Evolution of Communication

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Synonyms

Evolution of signaling and responding

Definition

Evolution of responses by a receiver to signals from a signaler.

Introduction

Understanding the evolution of communication has undergone several saltations in the past century. Nonhuman animals are now routinely recognized to have spectacular and complex forms of communication. Also, after decades of controversy, it is now clear that communication is a form of cooperation. The conditions for the evolution of cooperation have also become clear. All of these statements can no doubt still excite controversy, but beyond any contention, they raise issues for the evolution of human language, as an extreme case of complexity in communication.

This article summarizes developments in evolutionary biology relevant to communication in general and introduces some implications for the specific case of language. Another article, Design Features of Language, develops these implications in detail.

Comparative Study of Signaling

Study of communication by animals other than humans began in earnest with Darwin. Earlier concepts had placed organisms on an immutable *scala naturae*, with progressive elaboration of capabilities, including mental capabilities, from lower to higher, with a culmination among sublunary creatures in humans. Linnaeus' *Systema Naturae* instead formalized hierarchical classification of organisms, although humans still occupied first place with the unique attribute of wisdom.

Darwin first introduced natural selection of behavior in *On the Origin of Species* (1859), elaborated the possibilities in *The Descent of Man, and Selection in Relation to Sex* (1871), and illustrated applications to communication in *The Expression of the Emotions in Man and Animals* (1872). In subsequent decades, the study of animal behavior diverged into several paths: (1) experimental study of learning in a few convenient species, (2) experimental study of the sensory capabilities of animals, and (3) observational study of diverse organisms engaged in natural behavior. The first path quickly established

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unsuspected capabilities for learning in animals and then investigated these abilities in species amenable to experimentation. The second path revealed that many animals had unsuspected sensory capabilities, including some unavailable to humans, such as complex vision, including ultraviolet and polarized light, ultrasonic sound, electric and magnetic fields, and echolocation. Mental capabilities of animals were no longer just subsets of human capabilities. The third path, close observational study of animals, was at first pursued on the fringes of academic science. It eventually established at least six points important for a comparative study of communication.

1. Many animals have sizable repertoires of actions, including vocalizations, not directly related to nutrition, survival, or procreation. Often they are relatively conspicuous, discrete, and stereotyped. The term "display" was appropriate for them.
2. These displays are usually deployed in interactions between individuals and often evoke appropriate responses. They thus fit a basic criterion for communication. Furthermore, this communication is mostly among conspecific individuals. Both displays and responses are usually species-specific.
3. The structural and behavioral traits of these displays reflect the phylogeny of species. Indeed, for a while it seemed that comparisons of these displays might reveal phylogeny better than morphology could. They appeared to have evolved in arbitrary directions, without the complications of convergent adaptations. Yet their stereotypy and elaboration (called ritualization) suggested adaptations for communication (Cullen 1966), and eventually it became clear that displays include many adaptations to their environments and their functions in communication (Wilson 1965; Wiley and Richards 1982; Endler 1992).
4. Detailed comparisons of behavior between and within species suggest that displays have often evolved by elaboration of much simpler actions, either actions for individual maintenance, incipient actions in other contexts, or actions that seemed partially inhibited or redirected in the circumstances (Tinbergen 1952, 1960).
5. Experiments show that animals often respond only to a few simple features of displays (Tinbergen 1951). These "sign stimuli" often elicit relatively stereotyped responses, a finding that provided opportunities for a comparative neurobiology of behavior.
6. The ontogenetic development of these displays and their corresponding responses often does not depend on shaping by reinforcement or encountering models. In other words, they are in many cases "innate" or relatively canalized, in the sense that they develop in a stable way despite normal variation in individuals' experiences. In contrast, other actions and responses, equally complex and stereotyped, are learned by experience. In some cases, perhaps always, this learning is subject to constraints, predispositions such as sensitive periods, or templates. The first such case was imprinting of the following response by newly hatched precocial birds. Another was imitation of species-typical patterns of singing by songbirds. Predispositions in these cases are more canalized, within normal variation of experience, and simpler than the subsequent learned displays or responses. These examples of constrained learning have become epitomes of the interaction of genes and environment in the evolution of behavior, in particular, communicative behavior (Bateson 1981; Marler and Peters 1977; Marler 1990; Soha and Marler 2001a, b).

The discovery of such widespread and complex communicatory behavior in animals, generated by nonintuitive developmental processes and enmeshed in diverse social interactions, raised many questions about its evolution.

Evolution of Honesty

Until 50 or so years ago, the evolution of societies was explained by cooperation among individuals. Because cooperation is mutually beneficial, the action of natural selection in promoting cooperation seemed easily understood. This naïve attitude was overturned by George Williams' *Adaptation and Natural Selection* (1966) and Richard Dawkins' *The Selfish Gene* (1976). In the first place, not all individuals in an ostensibly cooperative society benefit equally. Individuals, for instance, might reduce their exposure to predators by herding, but those near the outside of a herd have more exposure than those in the center. Williams and Dawkins emphasized that, if differences in individuals' social behavior are associated with differences in the genes they carry, any allele (variants of genes) associated with behavior contributing to greater survival and reproduction spreads in a population, while others do not. Thus an explanation for the evolution of social behavior by natural selection requires an analysis of how each individual's behavior in social interactions affects its reproduction and survival.

