- 22. E. Leete, Chem. Ind. London 1957, 1270 L. Leete, Chem. Int. London 1957, 1210 (1957); L. M. Henderson, J. F. Someroski, D. R. Rao, P. L. Wu, T. Griffith, R. U. Byerrum, J. Biol. Chem. 234, 93 (1959).
 E. Leete, L. Marion, I. D. Spenser, Can. J. Chem. 33, 405 (1955).
 F. Leete, Chem. Ind. London, 1958, 1477.
- Leete, Chem. Ind. London 1958, 1477
- (1958)25. T. Griffith and R. U. Byerrum, Science 129,
- 1485 (1959) 26. G. R. Waller and L. M. Henderson, Biochem.
- Biophys. Res. Commun. 5, 5 (1961); J. M. Essery, P. F. Juby, L. Marion, E. Trumbull, Can. J. Chem. 41, 1142 (1963).
 A. R. Friedman and E. Leete, J. Am. Chem.

- A. R. Friedman and E. Leete, J. Am. Chem. Soc. 85, 2141 (1963); 86, 1224 (1964).
 D. R. Christman, R. F. Dawson, K. I. C. Karlstrom, J. Org. Chem. 29, 2394 (1964).
 U. Schiedt, G. Boeckh-Behrens, A. M. Del-luva, Z. Physiol. Chem. 330, 46, 58 (1962).
 L. A. Hadwiger, S. E. Bodiei, G. R. Waller, R. K. Gholson, Biochem. Biophys. Res. Commun. 12, 466 (1962).
- L. A. Hadwiger, S. E. Bodiei, G. R. Waller, R. K. Gholson, *Biochem. Biophys. Res. Commun.* 13, 466 (1963).
 T. Griffith, K. P. Hellman, R. U. Byerrum, *Biochemistry* 1, 336 (1962).
 M. V. Ortega and G. M. Brown, J. Biol. *Chem.* 235, 2939 (1960).
 D. Gross, H. R. Schütte, G. Hubner, K. Mothes, *Tetrahedron Letters* 1963, 541 (1963).
 E. Leete, J. Am. Chem. Soc. 78, 3520 (1956).
 E. Leete, E. G. Gros, T. J. Gilbertson, *ibid.* 86, 3907 (1964).
 M. Grobbelaar and F. C. Steward, *ibid.* 75,

- N. Grobbelaar and F. C. Steward, *ibid.* **75**, 4341 (1953); P. H. Lowy, *Arch. Biochem. Biophys.* **47**, 228 (1953); A. Meister and S. 36. N.

- D. Buckley, Biochim. Biophys. Acta 23, 202 (1957); L. Fowden, J. Exptl. Botany 11, 302 (1960).
- (1900).
 A. V. Robertson and L. Marion, Can. J. Chem. 37, 1043 (1959).
 U. Schiedt and H. G. Höss, Z. Naturforsch. 13b, 691 (1958); Z. Physiol. Chem. 330, 74
- (1962).
- 39. E. Leete, J. Am. Chem. Soc. 85, 3523 (1963); 86, 2509 (1964). T. Sakan, A. Fujino, F. Murai, Y. Butsugan, 40.
- Sazui, Bull. Chem. Soc. Japan 32, 315 (1959)
- C. Djerassi, J. P. Kutney, M. Shamma, J. N. Shoolery, L. F. Johnson, *Chem. Ind. London* **1961**, 210 (1961); G. C. Casinovi, J. A. Gar-41. barino, G. B. Marini-Bettolo, ibid. 1961, 253 (1961).
- 42. G. C. Casinovi and G. B. Marini-Bettòlo, Abstracts A, meeting of International Union Pure and Applied Chemistry, London (1963), p. 285.
- 43. R. H. F. Manske and L. Marion, *Can. J. Res.* **B20**, 87 (1942).
- 44. H. Paulsen, Angew. Chem. Intern. Ed. Engl. 2, 555 (1963).
- 45. 46.
- S55 (1963).
 C. Sheehan, H. G. Zachau, W. B. Lawson, J. Am. Chem. Soc. 79, 3933 (1957).
 R. Thomas, Tetrahedron Letters 1961, 544 (1961); T. R. Govindachari, K. Nagarajan, S. Rajappa, Experientia 14, 55 (1958); E. Wenkert, J. Am. Chem. Soc. 81, 1474 (1959).
 E. Lette Chem. Ind. London 1058 (1958)
- Leete, Chem. Ind. London 1958, 1088 47. E (1958).
- 48. -, J. Am. Chem. Soc. **85**, 473 (1963).

Animal Communication

A communication network model for languages is applied to signaling behavior in animals.

Thomas A. Sebeok

to absorb logic, mathematics, and

linguistics entirely within semiotic.

"The whole science of language," the

logician Rudolf Carnap then reaffirmed

The term "semiotic," in its earliest sense equivalent to symptomatology, was introduced into philosophical discourse at the end of the 17th century by John Locke to label one of the three branches of contemporary science, to wit, the doctrine of signs. The real founder and first systematic investigator of the field, however, was the subtle and profound American philosopher, Charles Sanders Pierce. The unique place of semiotic among the sciences-not merely one among the others, "but an organon or instrument of all the sciences"-was insisted on by Charles Morris who, in 1938, proposed

in 1942, "is called semiotic," and, in 1946, Morris introduced further refinements when he distinguished among pure semiotic, which elaborates discourse about signs; descriptive semiotic, which focuses on actual signs; and applied semiotic, which utilizes knowledge about signs for the accomplishment of various purposes. In 1962, the anthropologist Margaret Mead proposed a variant, "semiotics," as a term which might aptly cover "patterned communications in all modalities," that is, for the global study of the interactional and communicational context of the human use of signs and the way in

