

Chapter 2

Signal Detection, Noise, and the Evolution of Communication

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Abstract Signal detection theory has had limited application in studies of animal communication. Yet by specifying constraints placed by noise on a receiver's performance, it provides a way to investigate optimal performance and thus the evolution of communication. Noise in this case is anything influencing a receiver's receptors other than a signal of interest. The essential features of signal detection theory are (1) a distinction between the detectability of a signal in noise and the criterion or threshold for a receiver's response and (2) a realization that any decision by a receiver to respond has four possible outcomes, not all of which are independent. Although presented here in terms of a receiver's threshold for response to one kind of signal, signal detection theory applies also to more complex criteria for response as well as complex discriminations among multiple signals. A receiver's optimal performance always depends on the payoffs of the four possible outcomes of a decision to respond and on the detectability of a signal. By incorporating detectability, signal detection theory can provide a complete explanation for the evolution of exaggerated signals. An alternative explanation, based only on sexual selection and necessary costs of signals, does not do so. In particular, signal detection theory shows that exaggeration of signals should evolve so as to improve the detectability of signals by receivers. By shifting the emphasis from a receiver's preferences and to its performance, this theory also clarifies the co-evolution of signalers and receivers. The result is a signal-detection balance, in which signals reach optimal but not ideal detectability and receivers reach optimal but not ideal performance. The crucial importance of the detectability of signals by receivers means that noise in natural situations, just as much as costs and benefits for the participants, determines the features of communication.

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2.1 Introduction

In recent decades, the study of animal communication has been transformed by steadily expanding research on the effects of noise on communication, as this volume demonstrates. Initially, interest focused on the attenuation and degradation of acoustic signals as they propagated from the signaler to a receiver. This work quickly led to questions about adaptations of signals to minimize these effects in different habitats. It also became clear that receivers could often use attenuation and degradation of signals to judge the distance to signalers. There was also some early interest in ways that animals can avoid masking of signals by environmental noise, but this possibility has recently received much more attention. It is now clear, as this volume shows, that animals counteract the effects of environmental noise on communication in several ways. The discovery that animals make these adjustments to anthropogenic noise, which presumably presents a novel challenge from an evolutionary perspective, suggests that these adaptations can result from behavioral plasticity in addition to or instead of evolution. With this diversity of interests in the effects of noise on animal communication, it seems appropriate to take a broad view of the role of noise in communication. This chapter reviews the argument that noise in communication is equivalent to errors by receivers and that receivers' errors have fundamental consequences for optimal behavior of both receivers and signalers.

People have always recognized that noise, as commonly conceived, is a problem for communication. People have also always known that communication is prone to errors. It was Shannon (1948), however, who first realized that noise in communication is nothing more or less than a receiver's errors (see Shannon and Weaver 1963). This insight provided the start for his mathematical analysis of the limitations on the rate of communication, now known as information theory. Shannon formulated communication as the process of reproducing, at one point, signals generated at another point. In addition to correct reproduction, he recognized that there are also the possibilities of two kinds of error, ambiguity, and equivocation (reproduction without signal and signal without reproduction). There is no need to pursue the mathematical details of Shannon's analysis to cast this situation into one familiar in the study of animal communication. Whenever a receiver samples the input of its receptors, in all but ideal conditions, and makes a decision to respond or not, there are four mutually exclusive outcomes possible. These four outcomes are a consequence of a combination of two possible situations (the presence of a signal or not) and a binary decision by the receiver (respond or not). Two outcomes are correct (correct detection and correct rejection) and two are errors (false alarm and missed detection). Just as Shannon first emphasized, when signals of interest to a receiver cannot be completely separated from other coincident events, the receiver inevitably makes errors in deciding whether or not a signal has occurred.

We return shortly to what constitutes a signal, but for the moment we need only recognize that examples of signals include the presence of an optimal mate or a

rival, the presence of a predator or parasite, the nutritional state of offspring, the identity of a nest mate, and so forth. An example of a correct detection is a response to an optimal mate or to a territorial intrusion by a rival, and a missed detection is a failure to respond despite signals from an optimal mate or a rival. A correct rejection is an absence of response to a suboptimal mate or to an individual that does not represent a threat such as a territorial neighbor still inside its own territory. A false alarm is a response to signals from such individuals. Experiments that present signals to territorial individuals or females seeking mates routinely elicit all four of these kinds of responses. Even “successful” experiments, in which the subjects respond with statistically significant probability to the “correct” signals and not to the “false” signals, nearly always include instances of false alarms and missed detections as well as correct detections and correct rejections.

Decision theory provides a method to determine the optimal decision when the outcomes of decisions are uncertain. It computes the expected utility of any decision from the payoffs (positive or negative) and probabilities of each of its possible outcomes. Von Neumann introduced a measure of the expected utility of a decision,

$$E(U) = \sum(i) U(i)p(i),$$

the sum of the utility, $U(i)$, times the probability, $p(i)$, of each of i mutually exclusive outcomes (von Neumann and Morgenstern 1944). Decision theory has since been widely applied in economics and has become familiar to behavioral ecologists, who routinely consider costs, benefits, and probabilities of alternatives in order to predict optimal behavior.

The optimal performance of a receiver facing four possible outcomes of any decision to respond or not is easily formulated in terms of decision theory. This fusion of decision theory and information theory occurred over a period of a decade or so and resulted in a general theory of a receiver’s performance known as signal detection theory (Green and Swets 1966). Perhaps because this theory was first introduced by psychophysicists interested in studying the sensory capabilities of humans and other animals, its application has not diffused widely. Nevertheless, for over half a century, signal detection theory has provided the foundation for psychophysics and cognitive psychology. In particular, it has provided a way to separate the motivation of subjects from the inherent detectability of signals. Although it has remained peripheral in studies of animal communication, this chapter will suggest that signal detection theory, by addressing the fundamental problems of noise, can explain some basic adaptations for communication and reveal some unrecognized problems.

The application of signal detection theory to animal communication has been presented in some detail elsewhere (Wiley 1994, 2006), so this chapter focuses on the generality of this theory for understanding communication and then develops ways it can help to think about the evolution of communication, including the co-evolution of an equilibrium in the performance of signalers and receivers.

