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The Analysis of Animal Communication

STEVEN GREEN AND PETER MARLER

INTRODUCTION

Communication consists of the transmission of information from one animal to another. Information is encoded by one individual into a signal. When received by another animal, this information undergoes decoding, while still retaining a specifiable relationship to the encoded information. The relationship is sometimes deterministic, sometimes only probabilistic. During such encoding and decoding, the carrier of the information and the format of the information undergo many transformations. Starting with the original designatum or referent, information passes through a series of steps internal to the signaling animal before effecting a change of state of the signaling organ. A signal is then propagated in a medium. Further steps follow, from transmitted signal to receptor organs of a recipient, from sensory to central processing, and eventually to a recipient's overt or covert response.

Viewed in this light, communication systems engage many scientific disciplines. Phenomena of memory and cognition are included as well as the physiology of transduction in receptor organs. Alterations in mechanisms can occur over many generations, with their fundamental regulation by natural selection, or by inter- and intragenerational learning, so that the study of animal communication impinges on the domains of sociobiology and evolutionary biology as well as ethology. We will not attempt to cover all of these areas but rather to highlight

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themes of current interest to students of animal behavior and psychology, in the context of a general scheme for examining animal communication. For our present purposes, the topic of animal communication includes only phenomena that satisfy the following three conditions:

1. *Nonconstancy of signals.* The signal itself is a discernible event, with its beginning and end marking a period much shorter than any phase of an individual's life cycle. Signal production is manifested by an observable change of state. Its detection by an observer is in some way contingent upon an external attribute that contrasts with the immediately preceding state. By use of this condition as a criterion, we intend for the most part to exclude from our consideration of signaling those attributes or signs that are constant within an individual's lifetime or that are strictly age-dependent.

Pelage color, for example, often mediates recognition of species, sex, age, or individual identity. With some special exceptions, such as fish (Baerends, Brouwer and Waterbolk, 1955; Leong, 1969; Heiligenberg, Kramer, and Schulz, 1972) and cephalopods (Moynihan, 1975), most body coloration changes occur over too long a period to qualify as signals by our definition. While the evolution of pelage color and pattern may well have incorporated selection for visibility or invisibility, these signs—and specialized structures that enhance visibility, such as the lamellae on butterfly wings—are not considered signals in and of themselves, although they may be used in signaling.

Some such features , involved as they are in recognition and discrimination of sex, age-classes, strangers, and kin, will fall within our purview, since any consideration of communication must clearly acknowledge that such basic information is often available to the communicant. However, we are inclined to treat them as contextual or ancillary components in the communicative process rather than as signals.

2. *Specialization.* Structural or behavioral adaptation for signal production and/or transmission and/or reception is a prerequisite for the phenomena we are considering, thus implying some specialization for communication. The energy transfer mediated by signal reception must serve as a response *trigger*, in the sense of Bullock (1961), rather than as a precipitant in its own right. To command someone to jump off a bridge is an act of communication; to push him is not (Cherry, 1966).

We shall be dealing primarily with intraspecific communication. There are, of course, cases of adaptive interspecific communication as in the signals of commensal beetles that live in ant colonies (Hölldobler, 1967, 1970). Interspecific communication may also be nonadaptive, as when an owl orients its strike to the squeal of a mouse. In such adventitious communication, one organism benefits from receiving another's signals without any benefit to the signaler. Such events may well be necessary precursors to natural selection for improved capabilities of receivers or for less readily detected signaling by transmitters, especially in communication between species. We will largely disregard adventitious communication, however, and concentrate instead on adaptations for mutually beneficial flows of information. For social communication, in the sense that we will use the term, potential two-way symmetry of communicating pairs is required, with both

members subject to natural selection for better information transfer, yielding co-evolved, bidirectional signal production and signal perception (Otte, 1974; Marller, 1977b).

3. *Internal processing.* Signaling and receiving animals behave as if they internalize the encoding and decoding of signals. Communicative responses to the same signals in the same context may vary at different times. The variation in internal processing that is implied engages more than just receptor states. Although verbal reports on introspection are the best way to approach this issue, they are available only for analyzing our own communicative behavior. There are other criteria, however, which provide a basis for logical inference about similar processes in animals (Griffin, 1976).

Responses are defined as any change in the probability of subsequent behavior compared to expectations in the absence of signaling. Although a change may occur immediately or in the indefinite future (Heiligenberg, 1977), the practicalities of research generally restrict us to short-term changes of large magnitude. The nature of responses serves to inform us indirectly about the internal processes of encoding and decoding.

Note that conscious intention is not included as a criterion. While *intention*, defined operationally as goal-directed behavior (MacKay, 1972), is widespread in animal communication, rigorous criteria for intention are currently applicable only in man, although the possibility of extension to other species should not be excluded (Griffin, 1979). Communication characterized by the three criteria we have given can occur without any consciously determinable intention. For example, body and facial language often contradicts purposeful lying (e.g., Ekman, Friesen, and Ellsworth, 1972; Ekman and Friesen, 1974), yet it satisfies our criteria and is also congruent with our commonsense notions of communicative phenomena. Communication can also be mediated by physiological processes with little or no nervous component, such as the odors or swellings associated with mammalian estrus. Although these would not usually be considered intentional, we accept them as communicative, as long as other criteria, especially brevity and the existence of discernible end points, are met.

Our requirements for nonconstancy of signals and for specialized adaptations for communication cover common ground with more restrictive formulations of animal communication. A communicative interaction is a social event. It represents the essence of sociality. Our internalization requirement indicates that the state of one animal, a signal emitter, alters the state of another animal, a receiver. The vehicle for this alteration is the signal. Determination of the change of state of the receiver is based on its behavioral changes, as compared with probabilities for a different signal or for no signal at all. This "state" of the emitter is an internal process, contingent on its perception of certain past or present external events, referents, or designata.

The overall characteristics of a communication system are the result of chaining together the individual transformation steps in signaling transmission and reception, to yield a mapping function that describes the transfer of information from organism to organism. Each step can be affected by noise, error, and inherent biological variability.

The usual subjects of descriptive studies of the communicative behavior of animals are the signals. Sometimes, the relationships between referents and signals are studied, though usually without examining the chain of transformations within the emitter resulting in signal generation. Correlations between a receiver's behavior and an emitter's prior or parallel signal action are also frequency examined (Wiepkema, 1961; Stokes, 1962a,b; Nelson, 1964; Altmann, 1965; Hazlett and Bossert, 1965; Dunham, 1966; Dingle, 1969; Andersson, 1976; Baylis, 1976; Rand and Rand, 1976). Nonexperimental studies often lump all modes of signaling other than the one being examined together with other aspects of the behavioral context. Experimental studies tend to manipulate only the signals and to separate the effects of other components of the situation by employing balanced controls. Each method emphasizes only a few of the many information transformations that occur in the complete communication process. Depending on one's perspective, some aspects of communication are inherently more interesting than others. Whether we are concerned more with the stochastics of behavior or with information theory, receptor physiology or signal detection theory, competition or reproduction, or the evolution or maintenance of animal societies, our preoccupations will determine the most appropriate strategy.

There are, however, many other major but as yet relatively unstudied questions about the physiological and evolutionary processes that dictate relations among referents, signals, and responses. Some issues have received more attention than others, in part because they are accessible for study but perhaps also because of the lack of a coherent theoretical framework for identifying central issues in animal communication. This paper introduces some hypothetical constructs that, although they do not necessarily bear a one-to-one relationship with identifiable anatomical structures or physiological processes, can be used to describe phenomena of communication and may aid in their analysis.

SIGNAL PRODUCTION, TRANSMISSION, AND RECEPTION

THE SENDER

From a sender's vantage point, a signal must be producible at an intensity or concentration adequate for transmission over a required distance so that it can be received and acted upon in a way advantageous, on the average, to the sender's inclusive fitness. Some degree of matching inevitably arises between the form signals take and the nature and mode of operation of the special organs and motor equipment available for their production. Zoologists, linguists, and anthropologists have described a vast array of specialization for the production of signals, whether electric, photic, acoustic, chemical, or tactile (Sebeok, 1977). Thus, the constraints on sound production by cricket stridulation are quite different from those on bird vocalization, and the sounds produced differ accordingly. At a more subtle level, both birds and man use respiratory air flow to produce communicative sounds, but songbird and human vocal tracts operate differently. Laryngeal and syringeal mechanisms must be understood before differences in the acoustic

structure of bird song and of speech become intelligible (Lieberman, 1967; Greenewalt, 1968).

By contrast with the diversity of studies on signal production, comparative information on the anatomical and physiological specializations for the encoding phases of signal production is virtually nonexistent. Only the comparison between man and nonhuman primates has yet been studied fruitfully. In this case, it is known that different parts of the brain relate to so-called affective and symbolic aspects of signal production (Robinson, 1975; Jurgens and Ploog, 1976; Laman-della, 1977).

Little is known about the direct consequences of signaling actions for the signaler, a potentially important issue, especially perhaps in cases where signal production is repeated continuously for some time (Haldane, 1953). Nelson (1965) has clear evidence that courtship actions of a male stickleback change the prospects of his future behavior. Eisenberg and Kleiman (1972, p. 26) have suggested that self-stimulation may be important to an olfactory signaler in some circumstances, in that production of a scent changes the odor field and arouses the individual in various ways, depending upon the nature of the change.

The hypothesis has been offered that adoption of the appropriate facial expression by human subjects facilitates a transition to the corresponding mood. Recent studies have supplied some supporting evidence (Izard, 1974; Schwartz, 1975; Schwartz, Fair, Salt, Mandel, and Klerman, 1976). Method-acting schools have expounded similar views for many years. If people gain some self-assurance by singing, whistling, talking, or shouting to themselves, why not animals? Such consequences for the signaler might involve not only positive but also negative feedback. In one of the few animal studies on this subject, Wilz (1970) has presented evidence that some of the courtship actions of the male three-spined stickleback function at least in part to change the state not of the female but of the male himself, in this case to reduce aggressiveness. Signaling actions that involve occlusion of sense organs, such as hiding the face, serving to "cut off" sources of stimulation may also have negative feedback consequences for the signaler (Chance, 1962).

THE RECEIVER

From a receiver's viewpoint, selective pressures operate on its ability to detect and react to signals so as to enhance its inclusive fitness. Signals are thus part of an evolutionary feedback system that also reflects features of the receiver's own anatomy and physiology. Aside from the obvious need for possession of receptor systems in the appropriate sensory modality, the existence of particular predispositions within a modality—such as zones of high sensitivity or acuity, for example, or qualitative quantization of stimulus continua, as occurs in color vision (Kolers and von Grunau, 1975; Bornstein, Kessen, and Weiskopf, 1976; Ratliff, 1976)—will exert obvious influences on signal evolution. The details of such relationships are virtually unexplored (see Hailman, 1977) except for those between perception and production of human speech (page 99).

The range of frequencies best heard by animals as different as fish and

orthoptera varies in parallel with the frequencies most strongly emphasized in their sounds (e.g., Nocke, 1972; Paton, Capranica, Dragsten, and Webb, 1977; Myrberg, 1978). Among birds, audiometric studies reveal species variations in frequency sensitivity, even though the overall range of audible frequencies may be similar across species. There is a general tendency for the emphasized frequencies of birdsong to be clustered around a species' own best frequency for hearing (Konishi, 1970, 1974; Dooling, Mulligan, and Miller, 1971).

Although there is necessarily coupling between signal structure and sensory systems, this is often very loose. Thus, one cannot predict that species with color vision will necessarily exploit colors in the design of their visual signals, although, if they do, a knowledge of the details of color perception should permit one to predict some of the rules governing how colors are used (cf. Hailman, 1977). Correspondingly, responsiveness to a wide range of sound frequencies is not necessarily predictive of an equivalent range in the vocal output.

Only when receptor systems are expressly and narrowly specialized for communication can knowledge of them permit precise predictions about properties of signals of the species. With social signal detection as the prime function, it may drive the structure and physiology of receptor design to the exclusion of other concerns. More versatile receptor systems, responsive to wider ranges of stimuli, are subject to many other selective influences, and the match with features of conspecific signals is correspondingly loosened.

Chemoreceptors of moths and hearing organs of frogs illustrate the close relationship that *can* evolve between signal structure and highly specialized receptors. Species differences in the chemical structure of female moth sex pheromones are sometimes, though not always, matched by the responsiveness of male antennal chemoreceptors (Schneider, 1962; Payne, 1974). In frogs, species differences in the frequency structure of male calling songs are beautifully matched to the best frequencies of the audiogram originating in the two primary hearing organs, the amphibian and the basillar papillae (Capranica, 1976). However, there is an obvious price to be paid for such specialization in that a species cannot maximize specificity to conspecific signals while retaining sufficient generality of responsiveness to be sensitive and efficient in detecting other stimuli.

SIGNAL DIRECTION

The ease with which a receiver can determine the direction of a distant signal varies with the sensory modality and the design of the receptor system that is used. Except for species with the most primitive light receptors, an animal can hardly detect a visual signal without at the same time getting a fair idea of where it comes from. Still, the accuracy of localization varies according to such structural features of the visual organ as retinal cell density, accommodation abilities, or, for compound eyes, whether ommatidia are of the apposition or superposition type (Horridge, 1975).

Unlike light rays, a diffusing chemical has minimal inherent directional qualities, so an animal sensing a pheromone from a distant source must localize it indirectly, by reference either to the differences in concentration at different

locations or to the direction of movement of the medium carrying the scent, such as a breeze or a current, or both (Wright, 1958; Farkas and Shorey, 1974). Thus, for organisms relying heavily on chemical communication, sensitivity to small variations in stimulus concentration is a great advantage. This is, in fact, a general characteristic of both vertebrate and invertebrate olfactory systems (Adrian, 1928). Equally important is an ability to register the direction of air or water movements, an issue studied in some invertebrates (e.g., Camhi, 1969) and in fish, but virtually unexplored in mammals, whose vibrissae would seem prime candidates for such a function. The ease of locating the source of a chemical signal also varies according to its volatility and rate of diffusion as well as durability and the rate of production at the source (Bossert and Wilson, 1963; Wilson and Bossert, 1963; Wilson, 1968; Regnier and Goodwin, 1977).

Perhaps the most elaborate adaptations for easing or hindering the localizability of a signal source occur in the auditory capabilities of birds and mammals. Unlike insects, many of which possess receptors that are directly responsive to the vectorial properties of a sound wave, the ears of terrestrial vertebrates typically employ pressure receptors and must therefore rely mainly on binaural detection of differences of intensity, time of arrival of a sound, and phase relations. In certain circumstances, they can use all three methods, and localizations are most accurate in such cases. The available cues vary with the type of sound. Localization by means of intensity differences can be most accurate with high-frequency sounds, since wavelengths shorter than head dimensions permit the sound-shielding effect to be greatest. Conversely, localization by means of phase differences is most accurate with frequencies low enough that their wavelength is longer than the distance between the ears (Konishi, 1977). Accurate localization by sensing the difference in time of arrival of the same sound at each ear depends on the presence of discontinuities and transient frequencies in the acoustic stimulus. All three types of cue are provided by sounds that are varying with time, broken, and repetitive, with a wide range of frequencies. These properties are shared by many animal sounds, but especially those where quick, accurate localization is at a premium (Marler, 1955).

However, a readily localizable signal is disadvantageous in some situations, as with small-bird alarm calls used in the presence of a hunting hawk or carnivore. If a sound is a relatively narrow-band pure tone, if its amplitude envelope begins and ends gradually, and if it has few transients or discontinuities, it is more difficult to locate, as Brown, Beecher, Moody, and Stebbins (1978) have shown with monkeys in the laboratory. Moreover, a high pitched sound, with its rapid attenuation with distance in air, can reduce the range of possible detection by predators while still effectively communicating danger to nearby companions (Konishi, 1973). Many birds and mammals have converged on the use of this type of ventriloquial sound as a signal for extreme danger (e.g., Collias, 1952; Orians and Christman, 1968; Melchior, 1971; Latimer, 1977; Vencl, 1977; Owings and Virginia, 1978), still localizable (Shalter and Schleidt, 1977; Shalter, 1978), but with greater difficulty (Konishi, 1973).

With signals originating close to the receiver or even directly touching its own body surface, as with the somesthetic and chemotactic senses, and with close-range

olfaction, localization is direct and immediate. Odor-trail laying, exploited by many vertebrate and invertebrate animals, is a special case of this kind of contact or close-range signal orientation, elaborated with considerable refinement by ants and used by many other animals (Wilson, 1962, 1971a; Myktytowycz, 1974; Shorey, 1976). In some such cases, the location itself may be part of the signal rather than ancillary information. Touch patterns, whether gradual or sudden, weak or strong, localized or stroking across a surface, provide one of the elementary and widespread means available for communicants to exchange varied information of profound social significance (Geldard, 1977). Just where on the body surface one organism touches another, as well as the nature of the contact, can transform its communicative significance.

Spatial characteristics also affect encoding possibilities with other sensory modalities. Their relevance is most obvious with visual signals. The directionality of light and the discriminability of separate light sources permit the use of spatial patterns in encoding to a degree that is inconceivable for signals mediated by the other distance receptor systems. Even when communicating primarily by some other means, animals often exploit the visual channel as well for the particular directional advantages that visual signaling possesses.

NOISE

The background against which a given signal must be discriminated if it is to mediate effective communication, including other similar stimuli, may be viewed as noise. In almost all habitats, there is a background of environmental noise of nonbiological origin. A wind creates various kinds of acoustic noise that interfere with the processes of auditory communication. One of the factors favoring dawn and dusk as times of day for acoustic communication is the likelihood that convectional air movements will be at a minimum. The frequency properties of wind noise vary with the type of vegetation, with as yet unexplored consequences for the best frequencies for communicative use. Noise of biological origin may be even more significant than physical noise in some circumstances, as with the din of insect sounds through which vertebrate sounds must be detected and identified in a tropical rain forest (Waser and Waser, 1977) or the ubiquitous background noise of marine environments (Myrberg, 1978).

Signals of other organisms constitute a source of noise that can generate strong selective forces for specific distinctiveness of signals. One solution is to avoid simultaneous signaling (see Cody and Brown, 1969; Smith, 1977), manifest in patterns of pheromone production of closely related insects (Shorey, 1976) and perhaps an explanation for the specifically distinctive timing of participation of different bird species in the dawn chorus. Short-term avoidance of song overlap has been demonstrated between a flycatcher and a vireo (Ficken, Ficken, and Hartman, 1974). The nocturnal production of long-range calls by certain populations of orangutan has been interpreted as avoidance of intense competition with other primates and birds for use of acoustic channels at dawn. In geographic areas where some of the competitors are absent, calling at dawn is more typical than at

night (MacKinnon, 1974). The contrapuntal singing of rival males of certain birds may also be viewed as a form of delivery that avoids temporal overlap.

Background noise of physical origin impinges even on electric communication in fish. A major source of electrical noise in tropical environments in South America and Africa, where electric fish are found, is lightning. Frequent thunderstorms produce interference in the same frequency range as those used by these fish for communication (Hopkins, 1973). Electromagnetic waves from lightning propagate with little attenuation, so that the pulses are detectable at great distances from storms. In the rivers in Guyana where the fish were studied, there was a steady but randomly organized background of electrical noise of this kind, against which the fish had to perceive each other's signals. Their tendencies to use continuous and regular trains of pulses is interpreted as an adaptation to favor contrast with this background (Hopkins, 1974), an interpretation also applied to the acoustic pulse trains of fish, amphibians, and birds in noisy environments (Myrberg, Espanier, and Há, 1978).

Presumably, chemical noise has a significant influence on the evolution of olfactory signaling, although it has been little studied. The chemical senses illustrate one means of dealing with the noise problem, namely, employing receptor systems narrowly tuned to a limited range of stimuli, thus eliminating masking that might result from the perception of stimuli outside that range (e.g., Roth, 1948; Tischner and Schief, 1954). The antennal olfactory receptors of some moths respond only to the sexual pheromone of females of the species and a few other closely related compounds (Schneider, 1962, 1970). With more versatile receptor systems that are responsive to broader ranges of stimuli, masking can be a serious problem, even when receptor subsets are narrowly tuned, as in audition (Scharf, 1970).

Adaptation to maximize contrast between signals and background is perhaps better known for the visual modality than for any other, though there has admittedly been little systematic effort to explore general relationships between variations in light quality in different environments and the visual signals used in them (Hailman, 1977; but see Burtt, 1977). There are many examples in animal coloration of patterns of color and shading that serve to emphasize the outlines of the shape of the body or some part of it (Cott, 1957). These are often focused on parts of the body exposed or moved in the course of signaling behavior, particularly those with significance to others, such as weapons or reproductive organs. Shading can emphasize three-dimensionality and hence, visibility. Black and white patterns or vivid coloration against a contrasting color of background also serve to increase discriminability from immediate surroundings (Hingston, 1933; Cott, 1957; Hamilton, 1973).

On the other hand, there is a rich literature concerning the opposite adaptation: animals subject to intense predation frequently blend with their visual background rather than contrasting with it. Similarly, some predators have visual aspects which make them difficult to detect, the tiger usually being offered as an example. Extreme cases are often exquisitely refined, involving resemblance not just to a general background but to a particular object or organism, gaining highly specific protection thereby (Tinbergen, 1951, 1953; Wickler, 1968).

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Even more basic to communication than the directionality of signals is the distance from the signaler at which they can be detected and discriminated. This is of particular concern in exploring the nature of signals that mediate the differing organizations of social groups in animals. Species vary widely in their patterns of spatial distribution and therefore also in the optimal distances at which signals should be perceptible to competitors and companions, kin and strangers, predators and prey.

What determines the distance a signal travels and the degradation and distortion it suffers in the course of transmission? Much depends on how the signal spreads from the source—whether it is beamed, deposited, or transmitted omnidirectionally so that its intensity rapidly decreases in any given direction. Obstacles in the signal's path may absorb, reflect, refract, or distort it. These issues are obviously different for visual, acoustic, electrical, and chemical signals, the former most impeded by obstacles, the latter least. There are also variations within a modality depending on the particular physical properties of the signal and the environmental conditions of transmission. The alternatives have been most thoroughly explored with sound, as reviewed by Waser and Wiley (this volume), who describe frequency "windows" in relation to sound transmission under certain conditions (Morton, 1975; Marten and Marler, 1977; Marten, Quine, and Marler, 1977).

An analogous situation can occur in the ocean with a steep gradient at the thermocline near the water surface and another near the ocean floor resulting from compression. Payne and McVay (1971) have indicated that the "sofar channel" thus created can refract sounds away from energy-absorbing contact with the water surface and the ocean floor, and it may well be exploited by hump-backed whales. This species produces its very loud and elaborate songs at the range of intermediate depths where this sound channel occurs, and Payne and McVay speculate that under these conditions, the whales may be audible to one another at distances of hundreds of miles. Their suggestion appears to be plausible in light of the use by submarines of the special properties of the sofar channel for long-distance acoustic detection and communication.