1006

- and J. B. Murrill, Tetrahedron Letters 49. **1964**, 167 (1964); A. R. Battersby and R. J. Francis, J. Chem. Soc. **1964**, 4078 (1964).
- Francis, J. Chem. Soc. 1964, 4078 (1964).
 50. N. Kowanko and E. Leete, J. Am. Chem. Soc. 84, 4919 (1962).
 51. E. Leete and P. E. Németh, *ibid.* 82, 6055 (1960); E. Leete, *ibid.* 85, 3666 (1963); E. Leete, *Tetrahedron Letters* 1965, 333 (1965); A. R. Battersby, R. Binks, D. A. Yeowell, Proc. Chem. Soc. 1964, 86 (1964); A. R. Battersby, R. Binks, J. J. Reynolds, D. A. Yeowell, J. Chem. Soc. 1964, 4257 (1964).
 52. E. Leete, J. Am. Chem. Soc. 84, 55 (1962); Tetrahedron Letters 1964, 1619 (1964).
 53. M. L. Louden and E. Leete, J. Am. Chem.
- 53. M. L. Louden and E. Leete, J. Am. Chem.
- Soc. 84, 1510, 4507 (1962). 54. B. G. Gower and E. Leete, ibid. 85, 3683 (1963).
- 55.
- (1963).
 E. Leete, E. G. Gros, T. J. Gilbertson, Tetrahedron Letters 1964, 587 (1964).
 E. Leete, Chem. Ind. London 1958, 977 (1958); J. Am. Chem. Soc. 81, 3948 (1959);
 A. R. Battersby and B. J. T. Harper, Chem. Und London 1953, 264 (1958).
 A. B. Battersby and B. J. T. Harper, Chem. 56. E (1958); J. Am. Chem. Soc. 81, 3948 (1959); A. R. Battersby and B. J. T. Harper, Chem. Ind. London 1953, 364 (1958); A. R. Bat-tersby, R. Binks, B. J. T. Harper, J. Chem. Soc. 1962, 3534 (1962).
- 57. E. Leete, J. Am. Chem. Soc. 82, 6338 (1960). 58. _____ and M. Yamazaki, Tetrahedron Letters 1964, 1499 (1964).
- 59. E. Leete, A. Ahmad, I. Kompis, unpublished
- 60. I thank the National Science Foundation and the U.S. Public Health Service for grants (NSF-GB-363, NIH-MH-02662) which have supported my work on alkaloid biosynthesis.

which these are organized in transactional systems involving all of the senses (1). "Zoosemiotics" was then coined (2) to identify a very rapidly expanding discipline within the behavioral sciences, one which has crystallized at the intersection of semiotics, the science of signs, and ethology, a field which Niko Tinbergen characterized, in the first book ever written on the subject, as "the objective study of behavior," but which he more recently-and more fairly-redefined as "the biological study of behaviour" (3). Zoosemiotics has not only emerged as a dominant theme in ethology, but "data on animal communication have contributed a thread of continuity that, in some ways and at some times, has seemed to be the principal axis of synthesis in the entire field of animal behavior" (4).

Modern developments in the study of animal communication stem largely from Charles Darwin (5). They received substantial impetus from the classic investigations of K. von Frisch, and were placed in their present academic frame by K. Z. Lorenz, Tinbergen, W. H. Thorpe, and many others. The period from Darwin until the end of the last decade has been conveniently summarized by Kainz (6), whose book may be complemented by a series of easily accessible review articles and a recent, semi-popular, survey of the field

The author is professor of linguistics and chairman of the Research Center in Anthro-pology, Folklore, and Linguistics at Indiana pology, Folklore, and University, Bloomington.

by H. and M. Frings (7). While zoologists tend to be taxonomically parochial, the understandably anthropocentric preoccupation of psychologists and linguists has, with a few notable exceptions (ϑ), severely limited the range of their respective contributions to the subject.

A Model of the

Communication Network

The elaboration of models of varying degrees of suggestiveness has recently become an international diversion among students of animal communication; although each of these models may be regarded as a useful guide to the classification of behavior, or as a means whereby predictions may be made, they are less assuming than a theory (9, 10). The model which is applied below derives from K. Bühler's field theory of language; in an expanded form, it has proved a valuable research tool for the exploration of the six basic functions of verbal communication (11).

In its traditional guise, Bühler's model envisioned language as an acoustic product viewed from the standpoint of one or more of three possible sign functions: the expressive function, which correlates sign and speaker; the appeal function, which correlates sign and hearer; and the referential function, which correlates the sign with "objects and states of fact," that is, whatever we talk about. This scheme postulated, essentially, that one system, a source, influences another, a destination, with reference to some designation. It has become necessary to amplify it by three additional factors, transforming Bühler's triadic model into a more sophisticated hexagonal one involving the following dimensions: an addresser who selects (that is, encodes according to specific statistical constraints) a message out of a code which, to permit decoding, must be at least partially shared by an *addressee*; the message requires a context apprehensible by the addressee, and a channel through which the participants are capable of establishing and maintaining contact. That portion of the message which originates with the addresser is commonly called the signal, and that which intrudes en route to the receiver, noise, the message being, normally, a mixture of the two. The relation between Bühler's model and an information theoretical 26 FEBRUARY 1965

model of a communication network may be illustrated by a Morley triangle (Fig. 1).

These six factors determine the hierarchical order of the corresponding functions so that the structure of the event depends primarily on the one which predominates. In language, orientation toward the context---the so-called denotative, cognitive, or referential function-is the principal burden of many messages, but each of the other five accessory functions is ordinarily present and must be accounted for. In paralanguage (12), as among animals, orientation toward the addresser-the emotive function-or toward the channel-the phatic function-is more likely to preponderate because, to a degree, denotation and reference are restricted by the medium itself. The heuristic implications of this model for the study of animal communication can be investigated by surveying the factors which constitute such an event.

The Role of the Channel

A linguist approaching a language he has not previously encountered is in the position of a cryptanalyst: he receives messages not destined for him and is initially ignorant of the code from which these are being selected. The zoosemiotician resembles a cryptanalyst as well, but he is faced with further problems which need not occupy the observer of speech: thus, at first, he cannot even be sure through what physical channel or, more likely, channels, the presumed messages are being transmitted. Since any form of physical energy propagation can be exploited for purposes of communication, and many forms are, in fact, at the disposal of animals, one of his first tasks is to specify the sense, or constellation of senses, employed in the message processing situation he is observing.

