interactions in birds.' *American Naturalist 131*, 175–202.

Jouventin P, Guillotin M & Cornet A (1979). '*Le chant du manchot empereur et sa signification adaptive*.' *Behaviour 70*, 231–250.

Kilner R M & Johnstone R A (1997). 'Begging the question: Are offspring solicitation behaviors signals of need?' *TREE 12*, 11–15.

Kilner R M, Noblet D G & Davies N B (1999). 'Signals of need in parent–offspring communication and their exploitation by the common cuckoo.' *Nature 375*, 667–672.

Lévy F, Kendrick K M & Keverne E B (1996). 'Physiological sensory and experiential factors of parental care in sheep.' In Rosenblatt J S & Snowdon C T (eds.) *Parental care: Evolution, mechanism and adaptive significance*. San Diego: Academic Press.

Mock D W & Parker G A (1997). *The evolution of sibling rivalry*. Oxford: Oxford University Press.

Schaal B, Coureaud G & Langlois D (2003). 'Chemical and behavioral characterization of the rabbit mammary pheromone.' *Nature 424*, 68–72.

Trivers R L (1974). 'Parent–offspring conflict.' *American Zoologist 14*, 249–264.

Trumbo S T (1996). 'Parental care in invertebrates and early vertebrates.' In Rosenblatt J S & Snowdon C T (eds.) *Parental care: Evolution, mechanism and adaptive significance*. San Diego: Academic Press. 3–51.

Tschanz B (1968). '*Trottellummen. Die Entstehung der persönlichen Beziehung zwischen Jungvogel und Eltern*.' *Zeitschrift Tierpsychologie Supplement 4*, 1–103.

Animal Communication: Signal Detection

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Introduction

Signal detection theory (SDT) addresses the problem of identifying signals in noise. SDT derives from a fundamental feature of any mechanism for detecting signals, whether sensory, electronic, or otherwise – signals and noise cannot be differentiated with certainty. Signals (patterns of energy or matter with significance for the detector) are not distinct from noise (random or irrelevant energy or matter impinging on the detector from outside or arising in the detector itself).

Imagine a territorial bird in a forest singing its own songs and listening for its neighbors 50 to 200 m away. Some neural mechanism must distinguish between a neighbor's song at an appropriate distance and innumerable other possibilities – a neighbor's song close enough to indicate a territorial encroachment, a song of a newcomer looking for a place to settle, a song of another species with similar notes or frequencies, other sounds in the forest, and even random sounds produced by wind and turbulence. At a distance, any song arrives at the listener distorted by attenuation, reverberation, random amplitude fluctuations, and masking by sound of similar frequencies (Wiley and Richards, 1982). All signals are degraded during transmission, and all mix with background energy. In practice, absolute differentiation of signals from external noise cannot occur in real life. The degree to which signals and external noise are separable in actual (as opposed to theoretical) situations varies widely but is never complete. Furthermore, any mechanism for identifying signals generates its own internal noise and confusions.

Principles of Signal Detection

To analyze this situation quantitatively, SDT assumes that any such detectors can be represented by some combination of simple channels, each of which has two possible responses: go and no-go. The output from such a channel depends on the level of the input. It further assumes that noise is normally distributed energy in the same channel as the signal. In this case, the problem of signal detection is represented by the overlap of the probability density functions of the noise and the signal plus noise. The detector uses some threshold of input for a response: A level of input below the threshold results in no response (no-go); a level above the threshold results in a response (go) ([Figure 1]).