Although whale sounds are audible over great distances, they are subject to considerable distortion in the process. The sound received at any one place is a sum of components that have different frequency-dependent histories of reflection and refraction. Parts of sounds with origins a few milliseconds apart may arrive simultaneously. An early part may be retarded by a longer transmission time if it has undergone more bends and bounces and hence travels a longer distance. Conversely, signals originating in a very short interval may arrive over a substantial spread of time. This raises an important but little studied issue. Signals detected at a distance may not only be faint but also degraded (Wiley and Richards, 1978; Richards and Wiley, in press). On both counts, they will be less easily detected against the background and less readily discriminated from each other, reducing the ease of selective identification. As we have mentioned earlier, selectivity and sensitivity cannot be simultaneously maximized, as the receptor

requirements differ. However, a signal may include features that allow adaptations for both detection at a distance, when specific details of the signal may be minimal, and also selectivity when at closer range.

By no means all signals are adapted to maximize transmission distance. The amplitudes of different sounds in primate repertoires vary extensively, in some degree of harmony with their apparent function, sometimes favoring close-range, within-group transmission, and sometimes allowing longer-distance transmission, perhaps favoring audibility to neighboring troops (Marler, 1973; Waser and Waser, 1977). Similarly, frequency adjustments may serve to limit the range of detectability. The very high pitch of some of the "ventriloquial" alarm calls of birds not only diminishes the cues available to predators for localizing the origin but also, perhaps more importantly, diminishes the transmission range because of the greater attenuation of high frequencies (Konishi, 1973). The acoustic signals of aquatic animals may be adapted to contrast with the ambient noise in their environment (Winn, 1967; Myrberg, 1978). Furthermore, certain components of complex acoustic signals may be more closely adapted for long-range transmission than others (Morris, Kerr, and Gwynne, 1975; Gerhardt, 1974a, 1975, 1976).

In the chemical domain, calculations of the "active space" of pheromones—such as an alarm signal of ants, on the one hand, and a sexual pheromone of a moth, on the other—show that they differ strikingly in accord with their function, the former being much larger than the latter (Bossert and Wilson, 1963; Regnier and Goodwin, 1977). Simple economy dictates some adjustment of the energy expended in production of a signal to the socially appropriate transmission distance. But it is also likely that long-range transmission of some signals is not just uneconomical but positively disadvantageous, as would be so if a local alarm pheromone spread to all corners of an ant colony, or a hen's tidbitting call for its chicks was as far carrying as a cock's crowing.

INTERNAL TRANSFORMATIONS IN SIGNAL PROCESSING

TRANSFORMATION RULES

Communication can be characterized as a sequence of procedures yielding a transfer of information. If one set of data is processed to yield a second set, the two are related to each other by the rules or instructions that dictate the procedure, plus any errors or noise introduced. Whether we examine large or small segments of a communication sequence, the same scheme can be used for depicting the information transfer that takes place.

If we look at a single organism, the first set might contain referents external to a signaling animal, and the second set the signals it produces. At the level of a social dyad or a social group, the second set might be responses by signal recipients. Even at the physiological level within a single organism, we can imagine viewing the internal procedures as arrayed in tandem. Referents, the first set, would be processed by the sensory apparatus and the brain to yield perceptions as the second set. These in turn would comprise the input set for generating a second

set of internal states, which we will call *assessments* of the referent data. Each assessment may or may not be processed to generate a signal, selected from the set of possible signaling outputs. Regardless of the scale we invoke, each link in the chain of information transfers in a communication system is logically and conceptually equivalent, although the physiological and psychological processes themselves may be quite different.

At each level, the result may be characterized by a process of mapping a body of input data onto output, which can in turn be part of the input for the next stage. The rules or instructions that describe how each member of the input is assigned to one of the possible outputs constitutes a mapping function.

The simplest kind of idealized mapping function is a listing of unique assignments: every member of the input set is linked to one and only one member of the output set, and vice versa. In such a case, as long as each of the specific links is given, knowing the identity of any member of either set implies knowledge of the identity of the corresponding member of the other set. In certain conditions, such a system can be very efficient. In the absence of noise and error, information transfer occurs without loss or degradation or the introduction of uncertainties.

In any natural process, particularly a biological one, these conditions are rarely satisfied. Noise (i.e., unpredictable variation in the linking process), misadventure (regularly mistaken connections at either the input or the output set), and dropouts (a lapse in the processing) are all apt to cause loss or spurious augmentation. The effects of such errors may be far from trivial, with a strong influence on survival and reproduction.

We can examine the ways in which natural selection should favor mapping functions to minimize the likelihood and severity of such hazards. As illustrations, we will present hypothetical rules that differ in the effectiveness with which they serve to transfer information. Some rules appear to be well represented by animal communication processes. Others seem to have major potential disadvantages and are not known to occur.

GENERALITY OF TRANSFORMATIONS

The rules governing signal selection are our first concern. When sensory input is combined with internalized information, either genetically determined or acquired, a signaling organism may assign the result to one of a number of assessment states. Assessments in turn become the input data linked to signal production. The links from input to output can be expressed as two parallel lists of assessments and signals, with each connection between them separately indicated.

For simple organisms, with few sensory inputs and small signal repertoires, a mapping function of this kind is readily envisaged (Figure 1). Even for complex organisms, well-endowed with sensory capacities, such a simple listing may suffice to describe the transformation of assessments into signals if, in the circumstances under study, the potential output set is limited. Consider, for example, a human infant in a state of discomfort. Although infants are complex organisms with multimodal sensory perceptions, each sensation and degree of discomfort may yield only a simple comfort assessment of "yes" or "no." These two assessments can

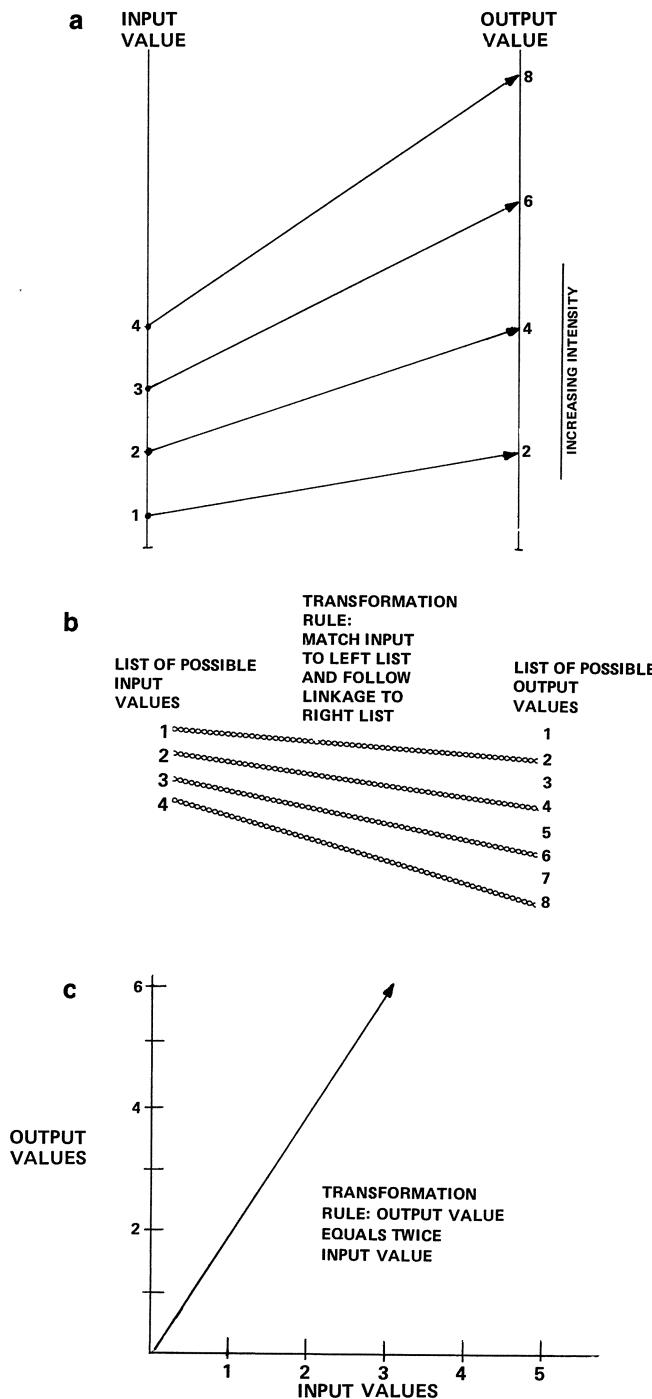


Fig. 1. (a) A diagram of relationships between input and output values that can be achieved either by (b) a set of linkages between parallel lists or (c) a general rule that can be applied to determine the output given any input. The same mapping function that describes (a) can be produced by the separate transformation rules shown in (b) or the general rule pictured in (c).

easily be mapped onto the vocal output set by a rule assigning "no" to crying and "yes" to silence or contented gurgling.

In more complex situations, however, it becomes less plausible to postulate a separate individual rule linking each and every pair of inputs and outputs. If, for example, an infant's assessments range over many intensities, reflecting different kinds and magnitudes of discomfort, and the output set varies from silence through minimal whimperings and thence louder and longer to full-blown screaming, then the list of rules linking each assessment to one of the vocal outputs would be extremely large. To internalize a list of rules embodying all such possible contingencies would require a staggering amount of information. An equivalent and more economical solution is achieved by applying one or more rules separately to each circumstance as it arises. A simple example would be a general rule specifying that the intensity value of the output data can be achieved by matching the intensity of the input. The greater the infant's hunger, for example, the louder its cry. Thus, one simple transformation function serves when needed to generate a relationship that maps input to output data and is fully equivalent to the separate determination of each output by matching the input against a list of input-output links. The result of transforming an assessment to a signal would be similar (Figure 1). Even with this type of more economical procedure, higher animals must have an enormous number of such rules, some as simple as this example, others much more abstract and complex.

SPECIFICITY OF THE TRANSFORMATION

If each possible input is transformed into one and only one output, we say every input value *specifies* an output value. The resulting specific links from input to output are all deterministic, whether produced by a list of links or by application of a general rule. Examples can be found in production of those signals that have been described as "released" or "triggered." The input data set for a newly hatched herring gull, for example, includes one member that is a particular configuration of adult bill length, coloration, and movement. The output corresponding to this sensory input, specified by the process of internal transformation, is vigorous pecking at the bill tip (Tinbergen and Perdeck, 1950; Hailman, 1967; Tinbergen, 1973). The output in this example serves the direct function of obtaining food, which the adult carries to the chick, as well as an indirect one by signaling a need to the adult.

More than one input may specify the same output. Systematic experimental manipulation of the input can then determine the boundaries of the portion of the possible input set specifying a given output. In gulls, various hues, degrees of color contrast, shapes, and sizes can yield the pecking response in addition to the optimal set. Without access to further information at the physiological level, it is not possible to evaluate whether different effective stimuli yield different assessments, all specifying the same response, or whether all the effective stimuli result in the same assessment, one that is specifically linked to that response (see Figure 2).

To the extent that a transformation rule connects more than one member of the possible output set to an input, the mapping function is not specific. Such unspecific links may be parallel or alternate. The parallel case implies that two or more output items are simultaneously determined, a situation we will examine later. In the alternate case, there may be (1) an equiprobable random selection among outputs; (2) a fixed sequence of outputs, in which case the link is specified by the prior history of outputs as well as by the assessment; or (3) a nonuniform probabilistic determination of a range of outputs, or any mixture (Figure 3).

UNIQUE DETERMINATION BY THE TRANSFORMATION

If each possible output results from a transform of one and only one input, then we say that every output is uniquely determined by an input. Uniqueness is then the mirror image of specificity (p. 86).

A unique transformation implies that we can examine the output and ascertain which member of the input set is linked to it, thus permitting us to make inferences about the signaling animal's assessment of its own inputs. Adoption by a

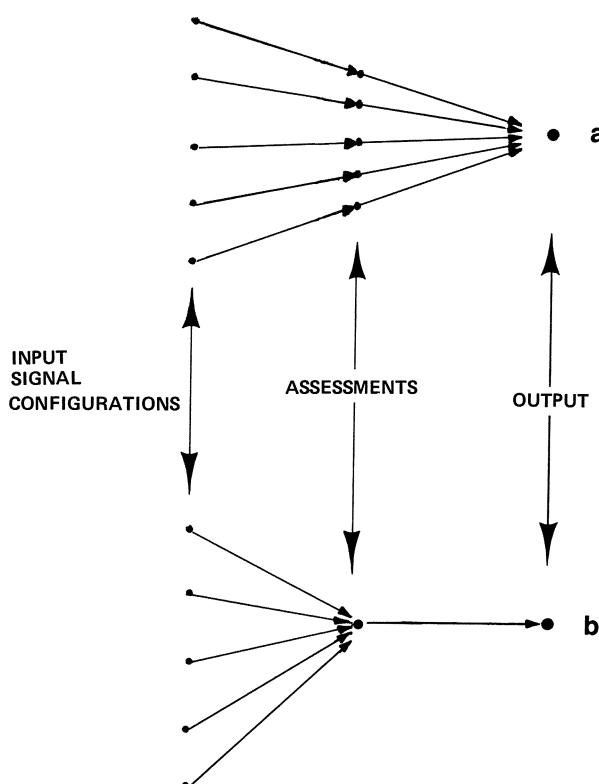


Fig. 2. Alternate routes for an array of input stimuli to yield specification of the identical output response. (a) Inputs are transformed into different assessments, each specifying the same output. (b) Each input is transformed into the same assessment, which specifies a single output.

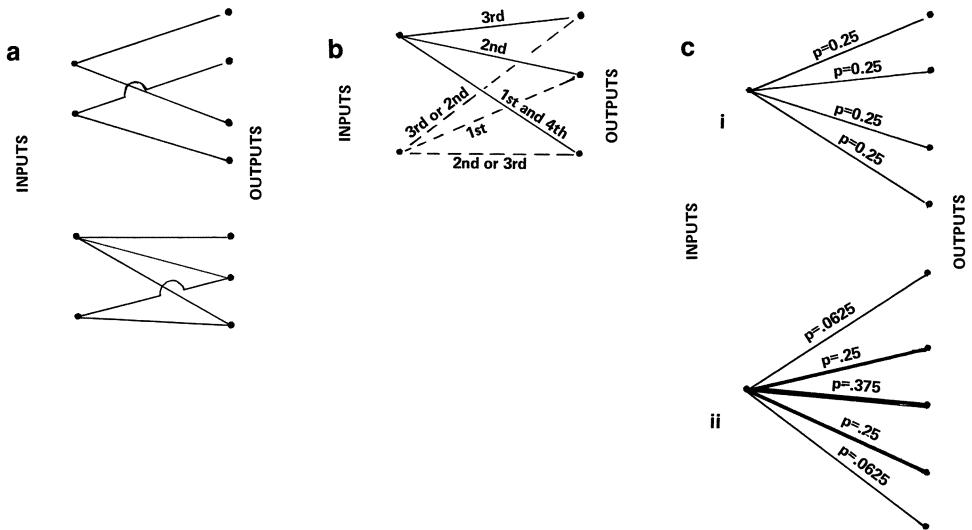


Fig. 3. Schematic diagram of transformation rules that are unspecific; that is, each input is linked to more than one kind of output. (a) More than one output is determined in parallel or simultaneous fashion. (b) Each input specifies an output that is not selected again until all other alternate outputs for that input have been specified. The sequence may be fixed or indeterminate. (c) Each input specifies an output with a fixed probability, but each such selection is independent of prior selections, so that (i) with equal probabilities of each output occurring, the transformations will be uniformly random, or (ii) with unequal probabilities, only the distribution of outputs can be predicted.

female bird of a typical precopulatory crouch would imply, if this posture is never otherwise elicited, that her assessment of the situation includes appropriateness for mating. Many sexual signals, however, appear in both mating and agonistic contexts. For these signals, which are not uniquely determined, no single inference is warranted. Examining additional signal components or knowing the broad context of signal production might provide further opportunities to refine our inferences (Figure 4).

UNIQUENESS AND SPECIFICITY

If each input is linked to exactly one output, and vice versa, the mapping is both specific and unique. Knowing the state of either input or output implies that we can infer the other. It must be remembered, however, that specificity and uniqueness are independent attributes of linkage relationships. Mapping functions may be fully asymmetrical relationships or only partly symmetrical.

Lack of symmetry presents an important practical problem when one attempts to examine the "assessment" of inputs by measuring responses. There is no *a priori* reason to expect exactly parallel mapping functions to link a single set of assessments to each of the separate possible output systems (Figure 5). The range of assessments that specify one output item might be much broader than those specifying another. If the outputs are used to gauge the richness of the assessments, it is easy to be misled by looking only at a single output system.

There are often arguments about whether animal signals and communication systems lack such attributes as digital coding, discreteness, arbitrariness, and openness. These terms are useful shorthand designations of extreme or limiting forms of transformation rules and the sets of signals or referent data on which they operate. Considering them as particular kinds of mapping functions provides a convenient, comparative framework for discussing human language and other animal communication systems.

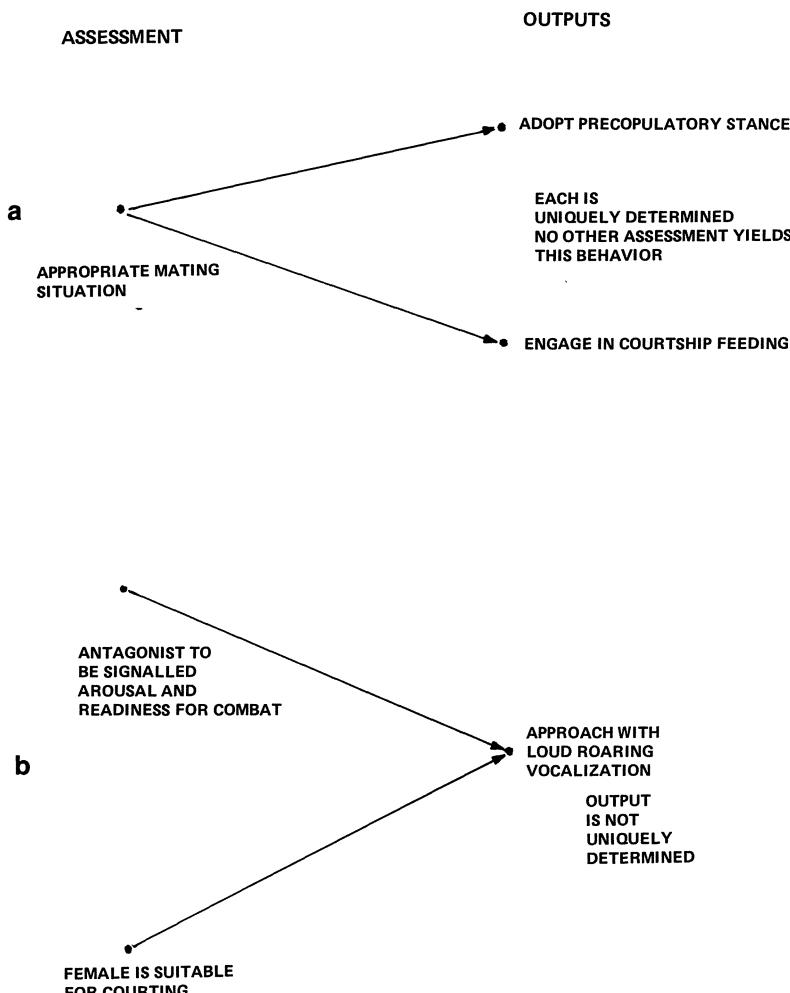


Fig. 4. (a) Precopulatory posturing and courtship feeding might each be uniquely determined by a bird's assessment that the situation is appropriate for mating. (b) A loud roaring vocalization by a male Japanese macaque is not uniquely determined; it may occur as part of a threat or during an agonistic chase or as part of a courtship sequence when approaching a female. An observer's inference after hearing the sound as to the male's assessment of the situation would be narrowed by knowledge of the context.

In signalers, we will take the input set as being the information available to the signaler and the output set as being the repertoire of possible signals. Thus, at the level of this discussion, two transformations are involved: input to assessment, and assessment to signal. For receivers, we will consider the next links in the chain of communication system transformations and reexamine signal transmission (the transformation from produced to received signal) and signal perception (reception through processing). For these receiver-oriented cases, the input set then consists of signals received, and the output set is an array of receiver's perceptions on which responses are based.

STEREOTYPY AND VARIABILITY

Lorenz (1935, reprinted 1970) originally focused attention on the existence of discrete, recurring, species-specific patterns of behavior in animals, epitomized in

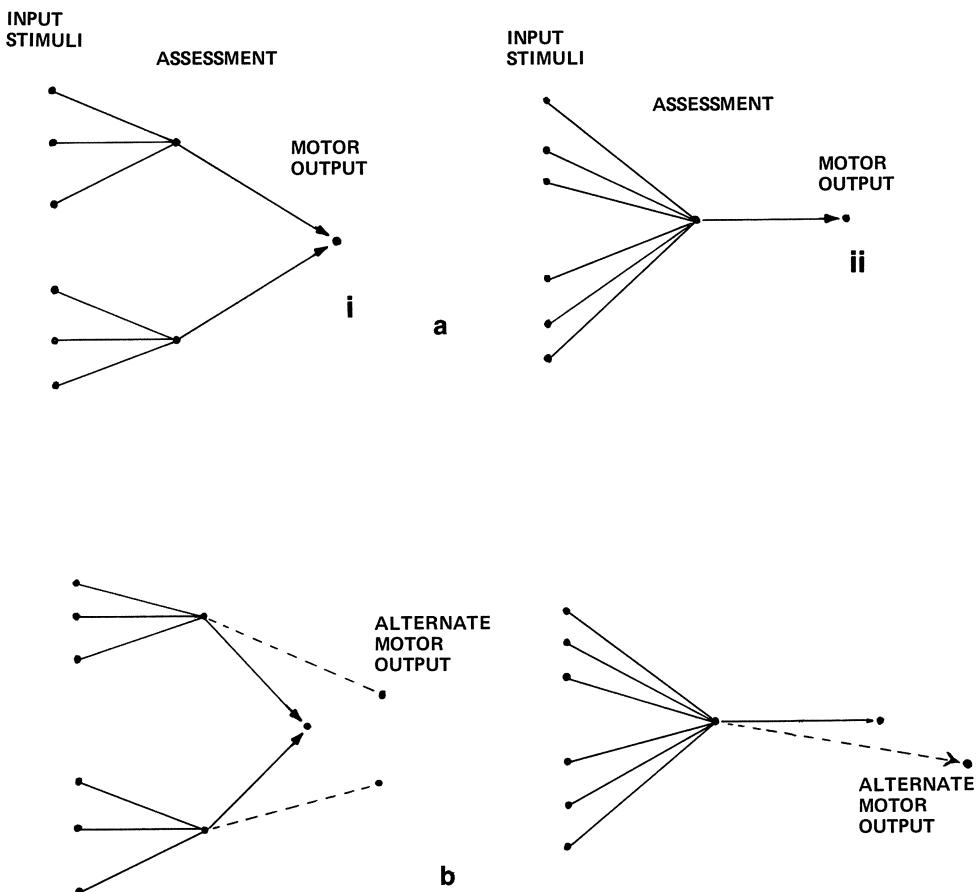


Fig. 5. (a) Alternate ways in which stimuli yielding the same or different assessments can be linked to a single motor output. Examination of the output does not allow one to distinguish whether the stimuli are perceived as the same or different: (i) stimuli are perceived to be of two kinds, but the same response occurs if (ii) they are perceived to be of the same kind. (b) The same stimuli may be shown to be perceived as different if a different response is measured as the output. Heart rate is frequently used, as it is often more sensitive than other measures.

his concept of the "fixed action pattern." Recently, ethologists have become concerned anew with the significance of signal variability. Substitution of the term *modal action pattern* is a significant step forward (Barlow, 1968, 1977), but there is still confusion about how to handle the problem of variation in the context of animal communication.