2.2 Signal Detection Theory as a General Model for Communication

To justify the general application of signal detection theory, we must address three issues: what constitutes a signal, what constitutes a receiver, and what constitutes an error by a receiver. In considering these issues, it will become apparent that many fundamental features of communication apply to interactions between machines or between humans and machines, as well as those between animals including those between humans. Indeed these features apply to interactions within organisms, among organs and cells, and even to those between molecules. So there arises a fourth issue, what special features apply to communication among living organisms? Although the following discussion of these four issues concentrates on animal communication, a wider scope is sometimes appropriate.

First, to qualify as a signal, an event must affect some receiver's behavior. In other words, signals are associated with responses, a point frequently emphasized. A response might be overt but it could also be covert. We often think of responses as actions quickly following a signal, but they could also be changes in a receiver's state that alter the probabilities of further actions. Beyond this basic condition for a signal, there have been proposals to separate signals from signs (characterized by representation), cues (characterized by a lack of intention or evolutionary specialization), or indices (characterized by an invariant relation with some property of interest to a receiver) (see for instance, Markl 1985; Maynard Smith and Harper 2003). These distinctions have inevitably proven difficult to characterize operationally.

The present perspective can ignore these distinctions. A signal is any event that influences a receiver's behavior, immediately or subsequently, without providing all of the power for that behavior (Wiley 1994). At least some of the power necessary for the receiver's response must come from the signal, because there must be enough to alter the receiver's sensory receptors. For most familiar kinds of signals, including human language and animal displays, however, it is clear that most of the energy for responses comes from the receiver. According to this definition, moving out of the way of approaching danger as a result of a push is not an example of communication, but jumping aside in response to a shout, or even responding to the sound of approaching danger, is. The essential feature of any signal, in this view, is its limited power, insufficient to produce the response. As a result, the receiver itself has a crucial role in determining the response. The receiver therefore is in a position to get what it wants, as Grafen (1990) has emphasized, although, as we see below, only within some limits.

Second, this definition of a signal leads to a conclusion that any receiver has three essential components. A receiver must acquire a signal, must differentiate it from other events, and then must generate the power and arrange the coordination for a response. Electrical engineers have distinct terms for these components: a transducer, a switch (or gate), and an amplifier. If the receiver is an animal, these three basic components are often neural: sensory receptors, associative neurons,

and motor effectors (in combination with a musculo-skeletal apparatus). These three components are sometimes not obvious, however. Acquiring a signal often involves transducing it from its original form of energy or matter to one appropriate for the receiver's nervous system (for instance, from sound waves to action potentials in sensory neurons). Differentiating between a signal and irrelevant events might involve no more than a filter, a simple physical, electrical, or chemical connection between an input and an output, but it could involve extremely complex connections, such as human cognition. Generating the power for a response might be a process that nearly consumes a receiver but in many cases it is nearly trivial. Even if it involves no more than cleaving one molecule of ATP, a response requires some energy from a receiver to amplify the direct effects of a signal. As already mentioned, an amplified response need not be an overt action. It could instead be an altered internal state, such as a memory, neural association, or other physiological state, that can affect future actions. The possibility of such covert responses recurs in all forms of communication. For instance, in electrical apparatus, capacitors and computer memories provide this possibility. Altered molecular states of a cell do too. In each case, receivers have the three fundamental components just mentioned. For living organisms, we might call the three components a sensor, an associator, and an effector. A crucial factor is the second one: all receivers must make associations between signals and responses.

Third, the insufficient power of a signal and the necessity of association by a receiver together impose a special state of affairs on any receiver. Receivers are, fundamentally, decision makers susceptible to error. This inescapable conclusion arises from the possibility that receivers cannot in every instance separate the occurrence of signals from other events impinging on them. It might be possible to arrange a situation in which a particular receiver can almost always differentiate correctly between particular signals and irrelevant events. Living organisms including humans might try their best to attain such situations, and they might evolve to maximize the possibility of these ideal situations, but it seems unlikely that they often achieve them in the real world. Later, in this chapter, it will become apparent that approaching this ideal of error-free communication has diminishing returns. Consequently, communication among living organisms is not likely to evolve, nor is communication among machines likely to be designed, in a way that reaches this ideal. At best, we can expect an occasional close approach to the ideal. In all but ideal circumstances, receivers make errors, more or less frequently.

What constitutes an error by a receiver? To recognize an error, one must have a goal. If our goal is to understand the evolution of communication, then our concern is the relative rates of spread of alleles associated with receivers that differ in their mechanisms for response. In this view, those responses that make a receiver less likely to survive or reproduce are errors and those responses that do otherwise are correct. For a living organism, this ultimate goal might be less prominent at any particular moment than a more proximate one of maintaining homeostasis and of managing its relationships with other individuals. Nevertheless, the goals of homeostasis and behavior are themselves ultimately subject to the goal of propagating alleles. Because there is a single ultimate goal, the ultimate costs of errors are

continuous with the ultimate benefits of correct responses. These costs and benefits are measured by decrements and increments on the same scale. In a more proximal view, scales for measurements of costs and benefits might coincide but they do not have to. For instance, the costs of errors and benefits of responses might both be measured by probabilities of obtaining a mate. On the other hand, they might be measured, respectively, by probabilities of attracting a parasite and attracting a mate. The ultimate costs and benefits would remain the same: differences in the spread of alleles associated with receivers' mechanisms for response.

This concept of error in communication includes the normal human concept of error. The human view becomes a special case of this general view. We think of error as an opinion or action that tends to thwart a person's own objectives or that fails to conform to the opinions or actions of other people. Error often seems to require a goal set by human judgment (or attributed by humans to divine judgment). For our purposes here, these cases all represent proximate mechanisms of human behavior subsumed in the ultimate one of evolution.

The common human approach also recognizes that error has two inevitable aspects, errors of omission and commission, although it seems to take some effort for humans to keep these possibilities routinely in mind. Nevertheless, the approach here emphasizes that these two aspects of error are a fundamental aspect of any decision. Because decisions are a fundamental part of any receiver, so are these two forms of error. Whenever an animal samples its sensors and decides to respond or not, it faces four possible outcomes, two of which are correct and two of which are errors.

