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The Logical Analysis of Animal Communication

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An attempt has been made to describe some of the responses evoked by communication signals in certain animals and to infer the kind of information which the signals transmit. Using the methods developed by C. W. Morris (1946) for the logical analysis of human language, identifiers, designators, appraisors and prescriptors can be distinguished. Animal signals are rich in designative information, and five sub-categories are distinguished: species-specific, sexual, individual, motivational and environmental information. The influence of natural selection upon the form of a signal will vary according to its information content. For example, the variable nature of some signals and the stereotypy of others can be related to the conveyance of different types of motivational information. A single signal often conveys several different items of information which are usually inherent in the whole signal and not represented by different parts of the signal. The form of some signals is arbitrary but the physical structure is often directly related to information content, in an iconic manner, or in other ways.

Introduction

By any reasonable definition of the term "communication" there can be no doubt that animals communicate with each other. Some authors even extend the term to include exchange of stimuli between organisms and their physical environment (Stevens, 1950), which is perhaps further than it is necessary to go. The position adopted in a recent book by C. Cherry (1957) serves very well to restrict the discussion to a social context. He defines communication as: "The establishment of a social unit from individuals by the use of language or signs". Inclusion of both signs and language in this definition ensures from the outset that studies of communication systems shall not be restricted to the languages of man. This simple step, which so many past authors have been reluctant to take leads Cherry into a lucid, illuminating account of the properties of communication systems and of the methodological problems which they pose. As a student of animal behavior who has been grappling with problems of animal communication the writer has been struck by the relevance to zoology of many of the ideas expressed in Cherry's book. This paper tries

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to apply some of them to animal communication and to show that they can open up new avenues to the understanding of the kind of evolutionary problems with which many zoologists are concerned.

THE ANTHROPOCENTRIC APPROACH

Comparative psychologists have neglected the subject of animal communication to a remarkable degree—remarkable, that is, until one reflects on the anthropocentric point of view of most psychologists. The strictures imposed by F. A. Beach (1959) on comparative psychology are nowhere more relevant than in the subject of animal communication. The main concern has been to differentiate man and the animals, rather than to determine the properties which their “languages” may have in common. Dozens of cases could be cited where this prejudice has influenced the questions that are asked, and therefore the answers obtained. Even in such distinguished contributions as the chapter on the social significance of animal studies by D. O. Hebb & W. R. Thompson (1954) in the “Handbook of Social Psychology” this bias is evident. After discussing the human capacity to combine and readily recombine sounds for different effects, they acknowledge that language has other distinctive characteristics but assert their belief that the above criteria “are enough to set it off fully from animal communication”. A promising discussion thus terminates at the point where it is about to become productive. In the field of linguistics attempts to analyse animal communication have also been marred by anthropocentric viewpoints (e.g. Revesz, 1956), although it is also a linguist, C. F. Hockett (1961), who has succeeded in defining the properties of human language in a manner that permits us to test for their occurrence in animals. In doing so, he has omitted “purposiveness” as one of the criteria. This concept, which may also be associated with an anthropocentric viewpoint, has bedevilled investigations of animal behavior in the past (Thorpe, 1956).

PURPOSIVENESS

Hebb and Thompson (1954) question whether the waggle dance of the honey bee (von Frisch, 1954) is purposive, suggesting that it would be if:

- (a) only the first of several returning bees made the waggle, since, if the message has already been conveyed to the colony by ten other bees, there is little sign of purpose in behavior that conveys it once more; and
 - (b) the worker still made the dance as though the audience was present even when it had been removed.
- (a) seems to be based on the misconception that the entire contingent of perhaps ten thousand workers can perceive the performances of a dozen

or so dancers. The solution to (b) is not certain, but personal observations suggest that an eager audience in the hive is certainly stimulating to a dancer. However, we may ask whether this is a sign of purposiveness, or whether the dancer is simply stimulated through palpation by the antennae of the audience.

If the concept of purposiveness has to be reduced to such a vague level before it can be tested, as Hebb and Thompson seem to imply, we may wonder whether it has not ceased to be valuable as a theoretical construct in the analysis of animal behavior. W. H. Thorpe (1956) has pointed out how difficult the subjective and objective aspects of purposiveness are to separate. It may be best to restrict the idea of purposiveness to a human context. Hebb & Thompson (1954) state that the essence of purposive communication is that “the sender remains sensitive to the receiver’s responsiveness during sending, and by modification of his sending shows that his behavior is in fact guided by the intention of achieving a particular behavioral effect in the receiver”. By this definition any dog-fight qualifies as purposive, as the authors admit. It is not clear what is gained by using a specialized and loaded term for a process which is basically a mutual communicatory exchange, unless to draw attention to possible subjective phenomena. If the latter, then we should recall Thorndike’s (1911) still relevant warning about the dangers of the introspective method in animal studies, notwithstanding Tolman’s (1932) demonstration that by placing special interpretations upon it, purposiveness can be given an objective basis.

AN OBJECTIVE APPROACH

The descriptive or taxonomic approach, which comes less readily to psychologists than to zoologists, has provided the bulk of our present knowledge about animal communication, as applied by such classic investigators as Charles Darwin and K. von Frisch. This in turn has led to new inductive generalizations by K. Z. Lorenz, N. Tinbergen, W. H. Thorpe and others which will provide the framework of future work for many years to come. Instead of approaching animal communication with anthropocentric preconceptions, they set out to describe the natural behavior in objective terms, seeking to derive conclusions about the evolutionary basis of behavior. Even such severe critics as D. S. Lehrman (1953) fully acknowledge the great value of the advances which this “ethological” school has achieved. Communicatory behavior has figured prominently in this work and provided the basis for much of the theoretical discussion in the early papers of Lorenz (1935) and Tinbergen (1940). The scope has subsequently been broadened to include other types of behavior, and the “ethological” school (Tinbergen, 1951; Thorpe, 1956) now provides a rationale for the analysis of animal behavior.