The observer, attempting to identify communication in a given group of animals, may choose to describe the process by the manner in which the signal is encoded, passed on, or decoded, but the classification emphasized will lead to quite different realms of discourse which are not always comfortably blended. Sometimes the action of an effector organ is featured; more often than not, properties of the intervening medium are the criterion; and sometimes the spotlight falls upon the action of a receptor organ. A signal encoded by one means, say chemical, may be variously interpreted, say, by the distal olfactory sense or the proximal gustatory sense. On the other hand, signals of quite varied originproduced, for instance, by the discoloration of the body's cover or by a gross movement (such as a change in the position of a horse's ear)may all be decoded through the visual

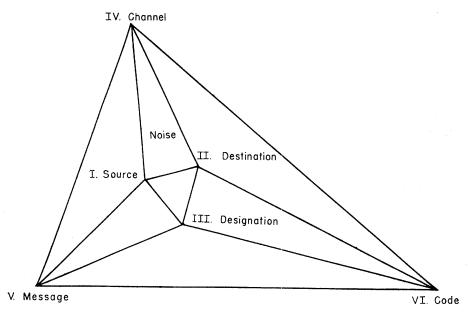


Fig. 1. A Morley triangle showing the relation between Bühler's model and an information-theoretical model of a communication network. Morley's theorem illustrates the relation between Bühler's model (the small equilateral triangle) and a more comprehensive information-theoretical model of a communication network. The encoder and decoder are often the same individual.

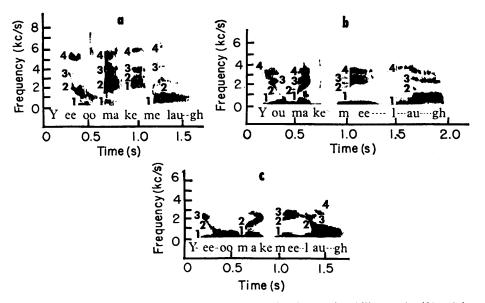


Fig. 2. The phrase "You make me laugh" spoken by (a) Indian hill mynah; (b) adult human male, New Jersey accent; (c) adult human female, New England accent (Thorpe, 15, Fig. 63, p. 118).

channel. A well-trained Indian hill mynah bird may coordinate its equipment of resonators to record a sound spectrogram that is hardly distinguishable from one of human origin (Fig. 2).

Of the six basic aspects of the communication event, the channel is usually the one most readily accessible to the human observer, and it is therefore not surprising to find that emerging subdivisions of zoosemiotics are often organized in terms of the properties of the channels used. One such new discipline which has recently taken definite shape but which has not, as yet, been named, focuses on "pheromones," the label given to chemical substances exchanged by many, perhaps most, animal species to convey information (13). The possibilities of modulating such

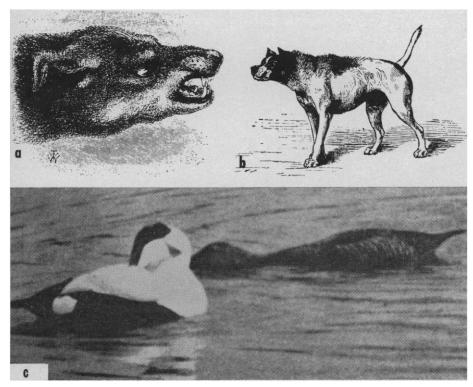


Fig. 3. (a) Head of snarling dog (5, Fig. 14, p. 118); (b) dog with erection of hair on back (5, Fig. 5, p. 52); (c) European eider male performing preen beside a female in prone posture. [F. McKinney, *Behaviour Suppl.* 7 (Brill, Leiden, 1961), Plate I, Fig. 2]

signals are severely restricted, but this lack is compensated for by the capacity of such signals to persist, especially when clinging to solid objects, and thus to convey information long after the addresser has departed. An individual can thus communicate with another in the future and, by delayed feedback, with himself in the future. Thus the graphic manifestation of language, script, has its functional analog elsewhere in the animal kingdom and in particular throughout the mammalian orders.

Another, far more advanced branch of zoosemiotics, "bio-acoustics" (14), is devoted to the study of mechanical vibrations that some animals communicate by in air (for example, 15), in water (for example, 16), or, more seldom, through a solid substratum (for example, 17). Of all the possible and demonstrated forms of animal communication, bio-acoustics boasts of the oldest as well as the most ramified literature, in part because of its immediate appeal to the imagination of men and in part because of technological refinements which became available in the decade after World War II. Yet this field is full of but dimly realized surprises, such as the sophisticated uses of sound in the communication system of the honeybee which have only lately been appreciated (18).

Considerable attention has also been paid to the nature of the visual channel, especially the function and mode of origin of certain postures and movements which, by an evolutionary modification called "ritualization," have led to the formation of a category of behavior ethologists prefer to distinguish as a "display." Displays are sometimes identified as incomplete movements signifying intention, as the snarling of a dog (Fig. 3a); autonomic effects, as piloerection (Fig. 3b); or seemingly context-irrelevant displacement activities, as the preening of drakes during courtship (Fig 3c) (19). In the case of diurnal species, this channel operates by means of reflected daylight, while a variety of other organisms, ranging from bacteria to fishes, those active in dark but transparent media, rely on bioluminescence (20).

Under communication through tactile perception are grouped rather disparate phenomena from various corners of the animal world. These comprehend physical conduits as different as the spider's web and tracks of silk, or the slime trails of snails and slugs, both of which may bear a functional resemblance to scent-trails; the many kinds of organic feelers required in environments where vision is more or less precluded; and miscellaneous contact aggregations, the precise social significance of which remains moot, in some higher vertebrates. Phenomena such as suckling, copulating, fighting, social grooming, and mutual preening all involve tactile perception.

It is well known that certain fishes generate electric fields (Fig. 4), and it seems increasingly probable that some of the feebler impulses are employed for signaling in at least those species where the frequencies and patterns of discharge are distinct. The rhythms of mormyrids are ascribed even a territorial function analogous to the singing of birds (21).

Matter as well as energy may serve as a message conductor, as in the honeybee, ants, and termites, where processes of food and water exchange (Fig. 5) transport not merely calories but also information vital to the survival of the colony. "Trophallaxis" is therefore not merely symptomatic but rather semiotic behavior.

Olfactory, optical, acoustic, and other mechanical signals are all employed for mutual communication in the bee society; a herd of mule deer achieves social integration by hearing, vision, smell, and touch (22, 23). In animals such as these, multiple strands of information are interwoven, as it were, in a single ribbon which is the topological measure of their worlds. Although, at this stage, it is both necessary and proper to distinguish the several channels, to concentrate on each in isolation, the redundancy which prevails among the multiplicity of bands in natural systems (an effect sometimes referred to as "the law of heterogeneous summation"), to the addressee's profit, must soon become an object of both theoretical and practical concern.