This sort of argument provokes questions about how the behavior (or any trait) of an individual is related to its alleles. This basic process of behavioral ontogeny is revealed especially clearly in the studies of constrained learning in animals. An individual's development involves an interaction, in the statistical sense, of its genes and environment throughout the course of its life. As a result, genes do not determine anything about an individual's development, but they influence all of it. The same is true of the individual's environmental experiences. Natural selection results from differences in the reproduction and survival of individuals, whose traits are thus influenced more or less, in one way or another, by their alleles.

An early application of this principle was the evolution of polygynous mating systems, those in which most females mate with a few males. An argument that successful males benefit from multiple matings is insufficient without an explanation for how females benefit. The "polygyny threshold hypothesis" proposed that in habitats with high spatial variability (for instance, grasslands and marshes, where many nesting birds have polygynous mating systems), a female could compensate for reduced parental help from a polygynous mate provided that her mate's territory provided access to more food and safer nesting sites (Orians 1969; Searcy and Yasukawa 1995). This new approach to the evolution of social behavior set the stage for a reassessment of the evolution of communication.

Communication often involves individuals in asymmetrical roles, males enticing female mates, opponents in aggressive encounters, and competitors for food or space. Mutual advantages or cooperation in communication is less clear in cases like these, in which one individual might benefit by deceiving the other about its strength or suitability. Honesty, in contrast, would require a benefit for an individual responding to a signal as well as a benefit for the sender. Dawkins and Krebs (1978) suggested that signals are usually not honest. Instead they manipulate receivers for the signaler's advantage, despite the receiver's disadvantage. They deceive rather than inform receivers. Alternatively, Zahavi (1975, 1999) suggested that receivers avoid this problem by responding only to costly signals, because only costly signals are honest.

Zahavi's original proposal included two specific conditions for honesty: (1) costs of signals must be wanton (more than necessary); and (2) signals must have a form that impacts the attribute that is of interest to a receiver. The first of these conditions separates the costs of producing signals into a necessary component, which assures detection by a receiver, and an excessive or "wanton" component, which ensures honesty. The second condition requires that a signal interferes with its own meaning, in the sense that it must compromise the condition of the signaler that interests the receiver. For instance, a signal indicating efficiency in collecting food might partially compromise an ability to find food; or one indicating skill at avoiding predators would partially increase a signaler's vulnerability, for instance, by attracting a predator's attention or approaching and perhaps taunting predators. Such a signal would assure a receiver that the signaler was good enough at the particular task to overcome the handicap. For these reasons, Zahavi stipulated that the "wanton" costs of signals are handicaps. Handicaps thus became conditions for cooperative communication in which both signaler and receiver benefited.

This handicap principle became a central tenet of the study of animal communication, primarily as a result of mathematical demonstrations that honesty in signaling required costs for signals. Grafen (1990a, b) and Maynard Smith (1991) used different approaches to show that (1) the cost of an honest signal must exceed 0 as a general rule but (2) the cost to the signaler or the benefit to the receiver could equal 0 when signalers were genealogically related to receivers. Maynard Smith and Harper (2004) nevertheless concluded that the costs for honesty must exceed a cost necessary to avoid ambiguity in communication. Many studies in the past three decades have demonstrated that signals are usually honest (receivers' responses have benefits in terms of survival or reproduction or have some correlated effect) and that signals have costs related to survival or reproduction (Searcy and Nowicki 2005).

The handicap principle, however, is vitiated by two problems (Wiley 2015, 2017; see also Getty 1998; Számadó 2011). (1) The mathematical analyses make no distinction between necessary and excessive costs and in fact demonstrate only that honesty requires signals with costs >0. It is difficult, perhaps impossible, to imagine a signal that has no costs whatsoever, in terms of energy, risks, time, or lost opportunities, any of which would affect survival or reproduction. These analyses thus make no predictions about how much cost honesty requires. (2) An analysis of the optimization of communication in the presence of noise (Wiley 2015) shows that there is no distinction between costs of signals that reduce ambiguity and those that do not. During joint optimization of signalers and receivers in the presence of noise, all costs are incurred in reducing errors by receivers. Furthermore, a distinction between manipulation and information in communication is misleading, once information is more clearly defined, as proposed below.

More important, Grafen's calculations confirmed, although without much emphasis, that receivers must benefit from their responses to signals, at least on average. If receivers incur net costs for responding to a signal, then these responses do not evolve, and thus the signals do not either. The same conclusion applies to responses to signals from potential mates, although in this case, a receiver's benefits from choosing a mate can include genes that influence survival and reproduction of the receiver's offspring (Pomiankowski 1987).

The principal conclusion of these analyses is thus not that honest signals must have costs but that both signaler and receiver must benefit from the responses. It is not necessary that every instance of a response to a signal has benefits. Instead, responses to signals must have benefits, on average, either immediate or delayed, for both signaler and receiver. Communication is indeed a form of cooperation, in which both parties do better on average by communicating than they can otherwise.