In proceeding thus far, it is the author's contention that some of the special circumstances surrounding communicatory behavior have been overlooked. Close attention has been given to the evolutionary basis of visual signals and the motivation which underlies them. Less attention has been given to the nature of the actual communicatory process; to the questions raised by the process of exchange of signals between one animal and another. The psychologists' concern with this aspect leads them to a consideration of purposiveness, but this does not prove to be a productive line of attack. A strictly objective approach is required which can be applied with equal efficacy to the communication of animals and of man. This paper seeks to show that the theoretical framework presented by Cherry (1957), building especially upon the ideas of Pierce (see Gallie, 1952) and Morris (1946), provides us with such an approach which can lead to advances in our understanding of animal communication.

Semiotic: The Theory of Signs

Dissatisfaction with the results of previous attempts to separate the subjective and objective aspects of human language led C. K. Ogden and I. A. Richards, in a book called "The Meaning of Meaning" (1923), to consider the implications of the theory of signs (or symbolism as they sometimes call it) as developed by the logician, C. S. Pierce. The relationship between a word or symbol and its external referent is shown to be elusive. Perception of external objects (referents) always involves sign situations. We respond only to a part of the whole object. That part comes to represent the whole object as a kind of symbol or sign. "If we realize that in *all* perception, as distinct from mere awareness, sign situations are involved we shall have a new method of approaching problems where a verbal deadlock seems to have arisen. Whenever we perceive what we name a chair we are interpreting a certain group of data, and treating them as signs of a referent." Narrowing down the discussion to the use of language they suggest that "when we consider the various kinds of sign situations... we find that these signs which men use to communicate with each other and as instruments of thought occupy a peculiar place". This comes to bear directly on our present problem with the statement that "the person actually interpreting a sign is not well placed to observe what is happening. We should develop our theory of signs from observations of other people, and only admit evidence from introspection when we know how to appraise it."

To explain the approach of C. S. Pierce to the problem of language analysis, W. B. Gallie (1952) gives the following example. "Suppose that in any particular case we are in doubt whether some sign made by an

individual A has been interpreted or understood by a second individual B. How should we set about trying to settle the question? Should we somehow or other try to discover directly what B's 'mental reaction' has been? It seems quite certain that we have no means whatever of doing this. What we would do, surely, is to try to discover whether B has made some overt response such as A's sign would justify." Cherry (1957) emphasizes the same point, that only a non-participant observer can make fully objective observations on communication systems.

The science of semiotic has arisen to deal with the kind of data that are obtained by direct, non-participant observation of communication systems. It is usually divided into three parts: *syntactics*, the formal study of signals as physical phenomena, and the laws relating to them; *semantics*, study of the "meaning" of signs; and *pragmatics*, the significance of signals to the communicants (Cherry, 1957). The application of syntactics to animal communication is clear, and great progress has been made by Tinbergen and others in this kind of analysis, especially in the sphere of visual communication (see Tinbergen, 1940, 1951, 1952, 1959). Semantics are of doubtful value in animal studies, and as Cherry points out there is considerable overlap with pragmatics, even in the sphere of human language. Pragmatics on the other hand forms the natural complement to syntactics, one defining the physical properties of signals, the other concerning itself with the role of those signals in the communicatory process, a role which we seek to establish by observing and interpreting the response which they evoke in other animals.

ANIMAL PRAGMATICS

The central problem is to determine the nature of the information content of communication signals. As Cherry points out "information content is not to be regarded as a commodity; it is more a property or potential". It cannot be discussed independently from the occurrences of responses to the signal in other organisms. We thus require a means of inferring information content from the nature of the response given. We may note in passing that the information theory developed by Wiener & Shannon (Shannon & Weaver, 1949) is of no help to us here since it operates only "at the syntactical level" (Cherry, 1957). The work of C. W. Morris (1946), however, is directly concerned with analysis of human language at the pragmatic level and can give us some clues as to how to proceed.

Morris seeks to distinguish between signals which function as *identifiers*, *designators*, *appraisors* and *prescriptors*. He emphasizes that this is not an exhaustive list, and elaborates some of them further to deal with special problems of human language. The four basic categories will suffice as a

basis for further discussion. We can describe each of them as conveying a corresponding type of information, provided that we can discern an appropriate response from a communicant. The categories are not mutually exclusive, so that one signal might convey one or all of the different types of information.

Morris defines the four categories as follows: "In the case of *identifiers*, the interpreter is disposed to direct his responses to a certain spatio-temporal region; in the case of *designators* the interpreter is disposed toward response sequences which would be terminated by an object with certain characteristics; in the case of *appraisors* the interpreter is disposed to respond preferentially with respect to certain objects" as manifest in a choice situation; "in the case of *prescriptors*, the interpreter is disposed to perform certain response sequences rather than others." So identifiers may be said to signify (i.e. convey information about) location in space and time, designators to signify characteristics of the environment, appraisors to signify preferential status and prescriptors to signify that specific responses are required. This classification cuts across the division of language into emotive and referential (or symbolic) which received so much emphasis from Ogden & Richards (1923). Morris shows how his classification is subject to testing in a way that the other is not. Moreover we can see that while prescriptors and appraisors embody much of the quality of "emotive" language, and identifiers and designators are more obviously "referential"; in nature, the latter can be emotive in certain circumstances. Thus the new approach is more precise and should be regarded as replacing the older terminology, as Morris suggests.