Messages which serve primarily to establish, prolong, or discontinue communication, to check, in brief, whether the channel works in good order, were dubbed by the anthropologist Bronislaw Malinowski "phatic communion . . . a type of speech in which ties of union are created by a mere exchange." This is the first verbal function acquired by human infants and commonly predominates in communicative acts both within and across other species. An interesting example of the former was found by Thorpe in shrikes of the genus Laniarius, where each pair in certain species tends to develop a particular

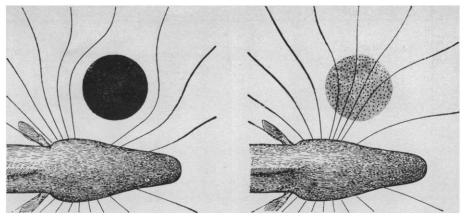


Fig. 4. Objects in electric field of *Gymnarchus* distort the lines of current flow. The lines diverge from a poor conductor (left) and converge toward a good conductor (right). Sensory pores in the head region detect the effect and inform the fish about the object. [H. W. Lissmann, *Sci. Am.* 208, 54 (March 1963)]

repertoire of antiphonal duet patterns in service of mutual recognition and maintenance of contact under conditions when visual display is ineffective; and the vocalizations of captive parrots and parakeets extend an interspecific phatic bond toward their human keepers (24).

Addresser and Addressee

The encoder and decoder of a message may be the same living animal, in a situation of rapid feedback, as in echolocation in bats or porpoises (25), or of delayed feedback, as mentioned above; but another addressee, present or future, is usual and the constant circuit must therefore be treated as a

The communicating organism's selection of a message out of its speciesconsistent code-as well as the receiving organism's apprehension of it -proceeds either in accordance with a genetic program dictating an almost wholly prefabricated set of responses, or with reference to each animal's unique memory store which then determines the way in which the genetic program is read out. E. Mayr has labeled the two extremes among possible combinations of behavior programs closed and open (26), but the relative proportions in the communicative behavior of most species are hardly known, in spite of Marler's detailed survey of the respective roles of inheritance and learning in the development of vocalizations (27).

special case of animal communication.

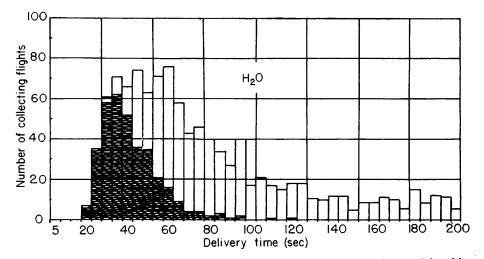


Fig. 5. A need for water is communicated to the forager bees by the receiving hive bees: the more quickly water is accepted by the hive bees, the more diligently will the forager bees collect more water. The number of water-collecting flights decreases as the time required for delivery increases. With very short delivery times (20 to 40 seconds; shaded columns), the foraging bees are even induced to perform an alerting dance after each collecting flight, to recruit new bees to help gather water (22, Fig. 14, p. 25).



Fig. 6. (a) Female mountain gorilla beats her chest, which may be done to attract attention (34, Plate 29); (b) a female gorilla with an infant on her back (34, Plate 17); (c) the striking individual differences in the facial features of gorillas are evident in this picture (34, Plate 18).

One would expect the open component to be important in the higher vertebrates, especially the primates, but useful details are not available. It is worth noting, however, that linguists are of late increasingly persuaded by evidence accumulating both from the study of natural languages and psychology that even certain fundamental features of linguistic structure are innate (28).

Once a message has been formulated, the output is encoded by the animal's appropriate organ or organs of emission, the morphological, physiological, and physical characteristics of which are more or less accessible to scrutiny. Similarly, when the message reaches its gan or organs of reception recode the sensory input for identification and integration with other messages. Every emitting organ and every receptor organ has its phylogenetic history, some of which is necessarily relevant to communicative behavior and all of which confines the range of the signals that can be produced and received. Much of the literature of zoosemiotics is concerned with the nature of the sense organs in their coding function, and the field is sometimes subdivided accordingly. A classification at the receptor stage of the total event would yield, on the whole, a simpler framework

destination, the animal's appropriate or-

but, as in speech, the motor organs and their movements are, by and large, better known.

As to their function, messages that are action responses to visceral and sensory stimuli, that chiefly serve to alert recipient individuals about the condition of the signaling individual, are emotive, a concept which ethological theory tends to shun as too obvious to merit attention but which linguistic theory is seriously reconsidering (29). In speech, orientation toward the destination may result in sentences devoid of truth value, namely, vocatives and imperatives; whether such messages, with a chiefly conative (or appeal) function, occur in subhuman species as well is controversial, and there has been a good deal of philosophical speculation about the question of whether all animal expressions are, so to say, monologues (that is, wholly directive) or sometimes dialogues (that is, partly purposive), this being another phase of the problem already alluded to of the ratio of closed and open behavior programs (6, pp. 176-185; 30). Barnett has argued that "the signalling of animals is performed, nearly always, without regard to the ability of other individuals to receive the signals" (31) but Wynne-Edwards rightly points to the necessary complementarity of the encoding and decoding processes: "Symbolic displays are largely wasted if there is no audience to receive and interpret them; and because of the ordinary necessities of life such as feeding and sleeping they cannot often be indulged in all day long" (32). In fact, a display delivered in the absence of a recipient is so unusual as to warrant some such special designation as a "vacuum activity," and corresponding explanations. There is little doubt that in many communicative events an affective state is generated in both agent and patient; even in human discourse. the monologue must be regarded as a complex superstructure which is by no means universal (save perhaps in the context of rituals requiring the accompaniment of verbal clichés). The flow of this two-way traffic of empathy is often described in terms that are impressionistic as well as mentalistic, but the intricacies of the situation in nature-where alone the circuit is whole -are so much greater than any faced by an ethnographer when he first enters an alien culture that there can be no objection to this interim convenience in usage.

Code and Message

The impressively documented hypothesis of Wynne-Edwards (which, however, still awaits genetic substantiation) about the mechanism of population control in animals presupposes social conventions of certain sorts which may be at the root of all social behavior in animals, including man, and demands a thorough study of the many forms which such governing "agreements" take. The practice of territoriality is a concrete example of a convention, and a convention is a kind of code.