Evolution of Cooperation

Cooperation begins by one individual helping another at some cost to itself. The first step is thus an act of altruism, one that benefits another at a cost to the actor, with benefit and cost ultimately in terms of survival and reproduction. Helping, including signaling, fits this pattern. Alleles cannot spread in a population unless the individuals that carry them survive and reproduce more effectively than others. Consequently, the challenge is to determine how alleles for helping can spread when helping individuals incur net disadvantages in survival or reproduction. It turns out that altruistic *individuals*, for which helping others decreases their own reproduction or survival, can persist in a population. Nevertheless, "altruistic" *alleles*, for which association with helping decreases their frequency, inevitably disappear from a population. To reconcile altruistic individuals with selfish alleles, two possibilities are now recognized: (1) helping genealogical relatives or (2) receiving compensating benefits in the future.

The first occurs, for instance, when individuals help to raise a relative's offspring while not themselves reproducing. The example of honeybees, which had perplexed Darwin, is such a case. Somewhat similar cases have now been studied in scores of birds and mammals as well as numerous social insects (Koenig and Dickinson 2004; Bourke 2011). In many cases the helpers (or workers) in fact reproduce to some extent either concurrently or later in life. Nevertheless, in some cases, such as honeybee workers helping queens to reproduce, the helping individuals almost never reproduce as much as the individuals they help. William Hamilton (1964, 1970) showed that alleles of individuals with lower chances of reproduction could nevertheless spread in a population provided these individuals helped close genealogical relatives. Close relatives can have a copy of any allele associated with a helper's behavior, as a result of their descent from a recent common ancestor. This "kin selection" is thus a special case of natural selection. If individuals sacrifice their lives to save the lives of more than two siblings (or more than eight cousins), any allele associated with this behavior would spread. The condition for the spread of an allele associated with helping is $C < rB$, where C is the cost in survival or reproduction for the actor, B is the benefit for the recipient, and r is the coefficient of genealogical relatedness of the actor to the recipient (one-half for a sibling, one-eighth for a cousin). Recent debate has clarified this possibility (Nowak et al. 2010; Abbot et al. 2011).

These ideas were quickly applied to mammals and especially to birds in which breeding pairs often have several helpers that feed or protect their young but do not (or are less likely to) reproduce. The evidence indicates that in most such cases, kin selection cannot provide a sufficient explanation for helping. Nevertheless, in the preponderance of cases, helpers are closely related to breeders. Kin selection in such cases contributes to the spread of alleles for helping even if it does not completely explain it. These principles apply to communication. We can expect individuals to accept uncompensated costs for signals or responses if the condition above is met.

The second case, when helpers receive later benefits, could apply to genealogical relatives and thus augment kin selection for alleles associated with helping. It might also apply to individuals without close genealogical relatedness. One possibility for later benefits is reciprocation: do unto your neighbor as you would have (or at least can expect) your neighbor to do unto you. Reciprocation though has its complications. Just because an individual helps another does not assure that the recipient will return the favor. In addition to inevitable random contingencies, a population could plausibly include individuals with alleles associated with accepting help but never reciprocating, in other words defectors or cheaters. The possibility for cheaters in an otherwise cooperative population is pervasive. Close attention to cases of helping reveals that reciprocation is not a physical necessity, so there is always the possibility of a mutant allele that predisposes individuals to cheat by skipping reciprocation. In any instance of helping, the recipient is always possibly a cheater and the helper possibly a sucker.

In communication, the norm is honesty, but the possibility of exploitation, in other words cheating, is always present, both for signalers and receivers. On average a signaler benefits from responses by appropriate receivers, but there is always the chance of an inappropriate receiver, such as an eavesdropping rival, predator, or parasite. These inappropriate receivers exploit the signals intended for appropriate receivers. This situation is the converse of deception. In deception, an inappropriate signaler exploits the responses intended for appropriate signalers. There is always the possibility that a signaler or a receiver is a cheater in normally honest communication, and there is always the possibility that a signaler or a receiver is a sucker.

The usual recourse for analyzing the evolution of reciprocation has been game theory. In particular, the prisoner's dilemma and many related games have provided a foundation for mathematical and experimental analysis of the evolution of cooperation. An early discovery was that the behavioral strategy of iterated tit for tat permits the evolution of cooperation by reciprocation (Axelrod and Hamilton 1981; Axelrod 1984). This strategy consists of helping any new partner on the first encounter and then on subsequent encounters, either helping or not depending on whether or not the partner has reciprocated (Axelrod and Hamilton 1981; Axelrod 1984). It is a practical variant of the golden rule: do unto each partner as you expect that partner to do unto you.

Many additional possibilities for the evolution of altruistic behavior have by now surfaced. For instance, altruistic behavior can evolve in local populations of sessile organisms, when individuals interact repeatedly with the same few partners as a result of their immobility. With the strategy win-stay-lose-shift, individuals help in their first interaction (or in random occasional interactions) and then help subsequent partners or not, regardless of whom they might be, depending on whether or not the previous partner reciprocated. In this case individuals do not keep record of their partners. Individuals might also develop a positive reputation for helping so that others would help them in the expectation that they would receive help in return. In this case, however, an individual's tendency to help would have to extend indiscriminately to other individuals. Alternatively individuals might develop a negative reputation so that others would have no expectation of reciprocation and thus refuse to help them. Finally, helpers might punish (impose extra cost on) defectors. In this case, helpers would themselves incur an additional cost for administering punishment. If the cost to each punisher was sufficiently small (perhaps shared among many helpers) and the cost to each punished non-reciprocator was sufficiently large (perhaps execution or banishment with little chance of survival or reproduction), this possibility could overturn the advantages of cheating but preserve most of the advantages of helping. Sharing the costs of punishment would, however, be another form of reciprocation, which would itself open opportunities for cheating (for instance, avoiding a fair share of taxes for policing). Sometimes cases of social approval or social disapproval are combined as contrasting examples of "social selection." All of these possibilities, when appropriate conditions are met, can explain how alleles associated with altruistic action can persist or spread in a population (Nowak 2006; for an example of punishment by monkeys, Hauser 1992).