We now have to demonstrate that this method of analysis can in fact be applied to animal communication systems. J. B. S. Haldane (1953; Haldane & Spurway, 1954) have already shown some ways in which this may be done, and the writer also made an attempt to analyse vocal communication in a small bird, the chaffinch (Marler, 1956) by a method similar to the one suggested here. A reinterpretation of those same data can serve as an illustration. In essence, given a knowledge of the response of other animals to the signal and of the other circumstances in which that same response is given, we can infer the nature of the "message" transmitted by the signal.

The song of the chaffinch is given only by the male. The species is normally monogamous, and the song is especially frequent in an unmated male, given only within his territory. An unmated female chaffinch in reproductive condition responds to repeated singing by persistently approaching the singing male, soliciting his courtship, and eventually establishing a pair bond with him. Circumstantial evidence suggests that some females learn the individual characteristics of their mates' song, and

subsequently respond to them in a preferential way. The behavioral exchanges consequent upon the female's response to the song are confined to a sexual context and are normally evoked by what we may describe as an "appropriate sexual partner". We may infer that frequent male singing conveys information about this particular class of objects which are the "designata" of the male's song, in this situation. What exactly is the information content which is implied?

An appropriate sexual partner for an unmated female chaffinch in reproductive condition is *an unmated male chaffinch in reproductive condition, in possession of a territory (within which nesting will take place), who is close to a location occupied by the female at the same time as she is there*. We are suggesting that all of these items of information are conveyed to her by the male's song. This does not imply that the song has any meaning for her, only that it performs selective actions upon her, appropriate to a certain input of information (Cherry, 1957). The male's individual identity may also be conveyed in some cases. To what extent can this be fitted into Morris's scheme?

"Identifiers" dispose the receiver to direct his responses to a certain spatio-temporal region. We can show that such identifying information is present in the male chaffinch's song which provides an abundance of clues for precise location of the singer in time and space (Marler, 1959). In some respects "locating" information might be a better description.

"Designators" dispose the receiver towards response sequences which would be terminated by an object with certain characteristics. Designative information is thus to be defined by the characteristics of the object normally evoking the response, in this case those of an appropriate sexual partner. This would encompass all of the items outlined above and we shall suggest in a moment that further sub-categories may be desirable.

"Prescriptors" dispose the receiver to perform certain response sequences rather than others. The response prescribed for the female chaffinch is to approach and to adopt certain postures which elicit male courtship. Prescriptors and designators may be confused in some cases because we need to know the kind of response prescribed before the object designated can be discovered. Circular reasoning can only be avoided when prescriptor and designator are contained in different signals. If they can be combined with other signals a different response can be prescribed with the same designator and the effects can be separated. When the same signal performs both functions, as seems to be common in animals, no logical separation between prescriptors and designators is possible.

Appraisors dispose the receiver to respond preferentially to certain objects. Although we have no quantitative information, the frequency with which a song is repeated probably conveys such appraisive informa-

tion. Within the range of song frequencies that will evoke a response, a female confronted with two singing males may be most likely to choose the one who is singing most persistently.

A more detailed breakdown of the nature of designative (and therefore prescriptive) information is required if this system is to aid us in analysis of the evolution of animal communication systems. Most critical from the point of view of natural selection is the presence of the *species-specific* information—that the singer is a chaffinch. We can also separate *sexual* information—that the singer is a male; *individual* information—that the singer is a particular individual; *motivational* information—that the singer is in reproductive condition; *environmental* information—that he is within his territory and has no mate. The criteria by which these types of designative information may be identified are as follows.

Species-specific information and its evolutionary implications

If the response given to the signal is normally evoked only by members of one species we may infer that species-specific information is conveyed by the signal. Usually a member of the same species will be involved, since many animal communication signals play a role in reproductive isolation. Information about other species could come into this category, as for example in the signals exchanged between a commensal and its host. There are also mimics which emit signals with a false species specificity.

Some signals are lacking in such species-specific information. For example, in a situation involving acute danger male chaffinches have an alarm call consisting of a high thin squeak. It is typically given in response to a hawk flying overhead. It evokes the same response from other chaffinches as the stimulus provided by the hawk, namely, direct rapid flight to the nearest cover. However, several other small woodland birds have converged upon the same type of alarm call presumably because, as mentioned below, it is a difficult sound to locate, and so exposes the caller to a minimum of danger. Chaffinches will respond to the corresponding alarm calls of other species as promptly as to their own. Such cases of interspecific communication are very common in the woods in which chaffinches live. Thus species-specific information is not present in this call. Degrees of species specificity may be expected, decreasing to the extent that signals are of mutual value in communication within a group of different sympatric species.

A signal functioning to transmit species-specific information will be subject to certain evolutionary pressures, since there must be a minimum of confusion with signals used by other species at the same time and place. Circumstantial evidence suggests that many auditory and visual signals have been selected for specific distinctiveness (see Sibley, 1957). Con-

versely signals with an interspecific function may be subject to selection for convergence upon a common type—or at least to a minimum of selection for divergence. Where species specificity is required, it is desirable that, as well as being specifically distinct, the signal should also be biologically improbable and conspicuous for effective communication against a background of environmental “noise” (Lorenz, 1951). A relative lack of variability is also required among members of the same species, or at any rate of the same population, an important point when we compare signals which convey individual information.

Sexual information. Responses associated with reproduction are normally evoked by members of the opposite sex when in the appropriate physiological condition. A signal evoking such a response may be said to convey sexual information. There are, however, cases where such behavior patterns are also evoked by members of the same sex in what may be called homosexual or pseudo-sexual behavior (see Morris, 1955). The incidence of sexual information varies considerably as manifest in the extent to which the sets of communication signals of the male and female overlap in different species. The same principles often apply to visual and auditory signals, so that the more sexually dimorphic finches, for example, also show the greatest discrepancy between the repertoires of displays and vocalizations in the two sexes (Hinde 1955–6). The principles governing these variations in the prevalence of sexual information in the signals of different species have not yet been worked out.

