is as yet poorly demonstrated and so I shall first consider briefly the problem of the origin of syntax, which may symbolically represented as:

$$AB \equiv BA \rightarrow AB \not\equiv BA$$

where the equivalence sign implies both semantic and pragmatic equivalence and the letters A and B stand for particular signals, produced in the order indicated. Now it is apparent that the second situation provides a channel with a greater capacity than the first but that this is associated with lower redundancy (hence greater probability of equivocation) and probably also with a requirement for more sophisticated information processing abilities. Thus if a change from the syntactically free to the syntactically bound is to be made, the pressures for increased channel capacity must be sufficiently intense to overcome the biological expense incurred by the developments of more sophisticated information processing devices and must include pressures to reduce equivocation to acceptable levels. The position of such syntactical innovations in the evolution of human language has been discussed by Hockett & Ascher (1964).

An alternative to a demand for increased channel capacity as a source of selection pressure in the development of syntax arises in the situation where one particular sequence of signals is superior to either a single signal, or any other sequence of signals in the transmission of information. The simplest case is where single utterances of a signal are replaced by repetitions of the same utterance, a change that has the effect of increasing redundancy and hence reducing the equivocation (Potash, 1972; cf. Schleidt, 1973, p. 364). As an illustration of a rather more complex case, we can consider the following hypothetical example.

One signal in the repertoire of a social group is a visual threat signal that, under the current conventions of usage, is given only in situations where there is face-to-face contact between the interactants. As well as information concerning the likelihood of aggression, the signal carries information concerning the identity of the sender and of the intended addressee. As a result of a change, say in the dynamics of social organization of the group, there comes to be an advantage in the ability to convey threat in other than faces to-face situations as well. Since a visual signal cannot be received unless there is visual contact between sender and receiver, this new situation could be met either by replacing the visual signal with, say, a vocal signal that does not have these constraints and can carry all of the necessary information, or by combining the visual signal with another signal that carries some directional information (see Marler, 1967, p. 770). In the latter case the additional signal permits potential receivers to orient to the sender and receive the other information carried by the visual signal. If this strategy is adopted, a constraint is placed on the sequencing of the signals and thus a syntactical rule introduced into the set of rules that specifies the operation of the communication system. The constraint is that the signal that carries localizing information must be received sufficiently before the end of the transmission of the visual signal that the receiver can perform the necessary operations involved in localization in time to receive the additional information carried by the visual signal. Thus it should be given either before or early in the transmission of the visual signal.

Relative information load. In the example above, it is clear that when the visual signal is glimpsed peripherally by the receiver and then brought to focus on the fovea[1] by reorientation, the directional information carried by it is being utilized. With the addition of a vocal signal, the responsibility for transmission of directional information is distributed over both signals. Let us suppose that 80% of the load is on the vocal signal and 20% on the visual. Then, if the signal can be expected from any direction, the vocal signal permits the receiver to localize the sender to within 72° of arc, precise localization within this sector being accomplished by means of the directional information carried by the visual signal. Now, suppose that localization of the vocal signal takes 0.4 s and localization of the visual signal 1.8 s under the prevailing environmental conditions, and that for communication to succeed, localization must be accomplished within 2.5 s of the beginning of signal generation. The time necessary to localize visually is probably proportional to the size of the arc that must be searched and inversely proportional to the visibility through the transmission medium between the sender and the receiver. So long as the visibility is not reduced to the point at which visual localization takes more than 2.1 s there is no problem of communication. If, however, visibility *is* reduced beyond this point, then for communication to succeed, more of the load for transmitting localizing information must be home by the vocal signal. This situation may provide a selection pressure to modify the vocal signal so that auditory localization can be accomplished to within say, a 36° sector, i.e. so that the vocal signal now carries 90% of the directional information.

It may be noted that under these circumstances, a further change in the environment that increases equivocation in the transmission of acoustically coded directional information is more crucial than would have been the same .change occurring in circumstances where the visual signal carried more of the directional information. This illustrates an important point, that in the adaptation of a communication system to its environment, the different sensory modalities act not as independent systems but as component parts
a single system, the nature of the relationships between them being of the utmost importance to the process of adaptation of the communication system as a whole.