There is one situation that does not allow such altruistic alleles to spread – badges identifying altruists. Altruistic individuals could increase the chances of reciprocation by recognizing each other by some badge associated with helping. Richard Dawkins labeled this possibility a "green-beard effect" (on the possibility that green beards might serve for such a badge). The problem is that a shared badge just creates another opening for cheaters, individuals that sport the badge but do not reciprocate. Alleles with pleiotropic effects might work temporarily but only until a mutation broke the association between helping and development of a badge.

From decades of discussion, two conditions have emerged that always increase chances for the evolution of mutual helping: (1) genealogical relatedness between actors and recipients and (2) cognitive abilities for remembering interactions with individual opponents. Genealogical relatedness promotes the evolution of cooperation even when it does not provide a complete explanation. Memory of individual opponents is a crucial part of some options for the evolution of cooperation by reciprocity, such as tit for tat. Some options, such as tracking individuals' reputations, require extensive memory of individuals. Nevertheless, even possibilities that require no memory of opponents, such as sessile neighborhoods or win-stay-lose shift, are even more likely to evolve reciprocity when memory of individual opponents is possible.

These possibilities for multiple contributing factors in the evolution of cooperation are often overlooked, because theoretical models have tended to take two directions, either focusing on the minimal conditions or on the maximal potential for cooperation. Those studying humans focus on the maximal possibilities for cooperation. Those studying other animals tend to focus on the minimal requirements for cooperation. Studies with humans in mind often assume complex cognitive capabilities without much comment and ignore the synergistic contribution of genealogical relatedness. They also can ignore the possibility that collaboration in a complex society, which results in unequal or uncertain advantages for individuals, generates natural selection for defection and for nothing-to-lose retaliation when disadvantaged. All these conditions for the evolution of cooperation apply to the evolution of communication.

Evolution of Individual Recognition

For the evolution of cooperation, all but the simplest possibilities rely on individuals' abilities to remember other individuals and to associate them with particular patterns of behavior. This ability requires at least minimal object constancy for another individual, discrimination of that individual from others, and association of that individual in memory with its previous behavior. Object constancy, discrimination, and association are mental processes, perhaps each some aspect of association in general, that recur in all discrimination learning.

Abilities of this sort are now well documented for many nonhuman organisms. There are important distinctions to be made about the complexity of recognition (Wiley 2013a). First, the specificity of individual recognition can vary. An experiment might reveal that subjects respond to a neighbor or a partner (or often just to some features of such an individual) in a different way than to other individuals. Such a discrimination could result solely from habituation to repeated experience with a familiar individual. It would thus constitute recognition of a particular individual only when no other individual could have such familiarity. In some cases it is still not clear whether or not animals recognize territorial neighbors, parents, offspring, or relatives as individuals or as small sets of familiar individuals and whether or not these small sets are distinguished from others by associative learning or solely by habituation. On the other hand, experiments have shown that many territorial birds, for instance, can identify specific individuals within the small sets of their familiar neighbors.

Specificity of individual recognition is crucial for the evolution of cooperation. Only when specific individuals are recognized can interactions with possible cheaters be avoided or reduced. One report of a nonhuman animal that fits the requirements for tit for tat provides an example. A warbler in eastern North American forests can use its ability to recognize individual territorial neighbors in order to cooperate with them once mutual boundaries are settled. Experiments with playbacks of songs show that they use tit for tat to retaliate specifically against defecting (trespassing) neighbors (Godard 1993).

The multiplicity of individual recognition can also vary, from recognition of a single other individual (for instance, a mate) to recognition of individuals in a small set (perhaps territorial neighbors, a small group, or current offspring) to recognition of potentially large numbers of individuals (as do humans). Some territorial birds are known to recognize several individual territorial neighbors, and primates (and presumably some other social birds and mammals) can recognize multiple individuals within their social groups and in nearby groups as well (Cheney and Seyfarth 1990, 2007). Associations with these individuals are probably not complicated in the case of territorial neighbors in particular locations but are possibly more complex in the case of group members encountered in diverse contexts.

Humans recognize large numbers of individuals with different degrees of specificity and different complexities of associations. There is a considerable literature on the influence of features, relationships of features, and contexts in peoples' abilities to recognize faces, but almost nothing is known about how many individuals a person can recognize nor about the cognitive complexities of how a person organizes these memories. This gap in our knowledge is surprising, because the memory, associations, categories, and relationships involved in individual recognition by humans seem to approach those needed for human language.

The hierarchical organization of many animal societies suggests possibilities for recognition that have parallels with language. The formation of a dominance hierarchy, it is important to acknowledge in the first place, might not require any individual recognition at all. Each individual can plausibly learn to recognize sets of higher- and lower-ranking opponents or even respond to one or more graded features (for instance, size, postures, or badges of dominance). On the other hand, individuals might recognize each individual opponent and respond to each in a different way. Associations with each opponent might allow inferences about the relative ranks of any two other individuals.