In discussing differences between the signals produced by male and female animals, Hockett (1961) has elevated the principle of what he calls “interchangeability” to the level of a major criterion in the analysis of communication systems. He suggests that while it occurs in animals, it is especially characteristic of human language, implying that any person can theoretically reproduce sounds made by any other person. He makes a distinction between language and paralinguage (Trager, 1958) and applies the principle of interchangeability particularly to the former. However the same distinction, which seems to rest on an intuitive judgement with reference to human language, cannot be made with animals. If we regard the difference between the sexes as a means of conveying sexual information, this information is obviously present as a conspicuous and more or less consistent difference in frequency between the speech of men and women. While the auditory signals produced by women share many characteristics with the corresponding signals of men, there are also in Western Society certain unavoidable differences of pitch, unavoidable, that is, for most women (Potter, Kopp & Green, 1947). In this respect the lack of “interchangeability” in human speech is more striking than in some animals, since even strongly sexually dimorphic species often have

some signals which are consistently identical in all respects in the two sexes.

Individual information. The transfer of individual information by a signal is implied whenever the response is normally only evoked, or most readily evoked, by the particular individual emitting the signal. The qualifications admit the possibility of appraisive information being included here, since the female chaffinch, for example, will respond to an unfamiliar chaffinch song, though she may choose a familiar song if given a choice. In many circumstances individual recognition of the signals of mates, rivals, young, and companions plays an important role in the social behavior of animals (Nice, 1943; Marler, in press).

A signal which transmits individual information is subject to selective influences different from those associated with species-specific information. The latter, as we have seen, is most readily transmitted by signals which show little variation, either in the individual or within a population of a given species. Individual information is again best conveyed by signals which vary little in the individual. But it is also a prerequisite that the signals emitted by individuals of the same species, especially within the same population, should differ from each other in a consistent manner. Circumstantial evidence suggests that there is an unduly high degree of intra-group variability in signals which are thought to be involved in individual recognition, such as visual signals originating from the head region of birds, and the songs of some species of birds (Marler, 1959, in press). Some bird songs appear to convey both species-specific and individual information by relegating the stereotyped and variable properties to different parameters of the song.

Motivational information. The last two categories of designative information, motivational and environmental, are the most difficult to define, the least understood, and perhaps ultimately the most important from an evolutionary point of view. The transmission of motivational information by a signal may be inferred if the response given is appropriate to a particular motivational state of the signaller. Such a signal conveys information about variations in the readiness of the signaller to engage in certain classes of activity, such as feeding, fighting or copulation and so on.

The male chaffinch's song evidently communicates to the female the fact that he is in a reproductive state. This condition usually lasts for about three or four months. Short-term changes in motivation may also be communicated by signals. When a mated female has built a nest and is preparing to ovulate she will allow the male to copulate at intervals for about four or five days. When actually ready for copulation she gives a special call which is restricted to this context. The male promptly

approaches and mounts. Similarly the calls given periodically by the young as they become hungry, cause the parents to bring food to them.

Information about still more subtle changes in motivation can also be transmitted. Here the best evidence comes from visual signals, and to discuss them we shall again have to anticipate consideration of the divisible parts of the signal and the information they convey. Many of the communication signals used by animals are subject to what Morris (1957) has called the "principle of typical intensity". This implies that the signal varies little or not at all, with variation in the level of motivation with which it is associated. Either it is given in "typical intensity" or it is not given. Such a signal can effectively communicate presence or absence of a certain type of motivational information but not variations in degree. For many purposes this appears to suffice. In general, a male chaffinch is either in reproductive condition or he is not, and an "all-or-none" type of signal can communicate this.

Other signals do not obey the principle of typical intensity, but vary widely in form, completeness and frequency with the intensity degree of motivation with which they are associated. Visual signals used in fighting behavior are particularly prone to vary in form with slight variations in the presumed balance between the tendencies to attack and withdraw. An opponent is often highly responsive to the slight shifts in motivation which these changes convey, advancing in response to signs of withdrawal, and vice versa, and the final outcome of the fight will normally be determined in this way. On the basis of his extensive studies of the behavior of cats, Leyhausen (1956) has been able to construct a Latin square of the changes in facial expression with changes in aggressiveness and readiness to flee, including all possible combinations between the two, a remarkable demonstration of the complex array of motivational information that such graded communication signals could convey. A function of this kind obviously has profound effects upon the way in which the signals will evolve.

The signals discussed above convey what we can describe as "positive" motivational information; they enable a receiver to "make a positive prediction" of the response which the signaller is likely to give when approached. The evolution of a second class of signals has been governed by a trend towards becoming the direct opposite of other signals, as Darwin (1872) pointed out with his principle of antithesis. His classical example is the behavior of a submissive dog which can only be described as the opposite in all respects of a dog which is fighting. Many other examples of such "antithetic" or "reversed" signals (Tinbergen, 1959) have been described, having the function of conveying something like "no offense meant", and so reducing the chance of an open conflict occurring (Tinbergen & Moynihan, 1952).