So far, this chapter has argued that the basic definition of a signal, as an event that evokes a response from a receiver but lacks sufficient power to produce the response, leads to the important conclusion that a receiver must have three components, one of which makes decisions prone to errors. The following section explores the nature of a receiver's decisions further and leaves us with a conclusion that all receivers face a double bind. Furthermore, we can see more clearly the relationship between errors and noise.

2.3 A Receiver's Double Bind

A receiver's dilemma results from the convergence of signal and noise. A simple example, in line with our focus on animal communication, is a sensory neuron tuned to a particular frequency of sound. In this case, a signal is a tone of this frequency emitted by an appropriate signaler, and any other sound with this frequency is noise. We must imagine that different occurrences of a signal have some random variation around a mean intensity, because the conditions under which the signal is produced and then received are never exactly the same. Likewise, the activation of a receiver's receptors by a signal varies. Nevertheless, we expect that the activity in a receiver's receptors, provided they are well matched to features of the signal, is often greater during the occurrence of a signal than during its

absence. Taking the variation into account, we find that the probability density functions for the activity of a receptor in the presence and absence of a signal often overlap (Fig. 2.1). If they overlap at all, then the receiver cannot completely avoid errors. As we have seen, receivers in the real world must usually, if not always, face such situations.

The possibility of error is thus the inevitable result of a decision by a receptor. A mechanism that makes a decision to respond or not requires a criterion for response. The simplest criterion is a threshold: if activity in the input reaches a predetermined level, then respond, otherwise do not. Of course, a criterion for response, even one based on just one receptor, can be more complex, and decisions can be based on the inputs from many receptors. The basic conundrum for a receiver, however, is not affected by the complexity of criteria or the number of inputs, a point discussed in more detail elsewhere (Wiley 1994, 2006). All the basic features of a receiver's conundrum are evident in the case of a simple threshold for activity in a single neuron (Fig. 2.1).

The receiver can adjust its threshold upward or downward. The location of the threshold is its decision. Such a decision might change from time to time depending on the receiver's physiology or development, and it might differ from individual to individual as a result of their genetic or epigenetic differences. Nevertheless, in any situation a receiver confronts, its threshold for response fixes four probabilities, one for each of the four mutually exclusive and exhaustive possible outcomes when the receiver samples its sensors.

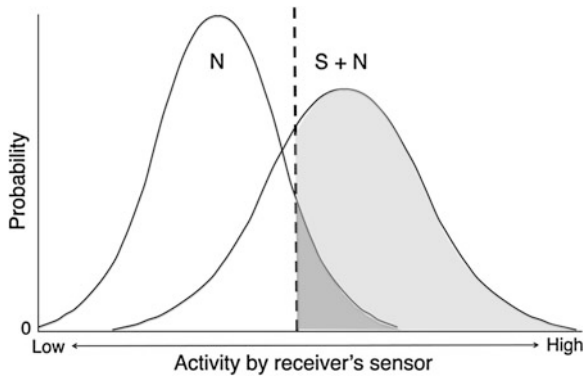


Fig. 2.1 Receiver performance depends on the activity of its sensors, the signal-to-noise ratio, and its threshold for response. Horizontal axis, the level of activity of the receiver's sensors. Vertical axis, probability that activity reaches any level when only noise is present (N) and when a signal is present with noise ($S + N$). The latter distribution would often have greater variance as a result of variation in the signal. *Dashed line*, an example of a threshold for response set by the receiver. *Light shading*, the cumulative probability of a correct detection when a signal is present and the receiver's threshold is at the indicated level. *Dark shading*, the cumulative probability of a false alarm when only noise is present. There are corresponding probabilities of a missed detection, when a signal is present, and a correct rejection, when it is not. A receiver can adjust its threshold for response in order to maximize the utility of its threshold and thus to optimize its performance

Furthermore, the four possible outcomes are not independent of each other. By raising its threshold, for instance, a receiver might reduce the chance of a false alarm, but it would concomitantly raise the chance of a missed detection. By lowering its threshold, a receiver might reduce the chance of a missed detection, but it would raise the chance of a false alarm. Receivers thus face an inevitable trade-off between the consequences of false alarms and missed detections (coinciding with this trade-off there is also one between correct detections and correct rejections). This trade-off is equivalent to the well-known trade-off in electronic receivers between sensitivity and selectivity. Only by accepting more false alarms (less selectivity) can a receiver reduce missed detections (more sensitivity). Evolution should thus result in receivers that optimize the expected utility, $E(U)$, of their criteria for response (Wiley 1994).

A receiver's criteria for response can vary in complexity. As described above, a simple case is a threshold on a single dimension of a signal, such as frequency or intensity. Other cases can include multidimensional criteria for responses to complex patterns of stimulation. Experimental demonstrations that a species' own vocalizations are easier to detect in background noise, for instance, indicate that channels for filtering and decision-making have evolved complex filters for detection of these signals (Okanoya and Dooling 1991; Dooling et al. 1992; Benney and Braaten 2000). Regardless of the complexity of a receiver's criteria for response, it faces the same inevitable trade-off in minimizing errors (Wiley 1994).

Although beyond the scope of our discussion here, it is also important to realize that a receiver only "knows" two possible states of the world prior to its decision to respond or not: input-above-criterion or input-below-criterion. The view presented here suggests that there are actually four possible states of the world, depending both on whether or not the receiver's input is above or below its criterion but also on whether or not a signal has actually occurred. We can imagine a privileged observer, one with a special vantage or special equipment for studying both signals and receivers simultaneously, who might realize these four states of the world. For the receiver, however, the world has only two states. And, going one step farther, we see that the observer, in deciding any "fact" about signals and responses, also sees only two possibilities: the evidence at hand is either sufficient or not. But we are not going to pursue this point here.

2.4 Applications of Signal Detection Theory to Animal Communication

The application of signal detection theory to human psychophysics has provided quantitative confirmation of many of its predictions. Controversies in this field have focused on the validity of assumptions for mathematical convenience, rather than on the underlying trade-off any receiver must face (reviewed by Wiley 2006).