Especially interesting are cases in which individuals' rankings include prominent subgroupings, and ranks across these subgroups do not follow gradations of individuals' features. In many primate groups, for instance, matrilineal groups as a whole are ranked as well as individuals within each matriline (Bergman et al. 2003). Thus a low-ranking young individual in a high-ranking matriline outranks a high-ranking older female in a low-ranking matriline. These nested hierarchies seem to arise because older relatives (mothers, aunts) shield younger ones from subordination by individuals in lower-ranking matrilines. Although the pattern and the interactions are well documented, there remains the question whether this pattern is conceptualized by individual monkeys as embedded subgroups or as an overall hierarchy. Some evidence suggests that the former is possible for baboons. Playbacks of calls indicating a reversal of ranks between matrilines evoke more attention than those indicating a reversal within matrilines, regardless of the differences in overall rankings (Bergman et al. 2003). Baboons evidently can conceptualize a dominance hierarchy as sets of embedded individuals, although wide overlap in the ranges of responses to the two conditions raises the possibility of inconsistency in this ability.

A similar situation results from "coattail" effects in dominance hierarchies of birds (Wiley 1990; Cristal 1995). Small groups of emberizine sparrows are allowed to form dominance hierarchies in large cages in winter, when competition for food is the predominant activity. Then the top half of the hierarchy in one cage and the top half from a second cage are combined in a third neutral cage. Surprisingly, the two groups often remain coherent in the newly formed hierarchy. Each individual's rank is nested in its group's rank. The mechanism is perhaps not dissimilar to that in primate groups. The two highest-ranking individuals in a combined group interact to determine their relationship, but once this relationship is decided, the higher individual creates a coattail for its familiar subordinates. In this case, and perhaps in the primate groups also, the principal effect of the dominant individual is to let its familiar opponents approach more closely than can others without aggression. Again the question arises: How does a relatively dominant member of a subordinate subgroup categorize opponents? First by subgroup and then by ranking within it or simply by overall rank.

Evolution of Mating Preferences by Sexual Selection

Mate choice is a well-studied example of communication. In many animals males perform conspicuous displays that increase their chances of mating. Darwin (1859, 1871) recognized that if females prefer males with certain traits, or if males with certain traits are more successful in competing with rival males, then these traits would tend to spread in a population. Even more than his theory of natural selection, this theory of sexual selection precipitated controversy among biologists. At first the primary sticking points were doubts about the cognitive abilities of females needed for preferences, but R. A. Fisher (1930) made it clear that a female's preference is no more than a neurophysiological response to a male's traits. Fisher then presented a verbal argument for accelerating evolution of male traits preferred by females. The process of sexual selection was terminated when the cost of the preferred male traits became too great.

It remained for proper mathematical analyses to verify the dynamics of this accelerating evolution (Lande 1981; Kirkpatrick 1982). Much subsequent work has confirmed predictions about mate choice in natural populations (Anderson 1994; Searcy and Yasukawa 1995). The key to the evolutionary dynamics is the genetic correlation produced when a female with a preference mates with a male with a preferred trait. Their offspring tend to inherit alleles associated with both preference and trait. The result is a genetic correlation between these alleles in the population. Within the genomes of individuals in the population, the presence of the preference allele is associated with the presence of the trait allele. This association is often called "linkage disequilibrium" by geneticists, but linkage is actually a special case of genetic correlation, not necessarily connected with mating preferences. As generations pass, females with preferences tend to spread not only alleles for the preferred male trait but also alleles for the preference (because both males and females tend to carry both alleles). As a result of the genetic correlation of the two alleles, the preference allele spreads by "hitchhiking" with the trait allele. Another way to look at it, the preference allele spreads itself. The genetic correlation that results from preferential mating produces accelerating evolution of alleles for both of the male trait and the female preference. Sexual selection is thus a special case of natural selection, one that happens whenever individuals of one sex with a particular trait mate disproportionately with members of the other sex with the same or different trait. Preferences and other traits, to reiterate a point above, develop under the influence of alleles.

There are several points to emphasize here. First, A preference for potential mates with a particular trait is a form of communication. In the most frequent case, males produce signals to which females respond discriminatingly. Nevertheless, the mathematical models of sexual selection do not require direct choice of males' traits. A female might instead exert a choice indirectly. She might set conditions for mating by provoking a contest between potential mates. For instance, she might limit her matings to a particular time and place, or she might indiscriminately advertise her readiness to mate. In these cases there is no discrimination between males' traits, yet females set conditions that result in selective mating. By mating with whichever male prevails in such contests, she would indirectly choose a male whose traits allowed him to prevail against all comers. Females would, in other words, define the contest for males and then take any winner as a mate. In the case of indiscriminate advertising, a female produces a signal to which males respond by approaching. In any of these possibilities for indirect choice, genetic correlation and subsequent sexual selection would result, just as in the case of direct choice.

Second, Alleles for preferences cannot spread if females with these alleles incur net costs in terms of survival and reproduction (Pomiankowski 1987; Grafen 1990b). Responses to signals, as we saw above, must result in net advantages, on average, for receivers or their close relatives. Furthermore, sexual selection also stops when males incur net costs, when the advantages of greater possibilities for reproduction are more than offset by disadvantages for survival.