In the light of the present analysis we can reinterpret this function as the conveyance of negative motivational information, making it possible for the receiver to predict that the signaller will *not* behave in a certain way when he is approached. All of the cases known so far occur in potentially aggressive situations and appear to function by reducing the chances of attack or flight, or both. Negative information about readiness to attack or to flee is conveyed in most cases. Once again there are evolu-

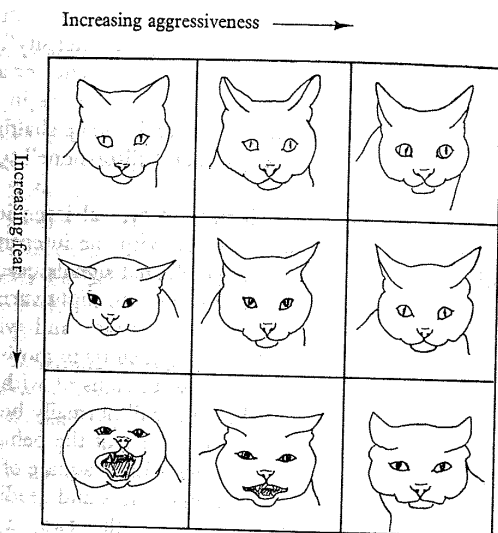


FIG. 1. Changes in the facial expressions of cats associated with variations in the intensity of aggressiveness and fear. (After Leyhausen, 1956.)

tionary implications which could be explored further. For example, aggressive displays usually have certain formal properties and also a certain orientation with respect to the opponent. A negative element can be introduced with respect to a certain receiver, both by reversing formal elements of the display and also by orienting away from the particular receiver. Both trends, in various combinations, can be traced in the examples given by Tinbergen (1959), ranging from simple reorientation of an aggressive display to the reversal of other aspects as well.

Environmental information. When Morris (1946) set up the category of designators he visualized their primary role as conveyors of environmental information, encompassing as they do the characteristically human tendency to give things names. In animals we may infer that a signal has

transmitted environmental information if the response it evokes is appropriate to some characteristic of the environment of the signaller at the moment or in the immediate past. The exact temporal relationship will be discussed in a later section. If, for example, a particular sound is produced in the presence of food, as occurs in herring gulls, and if others respond by approaching and looking for food, as Frings, Frings, Cox & Peissner (1955) have shown to be the case, we may infer that information about the presence of food was conveyed by the signal.

We have inferred that the male chaffinch's song conveys two items of environmental information, one positive, that he is within his territory, and one negative, that he has no mate. Other examples are mainly concerned with what are perhaps the two most important aspects of the physical environment to animals, food and predators. The use of signals conveying the presence of food is probably widespread within family groups. The mook pecking movements, by which a domestic chicken attracts her chicks to a supply of grain, are a familiar example. Special calls are probably also used in this context, though no examples are known to the author. The gull call mentioned above certainly attracts adult gulls as well as young (Frings, Frings, Cox & Peissner, 1955).

The best known signals concerned with the communication of food are the dances of honey bees, analysed in detail by Karl von Frisch (1954). The round dance communicates the distance of a food source in the neighborhood of the hive and its richness. The waggle dance, when given in the hive, also communicates the direction, as well as the distance and richness of sources which are further from the hive. This is, in a sense, another case of communication within a family group, for the worker bees are all daughters of the same queen. The dances are also used in the swarm, to communicate the distance, direction and suitability of new home sites (Lindauer, 1957). Here the dances are given, not on the vertical combs in the darkness of the hive, as in the case with the food dances, but on the surface of the swarm. Clearly the context in which the dance is given affects its communicatory significance. In both cases the signal is a mechanical one, received particularly by the bee's antenna and the mechanoreceptors at its base. The different items of information are conveyed by different aspects of the dance: direction by the angle of the waggle run with respect to the vertical; distance by the tempo of the dance; richness of the food source by the persistence of the dancing. Information about the latter might also be placed under the heading of appraisive information, since it determines the choice made between different situations, particularly in the swarm, where departure from the temporary resting place does not occur until the dancers have reached a degree of unanimity. The final decision is achieved by the scout bees discovering the best site who, by

their more persistent dancing, eventually sway those who have discovered alternative but less satisfactory sites (Lindauer, 1957).

If we place the environmental information conveyed by animal signals on a specificity-generality continuum it usually appears to be relatively unspecific in nature. Information is transmitted about food but not about which particular food. It is true that foraging honey bees may pick up the scent of flowers and so convey the identity of the nectar source to members of the hive (von Frisch, 1954), but the specificity of the signal has been evolved by the plant rather than by the bee. Similarly signals concerned with communicating danger usually seem to do little more than signify different degrees of danger without specifying which environmental agent is responsible. Many small birds have different vocal signals for sudden, acute danger, such as when a hawk appears overhead, and for less dangerous situations, such as when they discover a sleeping owl, or a cat on the ground beneath them. The responses which these stimuli evoke are quite different, sudden flight to cover and cryptic behavior on the one hand; approach to a safe distance and conspicuous "mobbing" behavior on the other. However, the circumstances may greatly modify the response to a given predator. In early spring a male chaffinch will normally give the call associated with acute danger only in response to a flying hawk. But later when he has nestlings, a variety of animals will evoke this call if they come near the nest. Thus we cannot say that the call communicates the presence of a hawk. There may be animals which convey more specific environmental information. Our knowledge is so fragmentary that we cannot begin to generalize. The European willow warbler is thought to have two mobbing calls, one given to a perched hawk, the other to a cuckoo, suggesting that more specific information may be conveyed in this case (Smith & Hosking, 1955).