Stereotypy and *variability* are terms implying judgments about the degree of variation of behavior. In most ethograms, such judgments are usually made without explicit indication of their basis, but there is usually some implicit assumption of a criterion of acceptable physical variation. No signal is absolutely stereotyped, with no discernible variation. Given a small enough unit as a criterion for stereotypy, all nonsingular samples of any signal could be judged as variable, that is, with variation exceeding the criterion. When *stereotypy* is invoked as a descriptor, it usually implies that an animal produces the same signal in a recognizably similar or identical pattern, upon successive occasions. Another use is at the population or species level, namely, that all individuals produce the signal in a basically similar fashion.

We propose here that a logical and quantitative basis for determining which among a repertoire of patterns are the "same" signals (i.e., those appropriate for measuring within-signal variation) is to be found in the transformation rules operating in sending animals. We also suggest that selection of the most appropriate criteria for judging stereotypy is best accomplished by reference to the transformation rules operating in receiving animals. These are the two sides of the coin usually tendered under the rubric "natural units of behavior" (cf. Altmann, 1962).

CATEGORIES OF SIGNALER OUTPUT

Consider a signal repertoire comprising three readily characterized patterns, say, click trains of one, two, and three identical click elements. Two divergent approaches are available to describe signal variation in this repertoire. The first is to ignore all information not inherent in the signal itself. In this case, we derive appropriate descriptive statistics from counting the kinds of signal patterns produced. The statistical parameters estimated from our sampling can be used to compare degree of variation with another sampling of a different individual or population.

The second approach takes account of other kinds of information that permit inferences about the use of this repertoire. Each of the three elements might appear to be predominantly associated with a different intensity of threat. We can gauge the probability of agonistic behavior by observing events other than the kind of click signal given. Then, rather than measuring every signal in a sample, we could elect to measure variation only in signals putatively associated with one level of intensity. If, for example, single clicks predominate at the lowest intensity and triple clicks at the highest, these subsets will yield different estimates of variation than those based on all observed signals.

According to this procedure, we examine the social data available as input to the signaling animal, infer its assessments, and sample the signals according to the

kind of assessment with which they seem to be associated. The measures of variation, although performed exclusively on the physical attributes of observed signals, reflect judgments about the mapping functions linking signals and assessments (see Figure 6).

Signals vary along many dimensions. One of the principal difficulties is to decide which parameters to ignore. The example of the click-train repertoire was phrased as if only the number of click elements was important in describing variation. Clicks may vary, however, in amplitude, rise time, frequency spectrum, beaming, phase relations, click duration, repetition rate, interclick interval, temporal modulation, and so on. Every signal can vary along the dimensions that physically describe it. Variation in some, however, may fail to be perceived. Thus,

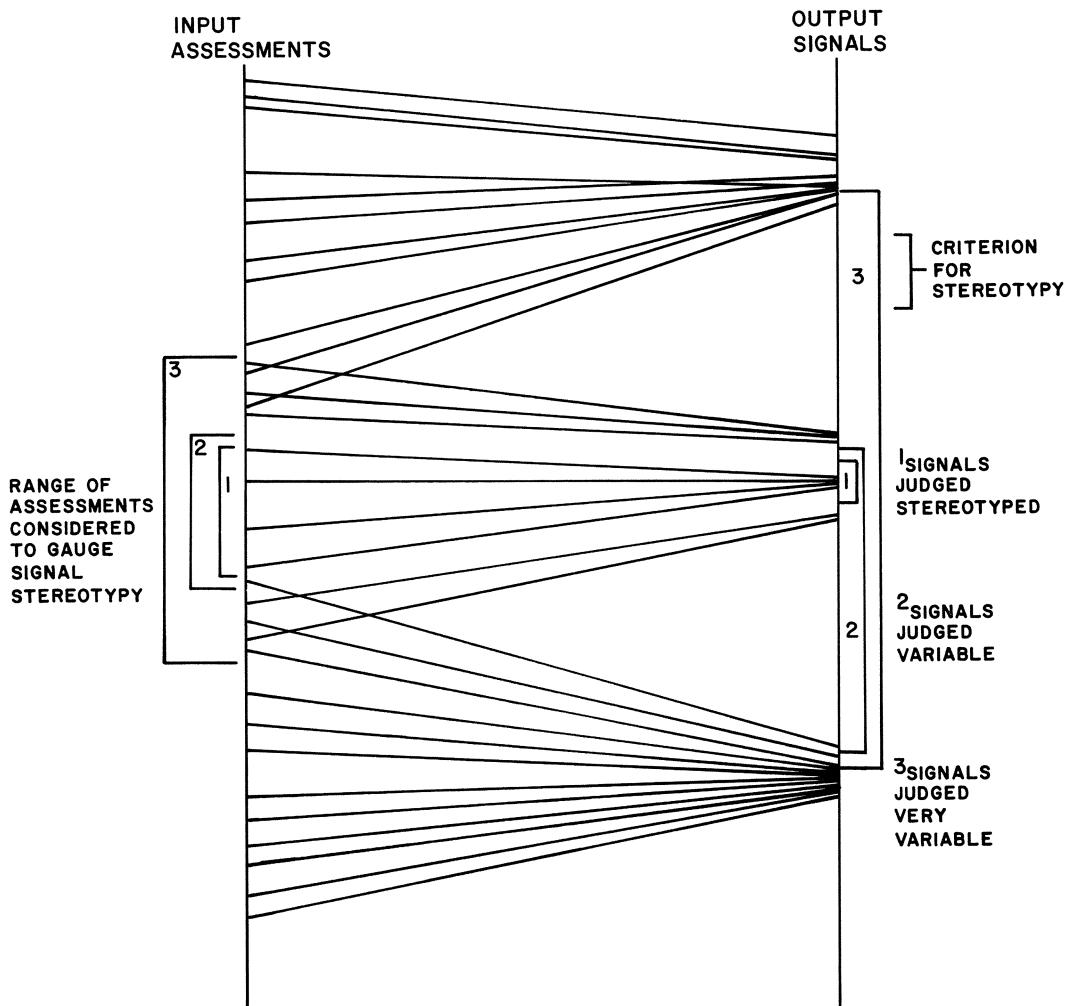


Fig. 6. A diagrammatic scheme of the way in which judgments of variation are dependent upon the breadth of the range of assessments transformed into signals. The signals linked to the smallest of the three ranges of input assessments, those within the #1 brackets, vary less than the indicated criterion for stereotypy. The variation of those linked to the assessments within the other two brackets exceed it.

not every bit of the signal-pattern information theoretically available is necessarily assessed or utilized by a receiver.

To decide whether physical variability is potentially meaningful to others, we must select a criterion and employ it systematically. The choice of subjects must be specified. The sample of signals for measurement may be obtained by repeating observations on one individual in the same circumstances, or it may be gathered in a naturally varied range of circumstances. The choice depends on the nature of the signal variation we seek to quantify. If we are examining population variability, the sample will be obtained from different individuals, either in the natural range of signaling circumstances or in some subset.

If any member of a sample set of signals differs by more than our criterion from some normative value, such as an arithmetic mean, we may say these signals are not stereotyped. We could equally well require a probabilistic rather than a threshold judgment of stereotypy, such as that no more than a certain fraction differ from the normative value by our criterion. If our measurements of the variable are taken along one dimension, the criterion will be a simple unidimensional constant. Analogous arguments apply for multidimensional signal variation. The major question is which criterion to use. Although any arbitrary value could be chosen for systematic comparisons, the particular selection predetermines whether signals are judged to be stereotyped or not. Procedures for sampling signals and for establishing criteria clearly determine whether our studies of stereotypy are biologically interesting or merely exercises in quantitative description.

Suppose that with our repertoire of three kinds of clicks, we try to characterize stereotypy looking at only the number of clicks. If we select one click as a threshold criterion for range of allowable variation, then any sample containing all three kinds of signals will clearly be considered variable; only samples that represent a single kind or just two kinds, including the double click, will be judged as stereotyped. With a criterion that variation should not exceed the mean or median number of clicks plus or minus one, then equal numbers of each kind of pattern will suggest a stereotyped repertoire. A different judgment of stereotypy could result if the same criterion is applied to a different sample taken from the same repertoire, one in which the single- and triple-click signals are not found in exactly equal numbers. Just as important as the magnitude of the criterion is how it is used and selection of the sample to which it is applied.

Another important consideration is the external-stimulus situation. By experimentally manipulating sensory input, we could probably find a narrow range of stimulation over which only one signal type would be elicited. The output would thus be deemed stereotyped. It might also be possible for a stimulus range of the same magnitude to cross a boundary between inputs linked to two different assessments, and to different signal types. We would then characterize the signals as variable (Figure 7). It is thus quite possible that the same restricted repertoire, produced from the same system and using the same criteria, would be characterized as stereotyped in some cases and variable in others.

In nonexperimental situations, such as is commonplace in field studies of communication, study of the combination of signals emitted in a given behavioral

situation and of the surrounding context can facilitate the formation of hypotheses about which input data are processed to achieve the same assessment. These can be tested by formal analysis, just as they are by the much-vaunted "intuition" of ethologists. The latter, although rarely explicitly recognized, is usually an internalized procedure for testing different ways of associating members of the signal set with external referents or presumptive internal states. Whether tested formally or intuitively, the basic procedure is the same. Variation of signals associated with one assemblage of input data is compared with variation under other schemes for classifying the signaler's input data and its inferred assessments. By a trial-and-error process, the assemblage that corresponds to the set of signals showing least variation is presented as the best estimate of the situation yielding that set of signals (Green, 1975a).

This method employs hidden assumptions about the relative importance of both signal variables and input variables. For senses that we ourselves possess, and for vertebrates, with which we have some empathy founded on familiarity and a

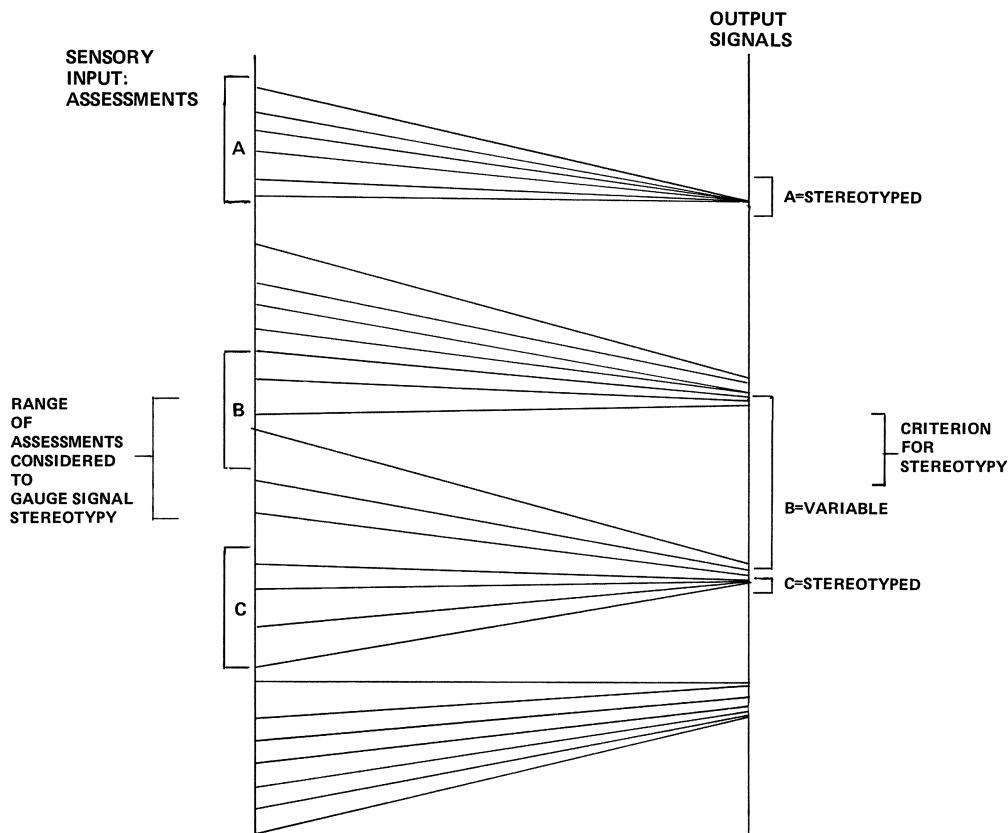


Fig. 7. A diagrammatic scheme of the way in which judgments of variation are dependent upon the nature of input assessments (represented by location) transformed into signals. Each of the three regions of input assessments covers a range of the same magnitude, but they are linked to signals with differing variation. Although the signals linked to ranges A and C would be judged stereotyped, those linked to B would be judged variable. The input range at location B includes a boundary between inputs mapped onto two different signal clusters.

shared evolutionary history, we rarely attack the issues of signal classification and stimulus-parameter salience from first principles. Instead, we usually rely, often quite appropriately, on a reasonable guess. Variation is measured on what we infer, using our own sense organs, to be the biologically relevant signal properties. Thus, for vertebrate vocalizations, we generally measure temporal changes of frequency and amplitude but ignore phase, unless we are concerned with localization problems. In the final analysis, only experimental manipulation can establish unequivocally which parts of a signal are relevant and therefore suitable for measurements of biologically meaningful variability, although this becomes glaringly obvious only when dealing with signals that activate sensory apparatus of other taxa quite different from our own (cf. Griffin, 1978). Lacking the ultrasonic sensitivity of bats or rodents, we are liable to lump all of their sounds as "squeaks," if we hear them at all.

RECEIVING ANIMALS: INPUT

Signal stereotypy implies not so much a lack of variation as a judgment of "sameness." If we assess the receiving animal's ability to distinguish one signal from another, the JND (just noticeable difference) so derived is one useful starting point for establishing criteria for stereotypy. Clearly, if the "sameness" criterion is set at much less than a JND, we will be labeling signals as variable that the recipients perceive as identical. Conversely, if it is set at more than one JND, then it is possible that two signals judged to be the same (i.e., stereotyped) could actually produce two different assessments by a recipient. A criterion roughly equal to the JND for a given dimension is a good starting point.

Most signals are complex patterns that vary simultaneously along several dimensions. Although sensory JNDs may be useful for examining biologically relevant similarities and differences among signal patterns that vary along a single dimension, we lack sufficient psychophysical expertise to combine them with confidence when considering more complex signals. Perceptual tests are required to inform us about the presence and magnitude of interactions that affect minimal discriminable differences between complex signals not readily predicted from separate JNDs. The interactions between hue, saturation, and intensity in color-vision tests are examples of such complex effects. If we are to use the responders' assessments of input data as guidelines for constructing signal measurement and classification schemes appropriate to each species and sensory modality, more such perceptual tests are essential.

Use of any criterion level for judgments of stereotypy must take full account of what is known about sensory psychophysics. Detectable differences might be of dissimilar perceptual magnitudes in different zones of the overall range of variation. A familiar example is the operation of the Weber-Fechner law, which describes ratio relationships for difference limens; we thus describe JNDs in logarithmic terms, as with decibels for acoustic intensity. In general, there is no *a priori* reason to expect JNDs to be uniform. The size of regions in which test pairs of stimuli are all labeled similarly by a receiver may vary, depending upon their absolute location on a stimulus continuum.

Given multidimensional signal variation, the interaction of JNDs on different

dimensions could yield perceptual categories of markedly different sizes. Small variations in one variable could lead to a judgment of difference between two test stimuli at one setting of the other parameters, while being judged similar at other settings (Gautier and Gautier-Hion, 1977; Beecher, Petersen, Zoloth, Moody, and Stebbins, in press; Zoloth and Green, in press).

It follows that judgments of variability or stereotypy are not generally made with sufficient information in hand to be taken at face value. As they appear in the literature, many such judgments are nevertheless informative because they are given in a comparative framework. When one species is judged as producing *more* or *less* stereotyped signals than another, this implies application of the same criterion to both species. Even though the criterion may not have been explicitly given, or perhaps even determined, such comparisons are valuable when considering the adaptiveness of signal morphology and evolutionary trends in signal usage.

DIGITAL VERSUS ANALOG CODING IN SIGNALS

These terms apply to signal structures with only two stereotyped signals or states possible (*digital*) and to those in which continuous variation is possible along a given dimension (*analog*). The terms are often confused with *arbitrary* and *iconic*, which apply to mapping functions and not to signal patterns themselves (see below). Analog signals can reflect assessments along a range of continuous judgments, for example, more-less. Digital signals are capable of reflecting two classes of input assessments, for example, yes-no. If a recipient perceives the two elements of a digital signaling system as different, the signals can form the basis for digital coding. A special case of digital signaling is presence versus absence of a single stereotyped element.

If the set of signal patterns in a repertoire, or the range of signal variants of a given type, is such that a receiver can detect an intermediate form between any two of them, then these signals form an analog array. They can thus form the basis for analogic coding.

Clearly, it is possible to have a repertoire in which some signal types are digital and others analog. Similarly, it is possible to have a repertoire in which some signals are stereotyped, each physically discontinuous from all others, and others are variable, with neighbors abutting or overlapping so as to form an analog continuum.

The recipients of such signals may assess them either by digital or by analog means, regardless of the digital or analogic nature of the signals themselves. Analogic signals may be assessed as present or absent regardless of which variant is received. In the case of a visual signal, for example, there is an intergraded set of variable threatening facial expressions common to many anthropoids (van Hoof, 1962, 1967). Regardless of which variant a dominant male gives, a youthful subordinate perceiving it is likely to respond by fleeing. An older respondent, more nearly a social equal, may, however, adjust its response to the "more intense" or "less intense" information coded analogically, rather than acting purely on the digital presence or absence of threat.

We can view every signal as conveying digital information in terms of its presence or absence. Thus, there is always some hierarchical duality of signal structure. Similarly, digital signals may be assessed by summing them over time, so that an analogic rate is derived from digital occurrences. These two kinds of mapping functions from signal input to assessment may even operate on the same signal (e.g., Konishi, 1963; Wilson and Bossert, 1963; Ramsay, 1969).

The signal and response ends of communication systems can then be described as employing digital and analog processes simultaneously at different levels. We may conclude that although digital and analog modes are clear logical alternatives, the terms by themselves are of limited usefulness without specifying which properties of the signal are being considered and which aspects of a respondent's mapping of the signal onto its assessment are under discussion.

ARBITRARINESS VERSUS ICONICITY

Signals are said to be arbitrary if the mapping function generating them cannot be described by a generalized transformation rule. In this case, each member of the signal set is linked to input information by specific assignments that can be characterized only by listing them separately. The spoken names of primary colors are arbitrary signals in this sense, each linked to a somewhat different sensory input range in different languages and cultures (Rosch-Heider, 1971, 1972).

Signals are said to be iconic if variations in the physical configuration of the referent are transformed into parallel variations along dimensions of the signal. Ordering relationships are preserved by iconic mapping functions, a change in the referent being mirrored by a corresponding change in some signal variable. For the signal to be completely iconic, all perceived properties of the referent need to be reflected in the signal; the signal would be in some literal sense an image. The hand signals of American Sign Language are rich in iconic imagery (Stokoe, 1975; Bellugi and Klima, 1976), and onomatopoeic sounds recur in our speech. A predator alarm signal in which duration or amplitude increases with the increased size of the predator could be said to represent predator size iconically.

Although a similar ordered relationship can occur between a signaler sensing the presence of a predator and its assessment of the degree of danger present, the resulting signals are not necessarily iconic if this danger assessment is transformed into alarm-signal variation. *Iconicity* refers directly to physical attributes and thus to external referents, not to internal assessments, even though the transformation process might be analogous.

The relationship between the perceived predator and the signal form that it elicits may be noniconic and yet by no means arbitrary. Although an arbitrary relationship between signal morphology and referent cannot, by definition, be an iconic one, and although an iconic one is never arbitrary, many regular relationships between signals and physical properties of their referents are neither iconic nor arbitrary.

A low-intensity call might be given with a certain predator seen at a great distance and become louder or longer at shorter distances. Such a series would not

usually be considered to iconically reflect distance, as ordering relationships are not preserved but reversed. They perhaps reflect the retinal image size and the visual perception of the predator by the signaler, but the signals then follow rules similar to iconic mapping of the assessment, not a measurable attribute of the referent. The referent has not changed its physical dimensions in the same way as the signal. Such a signal would usually be deemed analogic but not iconic. Note, however, that some situations can be difficult to classify. If there were an increase in signal repetition rate as the predator came closer, the time between signals *would* be iconically diminishing with decreased distance, but the average signal intensity over time would not. We therefore suggest that iconic be applied to situations where either positive or negative ordering relationships exist.

Perhaps the most celebrated of all animal communication systems, the dance language of honeybees, illustrates iconicity in the relationship between the direction of a resource in relation to the sun's observed or inferred position and the orientation of the waggle run. This is direct on a horizontal surface and angled to gravity when translated to a vertical surface (von Frisch, 1923, 1967; Lindauer, 1961; Gould, 1976). Other waggle-dance features bear an iconic relationship to resource distance. These include tempo, rates and numbers of waggles, and the duration of the bursts of sound produced in the waggle dance (Esch, 1961; Wenner, 1962), though it is still not certain which convey distance to other workers.

Dance meaning is further enriched both by olfactory and other cues brought back from the resource and by the context provided by the audience. The general excitedness of the dance corresponds with the relative "quality" of the food. However, "quality" relates in turn to current needs of the hive, conveyed to the dancer by how long it takes to share the incoming load with other bees. If this takes more than about a minute, dancing will rarely occur:

For example, water—which is used to air-condition the hive—is normally not well received by the colony. If the day gets hot, however, foragers returning with very sweet nectar will no longer be able to distribute their loads quickly. Bees gathering dilute nectar or water, on the other hand, will be relieved of their loads very rapidly. The nectar foragers will stop dancing while the water collectors will begin to dance vigorously. (Gould, 1976, pp. 215–216)

Only analog signals such as sound-pulse number or waggle-run duration in the dance language can be used for iconic representations of physical attributes that are themselves continuous, such as food distance (Gould, 1975). However, it is also logically possible for analogic signals to be linked in some *arbitrary* fashion to a continuum of intergraded referent data or assessments, although the likelihood of communication errors in such a system would restrict its evolution to very special situations (cf. Altmann, 1967).