A prime concern of information theory, in one formulation, is "to isolate from their particular contexts those abstract features of representations which can remain invariant under reformulation" (33), a representation being a construct the features of which purport to correspond in some sense with those of another. A code is that set of transformation rules whereby messages are converted from one representation to another, a message being a string generated by an application of a set of such rules, or an ordered selection from an agreed, that is, conventional, set of signs. The physical embodiment of a message, a signal, is a sign-event or a sequence of sign-events where, in the domain at issue, a small amount of energy or matter in the source, an animal, brings about a large redistribution of energy or matter in the destination, the same or another animal. The overall code which regulates an animal communication system often seems to include a set of subcodes, grouped in a hierarchy, fluctuations among which depend on such factors as the availability of alternative channels and the distance between source and receiver. Thus Schaller has convincingly shown that, in the mountain gorilla, vocalizations, employed in dense vegetation, serve to draw attention to the animal emitting them; these sounds "notify the others of a specific emotional state of the performer, alerting them to watch for gestures which communicate further information." Postures and gestures, especially facial expressions, coordinate behavior within the group when the distance among them decreases, while the visual subcode is in turn replaced by the tactile subcode when the distance is further diminished as between a female gorilla and her small infant (Fig. 6) (34).

Linguistic analysis resolves the physically continuous stream of speech into 26 FEBRUARY 1965 a finite series of discrete informational units, simultaneous bundles concatenated into sequences organized in a digital, "yes/no" type of code. Zoosemiotic analysis draws attention to a distinction with far reaching implications (35), that some other human and many forms of animal communication favor a basically different, an analog, "moreor-less" type of code: thus, as in the eastern wood peewee, "an increase in the rate of calling occurs with an increase in intensity of activity," so the louder a man shouts the angrier the impression he creates (36). A hypothesis (not necessarily implying sympatric diversification of one population) has been proposed that an analog code may function to produce behavioral isolation leading, in due time, to other genetic changes and thus to formal diversity within the subpopulations, whereas digital mechanisms were introduced later, when the scanning and integration of much larger quantities of information with more precision acquired adaptive value.

Another kind of distinction is suggested by a consideration of the observer's relation to the event observed and described: "The information an observer can collect depends upon his location within or without the system and upon his views of the boundaries" (37). That a student of animal behavior can occasionally penetrate within the system has been demonstrated. among others, by Jane Goodall: "Finally I was greeted almost as another chimpanzee-sometimes by a show of excitement and shaking of branches, and sometimes by a complete lack of interest" (38). If the observer is located within the communication system, he may submit the code to scrutiny from either end of the channel: as the message undergoes encoding, intention is transformed into display and, conversely, as the message undergoes decoding, the opposite process takes place, from display to meaning. In the latter aspect, the message is first a stochastic process the probabilistic properties of which may be analyzed as Stuart Altmann has in rhesus monkeys; the difference was underlined by Lorenz when he postulated an antistochastic model, to the effect that "There is no law that the sequence must be performed in its entirety. The opposite of an all-or-nothing law holds true of most instinctive movements, and the series may fade out or break off at any given point. But we

can state a law: The higher numbers of the series cannot be performed until after the lower numbers have been carried out" (39). The many ambiguities which bedevil the recipient of a message are unequivocal for the performer and are exploited perhaps to a maximum degree in mimetic associations of the Batesian type.

If a worker bee has found a good source of food less than 80 meters away, it performs a round dance, the odor of the blossoms clinging to its body giving the further information about how the food source smells. The dance and the smell are messages which, we say, designate the fragrant blossoms, enabling the informed searchers to hunt them out. Such messages are "simple" vehicles of communication. Consider now another situation in which the same osmic message is used. When a worker leaves the hive for field duties, it carries a sample of its particular colony odor (which, as a result of the actual flow of wax, pollen, and nectar, possesses a certain uniformity throughout the hive) locked in a special scent sac. Upon its return, immediately before landing, the worker opens its scent gland as though displaying a pass badge to the guard bees (Fig. 7). The odor of a strange worker causes bellicose behavior, but bees with the matching home odor are admitted and may go on to announce the discovery of the food source by a dance (40). When individual b_1 , of a colony C, sends a simple message m to individuals b_n of C, this event can be represented by a simple formula:

$b_1 \rightarrow m \rightarrow b_n$

In the second situation, however, the message consists of a special fragrance, C_r , which functions to insure that further communication, advantageous to that particular colony, can thereupon be initiated; an inappropriate stimulus may lead to an attack, followed by a scuffle, ending with the kill of the would-be intruder. The message has, therefore, a duplex function: it is used both as its own designation and, autonymously, it refers to the code; briefly, it is a metacommunicative message, M:

$b_1 \rightarrow M \rightarrow b_n \longrightarrow b_1 \rightarrow m \rightarrow b_n$

Exchanged cues about codification, elucidating interpretations about the mutual relations of addresser and addressee, are more common among animals than previously credited. Another

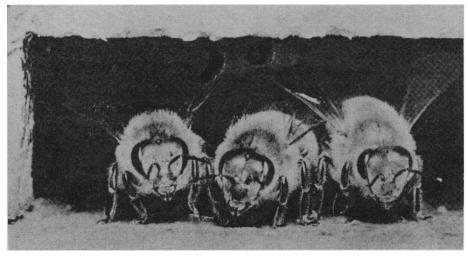


Fig. 7. Guard bees on duty at the entrance of the hive (22, Fig. 5, p. 11).

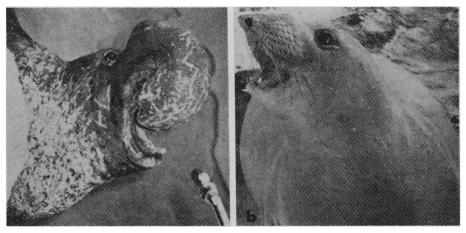


Fig. 8. (a) Adult male elephant seal giving a clap-threat into a microphone (47, Plate IV, Fig. 11); (b) adult female barking (attraction call) (47, Plate IV, Fig. 10).