Conclusions on information content. Although identifiers (or locators) and appraisers occur among the communication signals of animals, designators seem to be most richly represented. Five different categories of designative information have been described, all having particular implications for the evolution of animal communication systems. Perhaps the most prominent category in human language is environmental information, the one to which investigators most often turn when they wish to compare the animals with man. The basic capacity, to convey environmental information by signals, is present in both. However, the time element in this process is significant as several authors have pointed out (Haldane, 1956; Haldane & Spurway, 1954; Hockett, 1961). In animals the delay between perception of an object in the environment and emission of a signal conveying information about that object is usually a short one. In man the delay may be extended almost indefinitely, illustrating what Hockett

(1957) calls "displacement". The only well documented case involving a longer delay in animals comes again from the honey bee where the dance occurs after the forager has returned to the hive (von Frisch, 1954). Here there are finite limits to the delay, which is short by human standards in any case, and it would hardly be useful to the honey bee if it were any longer since the food supply from a given plant varies from hour to hour. Human capacities in this direction are probably unique, although one may wonder if any but the most educated observer would be able to detect such extensive time delays in animals even if they occurred.

The context may have considerable significance to the animals themselves. Hockett (1961) has pointed out how the responses of honey bees to dancing differs when it takes place in the hive and on the swarm. In speaking of the communicatory process as though it were mediated by signals alone, we have thus been guilty of over-simplification. The response evoked by a signal—and therefore the information it conveys—may vary with changes in the circumstances both of the sender and the receiver. The song of a male chaffinch is seen in a different light if we observe the response of male chaffinches instead of females. A male chaffinch intruding into another's territory will flee if he hears the owner's song, implying reception of a further item of motivational information, that the owner is ready to attack male chaffinches found within the boundaries of his territory. The response of a male in an adjacent territory will be different again, and so on. The separation of all of the factors which bear on a given act of communication is thus an imposing task. The additional possibility always exists that the signaller may be emitting several different cues at the same time, as seems to be the case in rats, for example, where olfactory, tactile, visual and auditory signals may all play a part in the female's sexual responses to the male (Beach, 1942, 1947).

Divisible Elements of the Signal

In trying to determine the role of prescriptive information in animal signals we have been confronted by the dilemma that it cannot be distinguished from designative information in signals consisting of one indivisible unit. Only when prescriptors exist in physically separate parts of the signal can an unequivocal separation be made. It thus becomes important to transfer our attention from pragmatics to syntactics to consider the physical nature of some of the signals used in animal communication.

CONTINUITY VERSUS DISCRETENESS

Attention has been drawn to the fact that some signals vary to the extent that they sometimes grade continuously into other signals; others tend to appear in an all-or-none fashion, so that they are separate and discrete from

all other signals. The degree of variation observed can be correlated to some extent with the information which the signal conveys. A degree of continuous variation may occur in at least three different circumstances.

First, appraisive information appears to be most commonly conveyed in animals by signal characteristics which vary in a continuous manner. The frequency with which the chaffinch song is repeated probably conveys appraisive information to the female about the male's relative suitability as a mate (cf. page 302). Similarly the persistence of dancing in the honey bee, as expressed by the number of dances given before the sequence is broken, conveys appraisive information about the richness of the food source or the suitability of a new nest site to other members of the hive. Cases may exist where appraisive information is conveyed by a discontinuous series of signals. For example, the remarkable series of postural displays given by the black-headed gull correlated with variations in the relative and absolute levels of tendencies to attack and to flee should come into this category, for while some intergrade, others are discrete, with a sudden switch from one to the other as the balance of motivation shifts (Moynihan, 1955; Tinbergen, 1959). However, it appears that this condition, which is characteristic of human language, is rare in animals.

Another function of continuously variable signals is the conveyance of subtle changes in motivational information. Some signals, as Morris (1957) has indicated, vary little with slight changes in the signaller's motivation, whereas others mirror the changes in motivation very closely (cf. page 308). Particularly in fighting behavior, where the communication of such subtle motivational information can assume great importance, such variable signals are often used. Human language is in some ways less well adapted to convey such continuously variable information because of the tendency to divide continuous phenomena into discrete classes, which is perhaps one of the reasons why animal signals of this type are difficult for zoologists to describe.

Continuously variable signals also occur as a means of conveying environmental information of a continuously variable nature. The best example is again from the honey bee dances, in which both the direction and distance of the food source are communicated. The former is conveyed by the angle of the waggle run with respect to the vertical, the latter by the tempo of the dance, both varying in a continuous manner. No doubt further examples will be discovered.

We may conclude that continuously variable signals have an important role to play in the communication systems of animals. More stereotyped, discrete signals are also common and, for example, make up the bulk of the vocal signals of such birds as the chaffinch. Continuously variable signals have certain disadvantages. Their interpretation may be slow, and