Third, Sexual selection does not spread alleles until the frequencies of the preference and trait alleles in the population exceed a threshold (or the level of genetic correlation crosses a threshold) (Lande 1981; Kirkpatrick 1982). Sexual selection does not spread mutations ab initio.

This hurdle applies to the initial evolution of any signal and response. No matter how advantageous communication might be, neither a response nor a signal can spread by itself. A rare mutant for a new response cannot spread without sufficiently frequent signals, and vice versa a new signal cannot spread without sufficiently frequent responses. Mutualistic signal and response must overcome a hurdle before they can spread.

Furthermore, all mutualistic interactions spread in an accelerating way once started. Responses become more advantageous as the frequency of signals increases and vice versa. It is still not clear whether R. A. Fisher (1930) had genetic correlation in mind when he proposed accelerating evolution of sexually selected traits or whether he was just thinking of the accelerating spread of any frequency-dependent mutualistic interaction (Wiley 2015). The rate of spread eventually slows down as the frequencies approach fixation, because increasing frequency of signalers results in diminishing advantages for receivers and vice versa.

Sexual selection, despite its specific application to communication during mate choice, includes parallels with the frequency-dependent evolutionary dynamics of all forms of mutualistic interaction and thus of communication in general. The evolution of mutualistic communication between individuals other than mates does not receive the extra boost from the genetical correlation that results from mating. Nevertheless it does share the initial hurdle and the subsequent acceleration that apply to all frequency-dependent mutualism.

A final point should be emphasized. The original mathematical models (Lande 1981; Kirkpatrick 1982) and subsequent derivations include the possibility that female preferences might be arbitrary. Arbitrary in this context means that mating with a preferred mate provides no benefit whatever to the female (we have already emphasized that it cannot incur a cost to the female). There are three reasons to think that such completely arbitrary preferences are unlikely to evolve. First, if alleles for two preferences exist in the same population, the one that results in a greater benefit to females spreads faster. So any preference with a benefit for females spreads to the exclusion of an arbitrary preference. Second, the same applies to the costs of male traits. Of two alleles associated with traits equally preferred by females, those with lower costs spread fastest. Finally, preferences for traits are a form of communication. Noise in communication makes the evolution of completely arbitrary signals and responses unlikely. The parameters, some ten of them, that influence the utility of a signal for a signaler (an advertising male, for instance) and the utility of a criterion of response for a receiver (a choosy female, for instance) would have to balance exactly to produce zero net utility for both signaler and receiver (Wiley 2015, 2017). Communication for mate choice, like all communication, is inescapably noisy.

Evolution of Communication in Noise

Noise requires a new approach to understanding the evolution of all forms of communication, one that is compatible in part with the preceding approaches but has advantages of defining some crucial concepts, presenting a thorough optimization of the behavior of signalers and receivers and incorporating the consequences of noise for communication. Noise opens a new perspective on the evolution of communication. Most surprising is the realization that evolution is not expected to produce noise-free communication.

Everyone is aware that noise can interfere with communication. Communication requires two parties, a signaler and a receiver. Even when more than one signaler or receiver is active at the same time, each instance of communication is a relationship between a signaler and a receiver. A signaler produces a signal to which a receiver might respond. A signal is any pattern of energy or matter that can elicit a response from a receiver, without providing all of the power for the response. A response need not occur every time a signal is perceived, but unless a response occurs more often than at random, there is no evidence for communication.

Most previous definitions of a signal agree in stipulating that a signal must evoke a response, although it is less often emphasized that responses need to occur only more often than random. Previous definitions also require that a signal must have evolved for the purpose of communication or have a goal (or intention or function) of evoking a particular response. Often there is a complementary condition: a response must have evolved for a particular signal. These stipulations are confusing and circular: signals and responses evolve for communication which consists of signals and responses.

A signal defined as a pattern of energy that evokes a response but does not provide all the power for the response avoids this confusion. The restriction on the power of a signal excludes cases in which one individual simply overpowers another, as, for instance, in predation. A signal, on the other hand, must provide some power, enough to activate the sensory receptors of a receiver. The receiver must then provide some, often most, of the power for the response. Consequently, receivers have the final control of responses.

Signals defined in this way can originate from inanimate objects as well as living ones. Previously most definitions have excluded this possibility by insisting that signals have functions; signals without functions are instead called cues. But this measure is unnecessary. From a receiver's point of view, it makes no difference what the source of a sensation is. Signals from any source produce sensations for receivers, and receivers have final control of responses. For any receiver, including humans, information about the inanimate world has the same footing as information about the behavior of other organisms.

Nevertheless, signaling and responding by organisms can evolve. As discussed above, signals by evolving signalers are expected on average to produce net advantages in terms of survival or reproduction for signalers; responses produce such advantages for receivers. Signaling and responding by living organisms evolve jointly.