Experiments in psychophysics have repeatedly demonstrated that a receiver's performance increases with higher signal-to-noise ratios, in other words higher contrast between signals and noise. Furthermore, performance improves under any conditions that allow a receiver to predict the timing and features of a signal. Identifying intervals when a signal might occur by means of alerting signals, using signals with features known in advance, and including redundancy (predictable temporal or spatial structure) all increase performance (reviewed by Wiley 2006). Other aspects of receiver psychology (Guilford and Dawkins 1991, 1993), including the "peak shift" so frequent in discrimination learning (Enquist and Arak 1998; Lynn et al. 2005), also follow from signal detection theory.

These results from experimental psychophysics have analogies with communication in natural circumstances (Wiley 2006). Adaptations that increase contrast between signal and noise, for instance, are widespread. Birds and mammals, including humans, increase the intensity of their vocalizations in the presence of background sound (Brumm and Todt 2002; Pytte et al. 2003; Brumm and Slabbekoorn 2005; Leonard and Horn 2005; Brumm and Zollinger 2011). In another case, two closely related populations of birds differ in the dominant frequencies in their songs, so that each minimizes overlap of its songs with background noise (Slabbekoorn and Smith 2002a). Many long-range acoustic signals of birds and mammals have attributes that reduce attenuation and degradation during transmission through their natural habitats and thus increase contrast between signal and noise for a receiver (Morton 1975; Wiley and Richards 1982; Wiley 1991; Brown et al. 1995; Mitani and Stuht 1998; Boncoraglio and Saino 2007; Brumm and Naguib 2009; Ey and Fischer 2009). Visual signals also provide evidence for adaptations that improve a receiver's signal/noise ratio. For instance, the movements in territorial displays of *Anolis* lizards are faster than the movement of vegetation in the background (Fleishman 1988; 1992). To maintain this contrast, lizards increase the speed of movements in their displays in windier conditions (Ord et al. 2007). The contrast between a bird's coloration and its background depends on the spectral properties of ambient light (irradiance) as well as the reflectance of the bird's plumage and the nearby vegetation (Endler 1990). The colors of manakins and other lekking birds of neotropical forests contrast best with the background at the sites where they perform their displays (Endler and Théry 1996; Heindl and Winkler 2003; Doucet et al. 2007). Species that display on the forest floor clear away leaf litter in order to increase the contrast of their plumage with the ground (Uy and Endler 2004).

It has also become apparent that animals include alerting components in their signals—introductory components poor in information that serve to attract the attention of potential receivers to subsequent components rich in information (Richards 1981; Wiley and Richards 1982; Peters and Evans 2003; Mitchell et al. 2006; Ord and Stamps 2008). In at least one case this alerting component becomes longer and more conspicuous in noisy conditions (Peters et al. 2007).

Redundancy is also prominent in many animals' signals, sometimes producing spectacular patterns in time or space. Temporal patterns in signals include simple repetition of movements or acoustic elements, as well as complex arrangements.

Spatial patterns of coloration and movement are also prevalent. Nevertheless, there has been little attention to the possibility that levels of redundancy differ in different levels of noise. Humans, in the presence of noise, speak more distinctly (as well as more loudly, as mentioned above) and thus with greater redundancy in enunciation, a change that improves intelligibility (van Summers et al. 1988). Birds close to noisy waterfalls and torrents repeat their songs more often (Brumm and Slater 2006), and birds also increase their rates of signaling in the presence of artificial ambient noise (Potash 1972). The use of multiple “ornaments” for communication might also provide redundancy (Møller and Pomiankowski 1993; Johnstone 1996; Candolin 2003). If the expression of these ornaments were positively correlated, they might improve detection (provide “backup” for missed detections), as predicted for increased redundancy. In contrast, multiple ornaments with negative or no correlation might serve as separate signals for distinct sets of receivers or responses (Andersson et al. 2002). So far, theoretical treatment and experimental investigation of multiple ornaments have only tangentially considered the possibility that features of signals correlated in time or space might improve detection by increasing redundancy.

Receivers might evolve adaptations to background noise as well as signalers. The optimal frequency for detection of sound by great tits *Parus major* is higher in the presence of natural noise such as wind in a forest than it is in quiet conditions such as in a sound-attenuating chamber. The higher optimal frequency in natural conditions is a better match for the dominant frequencies in the species’ vocalizations (Langemann and Klump 2001).

Among the more important consequences of background sound is the limit it sets for the active space of a signal (Brenowitz 1982; Römer and Bailey 1986; Janik 2000; Nemeth and Brumm 2010). A striking example of this limitation occurs in choruses of frogs. The phonotactic responses of female green treefrogs *Hyla cinerea* to calls of individual males differ in the presence and absence of sound from a chorus of these frogs (Gerhardt and Klump 1988). Females preferentially approach a male’s calls only when the calls exceed the sound of the chorus by 3 dB. A male’s call attenuates by spherical spreading alone to this level in a distance of about 1 m. Female frogs in such a chorus would thus respond to individual males only within this short distance. As a result of the spacing of calling males, even in the densest part of a chorus, a female is within this distance of only 2–3 males at a time. To sample more males, she would have to move around and thus risk exposure to predators such as snakes. A similar conclusion was reached by Wollerman (1999) for female *Hyla ebraccata* at a large chorus with eight species of frogs in a Costa Rican rainforest. Because of background noise, a female’s choice of males is much more limited in a large aggregation than we might imagine.

The adaptations of receivers to noise might explain one of the striking features of sympatric animals’ signals. Biologists have long realized that sympatric species usually have signals with distinctly different features, at least for communication with conspecifics (Marler 1957). Evidence suggests that signals of closely related species can diverge in sympatry in comparison to allopatry (reviewed by

Slabbekoorn and Smith 2002b; Pfennig and Pfennig 2009). Sympatric species' signals, however, are not only distinct but also disjunct. In other words, the signals of sympatric species are separated by gaps in signal space (the multidimensional space with axes defined by the features of signals). This disjunction of sympatric species' signals occurs even in highly diverse faunas, such as among birds in neotropical rainforests. In these situations, sympatric species' signals can diverge enough to produce significant overdispersion in signal space (Luther and Wiley 2009).