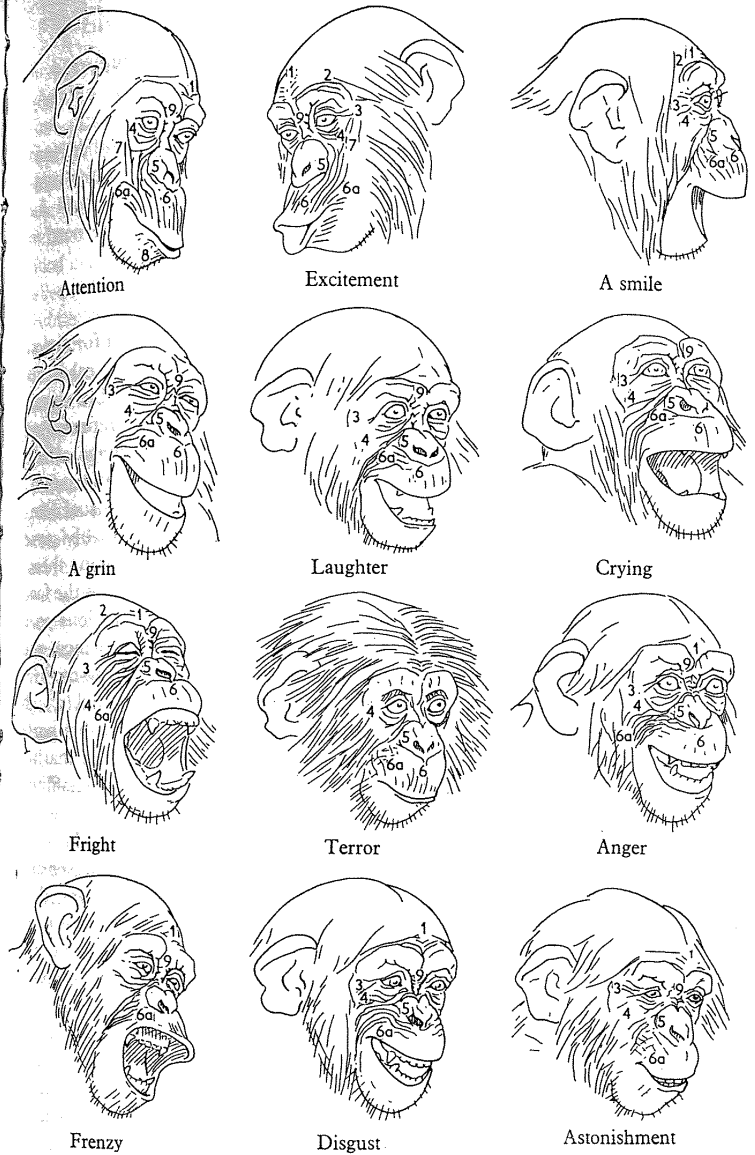


FIG. 2. The facial expressions of a young chimpanzee in various moods. The creases on the face are numbered to emphasize that each one may be involved in several different expressions. (After Kohts, 1935.)

subject to error. Also appropriate inborn responsiveness to all properties of the signals, which characterizes the communication systems of many animals is more easy to visualize with discrete signals than with continuously variable signals. Finally there may be conflicts with other items of information conveyed by the same call. We have seen that the communication of species-specific and individual information both call for stereotyped signals, a requirement which may well override the need to convey subtle changes of motivation.

DIVISIBILITY

The impossibility of separating designative and prescriptive information hinges on the fact that in animal communication systems several items of information seem to be conveyed by one discrete, indivisible signal. We do not normally find the different items of information represented by different elements as is commonly the case in human language, where the component elements can be rearranged to create new "messages". However, this does seem to occur in some cases, particularly in visual communication signals. The facial expressions of chimpanzees probably serve as signals in intraspecific social behavior (Hebb, 1946). In describing them, Kohts (1935) took great care to point out that the same creases on the face may be involved in several different circumstances, the expressions as a whole presumably conveying different information. In her drawings, she even went so far as to number the facial lines to emphasize this point (Fig. 2). Assuming that all elements are necessary for the complete signal (which is difficult to test with visual signals), it appears that the divisible parts can be rearranged to create new "messages". In a similar way the sharing of components by different visual displays of such birds as the chaffinch may imply something similar.

Examples may also be found among vocal signals, but we have to proceed with care. Thus Hockett (1961) quotes Lanyon as presenting evidence that basic motifs in the songs of certain birds are rearranged in different ways to create new songs. A number of cases of this have been described, but there is no evidence that these recombined elements differ in any way in information content. Better examples are likely to be found in the alarm calls of certain birds. Some species have several discrete calls which are given, sometimes alone, sometimes together with other calls. The sequences of different signals may conceivably contribute to one overall signal whose information content varies with the constituents of which it is made up. If this proves to be the case, we are then approaching, at a very primitive level, the kind of lability in the manipulation of the information content of signals which is such a distinctive property of human language.

We must not assume that the lack of such lability among animals is simply a result of incapacity of the nervous system to handle such complex information. The way of life of most animals is so stringent and fraught with dangers that a high premium is placed upon quick production of brief signals, which can be accurately interpreted by receivers, often without the opportunity for previous practice. Given that the fight for survival is controlled by a limited number of factors, such as reproduction, fighting, food and predators which, as selective factors, dominate all others in their effect, there is little place in the biology of most animals for the kind of subtleties of communication which human language permits. Nor must we forget that communication is a social activity which often runs counter to the trend towards competition which characterizes most animal communities. A very elaborate social organization is required before the survival of an individual's genotype becomes so dependent upon survival of the group that natural selection will encourage individual sacrifice for the sake of the community. In most cases we may expect this to occur only within the family group which is one of the reasons for the strong emphasis on individual information in communication signals. With a more elaborate social organization and division of labor among its members, the immediate pressures upon individual survival are alleviated, and the stage is set for the exploitation of the more subtle gains arising from further elaboration of the systems of communication. The most elaborate communication system known in the animal kingdom occurs in the honey bee, whose social organization particularly from a genetic point of view begins to approach the ideal conditions we have postulated above.

RELATIONSHIPS BETWEEN INFORMATION CONTENT AND SIGNAL STRUCTURE

Human language is usually regarded as consisting of arbitrary symbols, bearing no direct physical relationship to the information which they carry. The communication system is thus based upon a convention. Some zoologists have asserted that the communication signals of animals are arbitrary in the same sense (Lorenz, 1935, 1951) and many of them seem to satisfy the criteria. However, in some cases physical structure is intimately related to the corresponding designata.