Information is another term that has caused confusion. Shannon in his pioneering papers on information theory (Shannon and Waver 1949) described the simplest intuitive way to measure the quantity of information, but he only hinted that the quality of information ("what" rather than "how much" information) depended on the state of the signaler. A signaler's state results from its ontogeny, as described above, the accumulated influences of genes and experiences during the course of its life to present. Its state is the current condition of its body, including its nervous system and thus also its recent perceptions. The quality of information, regardless of its quantity, is the correlation between a signal and the signaler's state (Wiley 2013b). If a signal has information relevant to a receiver's survival or reproduction, alleles associated with responding appropriately to such a signal can evolve (increase or decrease in frequency in the population). If such a signal evokes a response affecting the signaler's survival or reproduction, alleles associated with producing such signals can evolve. Thus the quality as well as the quantity of information in a signal influences its evolution. Evolving signals must include some information about the signaler's state. Note once again that responses can include delayed and covert effects, such as memory or physiological changes affecting later behavior. It might include complex perceptions as well as simple reflexes.

With collateral issues resolved, a criterion for noise is possible: noise is errors by receivers. This insight by Shannon is as important as that about information. Anything that results in errors by receivers counts as noise. It can include irrelevant background energy that interferes with a receiver's detection or discrimination of signals. Background energy can include turbulence and extraneous energy impinging on the receiver's sensors. It can include signals of other species or individuals irrelevant to the receiver in question. Noise can result from attenuation and degradation of the patterns of signals during transmission from signaler to receiver, in the atmosphere or water or even at the interface between a finger or a tongue and a receiver's skin. Noise also occurs in nervous systems. Nearly all neurons produce action potentials continuously at irregular rates, which are combined with the firing rates elicited by sensory stimulation. Little is known about how this neural noise affects perceptions of sensory sensations. Both signalers and receivers are subject to neural noise. Signalers do not always produce signals perfectly correlated with their states; receivers do not always respond appropriately to signals (Wiley 2015, 2017).

The basic insight of signal detection is that a receiver must make a decision each time it checks any of its sensory inputs (Macmillan and Creelman 1991, 2005). Because relevant signals combine with noise in a receiver's sensors, a receiver must decide whether a sensation correctly indicates the occurrence of a signal or not. Normally the combination of signal plus noise results in greater stimulation than does noise alone. Both signals and noise vary, so each produces a probability density function (PDF) of levels of excitation of a sensor. Whenever the PDF for signal plus noise and the PDF for noise alone overlap to any extent, the receiver cannot respond to appropriate signals without some error.

Another insight of signal detection is that receivers are subject to two kinds of errors, false alarms and missed detections (or errors of commission or omission or Type I and II errors in statistical comparisons). These errors result from a receiver's criterion for a decision to respond or not. The simplest criterion for response is a threshold. If the level of excitation in a sensor exceeds the threshold, then respond; otherwise, do not. More complex sensors can include filters and combinations of thresholds and filters to produce specific cognitive criteria for a response. A response, as emphasized above, can be either overt or covert, an act, a perception, or a memory. Any response might be an error.

Every time a receiver checks its input, exactly four mutually exclusive outcomes are possible. The level of excitation in its sensor might exceed its threshold (or other criterion for response) or not; in each case, a relevant signal might have occurred or not. Excitation above threshold when a signal is present results in a *correct detection*. With no signal, only noise, the result is a *false alarm*. Excitation below threshold when only noise is present results in a *correct rejection*; with a signal present, albeit attenuated and masked with noise, the result is a *missed detection*.

A receiver in this situation can adjust its rates of error by adjusting the level of its threshold. Yet every adjustment of a threshold changes the probabilities of all four possible outcomes. For instance, by raising its threshold for a response, it would reduce its chances of a false alarm. Its chances of correct detection also decrease. On the other hand, missed detections and correct rejections increase. If a receiver lowers its threshold, its chances of a missed detection decrease, but again the probabilities of all other outcomes would also change. Most important, the two kinds of error, false alarm and missed detection, always change in contrary ways. A receiver cannot reduce one kind of error without increasing the other. Every time a receiver checks its sensors and decides to respond or not, it is in an inescapable double bind.

Signalers can influence the relationship between signals and noise for receivers. In general the more powerful or concentrated a signal, the greater its impact on the sensors of a receiver at any particular distance. Signalers thus can increase the probability of a correct detection (an appropriate response) by a receiver by increasing the exaggeration of a signal. The probability of a correct detection by an appropriate receiver in turn affects the benefit from signaling for a signaler.

The next objective is to calculate how natural selection can affect the evolution of signalers and receivers in noise. Does evolution by natural selection produce a joint solution for signaling and responding? Are there mutual advantages for signalers and receivers? Is noise eliminated by natural selection on communication? The first step is to specify net advantages and disadvantages for potential options for both receivers and signalers (Wiley 2015). For receivers, this step requires calculation of the utility of the receiver's threshold, each time a receiver checks its sensors and decides to respond or not. This utility is a function of the signal/noise ratio (more accurately, the relationship of the PDFs for signals plus noise and for noise alone), the probability of a signal, and the level of the threshold. The threshold affects the probabilities of each of the four possible outcomes. For investigating evolution, the utility is expressed in terms of the receiver's survival × reproduction.

A similar process can specify the utility of signal exaggeration for a signaler as a function of the cost of producing a signal with a particular exaggeration and the probability of a response from an appropriate receiver. The utility of a receiver's threshold thus depends on the signal/noise ratio, which depends on the exaggeration of a signaler's signal; conversely, the utility of a signaler's exaggeration depends on the probability of a correct detection, which depends on the level of a receiver's threshold. With some calculus, it is possible to find the optimal level of a threshold for a given exaggeration of a signal or, alternatively, the optimal exaggeration of a signal for a given threshold. Further computation reveals that in most situations, thresholds and exaggeration evolve by natural selection to a joint optimum, a Nash equilibrium at which both receivers and signalers have advantages and both do as well as possible provided the other does also (Wiley 2015).