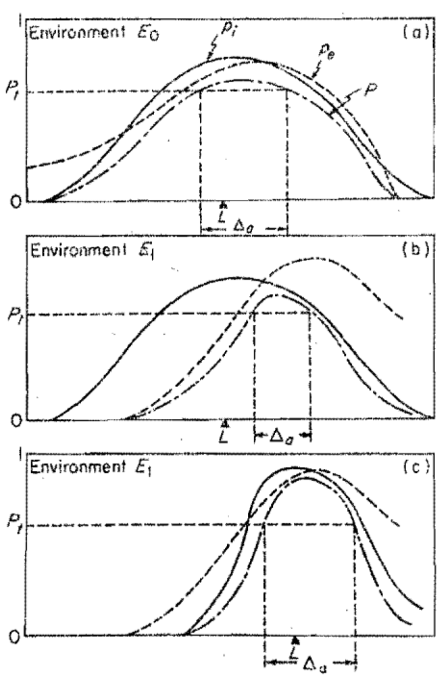

Fig. 5. Mechanism of change in the legisign under changing environmental conditions. In each diagram, the solid curve represents the probability (p_i) of a sinsign expressing the correct interpretant if it is received with no equivocation, the broken curve the probability (p_e) of error-free transmission and the semi-broken curve the probability (P) of a sinsign expressing the correct interpretant under the particular environmental conditions. "L" indicates the position of the legisign in each case.

(ii) *Equivocation*

Signal form. Although the capacity of the channel can be increased by increasing the signal number or by introducing syntactical rules to raise the entropy of the source, the additional information processing requirements that are placed on the population by this strategy mean that reducing equivocation by selecting for optimum signal form is likely to be a appropriate strategy for increasing channel capacity in most cases.

It should be pointed out here that the definition of the tolerance space (p. 54) as having probabilistically defined edges is crucial for any theory that holds that a change in signal form is possible, for it gives the boundaries of the tolerance space a flexibility that is ultimately transmissible to the legisign.

For any particular qualisign Q_a that can be measured by some parameter *a* consider two probabilities: p_i, the probability of a sinsign expressing the appropriate interpretant if it is received with no equivocation; and p_e the probability of error-free transmission. Fig. 5(a) shows the distribution of p_i and p_e over *a* under conditions E_0. The probability of any particular sinsign expressing the appropriate interpretant under the appropriate conditions is thus:

$$P = p_i p_e.$$

There will be some value P_t , such that if $P<P_t$, communication is unacceptably equivocal; that is, for which the disadvantageous effects of frequent (1 - |P) misinterpretation are more important, evolutionarily, than the advantageous effects of infrequent *(P)* correct interpretation. The range within which $P \geq P_t$ is shown in Fig. 5 as Δa. Suppose now that conditions change from E_0 to E_1 [Fig. 5(b)]. Although the distribution of p_i remains the same, that of p_e changes, most probably in such a way that Δa is reduced. If Δ_a remains the same, or increases, the population is said to be preadapted the change from E_0 *to* E_1. Insofar as there is selection for unequivocal communication, there will be selection for an increase in the p_i lying within Δa and for a decrease in the p_i lying outside Δa. Thus the distribution of p_i over *a* will change as shown in Fig. 5(c), resulting in an increase in Δa. The advantages to having a large Δa are that (1) there will always be some variation in the form of the sign-vehicles produced by the population and a large Δa increases the number of them that are acceptable as sinsigns and so increases the feasibility of communication; and that (2) the qualisign Q_a *is* just one of the qualisigns associated with the legisign and that given the range of local conditions in E_0 there is probably no single value or small set of values of *a* that will allow $P \geq P_t$ for all of these qualisigns simultaneously, over any substantial part of this range. A disadvantage to a large Δa is that by admitting a larger range of stimuli as sinsigns, the specificity of communication tends to be decreased. Generally a balance must be sought between these antagonistic effects. Because of the way in which the legisign would seem to be defined in natural, non-linguistic communication systems, by conventions of usage rather than by executive fiat, this shift in the distribution of p_i over *a* leads necessarily to a shift in the definition of the legisign [Figs 5(c)]. It is clear that without the probabilistic definition of the tolerance space given earlier, no such shift would be possible, since *P* would always equal zero for values of *a* lying outside the tolerance space and would equal P_e for values lying within it. As the distribution of p_e over *a* changed, *P* would get smaller for all values of *a* within the tolerance space, leading eventually to a breakdown in communication.