This formulation separates two aspects of signal detection. The inherent detectability of the signal is represented by the normalized distance between the peaks of the probability distributions for noise and signal plus noise. The bias of the detector is represented by the position of the threshold for response. By quantitatively separating the detectability of a signal from the subject's bias, SDT has made an important contribution to the study of sensory thresholds in psychophysics (Macmillan and Creelman, 1991; Macmillan, 2002).
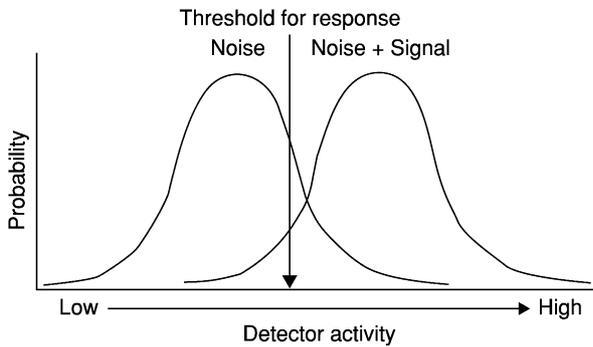
Figure 1 Representation of the general problem addressed by Signal Detection Theory. Noise (random or irrelevant energy in a channel) produces a measurable level of activation of a detector. A signal is added to this noise to produce a higher level of activation. The detector responds or not, depending on whether or not the level of activation exceeds some threshold, which can be adjusted to higher or lower levels of activity.

Applications to Animal Communication

Signal detection creates some serious problems for animals in natural situations. Communication between widely separated individuals, as just described, often requires receivers to deal with heavily degraded signals. Communication in large groups of conspecific individuals requires receivers to identify signals (for instance, a mate's or offspring's call) in a background of other similar signals. This latter situation is traditionally called the Cocktail-Party Problem.

The attraction of female frogs to calls of potential mates in large choruses provides an example (*see* **Frog and Toad Communication**). A gravid female frog in a quiet environment usually approaches a loudspeaker playing a conspecific male's call. If the male's call is mixed with the sounds of a natural chorus of hundreds of males or with random noise in the same frequency band, the female approaches the speaker only if the signal/noise ratio (SNR) is sufficiently great. Apparently, below some SNR, the male's call is not differentiated from the background. If we now imagine a female in a natural chorus, listening to hundreds of males, we can calculate how many of those males' calls exceed the critical SNR for detection by the female. Because sound spreads approximately spherically from a frog, and thus attenuates approximately 6 dB for every doubling of distance from the source, only calls from nearby males exceed the critical SNR. The density of males in the chorus thus determines how many of them a female can hear distinctly from any one point. Two such studies have suggested that females can hear only two or three individual males in a chorus at a time (Gerhardt and Klump, 1988; Wollerman, 1999). The hundreds of others become indiscriminable noise. Although immersed in

hundreds of potential mates, a female actually has only a few choices at any one moment. She must move around and thus take risks of predation to sample more than these few.

When presented with two loudspeakers and two males' calls, a female (at least in some species) usually approaches the one with the lower dominant frequency, an indication of its larger body mass. When these males' calls are mixed with background sound from a natural chorus, females do not make this discrimination so easily. Again there is a SNR below which the female no longer prefers the call with the lower dominant frequency. Apparently, her nervous system no longer distinguishes the difference. As predicted by SDT, this more complex task of discriminating between two signals of interest requires a higher SNR than the simpler task of detecting the presence or absence of a signal (Wollerman and Wiley, 2002). There are thus levels of SNR that allow detection of a signal but not discrimination among similar signals. A female frog in a chorus is even more constrained in choosing an optimal mate than she is in finding any mate.

Theoretical treatments of direct mate choice (discrimination) as a factor in sexual selection should consider these constraints on signal detection in real situations (Wiley and Poston, 1996).

Implications for the Evolution of Communication

Signal Detection Theory offers a way to address the effects of these constraints on the evolution of communication (Wiley, 1994, 2000). The inability of detectors, neural as well as others, to separate signals from noise in real situations leads to the inevitability of error in communication. Every time a detector samples its input and either responds or does not respond, there are four possible outcomes: a correct detection (when a signal is present and the detector responds), a false alarm (when the detector responds but no signal is present), a missed detection (when a signal is present but the detector does not respond), and a correct rejection (when no signal is present and no response occurs). The probabilities of each of these outcomes depends on both the inherent detectability of the signal and the bias (threshold) of the detector.

The idea of error in animal communication can cause confusion, but evolutionary adaptation provides a clear framework for thinking objectively about error. If a response to a signal is evolutionarily advantageous for a receiver in a particular situation (in other words, if it results in greater survival or reproduction of such receivers and ultimately in the

spread of alleles associated with this response), then false alarms and missed detections represent errors by the receiver.