This disjunction of signals raises an evolutionary problem. Although it is clear that natural selection for character divergence might result in differences in the signals of two populations, the strength of this selection should fall to zero once the signals no longer overlap (distinct signals). So it is hard to see how natural selection for character divergence could routinely produce gaps between sympatric populations' signals (disjunct signals). A possible resolution of this problem comes from experiments in Neotropical forests on two bird species with similar (but disjunct) songs (Luther and Wiley 2009). The results showed that receivers have a broader scope for responses than do conspecific signalers for producing songs. When digitally synthesized songs were morphed to produce exemplars intermediate between the two species, playbacks revealed that individuals of each species responded to exemplars beyond the natural range of conspecific songs. The responses of the two species left no gaps in signal space. Receivers' responses were thus not disjunct and not even quite distinct. Presumably, the greater scope of receivers' responses allows them to compensate for variation in noisy signals. Receivers' scope for responses is thus wider than the scope for signals as produced by signalers and measured in clean recordings. If this result applies to animal communication broadly, the disjunct signals of sympatric species are not explained entirely by selection on signalers but also by selection on error-prone receivers—in other words, by noise.

2.5 Detection Versus Discrimination

The problem for a receiver becomes more complicated when the task is to classify two or more relevant signals as well as to detect the presence or absence of any one (Miller et al. 1951; Green and Birdsall 1978; Wiley 2006). This problem arises whenever a receiver must make appropriate, but different, responses to more than one signal. An animal that must respond in different ways to different types of prey or food might face this situation. Social situations that require recognition of several different individuals also fit this situation. Another occurs when appropriate responses must be given to signals warning about different kinds of predators (Owings and Leger 1980; Cheney and Seyfarth 1990; Blumstein and Armitage 1997).

These situations require classification (often called discrimination) of signals, in other words, different responses to each of several signals. In contrast, detection requires the same response to exemplars of one signal. A test for discrimination

thus requires a comparison of responses to two different sets of signals, each mixed with noise, and to noise alone. A test for detection, as described above, requires only a comparison between responses to one set of signals, mixed with noise, and noise alone. A complete analysis of discrimination thus requires three situations, noise alone and with each of two sets of signals, whereas an analysis of detection only requires two situations.

In a complete analysis of discrimination between two signals, there are nine possible outcomes as viewed by a privileged observer, instead of the four possibilities for detection. There are three states of the world (noise with signal one, noise with signal two, or noise alone), and there are three possible responses of the subject (appropriate for signal one, for signal two, or none). The analysis of this situation is correspondingly complex, with more than twice the number of relevant probabilities and utilities.

Despite this complexity, applying signal detection theory to discrimination leads to an important prediction (Macmillan 2002; Wiley 2006): performance of receivers in tasks that require discrimination is lower than performance in tasks with detection only. Consequently, we expect to find that individuals can detect signals in higher levels of noise but can discriminate among them only in lower levels of noise. Humans, for instance, can detect occurrences of a single known word in higher levels of noise than they can discriminate between two or more words (Miller et al. 1951).

This difference between detection and discrimination applies to female frogs mating in a dense chorus. In a number of species of frogs, we know that females prefer conspecific male advertisement calls with lower dominant frequencies. This preference has, for instance, been confirmed for *H. ebraccata* in Costa Rica (Wollerman 1998). As already discussed, we also know that female frogs, including *H. ebraccata*, have difficulty detecting individual male's calls in large choruses. Do they have even greater difficulty discriminating males' dominant frequencies?

In a test of discrimination in natural levels of noise, Wollerman and Wiley (2002) presented gravid female *H. ebraccata* with males' calls mixed with the background sound of a chorus. One speaker presented calls with a dominant frequency at the population mean, while a second speaker presented calls with a dominant frequency two SD below the mean. With no added chorus noise ($S/N > 25$ dB), females reliably preferred the lower frequency. With added chorus noise ($S/N = 6$ or 9 dB), they no longer preferred the lower frequency, although they still detected (responded preferentially to) a single male's calls in chorus sounds. The discrimination made in relatively quiet conditions thus disappeared in conditions that still allowed detection of the signals. This result is thus in agreement with the prediction of signal detection theory: discrimination requires a higher S/N ratio than does detection.

2.6 Evolution of Receivers

By providing a method for analyzing the performance of a receiver, signal detection theory allows us to determine a receiver's optimal performance and thus the expected evolution of communication. The constraints on a receiver's performance can provide a sufficient explanation for such problematic features of communication as the prevalence of honesty, the persistence of deception, and the exaggeration of signals. In addition, signal detection theory suggests that the co-evolution of signalers and receivers (or the behavior of signaling and receiving) lead to a signal detection balance.

Because receivers provide the power necessary for a response, they evolve to optimize performance in the conditions they experience. The first step in understanding the evolution of communication is thus an explanation for a receiver's decisions to respond or not. As we have seen, this explanation requires optimization of the expected utility, $E(U)$, of the receiver's criterion for response. Procedures for calculating optimal thresholds for response have been presented elsewhere (Wiley 1994). Here we use some limiting cases to illustrate the main conclusions. Compare, for instance, situations in which missed detections have relatively high costs with those in which false alarms have relatively high costs.

Missed detections might be especially costly when an individual is listening for alarm calls. A missed detection (failing to respond to an alarm call) is likely to mean increased exposure to a predator. A false alarm (briefly fleeing when there is no alarm call) would often require only a little energy and a little time lost from other activities. If predators are a relatively frequent danger, the cost of a missed detection multiplied by its probability might well dominate other terms in the expected utility of any threshold for response. In this case, a low threshold is optimal. The result would be a receiver with "adaptive gullability" (Wiley 1994), one prone to false alarms but subject to few missed detections. Such an individual would be susceptible to frequent deception, for instance, when calls that mimic alarms allow a subordinate individual to take advantage of a dominant rival.

Examples of adaptive gullability include birds that respond to false alarms by subordinating that usurp food or by rivals that interrupt sexual activity (Munn 1986; Møller 1988, 1990). Monkeys are also manipulated by subordinates in this way (Cheney and Seyfarth 1990). Another example comes from species in which satellite males encroach upon matings by dominant males. In many cases, the subordinate males look like females. Dominants trying to detect cheating males thus run the risk of false alarms, with the consequence that they chase away some females. When missed detections are expensive, adaptive gullability should evolve and dominant males should fail to exclude all satellites from matings.