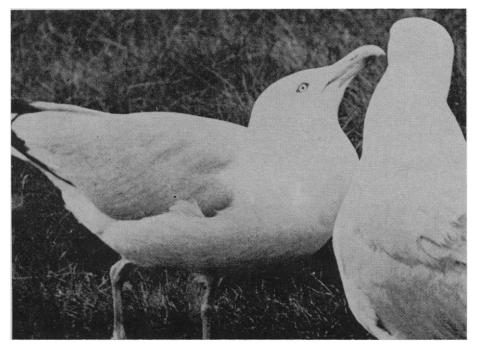


Fig. 9. Female herring gull begging for food from the male (49, Plate 3b). 1012

clear instance of such hypostatic interchanges is found in play encounters among rhesus monkeys: preceding and accompanying play, these monkeys go through certain motions that signal to the other members of the play group that any aggressive behavior in that situation would not be "real" aggression; "the metacommunicative messages that enabled the monkeys to distinguish between play and nonplay acted like mechanisms that somehow switched the monkeys from one entire set of response patterns to another" (41).

Roman Jakobson has illustrated how the message and the underlying code both function, in language, in a duplex manner-that is, may at once be utilized and referred to: thus a message may refer to (i) the code (metacommunication) or (ii) another message ("reported speech"); and, on the other hand, the general meaning of a code unit may imply a reference to (iii) the code (proper names) or (iv) the message ("shifters") (42). Of these duplex forms of semiosis, I have cited examples of (i) in insects and primates; I know of none of types (ii) and (iii); and will examine the prevalence of (iv) below.

The Role of Context

"One of the most significant but difficult aspects of meaning, namely the influence of context" (43), constitutes a major, if chaotic, topic both in linguistics (44) and in zoosemiotics. In the last analysis, all animals are social beings. The chief implication of this assertion of Lindauer's is that all organic alliances presuppose a measure of communication: Protozoa interchange signals; an aggregate of cells becomes an organism by virtue of the fact that the component cells can influence one another. Metazoa assemble in various kinds of alliances. It is essential for them to come together to form a temporary tandem for mating, thus enabling their species to continue. When the sexual partners remain together until the offspring appear, we may speak of a family community, that is, a group whose members stay together but become differentiated-a type of process realized in most dramatic fashion by insect colonies. On the other hand, members of a species not necessarily stemming from one mother may come together and become integrated into "interest communities," joined together,

for instance, for mutual protectionlike a school of porpoises. In all such unions-whether transient or persistent, closed or open, divergent or convergent, simple or complex-creatures of the same species must locate and identify each other; moreover, they must give information as to what niche they occupy in territory as well as status in the social hierarchy, and as to their momentary mood. Intraspecific messages furthering ends such as these are coarsely categorized, by their ecological or functional contexts, as "expressions of threat, warning, fear, pain, hunger, and, at least in the highest animals, such elemental feelings as defiance, well-being, superiority, elation, excitement, friendliness, submission, dejection, and solicitude," by Wynne-Edwards (32, pp. 24-25), who claims, tersely, that these "could if necessary be systematically analysed." Then there are interspecific messages, which he divides into four main categories, "not rigidly separated," namely, warning signals, intimidating signals, decoying signals, and positive or negative masking signals. Collias (45) divides all acoustic messages into five contexts, relating them, respectively, to food, predators, sexual and allied fighting behavior, parent-young interrelations, and aggregations and group movements. Armstrong (46), with due cautions about difficulties and uncertainties, tabulates the following categories required to cover the range of contexts birds communicate about by auditory means:

Identity	Motivation	Environment
Species	Sexual	Location
Sex	Need (other	(a) Individuals
Individ-	than sexual)	(b) Objects
uality	Escape or	Territory
Status	alarm	Predators

Finally, Moles (10, pp. 125–126) provides this six-word Gallic dictionary for grasshoppers (Acrididae):

Signal I:	It is fine, life is good;
Signal II:	I would like to make love;
Signal III:	You are trespassing on
	my territory;
Signal IV:	She's mine (of the female
	of course);
Signal V:	Oh, how nice it would be
	to make love!
Signal VI:	How nice to have made
	love!

The exhibition of rough, subjective classification schemes such as these is intended to illustrate that "zoosemantics," unlike those relatively more mature areas of zoosemiotics which deal with physical channels, coding mechanisms, or the "zoosyntactic" properties of codes and messages, does not exist

26 FEBRUARY 1965

as a scientific discipline but merely a heterogeneous collection of ad hoc proposals. Indeed, Marler was moved to dismiss semantics entirely, as being of doubtful value in animal studies. There are practical reasons why this should be so; but, more fundamentally, semantics suffers altogether from lack of an adequate theory and must first learn to cope with the facts of natural languages before it can hope to accommodate data relevant to animal communication. Little is gained, furthermore, by substituting-as Marler does, for example, in his ingenious analysis of the song of the chaffinchan explicitly "zoopragmatic" approach, which endeavors to get at the problem of context by inferences projected from the response chosen by the addressee, а female chaffinch, from the total repertoire of responses at her disposal; or from the parallel procedure of Bartholomew and Collias, who grouped the sounds made by adult elephant seals into two sorts, threats or attraction calls (Fig. 8), as inferred from the responses observed in other individuals to specific vocalizations in natural situations (47). One obvious difficulty stems from the fact of selective perception. since no response is ever entirely overt and any response could be wholly covert and hence very hard to observe, let alone evaluate.

An even more delicate set of problems is posed by a particular, but by no means rare, class of code units I would call "shifters," adapting Otto Jespersen's linguistic label for that class of words, as personal pronouns, "whose meaning differs according to the situation" (48). The honeybee's tail-wagging dance has more than one denotatum, for it designates either a food source or a nesting site: its pragmatic import depends not upon variation in the formal expression but solely the attendant physical context of an identical gesture pattern. The herring gull's head-tossing has more than one function: it occurs as a pre-coital display, but this is "indistinguishable from the head-tossing shown by the female begging for food" (Fig. 9) (49). The tail-wagging and the head-tossing are movements associated with their respective contexts by conventional rules; they are, therefore, symbols. Moreover, since they stand in existential relations with this or that context (that is, they point), they belong to the class of deictic symbols. Indexical symbols are a complex category of code constituents which

can be defined only by their compulsory reference to a given message, and the analysis of shifters used by animals requires an appreciation of this overlapping relationship in which a signal is coupled with its context. Incidentally, when an acoustic signal happens to be a shifter, playback experiments are bound to yield displaced or negative results: for example, when high-fidelity recordings of killer whale sounds were repeated to porpoises in a tank, no effects could be observed.