The fundamental conclusion from Signal Detection Theory is that receivers must compromise between decreasing their chances of false alarms and missed detection. If a receiver raises the threshold for its detector in order to decrease the chance of false alarms, it thereby increases its chance of missed detections ([Figure 1]). These two probabilities cannot be simultaneously minimized.

By combining SDT with Decision Theory, we can calculate the optimal threshold for a receiver in a particular situation. Decision Theory calculates an expected utility for any decision (such as any level of threshold for response by a detector) as a linear combination of the payoffs for each outcome times their probabilities of occurrence. The probability of a correct detection when a detector samples its input equals the probability that a signal is actually present times the probability that the detector will respond when a signal is present. The probability of each of the other three outcomes is calculated in an analogous way. In the end, the expected utility for a particular threshold for response depends on the payoffs of all four possible outcomes, the frequency of encountering a signal (the probability that a signal is present at any moment), and the effect of the threshold on the probabilities of response when a signal is present and when one is not.

Theoretical treatments of the evolution of various features of communication have sometimes included the possibility of error by receivers. Often, error is included by making the probability of response to a signal less than 1.0. Sometimes, formulations include the payoffs of two alternative responses (or response and no response). Few, though, have included all of the complexity of the expected utility of a receiver's performance.

Adaptive Gullibility and Fastidiousness

One application of expected utilities to the behavior of receivers reached the conclusion that receivers could evolve either adaptive gullibility (allowing relatively more false alarms but fewer missed detections) or adaptive fastidiousness (allowing fewer false alarms but more missed detections), depending on the payoffs of the possible outcomes and the frequencies of signals (Wiley, 1994).

Responses to alarm calls might often evolve adaptive gullibility. Mate choice might often evolve adaptive fastidiousness. Adaptive gullibility is a situation in which receivers are inevitably vulnerable to deception. Adaptive fastidiousness is a situation in which receivers are usually unresponsive even to appropriate signals.

Signal detection also has consequences for the evolution of signalers. The expected utility of producing a signal depends on the probabilities and payoffs of responses by the intended receiver and by any unintended receivers (such as rivals, predators, or parasites). One consequence is that signalers must compromise between the advantages and disadvantages of more exaggerated (and thus more inherently detectable) signals as a result of responses by intended and unintended receivers.

Another consequence is that fastidious receivers (in the sense just described) favor signalers that produce inherently more detectable signals. Evolutionary exaggeration of signals to increase detectability can thus result from evolution of fastidiousness in receivers. Because mate choice often evolves toward fastidiousness, adaptations for signal detection can explain the exaggeration of signals for mate choice. In this way, signal detection theory provides an important complement to sexual selection as an explanation for the evolution of many signals in animal communication (Wiley and Poston, 1996).

See also: Alarm Calls; Animal Communication: Deception and Honest Signaling; Animal Communication: Long-Distance Signaling; Animal Communication Networks; Animal Communication: Overview; Animal Communication: Parent–Offspring; Animal Communication: Vocal Learning; Bats: Communication by Ultrasound; Birdsong; Communication in Marine Mammals; Fish Communication; Frog and Toad Communication; Individual Recognition in Animal Species; Insect Communication; Nonhuman Primate Communication.

Bibliography

Gerhardt H C & Klump G M (1988). 'Masking of acoustic signals by the chorus background noise in the green tree frog: A limitation on mate choice.' *Animal Behaviour 36*, 1247–1249.

Macmillan N A (2002). 'Signal detection theory.' In Pashler H & Wixted J (eds.) *Stevens' handbook of experimental psychology,* vol. 4, 3rd edn. New York: John Wiley and Sons. 43–90.

Macmillan N A & Creelman C D (1991). *Detection theory.* Cambridge: Cambridge University Press.

Wiley R H (1994). 'Errors, exaggeration, and deception in animal communication.' In Real L (ed.) *Behavioral mechanisms in ecology* (Chap. 7). Chicago: University of Chicago Press. 157–189.