False alarms, on the other hand, might have especially negative consequences when individuals make infrequent but crucial choices. Mate choice might often fit this situation. In most species, a female chooses a mate infrequently and yet mistakenly mating with a low-quality male, a male with inadequate resources, or even another species could substantially reduce the spread of her genes. In this

case, a high threshold is optimal. The result would be a receiver with “adaptive fastidiousness” (Wiley 1994), one liable to miss detections of suitable signals but subject to few false alarms. From a privileged observer’s perspective, such a receiver would appear to be “choosy” or “coy,” because they would often fail to respond to suitable signals.

This situation would apply whenever reproductive success of a female is limited by the number of eggs she matures, while reproductive success of a male is limited by the number of matings he gets. A mistake in mating in this case has greater consequences for a female than for a male. As Wiley and Poston (1996) have argued, females in many species have evolved choosiness in mating and males have not because the consequences of errors in mating differ for the two sexes.

Adding signal detection theory to an investigation of mating signals and preferences has advantages over the usual approach based exclusively on sexual selection. First, it emphasizes that the evolution of receivers is likely to depend on the probabilities and consequences of all four outcomes of an interaction. Second, it emphasizes the detectability of a signal, which in relation to the receiver’s criterion for response, determines the probabilities of the possible outcomes. Overall, it stresses features of communication with noisy signals in natural situations, as opposed to communication with clean signals in expurgated situations.

2.7 Evolution of Signals

Once the performance of receivers begins to evolve toward its optimum, the evolution of signaling should adapt to the changing behavior of receivers. On one hand, the presence of receivers with “adaptive gullability” opens opportunities for signalers that can manipulate receivers with misleading signals, like the deceptive alarm calls mentioned above. In this case, the evolution of deceptive signals is limited by the payoffs and probabilities of the four outcomes for receivers and by the probabilities of honest and deceptive signals (Wiley 1983).

On the other hand, the presence of receivers with “adaptive fastidiousness” favors signalers that produce exaggerated signals that exceed the high thresholds or other stringent criteria set by these receivers. For instance, among oropendolas and caciques, males of species with only brief interactions with females have displays with high repetitiveness and complexity (Price 2013). Signal detection theory predicts that the evolution of exaggerated signals should result in increased detectability or discriminability of signals by intended receivers (potential receivers whose responses would have advantages for the signaler). Evidence for greater detectability of exaggerated signals comes from a study of nestling birds begging for food from their parents. When begging, nestlings often reveal bright colors in their mouths, particularly red gapes and yellow flanges. Heeb et al. (2003) showed that nestling great tits with gapes and flanges that were more detectable under natural light conditions (the dim light available in nest cavities)

gained more weight than did other nestlings. The detectability of the markings was a better predictor of parental response than was their complexity or redness (which might indicate the nestling's nutritional state).

Studies of fish have revealed a connection between discriminability and the evolution of colorful signals for mate choice. In Lake Victoria, female preferences for the colors of males contribute to reproductive isolation between many coexisting species of cichlids. Sedimentation of the lake in areas with high agricultural runoff, however, has obscured colors and resulted in loss of reproductive isolation (Seehausen et al. 1997). Another case involves sticklebacks in lakes of coastal British Columbia. In some populations, males have bright red on their underparts and in others they lack red, differences that contribute to reproductive isolation between sympatric populations. In lakes with high concentrations of tannin, the tea-colored water masks red signals. In these lakes, males have lost their red markings, and females have lost not only their preferences for red males but also their sensitivity to red light (Boughman 2001 also see Fuller and Noa 2010). Colorful signals and receivers' responses to them thus persist only where the ambient light does not mask them. Between populations, lower thresholds for responses to red by females correlate with redder males. Within a population, on the other hand, females with higher thresholds for red should tend to mate with redder males.

2.8 Signal Detection in Relation to Previous Theories

This approach to the evolution of signals based on signal detection theory complements previous ones based on sexual selection and costs for the signaler and receiver. The effects of sexual selection on communication have attracted widespread attention, because the evolution of exaggerated signals, one of the most striking features of animal communication, is especially associated with mate choice. Not all mate choice is a result of communication, however (Wiley and Poston 1996). Mate choice, behavior that results in mating with some potential mates more than others, includes both direct choice (preferences for perceived traits of potential mates) and indirect choice (any other behavior that results in narrowing the set of potential mates). It is direct choice that requires communication between potential mates. Both forms of mate choice generate sexual selection, the evolution of alleles associated with the traits of mating individuals. The distinctive feature of sexual selection, as opposed to other forms of natural selection, is the genetic correlation that inevitably results from nonrandom mating between individuals with a preference and those with the corresponding trait. This genetic correlation produces the explosive evolution that makes sexual selection distinctive. If this genetic correlation becomes sufficiently strong, the evolution of a preference and a corresponding trait become self-reinforcing, and alleles for a preferred trait spread in association with alleles for the corresponding preference until the benefit of additional matings is balanced by the cost of the trait (Lande 1981; Kirkpatrick 1982). Subsequent analyses have emphasized that alleles for a

preference can spread unless the direct costs of the preference (from searching for or interacting with males) completely compensate for the benefit (direct or indirect) of mating with a preferred male (Pomiankowski 1987, 1988). If a preference has no costs, then, a preference can spread even if it has no benefits. Matings of females with high thresholds and males with exaggerated signals produce the sort of genetic correlation that characterizes sexual selection.

At first it seemed that sexual selection could result in the evolution of arbitrary traits, those with no benefits for females and none other than multiple matings for males. This possibility provided an attractive explanation for many secondary sexual traits that seem exaggerated to an extreme of preposterousness. The expanded esophageal sacs of male greater Sage-Grouse *Centrocercus urophasianus*, so laboriously inflated during displays, provide an example (Wiley 1973). The selection on a male trait depends on the sum of direct selection as a result of its effect on the male's viability and selection as a result of females' preferences (reviewed by Heisler 1994). Taking both costs and benefits of male traits into account, sexual selection favors the evolution of preferences with the greatest net benefit for females and a corresponding trait with the greatest net benefits for males. Strictly arbitrary preferences (those with no costs for the choosy partner) and arbitrary traits (those with costs limited only by mating success of the chosen partner) seem unlikely to evolve.