Digital signals can also be used iconically, but only to represent physical attributes with just two states. Signaling systems that are neither analog nor digital can have some attributes of both. Repertoires may be formed, for example, of an array of discretely distinctive stereotyped patterns drawn from a continuum but without intermediates. If the range of variation within each pattern is much less than the distance between them, such signals are often called discrete. Signals of

this kind could be used as iconic representations of attributes that are similarly discrete, as if stepped levels of signal intensity represented the number of predators in an attacking group. They are also available as the output set from arbitrary transformations of either continuous or discontinuous assessments, or from a nonarbitrary mapping function that, although noniconic, is very regular, such as stepped intensities of signal representing degrees of threat. Such discrete signals cannot be used for iconic representation of any physically continuous attribute, such as predator size (Figure 8).

CATEGORICAL AND CONTINUOUS PERCEPTION

It is an obvious but often neglected point that what an animal makes of a signal it receives cannot be determined by analyzing the signal. The information transfer from sense organ to assessment is governed by rules that we are unable to discern no matter how closely we examine signal morphology. This point is exemplified by tests performed on humans listening to sounds of speech. Presented with neighboring pairs of stimuli from an array of speech sounds spaced equidistantly along a single acoustic dimension, listeners assign only one label to both members of some pairs, yet classify others as representing two different stimulus categories (Liberman, Cooper, Shankweiler, and Studdert-Kennedy, 1967). The dimensions tested include such features as voice-onset-time and formant slope. If we examine other aspects of performance during the listening task, however, it is apparent that information on within-category discrimination is available, although this is not evident if listeners employ the usual labeling procedure (Cooper, Delattre, Liberman, Borst, and Gerstman, 1952; Pisoni and Tash, 1974) (Figures 9 and 10).

As viewed spectrographically through time, normal speech is a continuously changing pattern of frequency and amplitude modulations. To the listener,

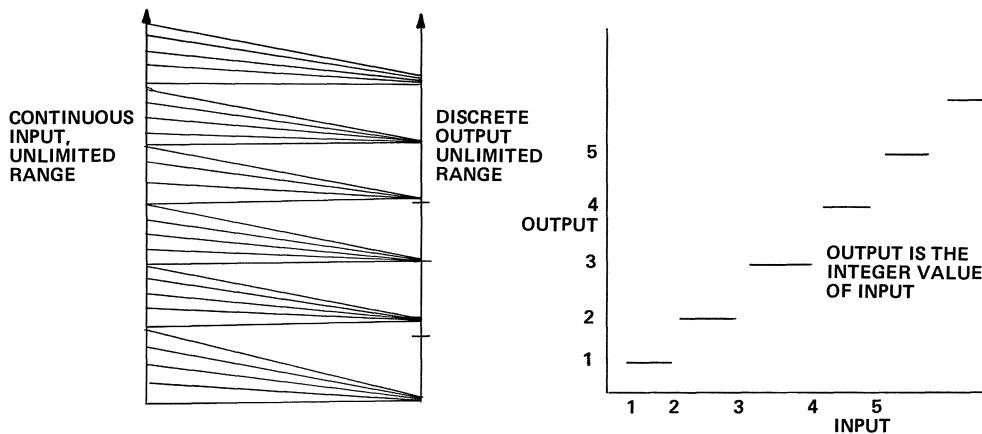


Fig. 8. To the left is a schematic diagram of a mapping function which transforms the continuous input at the left margin into the discrete outputs on the right. The graph on the right side illustrates the kind of orderly and non-arbitrary transformation rule which can generate such a regular and systematic, but non-iconic, mapping.

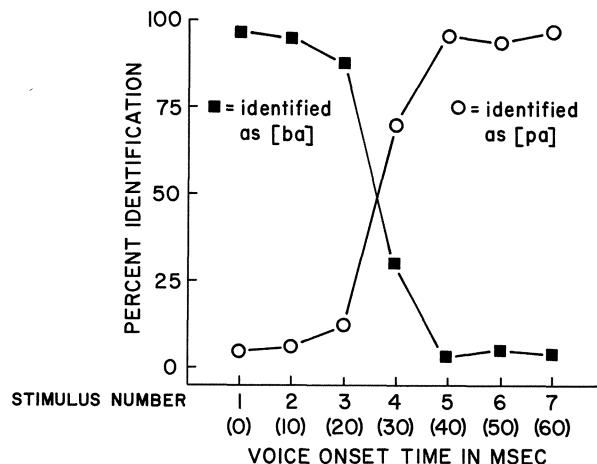


Fig. 9. Average identification scores of nine subjects listening to seven steps in a synthetic speech, voice-onset-time continuum (cf. Pisoni and Tash, 1974). There is a consistent partitioning of the stimulus continuum into the two categories [ba] and [pa]. Stimuli in which laryngeal voicing starts early in the sound are heard as the voiced consonant *b*. Sounds with a later voicing onset are heard as the unvoiced consonant *p*.

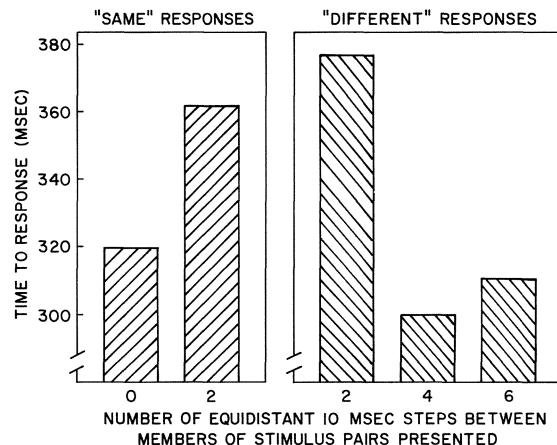


Fig. 10. Mean time for nine subjects listening to paired stimuli and judging them as "same" or "different" to respond correctly. The number of 10 msec steps between members of a pair is the difference between their assigned stimulus numbers, each (as listed below) representing a stimulus with a specific timing of voice onset as given in Figure 9. Within category (= same) pairs with zero difference are 1–1 (stimulus number one paired with itself) and 3–3 for [ba], 5–5 and 7–7 for [pa]; those with a two-step difference are 1–3 [ba], and 5–7 [pa]. Across category (= different) pairs are 3–5 (two-step [ba]–[pa]), 2–6 (four-step [ba]–[pa]), and 1–7 (six-step [ba]–[pa]). Note the across-category responses to stimuli near the category boundary (located between 3 and 5 in Figure 9) are slower than to those pairs whose members have a greater degree of acoustic disparity in the timing of voice onset. The within-category responses to the acoustically two-step different stimuli are slower than to pairs with identical members although in both cases the stimuli are each given the same phonetic label [ba] or [pa] by subjects. Thus, differences in processing are revealed which would be obscured if only the question of same or different identification or of phonetic labeling were addressed. (See Pisoni and Tash (1974) for a full account.)

however, it appears to be a stream of closely spaced discrete elements (Liberman *et al.*, 1967). The mapping function of speech perception is then of the kind shown in Figure 11, a set of discrete labels, or assessments, each linked to a small portion of the total range of intergraded signal morphologies. In the speech literature, this kind of transformation is called categorical processing of a continuous signal.

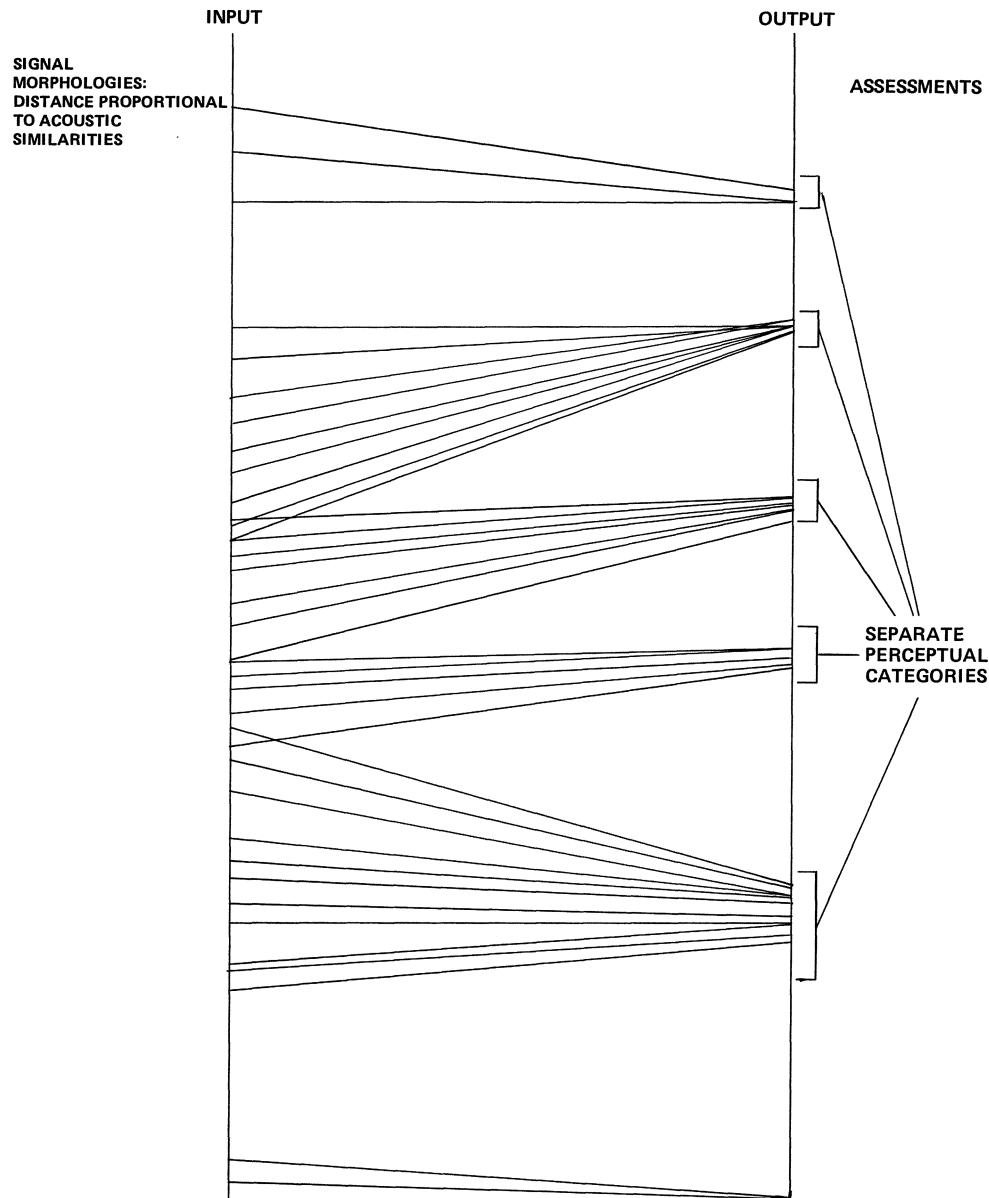


Fig. 11. Diagram of a mapping function describing categorical assessment of signals with continuous variation as revealed by listening tests using speech signals. Samples taken from acoustically continuous speech variation are labeled as belonging to separate perceptual phonetic categories. Variants within some ranges are all labeled similarly. Variants which differ by lesser amounts, however, may be labeled as belonging to two different categories. There are small boundary zones where variants are sometimes identified as belonging to one category and at other times another. Listeners do not identify sounds from these zones as belonging to an intermediate category.

We are as yet unable to define which of the physical attributes of the vocal signal are involved in most kinds of assessments made in speech processing. The labeling process leads us to infer that the processing normalizes for differences in the speaker's age, sex, systematic distortion (e.g., regional accent), and idiosyncrasies, all of which change the values of the parameters describing spoken phonemes. It appears that our only reliable method for establishing the salient units of speech is to employ human listeners, a situation with important implications for students of animal vocal signals (Marler, 1976c, 1977a; Green, 1977; Beecher *et al.*, in press; Zoloth and Green, in press).

The phenomena of categorical perception and the attendant normalization for cues that are irrelevant to phonemic identity dramatize the difficulty of deriving biologically relevant signal classifications. In some important intuitive sense, a variable sampling of the same spoken phoneme from a single speaker or a selection of different speakers contains signals more similar to each other than they are to other phonemes. To establish an analytic procedure yielding this same result, we would first have to determine the important dimensions used in speech-pattern recognition and then establish the appropriate criterion for stereotypy for different parts of the range of natural variation. This is somewhat of a paradox, since categorical perception implies that any criterion may be vanishingly small across boundaries between perceived categories, although the signals are clearly physically continuous. In fact, the differences between phonemes can be *less* than the variation within a sample of the same phoneme. Not only do extreme signal forms that abut a boundary differ little, but even central or median patterns of different kinds can differ less than the difference across the range of one of them. This perceptual phenomenon of auditory categorization is probably more general than is acknowledged (Cutting and Rosner, 1974; Kuhl and Miller, 1975; Pastore, 1976) and is likely to play an increasingly important role in analyzing animal communicative systems, especially as ethologists become more familiar with speech research.

The human propensity to perceive sounds categorically probably inclines us to label animal signal repertoires as stereotyped or discrete even when a physical analysis does not fully support this judgment (contrast Winter, Ploog, and Latta, 1966, with Schott, 1975). This may be a more serious problem in forming differences of opinion on vocal repertoire size and degrees of vocal variability than the lack of uniform criteria or the undersampling of repertoires. Similar processes occur in sensory modalities other than audition. Here, too, repertoire characterizations that rely on human pattern-recognition may be informing us more about the number of categories that we can comfortably erect than about the signals themselves (e.g., Miller, 1956; Moynihan, 1966, 1970; Bertrand, 1969; Wilson, 1972; Eisenberg, 1974, 1976).

Of course, continuously variable signals are not necessarily perceived categorically and may also be assessed in a continuous fashion. It appears that the crest display of Stellar's jay, for example, yields a continuously variable assessment of the agonistic intent of the signaler (Brown, 1964, and Figure 12), as does the extension of median fins in fish (Rasa, 1969). Furthermore, continuous and categorical perception of the same continuum may occur together, but at different

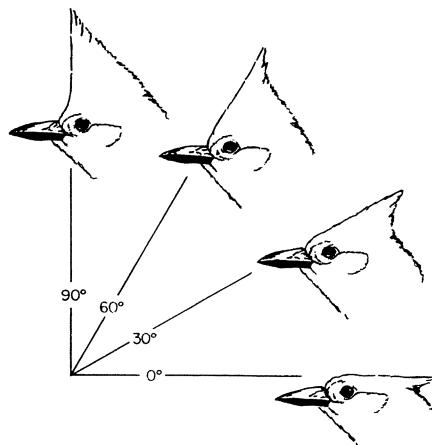


Fig. 12. Continuous gradation in the degree of crest elevation in Steller's jay in various behavioral contexts. After Brown (1964).

levels, just as there may be concurrent digital and analog processing. The best example, again, comes from human speech. While the linguistic content may be assessed by categorizing the speech signals into phonetic elements, intonation patterns can yield continuous assessments of mood.

Lastly, discontinuous or discrete signals may be perceived in a continuous or noncategorical fashion (Figure 13). Although rarely considered explicitly, the mapping function describing this kind of transformation may play an important role in many communication systems, as discussed next.

DISCRETE AND GRADED COMMUNICATION SYSTEMS

Consider an organism that produces signals in conjunction with a number of different assessments, each derived from differing combinations of current and previously internalized data. If we picture an animal using a regular, nonarbitrary mapping function, its signals will bear some readily specifiable relationships to the assessments. In this simple, hypothetical situation, assessments that are similar will be linked to similar signals. Those with distinctly different assessments will be linked to signals with very different parameters. The repertoire would then consist of some signals closely spaced along a dimension of physical similarity and others that are distant from their neighbors, the degree of separation reflecting relationships among their underlying assessments. There would be a complementary set of signal-assessment relationships in a receiving animal. By engaging the converse receptive mapping function, similar signals would yield neighboring assessments, while perceptions of distinctly different signals would yield very different assessments (assuming that the other inputs into the assessment, such as context and prior experience, remain constant).

Signal patterns necessarily change somewhat during transmission. If the effects of noise and degradation are equivalent for all elements of a signal repertoire, we can predict that certain relationships will be preserved. For a signal that is originally different enough from neighboring signals, transmission degradation will result in a received signal that still matches its own original form more

closely than any other. With lesser differences, two signals may be indistinguishable after transmission.

Given such a simple, generalized communication system, any input assessment by the signaler will produce a signal that elicits an assessment in the receiver within a defined range of probabilities. The size of the range and the sharpness of the probability peaks will be functions of such factors as the noise, error, and

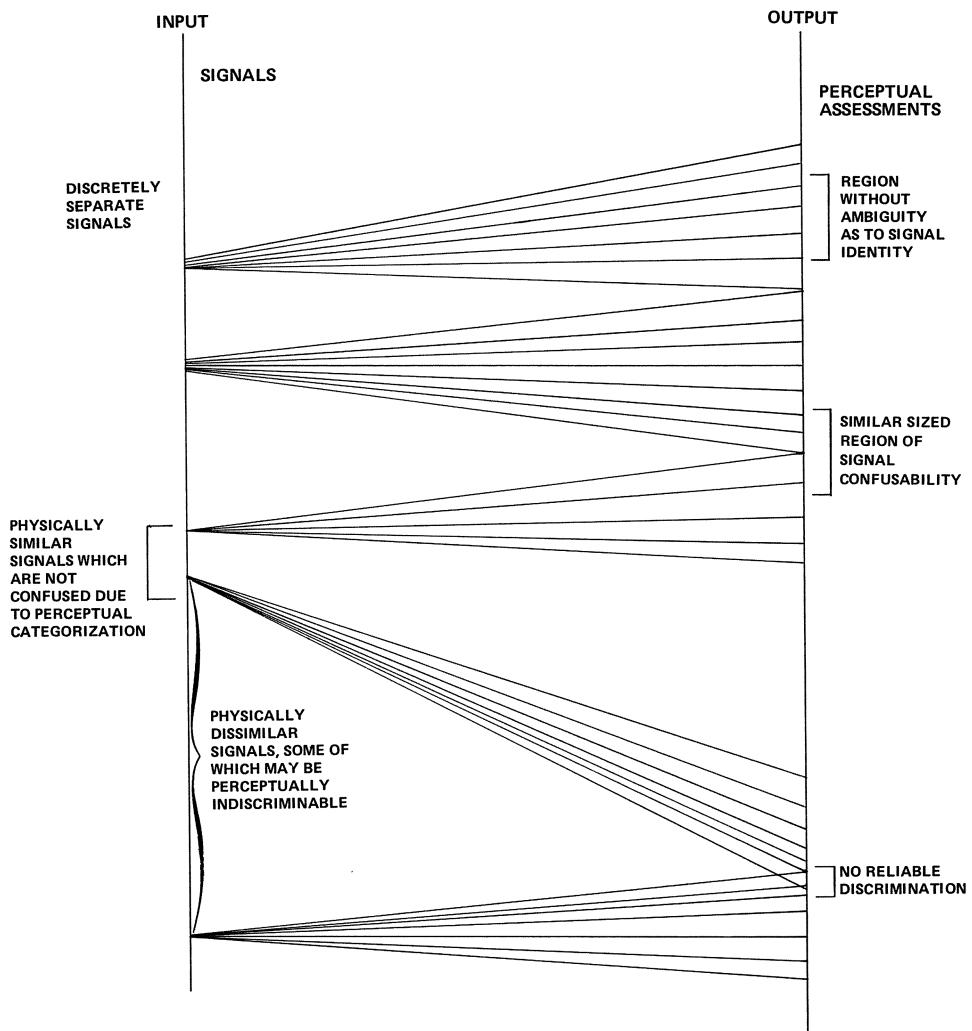


Fig. 13. Diagram of a mapping function by which discretely separate signals may not be perceived as such. The perceptual assessments represented by the upper bracket on the right all derive from one discrete set of signals. Those from the bracket below it can be generated from signals of two sets which are discretely separate. The signals embraced by the square bracket at the left generate widely different perceptions. Those more discontinuous embraced by the curved brackets generate a continuous range of similar perceptions including a range of overlapping perceptual assessments. Signal discontinuity of greater or lesser degree may or may not be transformed into continuous, discontinuous, or overlapping perceptions, depending upon the mapping function rather than exclusively upon the degree of signal similarity.

variability in sender and receiver processing; the continuous or categorical nature of signal perception in the receiver; the degrees of dissimilarity among closely spaced signals; and, particularly, for distinctively different signals, the effects of transmission.

If all the signal varieties in a repertoire that reflect different input assessments are so widely spaced that even after taking account of variation and allowing for the maximum signal degradation that occurs during normal transmission, differences between them larger than a JND are still preserved at the receiver, the result is a *discrete* communication system. Such a system is composed of stereotyped signals (regardless of the degree of physical variation), is digitally coded (each assessment is signaled in a yes-no fashion), and comprises signals that are perceived as distinct categories. With the categorical processing (i.e., there are very small JNDs at some boundary points between signals), discriminable signals can be relatively more similar to each other than with continuous processing. When transmission losses are negligible, as in operation over short distances, discriminability can be retained without increasing dissimilarity. Such a system permits completely arbitrary mapping functions to be used without diminished effectiveness or increased likelihood of error compared with nonarbitrary ones. It prohibits analogical communication, although with continuous processing of these discrete signals, some of the subtlety of analogic communication of ordered series can be preserved.

A *graded* communication system would be the opposite, one in which signals are both so closely similar to each other and also variable enough that a pair deriving from neighboring assessments will on occasion be judged to be identical. In this system, signals originally different by more than a JND may become indistinguishable after transmission. Analogic signaling would be possible and continuous perception likely. Although some of the advantages of discrete systems could be preserved by imposing categorical perception on the receiver, the disadvantages in terms of error would be enormous unless very regular nonarbitrary mapping functions for production and perception or some other error-reducing procedure were employed, such as a high degree of redundancy.

Probably only the very simplest organisms communicating in a single sensory modality can be characterized as having fully discrete or completely graded communication signals. Most animals are likely to employ a mixture of discrete and graded signal ranges within any sensory modality, although one can imagine a multimodal system that approximates a graded one by multiplexing signals of different modality, each of which operates discretely. No animal system is well enough known to determine whether the potential of such multimodal communication is realized.

The evolution of systems with discrete and graded properties has been treated by Moynihan (1964), Marler (1965, 1975), Gautier (1974, 1978; Gautier and Gautier-Hion, 1977), and others, although initially applied to signals and their transmission rather than entire systems. Briefly, they conclude that discretely organized primate vocal repertoires are favored when auditory signals must operate without complementation by other sensory modalities, as in signaling at night or in intergroup calling in the day over long distances in the forest.

Conversely, graded sound signals are more common in close-range signaling, often within-group, where rich supplementation by visual and tactile signals is the rule.