Wiley R H (2000). 'Sexual selection and mating systems: Trade-offs for males and females.' In Apollonio M, Festa-Bianchet M & Mainardi D (eds.) *Vertebrate mating systems*. Singapore: World Scientific Publishing. 8–46.

Wiley R H & Poston J (1996). 'Perspective: Indirect mate choice, competition for mates, and coevolution of the sexes.' *Evolution 50*, 1371–1381.

Wiley R H & Richards D G (1982). 'Adaptations for acoustic communication in birds: Sound propagation and signal detection.' In Kroodsma D E & Miller E H (eds.) *Acoustic communication in birds,* vol. 4. New York: Academic Press. 131–181.

Wollerman L (1999). 'Acoustic interference limits call detection in a neotropical frog *Hyla ebraccata*.' *Animal Behaviour 57*, 529–536.

Wollerman L & Wiley R H (2002). 'Background noise from a natural chorus alters female discrimination of male calls in a neotropical frog.' *Animal Behaviour 63*, 15–22.

Animal Communication: Vocal Learning

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That we learn many of the sounds that we produce is clearly one of the most striking features of our own species. This learning is the basis of our rich language, which has no equal in any other animal, and it also leads to the differences in space and time that are a striking feature of language: languages, dialects, and accents differ across the globe, and they also change with time so that new words spring up while others fall from use. Curiously, although all of these phenomena have their animal equivalents, to find them, at least in the vocal domain, one must search beyond our closest relatives. Among the apes, gibbons (Hylobatidae) have the most striking vocal repertoires, with pairs singing wonderful duets that resound through the forest at dawn. The members of a pair learn to coordinate the sounds that they produce, but do not learn the sounds themselves: Hybrids even produce songs intermediate between those of their parent species. Efforts to 'teach chimpanzees to speak' met some success using sign language, but were an almost total failure when the animals were called on to use their voices. Although the vocal repertoires of chimpanzees in different localities do appear to differ, and dialects are most likely to arise through learning, this sort of evidence is equivocal: animals recorded under different conditions, as, for example, when disturbances or provisioning differs between sites, may use different parts of their repertoires or call more excitedly in one place than another. Thus, the samples may differ without vocal learning necessarily being involved. The best evidence to date of vocal learning in nonhuman primates is probably in marmosets, where the calls of animals placed in pairs or groups show subtle modifications to match those of their cage-mates.

When we talk of vocal learning, we are concerned with animals learning to modify the form of sounds they produce as a result of experience, and this is sometimes called production learning. We must distinguish between this and two other processes. Usage learning is learning to produce sounds in a particular context, perhaps novel or simply more limited, as, for example, when a young animal initially produces a call in many different situations but gradually comes to link it only to that situation in which it is appropriate. Comprehension learning is learning to understand the meaning of sounds, so that over time an animal comes to respond to them in an appropriate manner. As a result of these two processes, a dog may learn to bark when it wants a door to be opened and that the word 'food' is a good sign that it should go to the kitchen. But there is no evidence that dogs can modify the sounds they produce. They are not therefore 'vocal learners.' Animals that do alter the sounds they make as a result of experience may, as many do, make precise copies of sounds they hear, or they may achieve individual distinctiveness by avoiding matching the sounds of others, or they may innovate, generating a whole variety of sounds that are different from any they have heard or produced before.

In what species is there evidence of vocal learning in this sense? Among mammals, apart from ourselves, it occurs in three groups: seals (Pinnipedia), bats (Chiroptera), and whales and dolphins (Cetacea). In seals and bats, the evidence is not extensive, but nonetheless convincing. A harbor seal (*Phoca vitulina*) in the United States, reared by a couple in Maine and transferred when a few months old to Boston aquarium, could produce various phrases including his own name, Hoover, all apparently uttered in an impeccable local accent. In bats, it has been found that the young of greater horseshoe bats (*Rhinolophus ferrumequinum*) have echolocation calls that match in frequency those of their mothers. The calls of mothers become lower with age, but the calls that the young develop are those appropriate to the age of the mother, giving strong evidence that these are learned from her. In greater spear-nosed bats (*Phyllostomus hastatus*), calls are group specific and