Although sexual selection can explain the explosive rate of evolution of preferences and traits, it does not explain the direction of evolution. Sexual selection puts no constraints other than costs on the nature of the preference or the corresponding trait. Even when we consider the costs and benefits of the partners, sexual selection could in principle result in preferences for either augmented or diminished traits. Nevertheless, sexual selection has always been assumed to produce augmentation of signals. This gap between theory and preconception poses a dilemma. The explanation for the exaggeration of signals by sexual selection alone is incomplete. To complete the argument, it has been proposed that high costs of traits are necessary to insure reliable (or honest) signaling of mate quality, which in turn insures a net benefit for females' preferences (Zahavi 1975; Grafen 1990; Johnstone 1995, 1997; Zahavi and Zahavi 1997; Maynard Smith and Harper 2003).

This expanded argument has plausibility. Exaggeration of signals should normally increase the costs for signalers. These costs might include any of those previously identified for signals: additional time and energy, developmental compromises with other traits as a result of physiological interactions or genetic epistasis, and risks of interception by unwanted receivers, like predators, parasites, and conspecific rivals (McGregor 1993; Zuk and Kolluru 1998). In many cases, exaggeration of a signal at a cost could increase the discriminability of high-quality mates, those able to absorb the additional costs. For a graphic demonstration of how costs produce honesty, see Fig. 2.2, from Wiley (2000, 2013); more or less similar graphs are presented by Johnstone (1997) and Getty (1998, 2006).

This argument for costly exaggeration of signals nevertheless raises problems. It has been pointed out that some costs do not insure honesty (Hurd 1995; Getty 2006; also consider the final comment in the legend of Fig. 2.2), so the argument

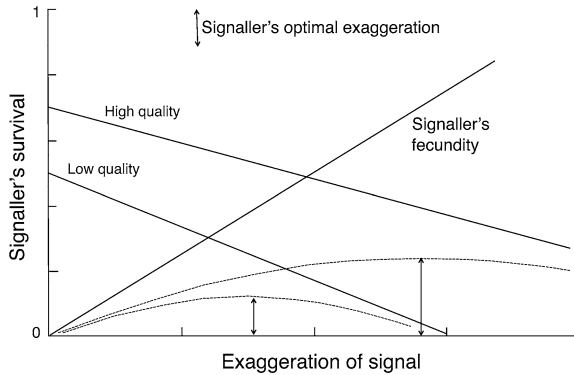


Fig. 2.2 Reliability of signals occurs when signalers of different quality adjust their levels of signaling to maximize fitness (the product of survival and fecundity). Signalers with higher quality have higher intrinsic survival than those with lower quality when no signal is produced and higher marginal survival when signaling. Females only respond to males' signals, so all males have the same fecundity for any level of signaling. A male's fitness as a function of his level of signaling (*dotted lines*) reaches a maximum at a higher level for males with higher quality than for those with lower quality. Signals of male quality are reliable (honest) unless the survival functions for males of different quality cross. In other words, reliability requires that quality correlate with intrinsic survival in the absence of signaling or marginal survival at any level of signaling. Otherwise the shapes of the curves do not matter. Notice that signals would still be reliable even if males had equal intrinsic survival provided their marginal survival correlates with quality—or if they had equal marginal survival provided their intrinsic survival correlates with quality (see Wiley 2013 for more discussion)

for exaggeration might then not apply. A more serious problem is that any level of cost can separate individuals with different capacities to bear those costs (Getty 1998; Wiley 2000). Formal arguments that costs are necessary for honest signals have shown only that signals must have some cost but not that a receiver's benefits must rise as a signal's cost rises (Grafen 1990; Maynard Smith 1991; Johnstone and Grafen 1992; Maynard Smith and Harper 2003). Because all signals presumably have some costs, these arguments do not explain why honest signals must have exaggerated costs.

There is now extensive evidence that preferred traits have costs. Less extensive, but still substantial, evidence shows that individuals with preferred traits also have high phenotypic quality, such as higher survival, lower resistance to disease, greater foraging abilities, or greater success in competition with conspecific. Some evidence indicates that females benefit from preferences for mating with these individuals, either directly as a result of greater survival or reproduction or indirectly as a result of genetic advantages for their offspring (Andersson 1994; Searcy and Nowicki 2005). Some of this evidence comes from comparisons of benefits for females mated to two categories of males, with higher or lower expression of a trait, and some comes from measurements made partly or entirely in laboratories, rather than in natural situations. Evidence that females' benefits correlate with the size of their partners' traits in nature is absent. In cases of extremely exaggerated

traits, it has sometimes not been possible to find correlations between the size of the trait and a preference for the trait or the benefits of the preference (Poston 1997).

A corollary has also been proposed that the costs of signals should be structurally related to their “meaning.” For instance, a signal must reduce foraging success in order to indicate a greater capability for foraging, or it must reduce survival in order to demonstrate a greater capability for survival (Zahavi 1975; Zahavi and Zahavi 1997). This corollary could also provide an explanation for exaggeration of signals. Some signals might have this feature, but it is possible to imagine cases in which they do not. An ability to fight could be indicated by a signal that imposes a cost on foraging, if reduced foraging reduced fighting ability. Or parental ability could be indicated reliably by a signal that imposes a cost on fighting, if success in fighting improved opportunities for parenting.

Despite a superficial plausibility, arguments that the reliability of signals is proportional to their costs so far have no formal proof and little if any confirmation in the field. Instead the theory of sexual selection indicates that, for any net benefit for receivers (as a result of the reliability of a signal), a signal should evolve to minimize costs. These arguments and the corresponding evidence do not produce a strong explanation for the widespread evolution of exaggerated signals.

2.9 Signal Detection Theory as an Explanation for Exaggeration

Signal detection theory, on the other hand, provides an unequivocal prediction that signals intended for choosy receivers should evolve exaggeration. Exaggerated signals evolve in response to high thresholds. High thresholds of receivers are a result of adaptive fastidiousness, which, as described above, occur when receivers face situations with low inherent detectability or discriminability of signals (low signal-to-noise ratio) and costly missed detections.