We must now turn to consider the source of variation that might lead to a shift in the distribution of p_i. As Shannon points out (Shannon & Weaver, 1949, p. 65), equivocation may occur either during transmission of the signal or at the points of transmission and reception. In order to deal with the problem of variation in signal form, I shall here consider those sources of equivocation that operate at the ends of the channel, between the message source and the transmitter and between the receiver and the destination (see Fig. 3), for it is these sources of equivocation that supply the raw material for a change in signal form.

The components of the communication channel mentioned above may be identified, respectively, with the particular location in the sender's memory where the set of messages corresponding to particular legisigns is stored, the mechanism whereby the message is encoded as a particular sinsign (and transmitted as a signal), the sensory organ of the receiver that transduces the signal and the executive system of the receiver that directs the nature of the response. Starting with the message set, a number of possible sources of equivocation may be identified, viz :

(a) The situation at hand is incorrectly appraised by the sender and thus the wrong message is selected for transmission. Assuming that no further equivocation takes place, the receiver will select an inappropriate response. Here the source of equivocation lies in the sender's nervous system, either at a peripheral or at a higher, evaluative level.

(b) The correct message for the situation at hand is selected, but the legisign corresponding to a different message is chosen for transmission. Since the source of equivocation in both cases (a) and (b) operate entirely within-brain, I see no way that they can be distinguished operationally.

(c) The appropriate legisign is selected but the sinsign that is transmitted does not conform to it. It may be that the sender is physiologically or anatomically incapable of setting up a signal that embodies an appropriate sign-vehicle. In this case, the sinsign that is transmitted may not correspond to any message in the receiver's alphabet of signs, in which case communication will fail until the receiver can acquire a new sign corresponding to the sender's sign-vehicle. This may easily happen if the differences between the sender's sign-vehicle and that used by the rest of the social group are small and consistent between separate instances of signal transmission. Differences of this kind, under appropriate circumstances, provide the raw material for evolutionary change in signal form. Breakdown of communication is most likely to occur when the legisign (as an imagined type or norm in the mind of the receiver; see Stephenson, 1973a, p. 54) and the sinsign carried by the transmitted signal show differences that are large and/or unpredictable.

A rather more trivial case is where the sender is capable of setting up an appropriate signal, but is prevented from doing so because of the immediate circumstances, as in the case of a person trying to talk with her mouth full. Under some circumstances this may not be so trivial, as it may provide a selection pressure to change the form of the signal, for example if the "immediate circumstances" are those that became more frequent as evolving hominids began to assume a bipedal posture.

(d) Equivocation may occur at the point of signal reception, if the receiver's transducing mechanism does not have the same set of operating characteristics as do those of other members of the society. In this case the disadvantages that result from small differences in the operation of the transducer are unlikely to be serious as they will simply produce a different series of within-brain semioses, ending, because of the possibility of moulding in the course of individual learning, in the same final interpretant or response. It is probable that within-brain semioses are different for all interpreters, given the same legisign, because of the effects on them of memory and idiosyncratic neural organization. The semioses of an abnormal individual will simply lie at one end or the other of this distribution. Where the dysfunction is very great, the communicative disabilities will probably be insignificant compared to the very much greater disadvantages of the perceptual disabilities resulting from the dysfunction.

(e) The final source of equivocation to be considered operates if a within-brain semiosis of the receiver following signal transduction generates an interpretant that lies outside the tolerance space of the legisign for the next semiosis (of which it is the sign, see p. 45 above). In this case an inappropriate response to the signal may be selected. Conversely, a response that is more appropriate to the situation may be selected, a phenomenon that, once again, supplies the raw material for evolutionary change.