Conclusions

Semiotics and ethology have converged in a new behavioral science, zoosemiotics. Those who are interested in the theoretical analysis of the complex problems of non-verbal behavior that arise where these two disciplines interact aim to treat comprehensively animal communication systems by the aid of representations that have proved illuminating in the study of sentences of human language. Students of zoosemiotics are concerned with codes and messages much as linguists are concerned with competence, or language, and performance, or speech. They thus face the twin tasks of constructing a model for the addresser to specify how a message is encoded and transformed into a signal carried by a variety of channels to the addressee; and of constructing a model for the addressee to specify the ways in which animals utilize their knowledge of their code to recognize the messages they receive. Finally, they assess the context of the communicative event in the hope of dissecting that which is relevant to the selection process from the rest of the background, a program for which there is as yet neither a procedural eliciting technique nor a satisfactory theoretical solution in sight.

Their distant goal is the provision of an ordered body of data as a basis for the investigation of the phylogenetic origins of interacting communicative behavior elements, including verbal. Any viable hypothesis about the origin and nature of language will have to incorporate the findings of zoosemiotics, whether embedded within the framework of current evolutionary theory or, as linguists now sense it must be, formulated in terms sufficiently powerful to explain the appearance of the faculty of language in its uniquely creative ramifications.

References and Notes

- 1. T. A. Sebeok, A. S. Hayes, M. C. Bateson,
- T. A. Sebeck, A. S. Hayes, M. C. Bateson, Eds., Approaches to Semiotics (Mouton, The Hague, 1964).
 T. A. Sebeck, Language 39, 465 (1963); Am. Anthropol. 66, 954 (1964); Science 147, 492 (1965) (1965)
- (1965).
 N. Tinbergen, Study of Instinct (Oxford Univ. Press, London, 1951); Z. Tierpsychol. 20, 411 (1963). For a recent survey of ethology, see also E. H. Hess, in New Directions in Psychology (Holt, New York, 1963).
 R. D. Alexander, Science 144, 713 (1964).
 C. Darwin, The Expression of the Emotions in Man and Animals (Murray, London, 1872).
 F. Kainz, Die "Sprache" der Tiere. Tatsachen Problemschau—Theorie (Enke, Stuttgart, 1961).

- 1961)
- 7. P. Marler, in Darwin's Biological Work: P. Marler, in Darwin's Biological Work: Some Aspects Reconsidered, P. R. Bell, Ed. (Cambridge Univ. Press, London, 1959), pp. 150-206; W. H. Thorpe, Ann. Rev. Psychol. 12, 27 (1960); M. Lindauer, *ibid.* 13, 35 (1962); D. G. M. Wood-Gush, *ibid.* 14, 175 (1963); W. A. Mason and A. J. Riopelle, *ibid.* 15, 143 (1964); T. A. Sebeok, Language 39, 448 (1963); R. A. Hinde, in Disorders of Communication: Proceedings of the Associa-tion for Research in Nervous and Mentel Dis-tion for Research in Nervous and Mentel Dis-tion for Research in Nervous and Mentel Dis-tion for Research in Nervous and Mentel Dis-Communication: Proceedings of the Association for Research in Nervous and Mental Disease, 1962, D. McK. Rioch and E. A. Weinstein, Eds. (Williams and Wilkins, Baltimore, 1964), pp. 62-84; H. and M. Frings, Animal Communication (Blaisdell, New York, 1964).
 8. Among linguists, see especially C. F. Hockett, whose pertinent writings are listed in Current Anthropol. 5, 166 (1964).
 9. P. Marler, J. Theoret. Biol. 1, 295 (1961); S. A. Altmann, Ann. N.Y. Acad. Sci. 102 (Art. 2), 338 (1962); T. A. Sebeok, Behavioral Sci. 7, 430 (1962); N. I. Zhinkin, in Acoustic Behaviour of Animals, R.-G. Busnel, Ed. (Elsevier, Amsterdam, 1963), pp. 132-80.
 10. A. Moles, in Acoustic Behaviour of Animals, R.-G. Busnel, Ed. (Elsevier, Amsterdam, 1963)

- R.-G. Busnel, Ed. (Elsevier, Amsterdam,
- R.-G. Busnel, Ed. (Elsevier, Amsterdam, 1963), pp. 112-31.
 K. Bühler, Sprachtheorie (Fischer, Jena, 1934); R. Jakobson, in Style in Language, A Conference, Indiana University, 1958, T. A. Sebeok, Ed. (M.I.T. Press and Wiley, New York, 1960), pp. 350-377.
 G. L. Trager, Stud. Linguist. 13, 1 (1958).
 E. O. Wilson and W. H. Bossert, Recent Progr. Hormone Res. 19, 673 (1963); W. H. Bossert and E. O. Wilson, J. Theoret. Biol. 5, 443 (1963).
- , 443 (1963).
- R.-G. Busnel, Ed., Acoustic Behaviour of Animals (Elsevier, Amsterdam, 1963).
 W. H. Thorpe, Bird-Song: The Biology of Vocal Communication and Expression in

NSF: 14th Annual Report Reveals

Efforts To Devise New Techniques

The 14th annual report* of the Na-

tional Science Foundation received

scarcely any public attention last week

when President Johnson routinely for-

warded it to Congress. But in many respects it is an extremely significant

document in the relationship between

in Science-Government Relations

Birds (Cambridge Univ. Press, London, 1961); M. R. Frings and H. W. Frings, Sound Pro-duction and Sound Reception by Insects: A