OPEN AND CLOSED SYSTEMS

If we define an open communication system as always having the potential for production of new signals, and a closed system as having a preordained signal set, the graded portion of any system is clearly open in the sense that intermediate signals can always be added to reflect intermediate assessments. With a shared regular, nonarbitrary mapping function and continuous perception, intermediate assessments by recipients would follow. Apart from transmission problems, the limits on such systems will derive from the receiver's capabilities for refined discriminations and from the signaler's capacity for fine control of signal output, so that intermediate signals are likely to reflect intermediate assessments rather than effects of noise or variation. Expansion can occur within these physiological limits until additional intermediates can no longer be reliably produced and accurately transmitted, received, and assessed. Such systems are not open, however, with respect to expansion of the range of input data to which signals are linked, since this is preordained by the original mapping function.

The discrete portion of any system is always open to expansion of the range of referents. This can be done by adding new discrete signals or by embroidering variations on existing signals. They can thus be transformed into a new graded portion of the repertoire, assuming that parallel changes in receiver processing and the other criteria are met.

Characterization as graded or discrete is least useful with systems in which signals and perceptions may differ, as, for example, if signals vary continuously and perceptions are categorical, and with a mapping function that is arbitrary or listlike. Such systems are always open in the sense that a lexicon is open: new signals can be assigned new links both for the emitter (to additional referent data configurations) and the receiver (yielding new labels or output assessments). Human language is our best-known case for this kind of openness, but the specification of new, arbitrary links may also occur in animal communication systems.

There are then two independent substrates on which evolution can act to provide for the openness of communication systems. On the one hand, there can be selection for the capacity to generate new arbitrary individual links. On the other hand, there can be selection of processing and producing systems that allow a precise refinement of signal variability and its perception. We usually think of the former as a capacity to learn and of the latter as refinement of neuromuscular and sensory skills, each known to occur to some degree in all animals.

While this is not the place to pursue an argument on the origins of social communication, we can suggest a few premises. First, *all* systems are open. The traditional distinction between open and closed systems is a matter of timetable, that is, whether new communicative usages occur within a single life span as opposed to more leisurely, evolutionary changes. If heritable augmentation of

signaling behavior occurs without the parallel or preexisting development of receiver capabilities, natural selection is unlikely to favor it. Thus, either perceptual capabilities develop earlier in phylogeny than the signaling behaviors that utilize them, or they emerge simultaneously. In the latter case, it is most likely that simultaneity would occur in progeny or siblings that have inherited part of the same parental genotype associated with the new signals. Regardless of which animal produces signals—parent, offspring, or sibling—corresponding perceptions and assessments are more likely to occur when common transformation rules govern both processes and are associated with the same genetic material, a point we return to in the next section.

In the case of new linkages, those that are relearned within each individual's development, social usage is likely to spread first among relatives, both because of kinship-related physical proximity in many animals and also as a result of their sharing whatever component of this learning capability that is heritable. To the extent that such new linkages enable greater individual success and inclusive reproductive fitness, the propensity for such learning will spread. Once the traits associated with such capabilities become widespread, the stage is set for the cultural transmission of these linkages, that is, of learned and shared agreement on the rules specifying signal usages, both in perception and in production. Perhaps bird and monkey vocal dialects are expressions of this process (Marler and Mundinger, 1971; Green, 1975b).

THE HEREDITY AND ONTOGENY OF COMMUNICATION

In the course of communication, signal senders and receivers can benefit most from the use of closely matched procedures. Errors will be reduced, and information loss will be kept to a minimum. Given the advantages of sharing basic procedures for signaling and reception, variations of lesser or greater effectiveness among individuals are subject to natural selection to the extent that the apparatus, rules, and procedures are heritable. The social organization of most animals requires that uniform rules extend far beyond a simple communicative dyad of mother and offspring or mated pair to include families, larger kin groupings, local clusters or aggregates, social networks, demes, all species members, and, to a degree, even broader phyletic units. A variety of means can be employed to ensure that the necessary degree of rule sharing is achieved.

Neither biologists nor psychologists have yet accumulated a sufficient body of empirical information to encourage formulation of theories about rule transmission in animals. Even in our own species, though language is a target of much current research, rules for linguistic, syntactic, and speech processing are still largely a matter of speculation. The deficiencies in studies of human communication are somewhat complementary to those in other species.

In animals, there is an extensive literature on the phylogeny of signaling actions, a major theme in ethological research since Lorenz's (1941) classical analysis of display behaviors in ducks. Ethologists have properly emphasized that

genetic mechanisms must play a dominant role, though some have argued that the importance of learning has been underplayed.

By comparison, there is almost no ethological information on the phylogeny or ontogeny of encoding and decoding procedures. While the development of many signal actions is largely innate, it seems probable that, at least in higher animals, learning plays an important role in the acquisition and development of functionally appropriate "assessments" of situations or signals. Thus, one may argue that the focus on the morphology of signaling behaviors in past animal research has led to overemphasis on the inherited component of the communicative performance.

If we compare the current state of understanding of the development of human behavior, a different bias emerges. Few hesitate to acknowledge the dominant or even exclusive role of individual experience in the ontogeny of language. This is perhaps in part because we are aware of the great diversity of human languages and dialects, and are introspectively conscious of the processes of encoding and decoding speech signals. In the minds of many, this environmental viewpoint extends to the development of all other human signaling behavior. However, this extension is probably less appropriate than is often supposed. Innate, species-specific components in human signaling behavior are in fact widespread in human facial expressions (e.g., Eibl-Eibesfeldt, 1972) and even in human speech behavior (Eimas, 1975; Eimas and Tartter, in press), although we are rarely conscious of them. In recent years, the revival of interest in nativistic interpretations of human communicative behavior has given promise of a more sensible balance, acknowledging both the essential role of hereditary influences in human communication and also the greater importance in animals of environmental influences, including some that may be properly viewed as cultural.

SIGNALING, SENSATION, AND PERCEPTION

Although we have indicated examples of extensive mutual evolutionary interactions between mechanisms of signal production and of sensation, such interactions are most evident in species with nonversatile receptor systems. When service for other functions is required in addition to communication, mechanisms of signal perception become more deeply embedded in the basic perceptual operations performed on sensory stimuli in general. Studies of perceptual development thus come to bear directly on the ontogeny of communication. We can hardly do justice here to a theme on which there is an extensive literature in both philosophy and psychology (e.g., Boring, 1942; Gibson, 1966; Uhr, 1966; Warnock, 1967; Gibson, 1969; Sutherland, 1973; Rosinski, 1977).

Perception involves not just the ability to sense changes in the environment but also the ability to organize and interpret what is sensed and to act on the basis of those interpretations. It is evident from this definition that the construct we have called *assessment* has much in common with perception in the broad sense. Indeed, it is probably best viewed as a special case of the more general phenomenon.

There is evidence that perceptual development includes something equiva-

lent to building up structural representation of the external world (Craik, 1943; Sutherland, 1973; Gregory, 1974). In ways that are still mysterious, objects and events become classified into categories, with definite boundaries between them. The process of assessment that we have invoked is closely allied to this classificatory process.

Aside from the purely sensory aspects of interaction with the external world that contribute to the ontogeny of internalized representations of external phenomena, there is a growing appreciation of the importance of motor involvement (Turvey, 1977; Weimer, 1977). In addition to the importance of actions that directly aid the gathering of sensations, such as searching movements with the distance receptors and their supporting body parts (e.g., Hebb, 1949 ; Yarbus, 1967), there is also evidence that functional involvement with the environment plays a role in the emergence of perceptual categories (Rosch, 1973, 1975; Nelson, 1974). Given the intimate association between human perception and action, it is but a small step to the invocation of sensorimotor interactions as a factor in the development of animal communication. In fact, such interaction is implied by the construct of *sensory templates* (reviewed in Marler, 1976b), invoked by students of auditory communication in animals as varied as crickets, frogs, and birds.

SHARED PROCEDURES FOR PRODUCTION AND PERCEPTION

We want to develop the notion that the perception and production of both human and animal signals requires only one kind of algorithm linking external signal to internal state. There is a sense of economy in designing communicative physiology so that common mechanisms serve this role in both signal senders and signal receivers. One line of argument favoring common physiological mechanisms underlying both signal production and perception derives from studies of effects of temperature on the behavior of cold-blooded animals. In a pioneering study, Walker (1957) demonstrated that a critical species-specific difference between the calling songs of males of different species of tree crickets lies in the rate of pulsation of the stridulatory sounds. Within groups of sympatric cricket species, he found that females respond selectively to conspecific male pulse rates by approaching the loudspeaker. It is well known that song pulse rates are temperature-dependent in a regular fashion, and Walker was able to show the responsiveness of females to pulse-rate changes in parallel, so maintaining specific discrimination over a range of temperatures that would otherwise completely confuse the discrimination process. It is economical to postulate that the temperature dependence of both male song production and female song responsiveness is mediated by a common mechanism. In another study of this type, Gerhardt's (1978) work with tree frogs has shown that species-specific pulse-repetition rates and pulse durations in male calling are highly dependent on temperature, and that female responsiveness for each species studied marches in parallel.

Study of the behavior of hybrid crickets leads to a similar interpretation. Having demonstrated that the calling songs of hybrids are uniquely different from those of either parental species, Bentley and Hoy went on to show that hybrid females prefer hybrid male songs to either of the two parental male songs (Bentley

and Hoy, 1972; Hoy and Paul, 1973; Hoy, 1974; Hoy, Hahn, and Paul, 1977). Common genetic control of signal production and reception is indicated, and Hoy *et al.* (1977) went on to speculate that

the existence of neurones common to both central pattern generators (male) and to hypothetical feature detectors or templates (female) would help explain the coupling of male and female auditory behavior. Genetic control could be achieved by identical sets of genes acting on the same neurone types in both male and female. Thus behavioral and genetic coupling would have a common basis.

BIRDSONG: PRODUCTION AND PERCEPTION

Studies of vocal communication in birds have provided another type of evidence in favor of sensorimotor neural templates as shared mechanisms for perceiving, producing, and responding to birdsongs. Since many songs are learned, it is possible to extend interpretations beyond what is appropriate for the cricket and frog findings, where the innate patterns of sound production are under more-or-less strict genetic control.

It is clear that learning plays a dominant role in the development of the perceptions that birds have of their own vocal signals. This is true even in cases where the patterns of production are not only innate but develop in the absence of auditory feedback, as in the domestic chicken (Konishi, 1963). In spite of this apparent lack of plasticity in the motor coordinations of sound production, there are strong hints that chickens derive much of their mature perception of conspecific sounds through learning (Evans, 1972; Evans and Mattson, 1972; Guyomarc'h, 1972, 1974a,b). Similarly, in birds with more plastic vocal behavior, a variety of evidence indicates that songbirds engage in extensive perceptual learning. While there is an innate basis for song recognition (e.g., Marler and Peters, 1977), songbirds also acquire responsiveness to many details of the male territorial song, such as local dialects, individual differences, and variations associated with changing motivation (e.g., Falls, 1969; Falls and Brooks, 1975; Milligan and Verner, 1971; Brooks and Falls, 1975a,b; Wiley and Wiley, 1977; Kroodsma, 1978).

Auditory learning plays a role in motor aspects of vocal development in many songbirds, so that their vocal behavior is abnormal if reared in social isolation (Marler and Mundinger, 1971). The accuracy with which sounds can be imitated indicates that vocal learning can proceed by reference to auditory information (Konishi and Nottebohm, 1969). The extreme abnormality of the singing behavior of males of some songbirds deafened in youth, before singing, is further evidence of the crucial role of auditory learning in vocal development (Konishi, 1963, 1964, 1965, 1966; Marler, Konishi, Lutjen, and Waser, 1973; Marler and Waser, 1977). In one closely related group of sparrows, deafening has been found almost to eliminate species song differences, again indicating the major role of audition in guiding species-specific signal production.

Sensorimotor interplay is also indicated by the tendency for singing to develop later than song learning. The initiation of the perceptual phase of song learning tends to precede production in many birds, sometimes overlapping in time and sometimes not. When singing begins, there is a gradual transition from

subsong to full song that often proceeds without further access to models. Sequences of vocal transformations occur such as might be expected if the bird were improving its skill at controlling operations of the complex syringeal apparatus, thereby achieving a better and better match with the memory of sounds heard earlier in life. We can conceive of the acoustic information used in this matching process as embodied in a sensory template that is modifiable through auditory experience (e.g., Marler, 1970).

A further role for perceptual mechanisms in avian vocal development is implied by evidence of selectivity in initial stages of the learning process. Whereas some birds are interspecific mimics, either by nature or in artificial circumstances of captivity, some species that develop a highly abnormal song when reared in social isolation are then nevertheless quite selective in what sound patterns they accept for imitation (Thorpe, 1958, 1961; Marler, 1970; Marler and Peters, 1977; Konishi, 1978). Evidently, some birds exhibit an innate auditory predisposition to learn certain classes of sounds more readily than others.

If recent studies are any guide, the initial specifications may be quite simple and incomplete (Marler, 1978). Although lacking in many details, the specifications are sufficient to endow the singing of a naive young male with more normal traits than is the case if he is deafened. Given auditory experience with normal species-specific songs, additional features are memorized, with delayed effects on learned song patterns when the male begins singing later. The learned song is obviously a closer match to the wild type than that of a bird without this experience. Thus, we may confidently postulate an engram or schema of the learned song, then used template fashion during the process of learning to sing. In the brain of an adult bird, equivalent processes are presumably used in song recognition as well as in song production (Marler, 1976b).

That mechanisms with some similar properties exist in the brains of nonsinging females is indicated by the elicitation of female song by treatment with male sex hormones. In the white-crowned sparrow, a species with well-marked song dialects, the normal male song is learned (Marler and Tamura, 1964; Marler, 1970). A female who hears a local dialect in her youth not only will sing under the influence of testosterone but will render that particular dialect (Konishi, 1965). This acquired information is presumably normally used in the process of mate selection by female sparrows (Milligan and Verner, 1971; Baker and Mewaldt, 1978). Thus, a common mechanism is indicated for perceptual and motor development, shared by males and females, though normally put to different uses by the two sexes.

Learning plays a major role in the development of this shared mechanism. The neuroanatomical nature of the mechanism is unexplored. Although it is conceptualized as having unity of operation, it may comprise few or many physiological components, with separate elements selecting different acoustic features from external sounds and from the animal's own vocal performance. Components exhibiting developmental plasticity may be distinct from or identical with those that underlie the innate selective perception of an untrained bird. Mechanisms might operate in series or in parallel, with control shifting from one to another as learning takes place.

While the particular structures involved are yet to be identified, together they achieve the template-matching function we have outlined. It also seems conceivable that they operate in analogous fashion to the developing internalizations of past experiences involved in the control of other kinds of perception and movement that physiologists are beginning to infer, however dimly, from interactions between operations in different parts of the brain (Evarts, Bizzi, Burke, DeLong, and Thach, 1971; Mountcastle, 1976).

THE MOTOR THEORY OF SPEECH PERCEPTION

There is a remarkable parallel here with the motor theory of speech perception as developed by Liberman *et al.* (1967; Studdert-Kennedy, Liberman, Harris, and Cooper, 1970). Noting that some anomalies of speech-sound recognition disappear if one thinks of them in terms not of acoustic features but of the vocal gestures producing them, it was proposed that a common mechanism underlies both perception and production. They suggest that we

think in terms of overlapping activity of several neural networks—those that supply control signals to the articulators and those that process incoming neural patterns from the ear—and to suppose that information can be correlated by these networks and passed through them in either direction.

In its original form, there was no commitment to any particular kind of ontogenetic history. In the seminal and widely used taxonomy of “distinctive features” of speech patterns, acoustic criteria mingle with production operations (Jakobson, Fant, and Halle, 1952). There has been some tendency to adduce primacy for mechanisms of sound production in view of our tendency to make use of gestures of tongue and palate that exhibit a degree of acoustic stability, with little variation in the sounds produced with errors of placement (Stevens, 1972; Lieberman, 1977). In other accounts, the metaphor is used of an internalized dynamic representation of the vocal tract and its operation, terms immediately reminiscent of the “schemata” used by psychologists to conceptualize other kinds of internalized perceptual phenomena (Bartlett, 1932; Oldfield and Zangwill, 1942–1943).

With the discovery that pre-speech infants are responsive to some of the same distinctions between phonemes that adults make (Eimas, Siqueland, Jusczyk, and Vigorito, 1971), it now seems reasonable to think of auditory rather than motor predispositions as taking the initiative in the development of the very complex task of analyzing speech sounds. According to this line of interpretation, perceptions of speech would first be elaborated in infancy. Then, speaking would begin, guided by memories of what has been learned, much as has been postulated in the learning of birdsong. There will follow a period of overlap between the ability to learn new speech perceptions and new productions, as mature speech behavior emerges.

A common mechanism is postulated, developing during infancy through the conjoint operations of speaking and listening to speech, which then takes part in the control of both kinds of operation in the mature organism. Processes of

encoding and decoding would thus employ some of the same brain mechanisms, an illustration of the kind of economy we may expect to be widespread.

SENSORY TEMPLATES AND SCHEMATA

Using examples from auditory communication, we have developed a case for overlap or even correspondence between the biologist's *sensory template* and the psychologist's *schema*. At least partly because we are conscious of the operation of our own external auditory feedback channel, the argument seems intuitively plausible in this case. Even with audition, however, it is likely that the bulk of sensorimotor matching occurs unconsciously. It is worth remembering that the neurologist Henry Head emphasized the frequency of unconscious processing in his original conception of brain "schemata" for bodily movements (Oldfield and Zangwill, 1942–1943; Mason, this volume).

Adult humans and chimpanzees, for example, are remarkably clever at imitating what they see others doing (e.g., Hayes and Hayes, 1952). This imitation extends to facial expressions. Recent studies have shown that 2-week-old human infants can imitate both facial and manual gestures, a result that implies a remarkable ability on the baby's part. It must first perceive the configuration of the stimulus face and then generate a matching motor output. This could only be achieved by reference to some internalized representation of patterns of previous proprioceptive experience from his own unseen facial movements or by direct mapping onto an appropriate motor output (Meltzoff and Moore, 1977). At least, as adults, we are not conscious of either kind of operation. During ontogeny, such sensorimotor brain mechanisms as are nevertheless implied for the infant must surely become enormously elaborated and also enriched by developing visual experience and growing skill in operation of the visual signaling apparatus. Again, we postulate the likelihood that shared mechanisms are involved in both perception and production.

In several of the examples we have discussed, much of the adult communicative behavior of higher organisms is heavily influenced by learning. There is nevertheless repeated evidence of perceptual constraints emerging early in life. In some cases, these are known to be innate. We view these indications as most important in understanding how perceptual abilities develop. The importance of shared rules for encoding and decoding of signals is obvious if communication is to operate efficiently. To the extent that signaling behaviors are modified and elaborated through learning, it becomes more difficult to ensure that an adequate degree of rule sharing for production and perception will persist among all communicants, especially with signals as complex as speech or human facial expressions. However, with both processes performed by common mechanisms that develop with some close degree of genetic control, we can visualize how this might be accomplished.

Innate instructions to the young organism as to how to embark on the process of perceptual analysis would be valuable both in ensuring a choice of efficient procedures and in encouraging all species members to tackle the problem in the

same basic fashion. It may be that some classical ethological illustrations of innate responsiveness are actually better interpreted as innate instructions for embarking on a certain trajectory of perceptual learning, rather than for designing animals as behavioral automata (Marler, 1978). To the extent that this strategy of innately guided perceptual development is successful, it will ensure a degree of rule sharing, while still allowing freedom for learned variability in both signal perception and production.

SIGNAL STRUCTURE AND FUNCTION

Although recent reviews have analyzed many aspects of animal signals and their contributions to patterns of social organization (e.g., Brown, 1975; Hailman, 1977; Sebeok, 1977; Smith, 1977), no comprehensive system is yet available for the study of animal semantics. More progress has been made in interrogating animals on questions of semantic meaning using human languagelike systems (e.g., Gardner and Gardner, 1971, 1975; Premack, 1971, 1976; Rumbaugh, 1976; Fouts and Rigby, 1977) than by studying communication in nature. Clearly new approaches are needed.

THE IMPORTANCE OF CONTEXT AND PAST EXPERIENCES

We sometimes think of a signal receiver as though it were in a passive, neutral condition, waiting for external instruction as to what to do next. It is obvious, however, that in all but the simplest animals, a potential recipient already has a great deal of foreknowledge it can call upon in planning future action. A bird that has just passed through a section of woodland has gathered information about who else is there and what they are doing. Probability judgments have been possible about the likelihood of a neighboring rival's encroaching, or whether he is too preoccupied with newly hatched young. Memories of unduly anxious behavior by recently encountered neighbors may hint at the possibility that a hawk has changed its hunting beat and could soon pass over again. Awareness of the changing seasons may rekindle older memories of annual migrations of other species, preparing expectations of encounters with unaccustomed signals, some perhaps similar enough to its own to have been confusing in the past and thus the object of refined discriminative learning.

An exhaustive list of internalized contextual information would be enormous, requiring much deeper empathy with the perceptual world of animals than we now possess. Yet, it is clear that when an animal receives a signal, various kinds of information stored in memory can influence its assessment of what a given signal means (Wiley, 1976). The communication of animals, like that of people, must involve a great deal of guesswork. The more information from the past that can be brought to bear on a given situation, the better the chance of guessing correctly. For this reason, if no other, it would be surprising if animals were not constantly consulting their memories in deciding what signals mean (cf. Griffin, 1976).

It must often happen that an animal receives a faint sound, an odor, or a glimpse of a display, sufficient to ascertain receipt of a signal but not enough to determine its precise nature. Memories of past events often suffice, however, to form a reliable judgment as to the signal's probable nature and meaning—that a neighboring rival has chosen this moment to make its customary evening transit for water or has discovered the predator that has been sleeping for the past few days in a boundary tree. Above all, such an unidentified signal specifies a moment in time at which a receiver might well choose to pause in ongoing maintenance activities for attentive surveillance. By consulting past knowledge and present perceptions of the organization of natural events in familiar habitats, it is often possible to make a reasonable guess at the nature of the unknown signal and to plan accordingly. It is hard for the laboratory scientist to appreciate the extent of this kind of ordering, which prevails in both time and space in the natural flow of events. There is every reason to suppose that many animals can become aware of such patterns, but few serious attempts have yet been made to incorporate this possibility in the interpretation of communicative behavior.

Suppose that an animal receives an unidentified signal, which may or may not be repeated. What might be inferred from variations in the timing of delivery alone? Schleidt (1973, 1977) has drawn a useful distinction between phasic and tonic signals, many of the latter being invariant and thus excluded from consideration here. While some signals are given singly, or in relatively brief bursts at irregular intervals, others are given at a regular rate over periods of time. These two delivery patterns relate to phenomena with different time courses, and a receiver might draw some inferences about them even in the absence of any other input from the signaler. A phasic characteristic correlates with a rapid change in a signaler state, as might ensue upon perception of a discrete event. A tonic pattern of delivery is more likely to designate an ongoing, or only slowly changing, state of the signaler. Examples of the former might be discovery of a predator or food. The latter might include the onset of physiological readiness for mating or parental care, though only general temporal features would be specifiable without further information.

Depending on its own circumstances and its physiological condition, a receiver may respond either phasically or tonically to a tonic signal. A continuously reiterated male birdsong may elicit slow physiological changes culminating in the ovulation of a mated female, while also evoking the rapid, phasic response of fleeing by a casually intruding male neighbor.