The conveyance of locating (i.e. identifying) information by sound signals is directly related to physical structure, since this controls the ease with which the sound source can be located. Vertebrate animals, for example, rely primarily upon differences of intensity, phase and time of arrival of sound at the two ears. The easiest sounds to locate are those providing all of these clues, the ideal being something like a repetitive click. This type of sound, used by many species of birds when they are mobbing an owl (cf. page 308), is a readily located call serving to attract the attention

to the position of the owl. Conversely the calls given when a hawk flies overhead have a different structure which minimizes the clues available for location, making the source of the sound difficult to determine. Insects with different types of receptors which respond, not to pressure changes but to the actual displacement of molecules of the medium, are able to determine the direction of sound directly by reference to the vectorial properties of sound, so that their signals are not affected by the problems of location which confront vertebrates (Marler, 1959).

We have noted that appraisive information is sometimes conveyed by the frequency or length of time for which a signal is repeated. The honey bee dances longer for rich food sources than for poor ones, which implies an iconic relationship.

With the sub-categories of designative information we are on surer ground. Consider for example some of these signals in the light of the most commonly accepted alternative to "arbitrary" which is "iconic". A degree of direct physical correspondence between the signal and its referent is implied (see Cherry, 1957; Hockett, 1961) as with a picture for example. The portion of the honey bee's waggle dance that communicates the direction of the food source conveys this environmental information in an iconic manner by transposing directly from the direction with respect to the sun, to direction with respect to the vertical (Hockett, 1961).

Some other signals conveying environmental information appear to be non-iconic. Thus the various alarm calls of birds bear no relationship to the dangers which are their designata. However their physical structure is by no means arbitrary, in relationship to the locating information which they may convey. Thus the adjectives arbitrary and iconic cannot be applied to a signal as a whole, only to the relationship between signal structure and particular items of information which they communicate.

Signals conveying motivational information may be iconic or arbitrary. Most sound signals probably come into the latter category, although sounds used by many birds and mammals in fighting, having a grating, growling or rattling quality may be related in iconic fashion to the snapping of beaks or teeth which occurs in actual combat. Visual signals which are known to have originated as what zoologists call "intention movements" (Tinbergen, 1940, 1952; Daanje, 1950), which Darwin (1872) recognized as "serviceable associated habits" are more obvious illustrations. For example, many aggressive displays undoubtedly originated through emphasis of the actual physical preparations for attack—baring of the teeth, tensing of the muscles, and so on. More than one type of motivational information may be iconically represented in the same signal, conveying information about the existence of two or more types of motivation in the signaller at the same time. Many insights into the evolution of visual signals have arisen

from the Tinbergen's discovery of this phenomenon of multiple motivation in communicatory behavior.

In the same way signals conveying *negative* motivational information are not arbitrary, since their physical structure is related in an inverse manner to the structure of other signals. These constitute a special class of iconic signals. Finally the need to communicate subtle changes in motivation has repercussions on signal structure, encouraging the use of signals which vary in a continuous manner instead of being discrete, in the appropriate circumstances.

Sexual information may equally well be arbitrary or iconic. The red breast of the reproductive male stickleback, which functions as a signal (Tinbergen, 1951) is arbitrary, whereas the swollen belly of a gravid female, also a signal, is iconic. Individual information also may be arbitrary or iconic. Arbitrariness becomes prominent with species-specific signals. It is no accident that Lorenz's (1951) emphasis on arbitrariness was largely derived from intensive study of the plumage and courtship behavior of ducks and other birds, as they play a role in reproductive isolation, all with a strong emphasis upon species-specific information.

The requirement here is that the signal should be readily distinguished from those of other species likely to be transmitted at the same time and place. The way in which they differ is arbitrary, as long as it is readily perceptible to members of the species. The evidence suggests that this has resulted in specific divergence in a wide variety of animal communication signals which function in reproductive isolation of the species. Even here the signals are not entirely arbitrary, since they are excluded from overlap with the signals of other species.

It will be clear from the above discussion that the classification of signals as either iconic or arbitrary is unsatisfactory. A signal may fail to be entirely arbitrary in several ways, which do not all conform closely to the usual definition of iconic. The structure can, however, be related in different ways to the different types of information being conveyed, be it locating, appraisive, species-specific, environmental, motivational and so on. It may be an aid to further progress if we treat signal structure from this point of view, instead of placing all non-arbitrary signals in the iconic category.

Conclusions on the Evolution of Signals

A detailed review of the evolution of the communication systems of animals is beyond the scope of this paper. We would need to present comparative data, on a much larger scale, and much of the evidence has been reviewed in recent papers (e.g. Tinbergen, 1952, 1959; Morris, 1956, 1957; Marler, 1959) together with discussion of the special problems which arise

with the different sensory modes. We may note that evolution from iconic to arbitrary signals is probably quite a common occurrence, as part of the process known as ritualization (Tinbergen, 1952; Blest, in press). The ontogenetic basis of sound signal systems has been considered in several recent papers (Sauer, 1954; Thorpe, 1958; Messmer & Messmer, 1956; Thielcke-Poltz & Thielcke, 1960; Lanyon, 1957) establishing that while the majority of signals are genetically controlled, some are passed on by the learning of traditions. In contrast we know almost nothing about the ontogenetic basis of responsiveness to signals. Learning probably plays an important role here, even in lower animals. All of these issues need to be considered in a complete analysis of the evolution of the communication systems of animals.

The aim of this essay is more restricted. It seeks only to demonstrate that by using the response evoked by signals as an index, we can derive a picture of the kind of information conveyed. An attempt is made to classify some of the types of information involved, and to show that the effects of natural selection upon the evolution of signals may be clarified by such an approach. The categories suggested are neither final nor exhaustive. The existing knowledge about animal communication is so scanty that we have little to use as a basis. Nevertheless we may make more rapid progress if we approach animal communication systems as a whole instead of treating each aspect as a separate issue. The problems occupy a unique position in the study of the evolution of behavior. It is a challenge for us to try to solve them, even at the most elementary level.

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