- duction and Sound Reception by Insects: A Bibliography (Pennsylvania State Univ. Press, University Park, 1960).
 16. W. N. Tavolga, Ed., Marine Bio-Acoustics (Macmillan, New York, 1964).
 17. A. M. Wenner, Science 138, 446 (1962).
 18. —, Sci. Am. 210, 117 (Apr., 1964).
 19. G. P. Baerends, Arch. Néerl. Zool. 13, 401 (1958); P. Marler, in Vertebrate Speciation: A Conference, University of Texas, 1958 (Univ. of Texas Press, Austin, 1961), pp. 96-121.
 20. W. D. McElrov and H. H. Seliger, Sci. Am.
- 20.
- 96-121.
 W. D. McElroy and H. H. Seliger, Sci. Am.
 207, 76 (Dec., 1962).
 F. P. Möhres, Naturwissenschaften 44, 431 (1957); H. W. Lissman, J. Exptl. Biol. 35, 156 (1958).
 M. Lindauer, Communication Among Social Rese, Combridge 1961) 21.
- M. Lindater, Communication Among Social Bees (Harvard Univ. Press, Cambridge, 1961). J. M. Linsdale and P. Q. Tomich, A Herd of Mule Deer; A Record of Observations made on the Hastings Natural History Reser-23. vation (Univ. of California Press, Berkeley,
- W. H. Thorpe, Nature 197, 774 (1963); O. H. Mowrer, Learning Theory and Personality Dynamics (Ronald, New York, 1950), chap. 24.
- D. R. Griffin, Listening in the Dark; The Acoustic Orientation of Bats and Men (Yale Univ. Press, New Haven, 1958); W. N. Univ. Press, New Haven, 1958); W. N. Kellogg, Porpoises and Sonar (Univ. of Chi-cago Press, Chicago, 1961). E. Mayr, Proc. Natl. Acad. Sci. U.S. 51, 939 (1964). The distinction was first mentioned
- W. J. Smith, in preparation.
 P. Marler, in Acoustic Behaviour in Animals,
- R.-G. Busnel, Ed. (Elsevier, Amsterdam, 1963), pp. 228-243, 794-797.
 E. H. Lenneberg, in *The Structure of Language*, J. A. Fodor and J. J. Katz, Eds. (Prentice-Hall, Englewood Cliffs, N.J., 1964), CTC (COL).
- (Prentice-Hail, Englewood Cliffs, N.J., 1964),
 pp. 579–603; and in New Directions in the Study of Language, E. H. Lenneberg, Ed. (M.I.T. Press, Cambridge, 1964), pp. 65–88.
 E. Stankiewicz, in Approaches to Semiotics,
 T. A. Sebeok, A. S. Hayes, M. C. Bateson,
 Eds. (Mouton, The Hague, 1964), pp. 239–264. 29.
- 264.
 W. H. Thorpe, Learning and Instinct in Ani-mals (Harvard Univ. Press, Cambridge, 1963).
 S. A. Barnett, The Rat: A Study in Behav-iour (Aldine, Chicago, 1963), p. 98.
 V. C. Wynne-Edwards, Animal Dispersion in Relation to Social Behaviour (Hafner, New York 1962) p. 16
- York, 1962), p. 16. 33. D. M. MacKay, Cybernetics: Transactions

of the 8th Conference, H. von Foerster, Ed. (Josiah Macy, Jr. Foundation, New York, 1952), p. 224. 34. G. B. Schaller, The Mountain Gorilla: Ecol-

- G. B. Schaller, The Mountain Gorilla: Ecology and Behavior (Chicago Univ. Press, Chicago, 1963), p. 272.
 T. A. Sebeok, in Natural Language and the Computer, P. L. Garvin, Ed. (McGraw-Hill, New York, 1963), pp. 47-64.
 W. J. Smith, Am. Naturalist 97, 122 (1963); compare T. C. Schneirla, in The Nebraska Symposium on Motivation, vol. 7, M. R. Jones, Ed. (Univ. of Nebraska Press, Lincoln, 1959), pp. 1-42. 1959), pp. 1-42.
- 37. J. Ruesch, in Toward a Unified Theory of Human Behavior, R. R. Grinker, Ed. (Basic Books, New York, 1956), p. 37.
- 38. J. Goodall, Natl. Geograph. Mag. 124, 293 (1963).
- (1963).
 S. A. Altmann, J. Theoret. Biol., in press;
 K. Lorenz, in Group Processes: Transactions of the First Conference, B. Schaffner, Ed. (Josiah Macy, Jr. Foundation, New York, 1955). 39. 1955), p. 179. 40. F. Köhler, Z. Bienenforsch. 3, 57 (1953).
- S. A. Altmann, in *Roots of Behavior*, E. L. Bliss, Ed. (Harper, New York, 1962), pp. 277-285.
- Z11-285.
 R. Jakobson, "Shifters, verbal categories, and the Russian verb" (mimeograph, De-partment of Slavic Languages and Literatures, Harvard University, 1957).
 C. E. Shannon and W. Weaver, The Mathe-matical Theory of Communication (Univ. of Ulinoin Persec Urbana, 1949) p. 117
- Illinois Press, Urbana, 1949), p. 117. T. Slama-Cazacu, *Langage et (* (Mouton, The Hague, 1961). Contexte 44.
- N. E. Collias, in Animal Sounds and Com-munication, W. E. Lanyon and W. N. Tavolga, Eds. (American Institute of Biolog-ical Sciences, Washington, D.C., 1960), p. 387.
- E. A. Armstrong, A Study of Bird Song (Oxford Univ. Press, London, 1963), p. 6. G. A. Bartholomew and N. E. Collias, Ani-mal Behav. 10, 7 (1962). 46. 47.
- O. Jesperson, Language: Its Nature, Develop-ment, and Origin (Norton, New York, 1964), o. 123
- N. Tinbergen, The Herring Gull's World (Basic Books, New York, rev. ed., 1961), p. 112. 49.
- p. 112. The preparation of this article was supported by USPHS research grant Nos. MH 07488-01/2, and profited from the comments of S. A. Altmann (University of Alberta), E. P. Hamp (University of Chicago), W. J. Smith (University of Pennsylvania), and W. N. Tavolga (American Museum of Natural History) 50. History).

to three questions which over the past couple of years have become subjects for concern in the scientific community and in Congress:

"Should the Foundation attempt to devise new or modified support programs rather than continuing to rely mainly on the project grant method?

"How can one be sure that the relative amounts of support being provided by NSF to the various fields are approximately correct?

"What changes, if any, should NSF make in its policies and procedures in response to the increasing concern over geographical concentration of Federal funds for research and development activities?"

News and Comment

the scientific community and its principal patron, the federal government. For in the report, NSF director Leland J. Haworth implicitly acknowledges that American science has passed through the postwar phase of rapid growth and now must devote attention to some serious administrative problems that have developed along the way.

The report, which covers Haworth's first full year as director, addresses itself

^{*} NSF-65-1, 14th Annual Report, available for 45 cents from the Government Printing Office, Washington, D.C. 20402. An accompanying pub-lication, *Grants and Awards*, *NSF*-65-2, is available for \$1. It lists all NSF-supported projects and investigators for fiscal 1964,