These considerations suggest that the definition of equivocation given previously may have to be amended, at least insofar as it is applicable to biological communication systems. The legisign may be thought of as a motor template held by the sender, and as a perceptual template held by the receiver; the sender learns, or is genetically equipped, to make the qualisigns associated with the sinsigns he produces conform to the legisign, but when he fails, the relevant semiosis does not take place and communication cannot succeed, even though the received signal may be identical to the transmitted signal. Thus equivocation may be more appropriately defined as occurring whenever the set of qualisigns associated with a sinsign set up in the course of some behavior is such that to the receiver the physical character of the sign-vehicle falls outside of the tolerance space of the legisign that is appropriate to the communication that is taking place [cf. (a) and (b) above].

Thus the main source of variation in signal form is anatomical or physiological variation among individuals, resulting in differences in the sign-vehicles actually set up by them. Variation that lies outside the range of p_i will tend to be selected against under any circumstances. Even under circumstances where transmission is 100% error-free, there will be some value of p_i for which the disadvantageous effects of frequent $(l - p_i)$ misinterpretation outweigh the benefits of infrequent (p_i) correct interpretation. Sign-vehicles having values of a for which p_i is below this level will also tend to be selected against. In conditions where there is a distribution of probabilities of error-free transmission, p_e, any sign-vehicle having a value of a that is associated with a $P < P_t$ will also tend to be selected against.

A change in sign-vehicle, given the same signal form, may be an alternative for adapting to an environmental change that introduces equivocation into the channels As mentioned previously, the sign-vehicle, which is that on which the selection pressure is actually exerted, is usually just one or a few aspects of the whole disturbance of the environment that is the signal. Thus, taking two of the qualisigns associated with the relevant legisign, the relationship between the observed range of variation in the form of sign-vehicles, the tolerance space and the range of observed variation in all of the other aspect of the signal that are invariably associated with the sign-vehicle may be represented as shown in Fig. 6. For the sake of simplicity, I assume that the signal is so well adapted to the environment that the tolerance space of the legisign is identical to the range of sinsigns that transmit with minimum equivocation, this range is not shown separately on the diagram. If the environment changes, so that the range of minimum equivocation after the change is as shown, those parts of the range of variation in other aspects of the signal that lie within this equivocation-free range will have greater potential as sign-vehicles than will those that previously acted as such. All that is required for these aspects of the signal to serve as sign-vehicles having the same referent and response is for the interpreters of the sign to be capable of forming an association (that is, acquiring a supplementary semiosis) by which the new sign-vehicle can stand for the old and hence, ultimately, replace it.

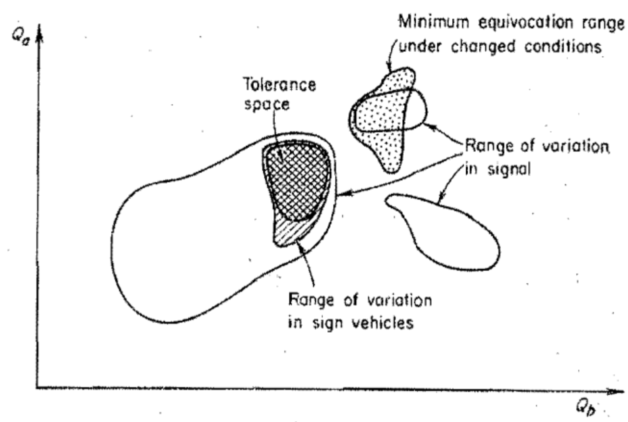

FIG. 6. Situation appropriate for the acquisition of a new sign-vehicle. The diagram shows a two-dimensional cross-section through n-dimensional space, indicating the relationships between the range of variation in all aspects of the signal, the range of variation in the sign-vehicle, the tolerance space of the legisign and the range of minimum equivocation under the changed environmental conditions. See text for full explanation.