Some General Principles for the Evolution of Communication

Several important insights about communication result from these calculations. First of all, adaptation by natural selection does not escape from noise. Noise is inevitable; communication in the absence of noise is unattainable. This conclusion follows from the basic insight that both signalers and receivers face conflicting advantages and disadvantages. They also face diminishing returns: in an approach to optimal signals or thresholds, advantages increase less rapidly than disadvantages.

Second, the variables in these calculations are completely general. They apply to signalers and receivers in all cases of communication. For instance, both exaggerations of signals and thresholds for response scale to the level of noise. Thus at close range, when background noise is minimal, optimal signals and thresholds decrease in relation to noise so that possibilities for error persist. In addition, this result applies not only to communication by nonhuman animals but also to humans and to all modes of human communication including electronic. It applies not only to communication between organisms but also to communication between and within cells. Molecular signals and receptors operate in a noisy environment, with multiple signals, multiple receptors, and chemical degradation. There is thus no reason to expect that adaptation by natural selection can eliminate noise in any form of communication. The same conclusion applies to perceptions of the external world. Optimal decisions by perceivers, based on signals from inanimate objects, cannot escape some probability of error, either false alarms or missed detections and errors of commission or omission.

Third, these calculations confirm the results of all previous calculations of the evolution of mutual interactions: neither signals nor responses can spread when both are infrequent. In the present calculations, when thresholds are too high (as when individuals have little tendency to respond to a particular stimulus) and when exaggeration of signals is too low (as when individuals have little tendency to produce them), communication collapses. Thresholds for response must not be too high, and exaggeration of signals must not be too low, for mutual communication to evolve ab initio.

Fourth, optimization of communication in noise opens many questions about adaptations for communication in different circumstances. Nearly every parameter in the utility functions has been measured or estimated in some case of communication (Wiley 2015), although never has there been a complete analysis of communication in noise in natural situations. There are clear predictions about the evolution of thresholds for response and for exaggeration of signals as a result of differences in signal frequency and the utilities of the four possible outcomes for receivers. A further prediction is that exaggeration of signals should not evolve in arbitrary ways but instead specifically in ways that increase the signal/noise ratio for appropriate receivers. There is evidence that evolution of both acoustic and visual signals follows this prediction (Wiley 1991; Endler 1992; Endler and Thiéry 1996; Gomez and Théry 2004; Kemp et al. 2009). It also seems unlikely that purely arbitrary signals could ever evolve even by sexual selection. An arbitrary signal would require the multiple parameters of communication in noise to balance exactly.

Finally, although communication is never expected to reach perfection, honesty is expected to prevail. At the evolutionary optimum, both signalers and receivers benefit on average. Nevertheless, some incidence of error persists. Some errors result from random events in the environment or in signalers or receivers. Evolved adaptations by inappropriate participants also affect optimal behavior by signalers and receivers.

Deception by inappropriate signalers can reduce the utility for receivers. Eavesdropping by inappropriate receivers can reduce the utility for signalers. Communication is expected to transfer information between signaler and receiver, in other words, a corresponding perception of the actual world to their mutual advantage but always with a possibility for random errors and for manipulation by inappropriate signalers or receivers.

Investigation of communication with a hypothetical absence of errors is thus unrealistic. Noise requires study as much as signals. Nevertheless, many studies of communication, whether theoretical, observational, or experimental, take steps to reduce noise as much as possible, in order to focus on signals or responses. Study of simplified situations has its place in science, but it can also produce unrealistic results. To understand communication in any real situation, noise is as important as the signals. In other words, communication of any sort cannot be fully understood without understanding its variation in practice.

It is also clear that all communication in noise is "inferential" and "intentional." If the "meaning" of a signal is the response it evokes in a receiver (whether overt or covert), the meaning in the presence of noise always requires a decision by a receiver. Meaning is thus "inferential."

Furthermore, signals are often accompanied by relevant as well as noisy contexts, both of which affect the receiver's decisions to response or not. These decisions must often depend on the receiver's previous interactions in a particular context and thus on the receiver's memory of any associations with this context. They thus are "intentional."

Signals always arrive within a context of noise. A receiver decides to respond based on its current state (including memory) and the sensations it receives. These sensations include signals (usually honest but with some noise) and relevant contexts (usually correct but with some noise). If "inferential" implies decisions by a receiver and if "intentional" implies associations for a receiver between a signal and its context, then all communication is intentional, between animals as well as humans. The decisions humans make in using language require complex criteria for responses. The distinctive features of human linguistic communication as opposed to other forms of communications lie in the specific complexities of these cognitive criteria, not in the importance of decisions or contexts in general.

Cross-References

- ▶ Design Features of Language
- ▶ Evolution of Cooperation
- ▶ Fisherian Runaway Selection
- ▶ Frequency Dependent Selection
- ▶ Game Theory
- ▶ Handicap Hypothesis
- ▶ Natural Selection
- ▶ Sexual Selection
- ▶ Signal Detection Theory
- ▶ Tit-for-Tat Cooperation

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