A different issue is raised by a receiver's past experience with the rate of signal reception in general. The significance of perceiving a single unidentified signal would be very different to an animal living in a group, surrounded night and day by a host of signaling companions, than to a solitary one with rare social contacts. In the latter case, the "stimulus contrast" would be high (Andrew, 1964), and the likelihood and nature of reactions would differ accordingly. The receiver accustomed to common signal reception is less likely to investigate an unidentified signal further than one for whom reception is rare.

Thus, even if a receiver has failed to identify an unknown signal, it can gain a great deal by interpreting the location, circumstances, and timing of the event in light of prior experiences of the probabilities of contextual events. Such information is equally relevant to a recipient's assessment of the meaning of accurately identified and highly differentiated signals. Thus, we fully concur with the emphasis placed by Smith (1965, 1968, 1977) upon the importance of context in understanding the meanings of animal signals.

IDENTIFYING SIGNALER SPECIES

What kind of assessment can a receiver derive when, irrespective of other aspects of signal meaning, the species of a signaler becomes known? Most ethological research on species recognition focuses on discrimination between the receiver's own species and others. Typically, little attention is given to the value of discrimination among "others." Cross-species identification can nevertheless make a valuable contribution to the context in which a species' own signals are assessed.

As migrating birds strive to locate appropriate summering or wintering habitats, a history of experience with the resident fauna in these habitats contributes to selection of opportune geographical locations for settling. On a more local scale, movements and foraging patterns of some species are closely correlated with those of others. Fish (Barlow, 1974a,b; Itzkowitz, 1977), monkeys (Gautier and Gautier-Hion, 1969; Struhsaker and Gartlan, 1972; Marler, 1973; Gautier-Hion and Gautier, 1974), and birds, especially in the tropical rain forest, habitually form mixed-species groups (Moynihan, 1962; Morse, 1970; Wiley, 1971; Buskirk, Powell, Wittenberger, Buskirk, and Powell, 1972). The gain from identifying another species can be substantial and immediate, such as locating a newly fruiting tree or a swarm of army ants which disturbs thousands of otherwise cryptic insects in the vanguard of its columns (Willis, 1966). There are equivalent illustrations of cross-species recognition in food location in temperate woodland birds (Krebs, 1973), predator communities on the African savanna (Kruuk, 1972; Schaller, 1972), and territorial defense in the coral reef (Myrberg and Thresher, 1974), all contributing to the contextual background for intraspecific communication.

Cross-species signal recognition can be equally important in the assessment of potential hazards, alarm calls being an obvious case, undoubtedly helping to sharpen assessments of the meaning of conspecific alarm signals. Interspecies dominance relations among food competitors is a significant source of selection pressure in some communities (e.g., Morse, 1970), and is probably sufficient to encourage the discrimination of other species' signals. An animal with food might well decide to behave cryptically upon detecting signals of another belonging to a dominant and competing species, again with implications for intraspecific signaling as well. It seems safe to assume that animals living in complex communities and with appropriate perceptual abilities rarely classify signals of other species into a single category. Rather, they tend to develop abilities to discriminate among them insofar as they constitute a sensitive and dynamic component in the contextual background for conspecific signal assessments.

There can be no doubt, however, that the discrimination of own from other species is the most critical of all. The functions served are legion. Some are relatively simple, as in aiding the location of suitable microhabitats for reproduction or overwintering or the choice of migration routes. Selection of a habitat by some lizard species is favored if they see other species members there, made more conspicuous by their frequent visual signaling (Kiester and Slatkin, 1974). A similar function has been suggested for male song in crickets (Ulagaraj and Walker, 1973) and for bird sounds (Falls, 1978).

SIGNAL SPECIES-SPECIFICITY

How are conspecific signals discriminated from others? Aspects other than signal structure sometimes play a critical role, as is illustrated by insect sex pheromones. While some species have pheromones with a unique molecular structure, others do not. Experiments show that sympatric moths may be equally responsive to one another's sex pheromones (e.g., Schneider, Kafka, Beroza, and Bierl, 1977). However, in nature there are different annual and circadian rhythms both of female sex pheromone production and of male responsiveness, resulting in a form of contextual species-specificity that does not rely on chemical individuality (Roelofs and Cardé, 1974; Shorey, 1976). In some beetles with the potential of cross-species chemical attraction, odors from other sources, such as the different trees on which they live, provide a species-specific context or act synergistically with pheromones that are inactive without them (Borden, 1974; Lanier and Burkholder, 1974).

Given the noisiness of most natural environments, the multitude of animal signals broadcast into them, and the frequent advantages of providing receivers with clear, unequivocal evidence of species identity, there is often strong selection pressure for signal distinctiveness within given animal communities. Species-specificity of signal structure can be achieved in many ways. In pheromones, as Wilson (1968) indicated, "organic odorants provide an immense array of potential signals. With an increase in molecular weight in any given homologous series, molecular diversity increases exponentially." Verifiable predictions have been made of the range of molecular weights that insect pheromones should have, with strong selection pressure for species-specificity (Wilson and Bossert, 1963). Signal specificity is sometimes matched by receptor specificity, so that pheromone receptors are highly tuned to respond only to the sex pheromone of the species and a few closely related compounds (e.g., Schneider, 1962, 1970).

The temporal patterning of damselfish chirps conveys precise information used in species recognition as well as for more subtle social functions (Myrberg *et al.*, 1978). In electric fish communities, both species-specific waveforms and the rates of repetition of electrical discharges differ distinctively among species members. The fish themselves prove to be clearly responsive to these features (Hopkins, 1974), and there is evidence that entire electroreceptor systems are attuned to waveforms of conspecific signals (Hopkins, 1974, 1976; Hopkins and Heiligenberg, 1978).

Species-specificity often accrues in a signal repertoire as a consequence of morphological adaptations that are primarily ecological rather than social in nature. When a number of similar species from a single taxonomic family are sympatric, they often form a series of distinct size classes, each with different niche specifications. In general, the pitch of acoustic signals bears an inverse relationship to the size of the sound-producing apparatus. Thus, the frequency contrasts that exist among sounds of species of frogs, birds, or primates that live together may be in a large part attributable to their ecological differentiation which results in species size differences (Blair, 1956, 1958; McAlister, 1959, 1961; Schneider, 1967, 1974, 1977; Martin, 1972a,b; Lorcher and Schneider, 1973; Bergmann, 1976; Eisenberg, 1976), although in some cases we also find divergent properties of structures involved in phonation, such as extralaryngeal vocal sacs and special neuromuscular control mechanisms (e.g., Negus, 1949; Gautier, 1971; Gautier and Gautier-Hion, 1977).

In crickets and grasshoppers, the sound spectrum of calling songs seems less dependent on body size or wing loading than on the way in which the file and scraper are employed (Dumortier, 1963; Morris, 1970)—that is, on patterns of neuromuscular activity, with or without afferent feedback interaction (e.g., Elsner and Hirth, 1978; review in Huber, 1975). While many orthopteran songs are relatively simple pulse trains, some require elaborate central motor programs for their production (e.g., Otte, 1972). In Uhler's katydid, with the most complex orthopteran song yet described, there is nothing unusual about the structure of the file of this species, implying that the complexities must be centrally generated (Walker and Dew, 1972). In frogs, a species-specific temporal pattern can be as important as size-related spectral structure in species recognition (Capranica, 1965, 1966; Loftus-Hills and Littlejohn, 1971; Capranica, Frishkopf, and Nevo, 1973; Gerhardt, 1974b), and again, central nervous pattern generators are implicated (Schmidt, 1974).

In European warblers, a survey of song revealed that some other features than song pitch also correlated with body weight. The tempo tends to be slower in heavier species, and song syllables tend to be longer (Bergmann, 1976). Moreover, some birds have special resonant structures that affect the pitch of their song (Stresemann, 1928). In general, however, syringeal structure is highly conservative among close relatives (Ames, 1971; Warner, 1972), and species-specific bird-song features must often be attributed to variations in the temporal pattern of neuromuscular activation of the syringeal musculature and respiratory patterns (Nottebohm, 1975).

Many such properties prove significant in the discrimination of conspecific song from others. Pitch differences are often relevant, as in the spotted sandpiper (Heidemann and Oiring, 1976), the golden-winged warbler (Ficken and Ficken, 1973), and in song discrimination by the sympatric goldcrest and firecrest (Becker, 1976). In the latter case, temporal features seem less important in species recognition, whereas in others such as the white-throated sparrow (Falls, 1969) and the brown thrasher (Boughey and Thompson, 1976), timing and sequential organization are more important than frequency. Descriptive analyses of song specificity often emphasize temporal differences (e.g., Guttinger, 1978). There is much

redundancy, however, in the species-specific information contained in male birdsongs, and the most common finding is that several acoustic features play a role in species recognition (e.g., Tretzel, 1965; Bremond, 1968a,b, 1972, 1976; Thompson, 1969; Schubert, 1971; Emlen, 1972; Shiovitz, 1975).

While there is a tendency for species to rely especially on features that are most stable throughout all members (Emlen, 1971, 1972), this is not necessarily the case (e.g., Bonelli's warbler, Bremond, 1976). By far the most attention has been focused on species-specificity of male birdsong, where selection pressures relating to reproductive and ecological isolation must place an especially high premium on rapid, reliable recognition. There are already indications that issues of species-specificity in calls, rather than song, may be just as important, even more subtle, and ultimately of even greater interest (e.g., Thielcke, 1971, 1976; Stephanski and Falls, 1972a,b).

Species recognition can be viewed as a special case of the more general phenomenon of discrimination of a signal from noise (p. 80). It follows that variations in signal environment will affect the kind of adaptations that optimize specific discrimination. The occurrence of "character displacement" is circumstantial evidence of such effects. Signals of related species presumed to be subject to selection for specific distinctiveness sometimes show more divergence in zones of sympatry than where they are allopatric (e.g., Brown and Wilson, 1956; Blair, 1968; Littlejohn, 1971; reviews in Straughan, 1973, and Brown, 1975). There are opposite cases in which signals seem to converge in zones of sympatry. When this occurs with birdsong, it appears that cross-species competition is especially intense, with evidence of interspecific territoriality (Marler, 1960; Cody, 1969, 1974), so that song assumes a rather different function than usual.

It should be emphasized that extreme signal species-specificity is by no means a universal advantage. While the benefits are obvious with signals that play a pivotal role in reproductive and competitive isolation, such as sex pheromones, typical birdsongs, and the "loud calls" of adult male forest monkeys, the advantages are much reduced with other signal functions. Some signals are very similar across species and are effective interspecifically. This seems to be true of some alarm signals, whether pheromones, calls, or displays, and also of some aggressive signals (Marler, 1957, 1973; Wilson and Bossert, 1963; Struhsaker, 1970; Zann, 1975; Gautier and Gautier-Hion, 1977; Morton, 1977), although this is not a universal rule (e.g., S. M. Evans, 1972).

A receiver's assessment of a signal identified as from a member of its own species depends on context (Prushka and Maurus, 1976). The song of a territorial male bird such as a chaffinch is assessed differently by reproductive and nonreproductive female chaffinches, by settled male neighbors, and by males seeking space for a territory (Marler, 1956). Such differences in the assessment of the same signal perceived in different contexts may be radical. Consequences may be cooperative in one case and competitive in another.

Consider, for example, an adult reproductive male rhesus monkey, recently emigrated from his natal group. While solitary, he will be seeking another group into which he can gain entry for reproduction. As he searches, any call identified as from a rhesus macaque, irrespective of other connotations, will lead to

approach, further investigation, and, if circumstances are propitious, attempts to become a group member. A few weeks later, that same signal experienced in a changed context would be assessed quite differently, as evidence of a competing group. Instead of advancing to solicit social acceptance, the same male, now a resident member of his group, may instead take part in an attack.

We are reminded that of all possible communicants, members of the same species offer by far the widest range of alternative assessments. While their signals are potential markers for social companionship, cooperation, and reproduction, they also signify the most potent and general class of competitors, with maximally overlapping needs and similar methods for satisfying them. Again, the major burden in assessing how to respond to conspecific signals in general must be carried by knowledge from other sources, both current and past. In this sense, meaning is again as much a function of context as of particular signal structure (cf. Prushka and Maurus, 1976).

This portion of our review emphasizes auditory signals, which have been the subject of a majority of signaling studies. Similar principles pertain to the visual domain, as exemplified by such systems as the flashing patterns of fireflies and other manifestations of visual communication in insects (Soucek and Carlson, 1975; Lloyd, 1966, 1977; Markl, 1974; Carlson and Copeland, 1978), the displays and colorations of lizards (e.g., Carpenter, 1962; Hunsaker, 1962; Kiester, 1977), and the displays, plumage patterns, and other morphological signaling characters in birds (Sibley, 1957; Hamilton and Barth, 1962; Moynihan, 1968; Brown, 1975; Smith, 1977). There is also an enormous literature on visual signals with a false species-specificity, mimicking other sympatric organisms and serving a wide variety of functions, with a multitude of complex and intricate adaptations brought into service (reviews in Cott, 1957; Wickler, 1968; Hailman, 1977).

FURTHER RECOGNITION OF SIGNALER IDENTITY

When a signal is perceived, there is a wide range of precision over which the signaler's identity may be ascertained. At one extreme is the basic discrimination between social signals and inanimate stimuli. At the other extreme is personal recognition of individual signalers. While individual recognition is virtually absent from insect societies apart from certain special exceptions such as bumblebees and *Polistes* wasps (Wilson, 1971b, 1975b), it is widespread among vertebrates.

INDIVIDUAL RECOGNITION

Wilson (1971b) offers the generalization that

the members of an insect colony employ signals that are for the most part uniform throughout the species. The one known exception is the colony odor, which is acquired at least in part from food and nesting material and is used to distinguish nest mates, all of them together, from members of other colonies. (p. 402)

Among vertebrates, however, individual signaler recognition probably extends through all sensory modalities, certainly olfaction, audition, and vision.

Olfaction mediates individual recognition in fish (e.g., Fricke, 1973) and is

involved in species and group recognition as well, along with vision (Myrberg, in press). Canids can discriminate individually among group members by smell, probably on the basis of proportions of salient compounds in urine and glandular secretions (Mech, 1970). In the vocal domain, wolf howling is individually distinctive (Theberge and Falls, 1967). Some nonhuman primate sounds are known to be individually distinctive, such as the pant-hooting of chimpanzees (Marler and Hobbet, 1975). Yet, while it may be widespread, only in a few cases has individual recognition of calls been confirmed by experiment or playback of recordings (Waser, 1975a, 1976; Hansen, 1976; Pereira and Bauer, in press). Nowhere is the personal individuality of signals more evident than in vocalizations of birds, and playback studies have repeatedly demonstrated that individuals are indeed discriminated by voice (e.g., Brooks and Falls, 1975a,b; Falls and Brooks, 1975; Kroodsma, 1976; Wiley and Wiley, 1977; Falls, 1978). Similarly, with visual signals, at least for social birds, there is evidence of individual recognition, which seems to involve especially features of the face (Guhl and Ortman, 1953; Candland, 1969).

Young Canada geese can reliably select group members from birds of similar age but from strange groups (Radesäter, 1976). However, it is not clear in this case whether this is a class discrimination of familiar versus unfamiliar age-mates or whether each group member is recognized personally. Parallel problems of interpretation arise in other studies of individual recognition. In much bird research, behavior related to hierarchical status is used as a criterion for individual recognition. But it is not always clear whether the data exclude the possibility that the discrimination involves not multiple individuals but two classes, one higher in rank and one lower (Wiley and Hartnett, in press).

The problem is confounded by the involvement of some of the visual characters, known by experiment to play a role in individual recognition, in the actual establishment of dominance rank. For example, both Guhl and Ortman (1953) and Candland (1969) found that of all disguises, modification of the comb of hens and cocks caused the maximum disruption of dominance relations. There is evidence that relative comb size is a good predictor of future dominance relations as birds become acquainted (Collias, 1943; Guhl and Ortman, 1953; Marks, Siegel, and Kramer, 1960), no doubt because it tends to reflect androgen levels. As an equivalent illustration from a nondomesticated bird, comb size in the willow ptarmigan also correlates well with dominance rank (Gjesdal, 1977). The antler size of deer covaries with social dominance and may help to establish rank (Esmark, 1964). Similarly, behavioral signals that correlated with dominance rank, such as tail position in baboons (Hausfater, 1977), might play a role in identifying hierarchies, without the *necessity* of individual recognition. Thus, care is needed to demonstrate personal recognition of group members unequivocally, even though general observation repeatedly confirms that it is indeed widespread.

DISCRIMINATION OF A FAMILIAR FROM OTHERS

More robust evidence is available that signals from particular individuals may be discriminated from those of all others as a class, as in the relationships between mates or between parent and young (e.g., Mills and Melhuish, 1974; Petrinovich,

1974). Miller and Emlen (1975), for example, changed the appearance and modified the sound production of ring-billed gull chicks, thus showing that they are discriminated from other young by parents after about seven to nine days posthatching. Visual cues were the more important of the two. The adequacy of vocal signals when they alone are available has been demonstrated with a variety of seabirds (e.g., Tschanz, 1968; reviews in Beer 1970, 1975). Similarly, in the relationship between a mated monogamous pair, as in gannets, experiments reveal that the discrimination of mate versus nonmate vocalizations can often readily be made (White, 1971).

Many species appear to rely on chance or growth-related differences in morphology or behavior as a basis for such discriminations, although the unusually high variability of such signal features as aspects of the face and the plumage patterns of chicks has been noted (Marler, 1961; Buckley and Buckley, 1970, 1972). In other cases, signal learning is clearly involved. Thus, in goldfinches, twites, and other cardueline finches, details of the flight call are modified so that mated pairs are matched. Playback demonstrates that they do indeed respond more strongly to the mate's call than to the calls of others (Mundinger, 1970; Marler and Mundinger, 1975). A more extreme case is provided by the elaborate, highly coordinated, and pair-specific duets that mates of some bird species produce (Todt, 1970, 1975; Helversen and Wickler, 1971; Payne, 1971; Thorpe, 1972; Wickler, 1972a,b, 1973, 1976; Kunkel, 1974; Seibt and Wickler, 1977; Wiley and Wiley, 1977).

Such behavior sometimes incorporates neighbors in addition to the mated pair, though their kinship relations are not known. Certainly, in species with close-knit and durable family bonds, one can readily see how signal-learning processes could encompass all members. Call modification of finches can occur in such circumstances (Marler and Mundinger, 1971), serving, along with other signals, to foster discrimination between members of other groups and members of the family, whether immediate or extended.

STRANGENESS, FAMILIARITY AND KIN RECOGNITION

For social birds and mammals, especially colony dwellers and herding species, animals are reared in a close-knit group in which everyone probably knows everyone else. The discrimination of strangers' signals from those of the familiar group is likely to be a component in the recognition process by which kin may be distinguished from nonkin. It is surely more than coincidental that strange conspecific individuals provide the strongest stimuli for hostility in a variety of species (see Bernstein, 1964; Southwick, 1967; Southwick, Siddiqi, Farooqui, and Pal, 1974; Rosenblum, Levy, and Kaufman, 1968; Scruton and Herbert, 1972; Wade, 1976, for primate examples; Ralph, 1977, for an avian example; review in Marler, 1976a). If we are to improve our understanding of the mechanisms of communication between animals, it is essential that we learn more about the distribution of familiarity in natural animal communities and about the rules governing its generation and decay. Not only is an understanding of this distribution basic to the

analysis of how animals assess signals in their daily lives, but it is also important from a theoretical viewpoint.

With our growing appreciation of the theoretical importance of kinship relationships in understanding the evolution of social structure, it is important to learn more about how kin networks are distributed in nature and about what means, if any—whether spatial, morphological, or behavioral—are employed for discriminating close kin from others and with what accuracy. One possibility would be communication by cues that directly reflect genetic constitution, perhaps most likely to be chemical in nature. Demonstrations of mating preferences among mouse strains bred for divergent immunological traits may hint of such a possibility (Yamazaki, Boyse, Mike, Thaler, Mathieson, Abbot, Boyse, Zayas, and Thomas, 1976; Yamaguchi, Yamazaki, and Boyse, 1978). Another candidate is surely intimate communicative familiarity. There is no better way to appreciate the importance of this factor than to observe social reactions to complete strangers. As we have indicated, strangeness constitutes one of the most potent accentuators of aggression in many species. It has profound consequences for dispersing species members and groups (Waser and Wiley, this volume), acting as a powerful modifier of the effects of distance-increasing and -decreasing signals, as well as of those signals that maintain dispersal or proximity (Tinbergen, 1959; Marler, 1968, 1976a; Kummer, 1971). Xenophobia in man lends itself to the perpetration of a group structure in which spatial companions tend to remain together. These are likely to be kin in both man and many other species. Indeed most of the conditions we have listed as favoring intimacy of communication in a group tend to increase the likelihood that communicants will be more closely related than randomly selected individuals from a deme, a virtual precondition for the evolution of shared, compatible mechanisms for signal generation and perception.

Communicative familiarity thus becomes a fundamental issue. Much signaling may be designed to permit companions to expose themselves to each other in many different circumstances, with ample opportunity for each to know how the others smell and sound, as well as how they look and how they are likely to behave in a variety of situations. The dynamics of marginal acquaintanceship, of forgetting what companions are like and what they do, may prove fundamental in separating the in-group from the out.

We know of examples of animals' forgetting one another. Something like this must occur, for example, when a troop of primates divides, severing long-established bonds and gradually turning familiar companions into strangers (e.g., Angst, 1973). Species differences in social organization may derive in part from variations in the rates at which strangers can become familiar and differences in what they must do to achieve this familiarity. Equally important may be the rates at which previously familiar individuals become strangers, the divergence perhaps hastened by their failure to perform particular activities, such as mutual grooming or greeting behaviors, that might otherwise delay the schism (e.g., Barash, 1974a). The delicate balance between strangeness and familiarity may be the ultimate function of much highly redundant and time-consuming signal behavior (Marler, 1976a), perhaps also involved in within-group discrimination of immediate from more distant kin (e.g., Massey, 1977).

STEVEN GREEN AND
PETER MARLER

A more complex signal vehicle for discriminating kinship groupings from others is provided by learned dialects in some bird songs (Marler and Mundinger, 1971). Several attempts have been made to explain their functional significance by perhaps providing reproductive advantages for individuals bound in kin groups or regional demes. One possibility is that if the dialects serve as population markers and encourage birds to settle and mate with members of the birthplace population, they perhaps act to perpetuate local physiological adaptations or races (e.g., Marler and Tamura, 1962; Nottebohm, 1969, 1975, 1976; Nottebohm and Selander, 1972). Both male and female white-crowned sparrows are most sensitive to the dialect learned in youth. In addition, there is direct evidence that a dialect boundary blocks gene flow by diverting the settling patterns of the young of both sexes back into the natal dialect area (Marler, 1970; Milligan and Verner, 1971; Baker, 1974; Baker and Mewaldt, 1978).