The most favourable circumstances for such a change are those where the signal is associated with a context that may arise under a variety of conditions affecting transmission, for example over a range of distances or a variety of levels of background noise. Under such circumstances, transmission will be most difficult under certain of those conditions (say at longer distances) and it will be primarily with respect to the selection pressures operating here that the signal form will be moulded. Under other of the range of conditions under which the signal is given, the whole signal may be perceived more clearly, allowing an association to be built up between the sign-vehicle (which may be the only component of the signal received under the less favourable conditions) and other aspects of the signal that are frequently associated with the sign-vehicle. Under changed environmental circumstances where these other components of the signal transmit with less equivocation over the whole range of conditions, there may be selection for a more invariant association of these),with the old sign-vehicle. Eventually, the association may result in a supplementary semiosis being set up in which some part(s) of the signal come to stand for the old sign-vehicle and finally replace it altogether.

Terrace (1963) has shown that pigeons can learn to switch from a discrimination based on colour to one based on form with no loss of performance, if the form cue is initially introduced as redundant information to subjects performing at criterion on the colour discrimination, and the colour cue gradually eliminated. This suggests that pigeons at least have the necessary abilities to acquire a new sign-vehicle spontaneously if it becomes advantaeous to do so.

Situational context. The particular situations in which a signal is given may change in the course of evolution as a means of reducing equivocation. In this case, the immediate environment of the signal is altered and thus the physical properties of the signal with respect to its environment, which determine the equivocation, change. Although the situational context is not a part of the sign-vehicle and thus does not play a semiotical role in the process of information transfer, it may have an effect on those elements that do. Under some conditions it may be largely incidental to the transfer of information. Thus for example a particular signal may tend to be given while the sender is quadrupedal rather than bipedal, while on the ground rather than while in a tree, or while flying rather than while perched, but it may not be the case that any differences in the probability of clear transmission are associated with these differences in situational context.

This situation may change in two ways. In the first case, the environmental circumstances may change so that the probability of error-free transmission, associated with one context becomes greater than that associated with any other. In this case there will tend to be selection for generation of the signal under those conditions and not in any others, resulting in a contextual specialization of the signal. To the extent that this context is one that is in any case frequently associated with the generation of this signal, the population may be said to be preadapted to the change. In the second case the behaviour of the animals may change for some reason, so that the range of situational contexts changes and one that was not previously available turns out to be associated with a high probability of error-free transmission. Once again there will tend to be selection for signal transmission in this context rather than in others.

It should be pointed out here that a change in situational context may or may not lead to a subsequent or concomitant change in signal forms. Under the new conditions surrounding signal transmission that result from a change in context, new selection pressures may come into operation, resulting in the evolution of a signal form that is less susceptible to equivocation under these new conditions. Alternatively, the new context may indirectly exert selection pressure on the signal form, by affecting the organization of the anatomical and physiological bases of signal production and/or reception. This last point has been discussed by DuBrul (1958) in connection with the change in the geometry of the human vocal tract resulting from a bipedal posture and the possible consequences of this for the evolution of human speech.

(iii) *Semantic and pragmatic relationships*

The final aspect of the communication system that will be discussed here concerns the semantic and pragmatic relationships of the signals; that is the objects and interpretants of the signs involved. For convenience, we may first consider the semantic and then the pragmatic aspects of the problem, but it should be noted that a change in either object or interpretant generally necessitates a change in the other as well, since the relationship between them is determined on grounds of the biological appropriateness of the response to the referent.

Acquisition of objects and referents. In the discussion of a change in situational context above, it appeared that a signal may, under appropriate selection pressure, come to be invariantly associated with one particular context of those in which it is generated. Thus the condition has been set up in which the invariant features of the context, or some of them, may become the referent of the sign-vehicle involved. Whether or not this actually happens will depend on the constellation of other selective pressures that operate simultaneously on the communication system.

Many authors (e.g. Collias, 1959; Marler, 1955, 1961; Konishi, 1970) have drawn attention to the fact that the form of a signal may be correlated, in some instances and to some extent, with the nature of its referent. They have argued that a danger signal should have a form that makes it suitable for transmission over long distances but hard to localize and it has been pointed out that many bird warning signals, for example, do in fact have such a form (Marler, 1955). Under circumstances where a previously hard to localize danger signal becomes more easily localizable (for example as a result of a change or improvement in the mechanism of sound localization in a predator), either the form of the signal may change, or the referent may change so that the signal's relative ease of localization is not such a disadvantage. For example, it might come to be used by a mother to lure a predator away from her young, in which case it could well continue to serve its predator warning function as well, though perhaps secondarily.