In this case, however, there is no requirement that exaggeration of signals should correlate with their costs, although as we have seen this possibility might often arise. Instead, exaggeration of signals should correlate with their discriminability in the intended receiver’s local environment. Signals should evolve to reduce the possibility of confusion with irrelevant perturbations of the receiver’s receptors (Endler 1992; Wiley and Richards 1982; Wiley 1994, 2006). It is thus not the cost of a signal that is the primary consideration in its evolution, but its impact on the receiver. Exaggerated signals should evolve to become spectacular. The cost is a secondary consideration.

Just as signal detection theory requires shifting our emphasis from preferences to an emphasis on thresholds (or to criteria for response in general), it also requires shifting our emphasis from a receiver’s benefits to an emphasis on the expected utility of its threshold. In signal detection theory, the benefit of choosiness is a

result of the difference in payoffs from mating with an optimal partner as opposed to a suboptimal one, in other words the difference in payoffs for a correct detection and a false alarm. Other payoffs affect the receiver's optimal threshold as well. The cost of additional search is the payoff for a missed detection, when an optimal mate is actually present, or for a correct rejection, when no optimal mate is present. The inevitable trade-offs between these possible outcomes are summarized in the expected utility, $E(U)$, of the receiver's threshold, which depends on the payoffs and probabilities of all four possible outcomes.

This approach also reinforces the improbability of arbitrary mating preferences and traits. Preferences could have equal benefits for receivers only when different thresholds for response have equal expected utilities, $E(U)$. This condition requires that the four possible outcomes have equal probabilities and equal consequences for different thresholds (or exactly compensating effects on their expected utilities). In other words, alternative signals would have equivalent consequences for a female only if they had exactly the same correlation with male quality and exactly the same detectability by females (or exactly compensating effects). Meeting these conditions seems so unlikely that arbitrary signals and preferences seem doubly implausible. As a consequence, optimizing a receivers' performance would nearly always oppose runaway evolution of arbitrary thresholds and signals.

By shifting our emphasis away from the costs of signals and the strengths of preferences, as the explanation for the exaggeration of signals, to new emphases on the performance of receivers, we find that the dominant influence on the evolution of exaggerated signals is the detectability or discriminability of signals in the receiver's natural environment. From the perspective of signal detection theory, the costs of signals are secondary. Costly signaling should evolve only when it increases the performance of receivers. The primary consideration is the detectability of signals from the perspective of receivers. The detectability of signals depends on the prevailing signal-to-noise ratio, the relationship between the properties of signals and properties of irrelevant events that alter activity in the receiver's sensors. Noise is thus an inescapable, if not dominant, consideration in explaining the evolution of exaggerated signals.

There is a further benefit from an application of signal detection theory to communication. Although the evolution of signalers and receivers must be mutually related, it has not been easy to formulate the nature of this relationship. It is easy to see that the evolution of signalers must depend on the evolution of receivers, and vice versa. Furthermore, it is routine to show that the properties of signals are related to the properties of corresponding detectors. If males have certain traits, we can test the expectation that females respond to these traits and that their sensory mechanisms have corresponding filters. Conversely, females' preferences often provide a match for male's traits. Perhaps in the course of evolution one side of this relationship drives the other. Perhaps, as in the theory of sensory exploitation, the mechanisms of females' responses set constraints for the evolution of males' traits. Although never previously suggested, one could conversely imagine that males' traits might drive the evolution of females' preferences.

A more likely result would be coevolution of both receivers and signalers to a signal detection balance. By providing an explicit measure of a receiver's performance, signal detection theory can provide to a way to think about the evolution of this balance. As before, it becomes apparent that noise is a predominant consideration.

2.10 Signal-Detection Balance

Although we have discussed exaggeration mostly in terms of its implications for the costs of signals and the increased probability of responses (correct detections) by receivers, signal detection theory identifies an additional consequence of exaggeration: diminishing returns for a signaler. As a signal becomes more detectable to the intended receivers, the probabilities of errors by receivers decrease asymptotically toward zero and the probability of correct detections increases towards one. In the later stages of this process, any further increase in a receiver's threshold would result in progressively fewer additional correct detections and more additional missed detections. As receivers' thresholds stabilized, further exaggeration of signals would yield little or no increase in benefits for them. Selection on receivers for increasing thresholds would thus progressively decrease. Even if further exaggeration of signals had little or no cost, selection on signalers for further exaggeration would also progressively decrease as a result of the diminishing returns from improved performance of receivers. Although high costs of false alarms and noisy discriminations could result in the evolution of highly fastidious receivers and extravagant exaggeration of signals, both receivers and signalers face diminishing returns.

Eventually, an equilibrium between diminishing benefits and augmenting costs of exaggeration would put an end to further exaggeration of a signal. Furthermore, these diminishing returns suggest that this equilibrium would be reached at a point short of perfect discriminability of signals by intended receivers (Wiley 2013). At this equilibrium, receivers would make some mistakes, and signals would sometimes fail to evoke the intended response. Receivers would have evolved optimal, not ideal, performance, and signals would have evolved optimal, not complete, efficacy. Both receivers and signalers would have adapted to the constraints of environmental noise on signal detection or discrimination. We should therefore avoid a naive expectation that evolution leads to signals that are always detectable by receivers or receivers that never make mistakes. At a signal-detection balance, ideal signals and ideal receivers would not exist.

It seems likely that most communication is poised in such a signal-detection balance. If so, the properties of communication would be difficult to understand without an investigation of all the constraints on optimal performance of receivers and on optimal detectability or discriminability of signals. Noise, as much as costs and benefits of signals or responses, would determine the properties of communication.

Acknowledgments My approach to understanding communication has developed over several decades in the course of many discussions and experiments with students and colleagues at Chapel Hill, many of whose papers are cited in my chapter. Those who took a particular interest in signal detection included Douglas Richards, Lori Wollerman, Marc Naguib, David Luther, and Jonathan Micancin. In addition, many ideas were vetted in a course in animal communication taught jointly with Steve Nowicki with students from both Chapel Hill and Durham. Continuation of my work has always been supported in many indispensable ways by my wife, Minna Wiley.

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