Dialects may be a special case of a more general propensity for birds to vary their behavior according to the unfamiliarity of a stranger's song. Playback of recorded bird songs has revealed a widespread tendency for stranger's signals to evoke more intense attack and repulsion than the familiar songs of immediate neighbors (e.g., Falls, 1969; Kroodsma, 1976; Wiley, 1976). Given that young birds are prone to settle near their birthplace, repulsion of birds with strange songs may also encourage the formation of local kinship groupings. A significant amount of signaling behavior may in fact be directly or indirectly concerned with the genetic structuring of local populations, serving by one means or another to aid the discrimination of close kin from nonrelatives.

SEX AND AGE

Another significant contribution to social organization derives from signal features that permit a receiver to identify a signaler's sex and age class. Static properties of the organism are often involved, such as coloration or size of the body or external structures. The issue of sexual dimorphism in signals would merit independent treatment. There are many cases of signals that are present in the repertoire of one sex and absent from the other, as, for example, in bird vocalizations (Nottebohm, 1975). The extent of such discrepancies varies in relation to many considerations, one being the intensity of sexual selection (Selander, 1972). It is especially acute in polygamous species, which tend to exhibit the most extreme sexual differences in signal repertoires, as in grouse (Wiley, 1974).

Size differences may contribute to age-specific signal structure, as in anuran songs. In the bullfrog, sounds of intermediate pitch, such as are offered by subadult males, actually inhibit the responsiveness of fully adult males to them (Capranica, 1966). Gautier and Gautier-Hion (1977) have plotted the changes of pitch with age in *Cercopithecus* monkeys, proving a ready basis for determining the age of the signaler. More subtle are the increases in the song-repertoire size of canaries with age, described by Nottebohm and Nottebohm (1978). Age-related song features may recur in other songbirds, providing possible cues by which

females can compare the ages of potential mates. Even more elaborate in this regard are the temporal castes of social insects (Wilson, 1976).

THE SIGNAL ADDRESS

Some signals point to an addressee, and some point to an external referent. We need to distinguish clearly between these two alternatives. Hailman (1977) has adopted Charles Pierce's term *index* and has used it for both functions, although he indicated that the original application was for signs that point out their referent objects. We propose that the term *indexical* be kept for signals that indicate referents and that the term *deictic* be used for signals that point out addressees.

DEICTIC SIGNALS

The response given to a signal may vary, depending on whether a receiver perceives itself or someone else as the addressee. The possibilities of addressing vary with the sensory modality used. It is most direct and unambiguous with tactile and chemotactic signals (by touching the addressee) and with visual signals (looking toward or otherwise orienting to the addressee). As Hailman (1977) illustrated, there are abundant animal examples of deictic addressing in the orientation of threat or courtship displays by fish, birds, and mammals, often clarified by special structures and markings.

Students of human nonverbal communication have found multitudes of examples of the use of looking, either unilateral or mutual, in deictic specification of signal addressees. The mode and temporal patterning of looking also serves as a mediator for meanings of other signals, such as speech, for which it provides an important accompaniment (Kendon, 1967; von Cranach, 1971; Exline, 1971; Argyle and Cook, 1976; Duncan and Fiske, 1977). Primatologists are becoming aware of the importance of recording the directed gazes within groups of monkeys and apes in the process of establishing patterns of social interaction (Chance, 1967; Chance and Jolly, 1970). There can be little doubt that the study of social looking behavior would be revealing in other mammals and in birds.

In speech we use what may be defined as *nominal addressing* in the form of personal or group names. There is a sense in which the distinctive contributions that each pair member makes to duets in many birds and certain primates could be thought of as names, eliciting as they do a response from only one particular individual.

SELECTIVE ADDRESSING

Independent of the existence of deictic and nominal signal components, there is another sense in which one may think of signals as being addressed. Many signals appear to select a particular subset from the audience as respondents. We call this *selective addressing*. Consider, for example, an impala giving an alarm snort on seeing a leopard, a male bird singing on its territory, and an infant monkey

screaming after being left unattended by its mother. Even though there need be no deictic component in any of these, the implicit or selected addressees can be inferred in each case from the potential range of responding animals, varying from broad to narrow.

The range of potential responders to the impala call is large, including not only its own neighbors and kin but all other herd members and other species, including baboons, as well (Washburn and DeVore, 1961). The birdsong is also broadcast, but it is addressed to a narrower audience—a mate and several rival males—and normally evokes responses only from these two classes of receivers. The infant monkey, although not necessarily directing or beaming its screams, is nevertheless calling its mother and will probably evoke no response from any other group member unless eventually a sibling or its mother's sister responds.

Thus, one may think of the range of selected addressees for even a broadcast signal as broad in some cases and narrow in others. For each signal, the size of the class of respondent animals is a different proportion of all animals receiving it. This interpretation can be extended further. A sexual signal might be thought of not so much as commanding sexual behavior in respondents as selecting or "addressing" respondents already predisposed to sexual interaction.

When a receiver perceives a signal originating some distance away, often the first detectable response is no more than a change in its orientation or spatial relationship to the signaler. Indeed, the dynamics of social spacing are important in building the distinctive attributes of societies (Kummer, 1974; McBride, 1978; Waser and Wiley, this volume). Both aggressive and alarm signals may elicit the withdrawal of a receiver. Signals that eventually elicit very different responses—attack or copulation—may first elicit an identical response, namely, signaler approach. Response patterns diverge later in the interaction, only after further signals have been received or more contextual information is available.

Approach to a signaler may be followed by many types of interaction. While it is implicit in much of our thinking that the eventual response selected in the signal receiver is specified by the same signal that elicited approach, we must remember that not all who receive a given signal approach in the first place. This is obvious in the case of the infant monkey screaming for its mother or an adult female soliciting for copulation. A female monkey who has recently given birth has a different set of response predispositions than an adult male engaged in consortship behavior.

One may think of an infant distress call and a female copulation signal as being, in this sense, directed to different selected addressees, rather than simply as triggering sexual or parental behavior. The specification of selected addressees might comprise a supraspecies grouping, an individual or group of conspecific animals, or a subgroup of a particular age, sex, rank, or kin class. It might also be made according to transitory physiological states, as when a food signal evokes responses from hungry animals but not from satiated ones. Finally, the specification might also be made indirectly by selectively addressing respondents finding themselves in a particular context, as when alarm calls elicit a response from animals out in the open but not from others deep in cover. We are reminded that the receiver's context is just as important as that of the signaler in determining whether and what kind of response a signal evokes (Prushka and Maurus, 1976).

A signaler can indicate an external referent to a receiver indirectly, by iconic or noniconic means, or directly, by indexing. We have surely underestimated the power of indexing in animals by orienting the gaze, the body, or external structures such as a pinna toward the referent (Hailman, 1977). Indexing becomes especially informative in combination with affective expressions of arousal. The point is best illustrated with a quotation from Norbert Wiener (1948):

Suppose I find myself in the woods with an intelligent savage who cannot speak my language and whose language I cannot speak. Even without any code of sign language common to the two of us, I can learn a great deal from him. All I need to do is to be alert to those moments when he shows the signs of emotion or interest. I then cast my eyes around, perhaps paying special attention to the direction of his glance, and fix in my memory what I see or hear. It will not be long before I discover the things which seem important to him, not because he has communicated them to me by language, but because I myself have observed them. (p. 157)

AFFECT PLUS INDEXING

As long as the receiver is aware of the context of a signal production, the cooperation of indexical and affective signal properties has an enormously rich communicative potential. In a discussion of the origins of language, Premack (1975) developed further this theme that it is easy to underestimate the communicative potential of a combination of indexical and affective signaling:

Consider two main ways in which you could benefit from my knowledge of the conditions next door. I could return and tell you, "The apples next door are ripe." Alternatively, I could come back from next door, chipper and smiling. On still another occasion I could return and tell you, "A tiger is next door." Alternatively, I could return mute with fright, disclosing an ashen face and quaking limbs. The same dichotomy could be arranged on numerous occasions. I could say, "The peaches next door are ripe," or say nothing and manifest an intermediate amount of positive affect since I am only moderately fond of peaches. Likewise, I might report, "A snake is next door," or show an intermediate amount of negative affect since I am less shaken by snakes than by tigers.(p. 591)

Premack thus indicated the further increment in information about external referents that can accrue if a receiver not only perceives affective signal components but also identifies the signaler. Given foreknowledge of, for example, individual idiosyncrasies in feeding preferences or in fearfulness of different types of predator, a receiver may be able to guess at the nature of a particular signaler's external referent quite accurately, even without indexical signal elements. With these added, the precision is even greater. It seems probable that animals, like children (Goldin-Meadows and Feldman, 1977), do a great deal of communicating about external phenomena by this combination of relatively simple signal elements and a comprehensive knowledge of signaler predispositions based on intimate social familiarity.

ENEMY SPECIFICATIONS

Data are difficult to gather, but there are promising leads. Careful study of the external referents of alarm signals, for example, is yielding new insights. Even

with the alarm pheromones of ants, a high degree of enemy specification is sometimes achieved (Wilson, 1975a). The same is true of ground squirrels' alarm calls, although here there is also the possibility of supplementary information from the signaler's identity. There are striking sex- and age-class differences in the frequency with which different ground squirrels' alarm calls are uttered (Sherman, 1977). It would be most interesting to know whether the effective predator situations for alarm calling differ consistently between these classes and whether receivers can sex or age a caller and modulate their responses accordingly.

There is a potential for using signal indexing in enemy specification. Sherman (1977, p. 1251) described how alarm callers usually sit upright, often on prominent rocks, and look directly toward the advancing predator, thereby seemingly directing the attention of conspecifics toward it. He noted that "I could often locate the predator by following the gaze of several alerted animals, whether or not they were calling. I do not know whether ground squirrels also use this cue." He added, "In eleven instances a ground squirrel probably could not see an advancing predator because of the ground squirrel's position in a swale: on eight of the occasions (73%), the ground squirrel sat up and oriented itself in the same direction as a conspicuous, calling conspecific, thus towards the apparently unseen predator."

Melchior's (1971) study of Arctic ground squirrels adds a further component. Noting that an observer could follow the course of a ground predator through a squirrel population by orienting to the squirrel sounds, he added that if the predator moves directly toward a squirrel, the squirrel typically runs down its burrow, calling as it does so. The result is a series of fading chat calls that locate the predator's position more precisely, even if it is invisible to a human receiver. Whether the squirrels can also locate the position using this cue has to be determined.

Signal features that correlate with varying degrees of arousal elicited by the referent are important in locating an unseen predator by the calling of others. Leger and Owings (1978) studied alarm calls in California ground squirrels, which, like many squirrels, have two classes of alarm calls: "chatter-chats," especially for ground predators, and "whistles." The latter are given mainly for aerial predators, though occasionally in social chases. Leger and Owings went on to comment on whistles as follows:

It is also possible that the multitude of dimensions along which these calls vary provide sufficient diversity to permit division of the signal spectrum into a graded subset referring to predators and a second lower alarm level graded subset referring to social interactions. Our anecdotal observations are compatible with this latter hypothesis.

For example, whistles elicited by social chases seem to have lower sound intensities than those evoked by flying raptors. Similarly, predators such as bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) elicit highly frequency-modulated chatters with about seven notes, whereas one- or two-note noisy calls signal agonistic interactions (Leger and Owings, 1978). Equivalent data are reported for the round-tailed ground squirrel (Dunford, 1977).

There are, of course, many examples from animals of correlations between

such measures of signal intensity as concentration, amplitude, rate, and morphology, and the intensity of stimulation that the signaler receives. However, the ground squirrel data hint at the possibility that, assuming receivers to be responsive to such signal properties, they may infer more from such signal variations than just an intensity judgment, given access to enough additional information in natural contexts.

AROUSAL, EMOTION, AND EXTERNAL REFERENTS

While signals that are mainly a reflection of degrees of arousal can in some circumstances convey a great deal of information about external referents, there are obvious limits to what such a system can achieve. It would be advantageous if the signaler could add even a general indication of the class of referents being signaled about. Otherwise, a hungry youngster, for example, might approach a referent indicated by its mother as worthy of positive arousal, only to discover that it denotes not a choice morsel but a desirable mate. If only on the basis of time and effort saved, we would expect natural selection to favor means by which a signaler could indicate whether the referent is environmental or social in nature. Environmental referents might include hazards, such as predators or bad weather, or resources, such as food, drink, or a safe resting place. Social referents might include a favored companion or an infant in need of care, both worthy of approach. An enraged male or a protective mother would be social referents to be avoided.

If we consult the literature on the complexities of human emotional states and their classification, it is clear that much more than a single arousal dimension is involved. There is some concurrence that four dimensions go a long way toward a comprehensive classification of the various human emotions. As an illustration, we present here a diagram from Plutchik (1970), with the major categories in the center and some equivalent ethological categories of ongoing behavior about which signals might be emitted in the outer ring (see Figure 14). It will be noted that two of these, C and D can be matched with classes of social referents and environmental referents, respectively. The other two may be viewed as an arousal dimension (A) and an approach-withdrawal dimension (B). Such a hypothetical system for human emotions can reasonably be generalized to animals, at least to birds and mammals. Looking at the patterns of behavior indicated in the outer ring, one could readily assign different signals, both visual and auditory, to each of them and reasonably infer that a receiver's assessment would include the external referents so indicated.

Such a hypothetical emotion-based signaling system would provide an economical explanation for much of the signaling behavior of animals, especially if one allows for some degree of mingling of emotional states and for variations in the intensity of each. Both Eisenberg (1976) and Green (1975a) have described socially complex primate signaling-systems that can be viewed in this light. A system of this type would suffice for receivers to assess that a signaler has perceived quite specific referents.

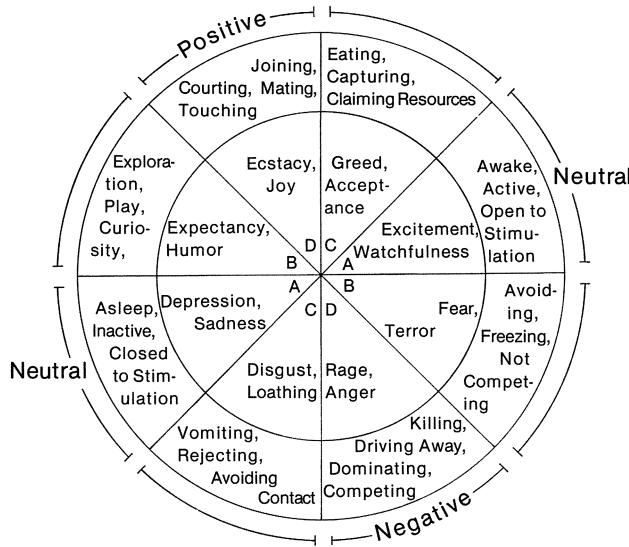


Fig. 14. Human emotional states (inner ring) with some equivalent ethological activities (outer ring) arranged according to whether their connotations are positive, negative, or neutral. A–A = a possible arousal-depression dimension. B–B = a locomotor approach–withdrawal dimension. C–C = an object acceptance–rejection dimension. D–D = a social engagement–disengagement dimension. Modified after Plutchik (1970).

FOOD SPECIFICATION

There are reliable descriptions of food calls in such birds as quail, jungle fowl, and other gallinaceous birds (Collias and Joos, 1953; Kruijt, 1964; Williams, Stokes, and Wallen, 1968; Stokes, 1971; Stokes and Williams, 1972; Anderson, 1978). The calls are used by males as a component of courtship feeding to attract females and by both sexes to attract young to food, often in conjunction with a visual "tidbitting" display. The melding of feeding and sexual behaviors perhaps illustrates the possibility of mixed emotional states already alluded to above and as is described in much of the ethological literature on display analysis (Tinbergen, 1940, 1952; Moynihan, 1955; Morris, 1956). Leaving on one side those species in which the behavior has become more ritualized and involves nonfood objects, such food calls clearly denote an external referent. Moreover, they are used not for just any edible item but for highly preferred foods, such as live insects (Williams *et al.*, 1968). That an intensity component is involved is indicated by the increased likelihood of quails' food-calling to nonpreferred food if they have been deprived (Williams *et al.*, 1968). Similarly, among primates, the rough grunting of the chimpanzee that this species uses as a food call (Marler, 1976c; Marler and Tenaza, 1977) attracting others to come and share is given only to highly preferred foods, such as palm fruits or bananas.

SYMBOLIC SIGNALING: ALARM CALLS

There are cases of more narrowly specified external referents, however, that seem to call for still further-refined internal representations. We have already

commented on the recurrence of two types of alarm calls in ground squirrels, one for terrestrial predators and the other for aerial ones. Owings and Virginia (1978) found that the great majority of California ground squirrels' whistles were given to flying raptors, usually when they were less than 15 meters above the ground. In the few cases of whistling in a social chase, there were indications that the calls were softer, as already mentioned. In separate tests with dogs as predators, whistles were heard as the dog rushed to the squirrel, which retreated into a burrow, but the great majority of trials elicited the chatter-chat alarm call instead. Owings and Virginia noted a further intensity dimension in that the number of notes per chatter-chat call increased when a dog abruptly changed its speed or direction of movement, and calling rates were higher at the beginning of an encounter with a dog than at the end. Note-duration and the number of calls containing an ascending frequency-modulation component also decrease in the course of a bout. Although there appeared to be several referent-related intensity dimensions to these calls, it does not follow that the most significant aspect of whistle and chatter-chat calls is stimulus intensity, as opposed to stimulus quality.

Leger and Owings (1978), in fact, made a special point of emphasizing the specificity of the external referents for these two kinds of calls. Their description of the responses to the playback of the two calls notes that a basic qualitative difference is exhibited even though there is always a quantitative element as well. Both kinds evoke immediate running, but whereas whistles then typically evoke walking and any upright posturing is considerably delayed, the upright position follows chatter-chat immediately, facilitating search for a terrestrial predator. Adopting the upright posture immediately after perceiving a call that signifies a nearby raptor would be an invitation to attack, a significant point since predators are known to pursue and strike at squirrels giving alarm calls (Sherman, 1977). Thus, the squirrels behave as though the two alarm calls have qualitatively different meanings for them, even though a change in the number of separate components in a chatter-chat also modifies the intensity of receiver responses.

Many birds have two equivalent classes of alarm calls for the same two types of predator (e.g., Marler, 1955, 1957). Again, there are referential intensity components, as when a male chaffinch that typically gives a whistle call to a flying raptor also utters it to a person approaching his nest with young. Yet, intensity variations alone do not suffice to explain the very different responses to the two calls: flight to cover, stationary crouching, and upward visual scanning in response to whistles, and conspicuous approach and mobbing behavior, in the case of the "chink" alarm call, the functional equivalent of the ground squirrel's chatter-chat.

Struhsaker (1967) discovered a remarkable array of alarm calls in the vervet monkey (Table 1). Two have rather generalized external referents and seem to function primarily to alert others. One, the "chutter," is associated with either a man or a snake, especially the latter, possibly with a difference in structure for these two referents. The "threat-alarm-bark" is given on sighting a major predator, typically a carnivore. It evokes not approach and mobbing, as is the case with the chutter, but precipitant flight to cover and ascent into trees. The "chirp" call of females has similar external referents, and receivers respond similarly. Finally there is a sixth call, the "rraup," for which the most typical referent is the initial sighting of an eagle, generally in flight. Here, the response is almost the opposite

TABLE I. VERVET MONKEY ALARM CALLS^a

	Uh!	Nyow!	Chutter	Rraup	Threat alarm-bark	Chirp
Typical stimulus	Minor mammal predator near	Sudden movement of minor predator	Man or venomous snake—but the chutter is structurally different for man and snake	Initial sighting of eagle	Initially and after sighting major predator (leopard, lion, serval, eagle)	After initial sighting of major predator (leopard, eagle)
Typical response of troop members	Become alert, look to predator	Look to predator, sometimes flee	Approach snake and escort at safe distance	Flee from tree-tops and open areas into thickets	Attention and then flight to appropriate cover	Flee from thickets and open areas to branches and canopy

^aAll calls are given by adults of both sexes, except the female "chirp." After Struhsaker (1967) and Cheney and Seyfarth (personal communication).

of that for the threat-alarm-bark and the chirp, namely, sudden dropping out of the treetops, as well as fleeing from open areas into thickets. Signal reactions are somewhat context-dependent, differing according to whether the receiver is in the treetops or out in the open. In each case, one can see the adaptiveness of the particular mode of response. Again, there are obvious intensity components, but variations in arousal level alone are inadequate to explain this remarkable array of signals and receiver responses.

The conclusion seems inescapable that these calls serve as labels or symbols for the different classes of external referent that they represent. This function is supplemented in many and perhaps all cases by varying degrees of arousal or affect that indicates to receivers the degree of priority they should give in assessing signal meaning.

ARTIFICIAL COMMUNICATION SYSTEMS

That there is a rich *capacity* for use of signaling behaviors as symbols for objects, attributes, operations, and even concepts is indicated by the performance of apes trained to use artificial communication systems based on human language and used between animals (Savage-Rumbaugh, Rumbaugh, and Boysen, 1978) as well as between animal and experimenter. Aware of the extent to which chimpanzees use their hands in natural communication, Gardner and Gardner (1971, 1975) used the hand sign language of the deaf, American Sign Language (Fouts and Rigby, 1977). With various training techniques, including shaping, guidance, and observational learning, as well as imitation, they were able to teach the young female chimpanzee Washoe to perform 85 signs, each equivalent to a word, in a three-year period. Included were many nouns, such as *flower*, *dog*, and *toothbrush*, adjectives such as *red* and *white*, prepositions such as *up* and *down*, and verbs such as *help*, *hug*, and *go*. Many words were used in appropriate combinations, such as the invitation for a walk, *You me go out hurry*, or the request *Please gimme sweet drink*. The appropriateness of combinations of actions and objects indicates a grammar not very different from that of young children in early two-word sentences (Brown, 1970; Gardner and Gardner, 1974). Another young chimpanzee, Lana, has demonstrated her prowess with a languagelike system based on keyboard signals to a computer, which talks back to her in a similar fashion (Rumbaugh, 1976).

The chimpanzee Sarah was trained by Premack (1971) to use colored plastic shapes instead of words, these shapes serving as symbols for objects and actions. A blue plastic triangle served as the symbol for *apple*. The one for *banana* was a red square, and so on. The relation between symbol and referent was noniconic, the shape lacking any physical resemblance to the object to which it referred. After Sarah was trained to present the appropriate shapes when she wanted a piece of fruit, other nouns and then verbs were introduced, such as *give*, *wash*, and *insert*, each performed by the experimenter when Sarah presented the appropriate symbol.

Within her repertoire of about 130 words were not only many nouns, verbs, and adjectives but also more complex constructions, such as *same*, and *different*, questions, and the conditional *if-then*. A particular word order was required of

Sarah in arranging the symbols on a board. Premack aimed more to test the conceptual abilities of Sarah than to see whether she could use language, reasoning that in our own species, the one is closely mirrored in the other.