A source of variation that might provide the raw material for a change of this kind was discussed above as a source of equivocation that operates prior to the transmission of a signal. Occasionally the wrong legisign for the situation at hand will be chosen for transmission, an error that under normal circumstances will be selected against. If, however, such an error is made under circumstances where the "incorrect" legisign is a better vehicle for the transmission of information appropriate to the situation, then its use in such situations will tend to be selected for. Now it is obvious that in order for such selection to occur, it is necessary for the response to the signal to change as well, so as to become appropriate to the new situation. Thus we must consider ways in which a sign can acquire a new interpretant, since this is the process that is involved in the acquisition of a new response.

Acquisition of interpretants and responses. From the point of view of adaptation, the impact of selective pressure is on the final interpretant and so it is variation in this element, rather than in intermediate, within-brain interpretants that is of interest. Insofar as the response subsequently serves as a sign in an on-going process of communication, it is associated with a tolerance space, whose limits cannot be exceeded (except as discussed on p. 63 above). Insofar as it constitutes adaptive behavior (i.e, as a response to some environmental contingency) it also may be thought of as having an “adaptation space”, within whose limits (under specified conditions) there exists a high probability of success in meeting the contingency. Where both functions are served simultaneously, the two spaces must overlap to some extent. As discussed above, it is probable that all within-brain series of semioses are different in different individuals, given the same initial legisign and final interpretant, because of the effects on them of memory and idiosyncratic neural organization. Nonetheless, appropriate responses are evoked because the series eventually converge on the same or closely similar final interpretants. The sign in each of a series of within-brain semioses has associated with it a tolerance space, within which the interpretant of the previous semiosis must fall if it is to serve as a sinsign of the appropriate legisign. It may be that in some individuals, one interpretant in this series falls outside of the tolerance space of the sign in the next semiosis, and within that of a sign in a different non-convergent series of semioses, in which case a different response will be elicited. In most cases the new final interpretant will be maladaptive, but in a few cases it may fall into a region of the adaptation space associated with a higher probability of success and so it will be selected for.

The acquisition of new referents and new responses in the manner just described involves the co-ordinated occurrence of events with inherently small probabilities. If the new referent is completely different from the old, then the process requires that a new legisign, presumably selected at random, serve as well as or better than the old and that simultaneously a new final interpretant to the legisign is generated that is not only adaptive in the new situation but also preserves the continuity of ongoing social communication. The probability of any such unlikely combination of events being of any significance in the adaptation of animal communication systems is negligible. The probability is increased somewhat in the case where the new referent is similar to the old; this is particularly true if within-brain semioses are organized in such a way that small errors in the interpretation of a sign in one semiosis gives rise to interpretants in subsequent semiosis that are only slightly different than in the case where a correct interpretation has been made. There are good reasons for supposing that evolution would have supplied some such "error-reducing" capacity, for the inherent unreliability of biological systems is such that small errors of this kind must be common.

(C) SOURCES OF SELECTION PRESSURE

Any model of the adaptation of a communication system would have to identify the sources of selection pressure that might act on the systems These would include pressures acting directly on the system, as well as those that act indirectly as a result of a direct action on some other component of the larger sociobiological system of which the communication system forms a part. However, it seems that little could be gained from listing such sources here; several have already been mentioned in the preceding discussion. General discussions of sources of selection pressure may be found in articles by Marler (1956), Konishi (1970) and Moynihan (1970) and some specific observations of relevance have been made by Ficken & Ficken (1962), Crook (1967), Gartlan & Brain (1968, p. 270ff), Petersen & Bartholomew (1969), Morton (1970), Gerald (1971), Poirier (1972, p. 51), Vogel (1973) and Jilka & Leissler (1974), amongst others.

Notes:

[1] This argument is only relevant for animals having a fovea and/or binocular vision but for sake of simplicity I shall assume that we are dealing with such an animal.

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