Can one infer that Sarah thinks in the language of these plastic shapes? Premack says yes. One test, he feels, is the ability "to generate the meaning of words in the absence of their internal representation." Premack asked Sarah to perform a feature analysis of an apple, using the plastic words to name its color and shape, the presence or absence of a stalk, and so on. Asked to perform a similar analysis of the plastic word for apple, the blue triangle, she answered by describing an apple once more and not the blue shape. This test bears on a further point, Sarah's ability to consider something that is not there at the moment—implying internalization and illustrating the critical language requirement of displacement in time.

The importance of appreciating the natural motives of a subject in trying to understand its use of language is well illustrated by errors that Sarah made in the use of shapes for different fruits. Required to present the appropriate shape for a fruit before she was allowed to eat it, she chose the wrong word surprisingly often. In a moment of inspiration, Premack wondered whether Sarah was asking for what she preferred rather than for what was before her. An independent series of tests of her fruit preferences provided the explanation. The word for banana offered when confronted with an apple was not an error but an attempt to get the experimenter to give her something else, suggesting again that she truly understood the symbolic significance of the shapes.

The accomplishments of chimpanzees using languagelike systems of signaling to converse with an experimenter are surely the highest animal attainments demonstrated so far. Yet, they also raise a curious dilemma. If a chimpanzee can indeed achieve some elementary competence with language when provided with an appropriate vehicle, why is the evidence for symbolic usage in nature so limited? It may well be that the paucity of our knowledge of natural communication in animals is such that we can hardly judge whether such abilities are demonstrated in nature or not. However, it is also possible that in most social interactions, animals have little use for languagelike patterns of communication but that occasions do arise where those individuals and families possessing better cognitive capacities and signaling competence are more likely to survive, thus favoring the evolution of languagelike capabilities. The circumstances may be infrequent but the selection pressures strong.

From a biological viewpoint, symbolic communication is highly specialized, working most efficiently with particular kinds of problems. For many of the uses to which animals can put their signals—largely social in nature and taking place within groups in which members have become familiar with one another over a long history of acquaintanceship—other kinds of signal usage can probably do the job better.

SIGNALS AND INTERNAL REFERENTS

Our treatment of communication emphasizes the pivotal roles of internalization in both signal production and signal reception. Production depends on a

prior assessment of the situation made by the signaler. The instigation of an assessment is often triggered by an encounter with an external referent in a given context. However, we have noted that there are variations in the uniqueness of connections between a signal and its input data. One major source of multiplicity of inputs to a given signal arises from contributions to the assessment by both external and internal referents.

Thus we use the word *food* both in response to food placed before us and in association with memories of food, as when we become hungry. A nestling bird gives begging calls spontaneously when it is hungry, although calling can also be triggered by the sudden appearance of food or of a food provider, or even of a stimulus that is an adventitious but regular accompaniment of the arrival of the provider, such as jogging of the nest.

Similarly, an ovulating female finch may break into the sexual solicitation display spontaneously or upon confrontation by her courting mate. The situation is somewhat different here, however, than in the case of a begging nestling. While the external referent for the latter is clearly food or something associated with it, the appropriate external referent for a copulation call is not so easy to identify. It seems inappropriate to name the male mate as the external referent and more pertinent to name as an internal referent for the call the current, transient internal state of the female, namely, her readiness to copulate.

At this point, the importance of internalized assessments again becomes evident. The assessment incorporates not only external referents but the entire context, both external and internal. Thus, for a female finch at the time of ovulation, the arrival of her courting mate has a similar significance to that of her own current physiological state, namely, that this is an appropriate moment for copulation and for the production of a signal that will ensure this response from her mate. Similarly, in the case of begging calls, despite their potential linkage to both internal and external referents, the underlying assessment for spontaneous begging and for begging triggered by food is similar, namely, that this is an appropriate moment for feeding solicitation.

INTERNAL AND EXTERNAL TRIGGERING

It should be the rule rather than the exception that many signals can be both externally and internally triggered, since the same fundamental assessment can often be precipitated by different trains of events. As functional alternatives, internal and external triggering are, of course, vitally important. While internal triggering is frequent in the case of food signaling, it is rare or even absent for alarm calling in most ordinary situations. Alternatively, in the case of a male birdsong with largely tonic communicative functions (Schleidt, 1973, 1977; Heiligenberg, 1977), triggering is primarily internal, although again external triggering is possible on, say, hearing the song of a neighbor.

Giving internalized assessments a central role makes it easier to incorporate the contribution of affective or emotional factors to signal production. Say that a male signaler is in the mood for reproductive behavior. This might arise because of some long-term physiological trend that reflects such changes in the physical environment as day length, or because of an endogenous reproductive trend (e.g., Gwinner, 1975), or because of a carryover from recent sexual encounters, or

because of entry into an environmental situation in which sexual encounters have occurred in the past. These factors may all influence the assessment of, say, copulation calls from the female of a neighboring pair and may increase the likelihood that he will then invade their territory and direct aggressive signals at the neighboring male, perhaps then stealing a copulation from his mate. On another occasion, perhaps at a different season, when the male is preoccupied with feeding his own young, there might be no visible response to a female's copulation signals at all.

In no case can one ignore the role of internal factors in determining the nature of a signal-generating assessment. Indeed, this is true not only of signal production but of all stimulus-response situations. Even in the most reflexive behavioral mechanisms, internal factors play a major role in determining which sensations evoke responses and which properties of a response are stimulus-locked, rather than being internally programmed (Marler and Hamilton, 1966; Bullock, 1961).

Consider as another example a male black-and-white colobus monkey giving a threat display and roaring at an intruding group. The signals are clearly provoked by the intrusion, and members of a neighboring troop might be able to infer the presence of the invading group from the signals perceived. The assessment by members of the intruding group would include the fact of having been detected by the resident male. Although the referent is intrusion, the most significant aspect of the signaling male's assessment is that this is an occasion for expressing rage and, ultimately, physical assault. The linkage between signal form and underlying assessment makes it easier for us to understand the similarities, from the signaler's viewpoint, between these circumstances of colobus roaring and another situation in which it is given, namely, overflight by a monkey-preying eagle (Marler, 1972; Oates, 1977). There is no specific and unique external triggering that might be thought of as a referent for all roaring, but the signaler's underlying assessment might well be similar—that this is an occasion for a state of aroused hostility and alertness. Thus, members of a neighboring troop might not be able to distinguish on the basis of the roaring signal alone whether the referent is an eagle flying over or a colobus intrusion. The task would be made easier if males in other troops in the area began roaring, as often happens during eagle flights.

COMMUNICATIVE FAMILIARITY AND SOCIAL ORGANIZATION

Communication is both an instrument for organizing societies and a mirror for social organization. Just as processes of communication serve to establish and operate networks of social interaction among animals (Hinde, 1976; Hinde and Stevenson-Hinde, 1976), so the details of the social matrix within each society establish the contexts on which communication depends. When an animal makes an assessment of a signal with social import, it takes account of the current situation and of relevant past social experiences. The details of social networks vary from species to species and population to population. The chain of logical steps linking communication systems to diverse patterns of social organization is long and difficult to analyze, requiring a finer appreciation of social structure than

we now possess. While no comprehensive analysis of relationships between semantics and social organization is yet feasible, one general principle is likely to pertain.

In certain circumstances, such as when communicants are completely familiar with one another and with the events precipitating signaling, prior experience makes a maximal contribution to the process of signal assessment. Such circumstances are especially likely to arise with long-term pair bonds and in species that are long-lived, with overlapping and cohabiting generations residing in assemblages of relatively stable membership. Another factor favoring complete familiarity is a social structure in which, at one time or another, members play a variety of social roles, such as dominant and subordinate, mother and daughter, young and adult. Adding further to familiarity are individual life histories in which animals pass through phases more than once in a lifetime—as with recurring reproductive cycles as opposed to a single period in a lifetime. Thus, lengthy, multipurpose, mixed assemblages are more predisposing to general communicative familiarity than those formed for a special behavioral function, such as a reproductive lek or a transient feeding group. The physical environment intrudes considerably into social organization, and intimacy with particulars of geography is another predisposing circumstance, as arises in philopatric species that are either permanently resident in an area or return to it repeatedly in the course of a life span.

There are, of course, many difficulties with such a prediction, such as defining the extent of “familiar groupings.” It is obvious that a lion pride qualifies, but perhaps more solitary carnivores have a range of familiar acquaintances almost as wide, as Leyhausen (1975) has suggested for the domestic cat. The same may be true of other so-called solitary species (Eisenberg and McKay, 1974; Waser, 1975b). Both Brown (1964) and Barash (1974b) have shown in different ways that the range of acquaintanceship of solitary mammals and a pair-living bird extends into the neighboring community. In social circumstances that fulfill all of these conditions, many communicative interactions have been repeatedly rehearsed. As a result, participants are often able to anticipate the prospective features of evolving interactions. We may therefore expect to see effective communication achieved by experienced interactants with signals that are uncompleted and undramatized, including subtly changing points along graded signal continua. The social organization of most nonhuman primates satisfies these conditions remarkably well (Crook, 1970; Eisenberg, Muckenhirn, and Rudran, 1972; Struhsaker, 1975), and there is in fact evidence of very subtle acoustic discriminations used in their vocal communication (Gautier, 1974, 1978; Green, 1975a; Eisenberg, 1976; Gautier and Gautier-Hion, 1977). Other animals that might well qualify are wolves and lions, porpoises and whales, bats, elephants, some ungulates, and perhaps some birds such as the long-lived social species of corvids, larids, galliformes, anseriformes, and psittaciformes. In all of these, there is reason to suspect that within-group signaling is subtle and that contextual cues play a major role in determining how signal receivers respond.

NEW DIRECTIONS

While the framework we have suggested for viewing animal communication is, at best, a tentative formulation, it serves to reveal significant gaps in current

knowledge. Filling these gaps will be important for developing alternative frameworks. Progress will depend in a fundamental way on advances in understanding the evolution of sociality and the physiology of behavior. In addition, we suggest that attention to the following topics may be profitable.

SIGNALING: SPECIFICATION OF CONDITIONS FOR SIGNAL PRODUCTION

There is an urgent need for progress in understanding the rules, and perhaps the mechanisms, by which a signaling animal forms an "assessment" of a situation. In addition to defining the range of external situations in which signals occur, it is equally important to specify the internal conditions for the production of different elements of a signal repertoire. Means are not currently at hand to investigate much of the physiology of signaling behavior. For example, to determine just one small but crucial component of an animal's internal state, we need techniques for rapid tracking of circulating levels of hormones.

As a more indirect route to specifying the internal state of a signaler, one can describe its prior history and immediate context. If field studies reveal developmental histories that differ consistently among individuals producing different signals in the same situations, the variables identified can be systematically manipulated in experimental studies. As demonstrated by studies of the ontogeny of birdsong, control of experiential factors can illuminate sources of individual variability. Experiments ranging in complexity from habituation studies to investigations of the internalization processes that underlie imprinting, for example, are appropriate but all too infrequent in animal communication research. We are just beginning to see serious attention paid to the effects on signaling of the presence of strange as opposed to familiar recipients. Closer attention to the effects of proximity of a signaler's close relatives on its signaling can only help in solving some of the puzzles emerging in the study of the evolution of communication behavior.

SIGNAL FORM: SELECTIVE PRESSURES AND DESCRIPTION

When a study suggests that the structure of a few signals, or even an entire species repertoire, can be best understood as the product of selection for such characteristics as localizability or maximizing transmission distance, it seems likely that there is often more to it than that. If hypotheses about signal form and function are to have predictive value, descriptions of signal morphology are required that are sufficiently precise to facilitate a comparative review of variation of the appropriate signal parameters and experimental manipulation of them. Perhaps one reason that questions about the adaptive features of signals are so frequently suggested but so rarely pursued is that signal patterns are difficult to define empirically and thus are elusive as a basis for theorizing.

The apparent simplicity of the process of physically describing a signal is deceptive. With some sensory modalities, such as taste or odor, molecular characterization is conceptually straightforward although technically difficult. With other kinds of signals, such as visual and auditory, questions of classification immediately thrust one into the complex arena of multivariate pattern analysis.

Signals can be described parametrically, by the use of many variables. The

initial task facing a classifier is to reduce the number of items while retaining those that are biologically relevant to the species under study. Sometimes, an explicit statement of the grounds for selecting variables and strategies for subsequent signal classification is presented, but all too frequently it is lacking. Many investigators have understandably relied on the availability of instrumental methods to select the dimensions for analysis. Thus, temporal patterning, frequency modulation, and amplitude modulation of acoustic signals may be emphasized but phase rarely mentioned. By the time a scheme for classifying repertoires is presented, the rationale for categorizing some elements as together and others as apart is often obscure. The lack of uniformity among researchers, even when examining closely related species, can only hinder the advance of animal communication studies.

With these difficulties in mind, we offer a few suggested guidelines about information to include in signal descriptions. Often, the effort involved in establishing signal repertoire categories also generates the data needed for interpreting them. For example, an explicit discussion of the rationale behind the choice of the stimulus dimensions used would enhance the usefulness of many studies by serving as a basis for testing alternative descriptive schemes, as well as facilitating comparative work. If technically feasible, electing to describe and classify signals along variables known to be perceptually salient for a species is often illuminating. Sometimes, patterns of signal usage provide clues to the likely relevance and importance of variation in different dimensions. Similarly, if the choice of boundaries between signal categories and the criteria for gauging variability within categories can be related to what is known of the sensory psychophysiology of the species, the usefulness of the classification is increased.

The presentation of data can both encourage and impede their use for further comparisons. Scatter diagrams describing simultaneous variation in two dimensions reveal more about the animals' natural signal units than statistical digests of the same information given separately. In like fashion, a histogram of the incidence of signal elements arrayed against the parameters used to erect repertoire categories is more revealing than a listing of boundary demarcations and a simple judgment as to whether the repertoire is organized in discrete or graded fashion.

While it may seem pedantic to enumerate such basic concerns about the presentation of quantitative data, literature surveys have convinced us that a recitation that may be self-evident to most readers is not so to all. Trying to relate signal form to social, environmental, and phylogenetic determinants is difficult enough without the handicap of insufficient and unsuitable empirical evidence.

CORRELATIONS BETWEEN SIGNAL PERCEPTION AND PRODUCTION

One fundamental goal of studies of animal communication is to identify the distinguishing features of signals that receivers use to classify them into socially significant categories. A related objective is to characterize the relations between the structure of a signal repertoire and the nature of the perceptual processing brought to bear on it (e.g., Zoloth *et al.*, in press). It would be surprising if a species' signaling did not take advantage of the general sensitivity and acuity of its

sensory capabilities. We must also consider the possibility of perceptual specializations, mutually adapted for the processing of communication signals. As epitomized in the concept of "innate release mechanisms," such specializations have long played a cardinal role in ethological theorizing about the mechanisms underlying social communication (Lorenz, 1970; Tinbergen, 1951). However, the interpretation of any degree of matching between signal and perceptual categories necessitates developmental studies as well (Marler, 1978).

The most extensive developmental studies, those examining birdsong, are concentrated on production aspects. Only recently has attention shifted to the effects of experience on perceptual performance (but see Peters, Searcy, and Marler, in press; Marler, 1978). Hybridization studies, chiefly on orthopterans and anurans, suggest a common genetic basis for production and perception. Much more work is needed on species that depend heavily on experiential factors (our own species included) if we are to determine whether a common neural substrate is involved (Liberman *et al.*, 1967). In addition to deprivation experiments, cross-fostering and hybridization studies are also needed, using avian genera that require auditory feedback for song development. The fact that in some bird species females can be hormonally induced to sing provides another avenue of approach to the relation between signal perception and production.

Progress in characterizing any commonality of rules dictating signal production and their perception is probably limited more by the paucity of perception studies than by any other factor. While there is a long and distinguished tradition of studies of sensation, relatively few of these have explored the areas critical to communication. Even with audition, the most extensively examined modality, we have little information on JNDs for the discrimination of complex acoustic signals and virtually none on changes in JNDs over the range of the acoustic signal parameters pertinent to the perceptual processing of a species' signals. Except for a few investigators now probing categorical perception in animals, the nature of multidimensional stimulus categories is unexplored (see Bullock, 1977, for reports of a recent conference on these issues).

Perception of socially significant signals in animals, if it parallels perception in man, involves more than simply sensory processing. Context-dependence and attention sets are involved, as well as other phenomena that call upon memory and collateral information. Is it meaningful to ask, for example, whether an animal detecting a stimulus can process it either as a communicative signal or not, depending on its character, as some think man can do, after deciding whether a sound is speech or nonspeech (Lane, 1965)?

A related area of inquiry, also rarely addressed, is the degree to which there are cross-modal perceptual interactions such as masking, facilitation, or more complex possibilities, yielding different percepts entirely for multimodal signals than expected on the basis of simple additivity.

RESPONSES: EFFECTS OF SIGNAL PERCEPTION ON BEHAVIOR

Looking at what an organism does after receiving a signal would seem the most straightforward route for studying communication. The approach has been

put to fruitful use in many studies, attacking the issue of temporal or sequential correlations, as the principal way to establish putative cause-and-effect relationships.

In most descriptive studies, contingencies of acts in a behavioral sequence or social interaction are reported qualitatively; for example, "The male usually does cartwheels after the female nods her head and rolls over." Wiepkema's (1961) studies of bitterling reproductive behavior were influential in developing quantitative analyses of intraindividual sequences of actions. Stokes's (1962a) study of blue tits employed similar quantitative techniques but emphasized interindividual sequence pairs. The preceding action by one animal was considered part of a signal to the other, whose response was measured. By comparing the degree to which response frequencies were contingent upon the presence or absence of antecedent acts, a quantitative foundation for inferring effectiveness of communication was constructed. Dunham (1966) elaborated on these methods in studying grosbeaks. He also measured proportions of different response categories contingent upon preceding actions but then used different combinations of single elements as the initial action.

Altmann (1965) elaborated stochastic analysis further in rhesus monkeys by examining the preceding actions further antecedent than the immediately prior event and calculating the additional reductions in uncertainty obtained by taking these into consideration. Actions were classified as gross patterns of behavior, apparently occurring as "natural units" (Altmann, 1962).

With today's easy access to computation facilities far more sophisticated than those available when these pioneering studies were performed, it is surprising how little advancement there has been on this front. In spite of severe methodological constraints on combining data gathered on different individuals and different dyads for sequence and interaction analyses (Chatfield and Lemon, 1970), this approach should be used more often, with inferences presented in ways that are interpretable to readers who do not wish to wade through enormous transition matrices. The major weakness in many applications of stochastic methods appears to be the neglect of a temporal dimension. Often, sequential action pairs are scored identically regardless of the time interval between components.

Applying somewhat different analytic methods to hermit crabs, Hazlett and Bossert (1965) emphasized the difference between the number of actions (responses) of each kind observed after each category of prior action (signal) and the number otherwise predicted. Expanding on these methods, Dingle (1969) compared such differences at different stages of interindividual agonistic bouts in mantis shrimp. By contrasting the figures from early, middle, and final periods of these encounters, he could determine how responses to signal-category actions are influenced by the contextual factor of elapsed time. Baylis (1976) also employed a transition matrix of preceding and following acts and used it to compare divergences between observed and expected value but added the novel twist of using the observed values of one species of cichlids to calculate the expected values for a different species against which the observed for this latter species were compared. He was thus able to perform interspecific analyses that provide a quantitative basis for judging similarities and differences in patterns of social communication.

The analyses mentioned above, comparing observed and expected numbers of responses, all concentrate on responses that occur much more often than expected (facilitated) and less frequently than expected (inhibited). Many responses, however, appear to follow particular signals about as frequently as one would predict in the absence of that signal. The preceding actions are therefore anomalous as signals when examined by these response-oriented techniques. The methods, however, do not purport to look at the possibility of signal effects other than those reflected in the very next actions of the respondent.

Nelson (1964) addressed this issue in a study of courtship in glandulocaudine fish by methods that deserve further application. Employing the comparison of observed and expected frequencies of responses, he also added the cumulative effect of prior actions by combining them into categories of preceding behavior in a fashion similar to Altmann's (1962) calculations of higher-order stochastic transitions. Nelson's analysis also examined the responses at intervals of varying duration after the signal actions. His study thus combines many of the best features of the other methods, permitting the sorting of signal actions according to the time for which they influence subsequent actions of a partner.

Rand and Rand (1976) extended the stochastic analysis methods by not only looking at transitions from signal patterns to subsequent behavior but also examining the joint effect of sequences of signal exchanges between individuals. Feedback of information on the nature of responses to the signaler, though little studied, must be important in many social species.

These latter two studies begin to address the issue of internalization of signal information by social interactions, only later manifest in behavior. Studies of sensitive periods, as in imprinting or song learning, illustrate other cases in which adult responses are influenced by information internalized early in life. Effects of signals on responses over interim periods that are neither very recent nor during a sensitive period early in life embody the majority of an animal's experience. Yet, studies that explore effects of communication on an animal's behavior beyond the immediate future are virtually unknown. This neglected area is undoubtedly procedurally difficult, but the rewards could be substantial.

With Smith (1977), we have tried to emphasize that responses to signals vary as a function of context. In the above studies, only encounter duration was explicitly considered as a contextual factor, although some of the antecedent signal categories, as defined, included contextual variables. The significance of context is rarely examined in its own right, although for some considerations it may be of fundamental importance. Knowledge of the dependence of responses on the genetic relatedness of signaler and respondent, for example, will surely generate new hypotheses about the evolution of social communication. Studying the variability of responses to the same signal in different stimulus contexts will help to refine our understanding of signal perception much as figure-ground contrast experiments in visual perception led to a better understanding of the physiological mechanisms underlying vision (Ratliff, 1976). Similar methods can enable us to explore which signal dimensions become salient as a result of contrast with their long-term context, as in the classic examples of a hawk silhouette becoming salient to turkeys (Schleidt, 1961), and search images which are modified by the experience.

A special case of context-dependence in communication is the possibility of intermodal interactions of signals. Do signals received through different channels interact in semantic-like fashion or should we consider information in one modality a part of the context that influences responses to signals arriving in another modality?

Similarly, the effects of varying the temporal order of signal elements can be gauged best only by studies of conspecific responses. Are sequential signals combined syntactically, or are early ones incorporated by a respondent as contextual information that tempers responsiveness to later ones (Beer, 1976; Wiley, 1975)? Regardless of evidence gathered by studying signaling, only by directing attention to responses can such issues be resolved.

In all such research, we must guard against narrowing our attention too early. If an alien being were to study human speech as a nonparticipant observer, how impoverished our communication might seem if tiny details of phonology were ignored in favor of the major features of mood-conveying intonation. And how confused the observer might be by the change of responses to an utterance with the same phonemes but different intonations. Inability to participate fully in social interactions would be a serious obstacle, to be overcome only by learning about the social structure and the relationships and prior histories of individuals and by gaining an appreciation of the factors that lead to the stereotypy and variability of responses. Discovery of which features of signal variability are disregarded by respondents and in which circumstances would help a great deal. And at some stage, the experimental introduction of appropriate signals and signaler models would be essential to make a final choice between alternative hypotheses about the nature of communicative operations, the underlying physiological mechanisms, and the associated cognitive processes.

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