Signal Transmission in Natural Environments

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Introduction

All communicatory signals consist of energy or matter transferred from a signaler to a receiver, but not all transmitted energy is a signal. The fundamental property of a signal is its ability to elicit a response from a receiver without providing all the power for the response. Coercion is not communication. Instead, a signal produces a response that is mediated by the receptors, decision mechanisms, and effectors of the receiver. Even tactile signals are separated from coercion by this property of insufficient power and thus rely on the receiver for their effectiveness.

Insufficient power to produce a response assures that transmission is a fundamental property of all signals. Transmission of a signal to the receiver in turn introduces the possibility of alterations in the structure of the signal and of masking by irrelevant energy in the environment. These possibilities result in errors in the receiver's responses, and the possibility of errors has in turn some fundamental consequences for the evolution of optimal behavior by both receivers and signalers. Understanding signal transmission is thus fundamental to understanding communication in general.

The alterations and masking of signals during transmission are most easily studied and most thoroughly understood in the case of sounds in the atmosphere.

Acoustic Signals in Air

Spherical Spreading

Sound radiating from a point in a homogeneous medium spreads spherically, so that the density of energy in a unit of area (the intensity) decreases in inverse proportion to the square of the distance from the source. The energy emitted by a source at any instant spreads over an imaginary spherical surface that depends on how far the sound has traveled from the source. Once beyond about one wavelength and one diameter from the source (in the far field), sound propagates as a wave of pressure as a result of minute movements of the molecules in the medium. Closer than this distance (the near field), sound has somewhat different properties as a result of the larger movements of molecules in the medium. Although no real source emits sound exactly from a point and no natural environment is exactly homogeneous, nevertheless measurements have shown that, at least in the far field, sounds produced by animals in relatively homogeneous conditions spread approximately spherically. As a result, the intensity of sound in general attenuates at least in proportion to the inverse square of distance from the source. This attenuation equals approximately 6 dB for every doubling of distance from the source, by the definition of decibels as -10 times the log of a ratio, in this case $-10\log((1/2)^{\wedge}2)$.

In the presence of gradients of wind speed or temperature, sound no longer spreads spherically. These conditions result in sound that attenuates from spreading either more or less than the 6 dB for a doubling of distance expected from spherical spreading. Sound travels faster in warmer than in cooler air, so a temperature inversion (warmer air near the ground, because of sunlight heating the surface, and cooler air above) results in sound that refracts upward as it propagates over the ground. This bending reduces sound spreading horizontally. As a result, attenuation in a horizontal direction is greater than 6 dB for a doubling of distance. Probably for this reason, few birds in open environments sing near the ground on sunny days. Instead, many sing in flight well above ground, behavior that increases the horizontal distance at which their songs can be heard.

In forests during early morning, the air above the canopy warms faster than the air below the canopy. In this circumstance sounds produced in the canopy are refracted downward from the air above, so the intensity of the sound in the canopy attenuates less than expected by spherical spreading. Primates of tropical forests often vocalize in the canopy at this time and thus get the advantage of this focusing effect to boost the propagation of their vocalizations.

Gradients of wind speed have somewhat similar effects on the propagation of sound. Wind speed is slowest next to the ground (or other surfaces) and increases with height, sometimes for 20 m or so. In these conditions, sound propagating upwind refracts upward, and sound propagating downwind refracts downward. As a consequence, a shadow zone develops upwind beyond which little sound penetrates, whereas downwind, sound is channeled horizontally. Thus under windy conditions, sound attenuates more in the horizontal direction upwind but less downwind than expected by spherical spreading. Although this effect is prominent, there are no documented cases of animals that selectively communicate downwind. For instance, we might expect in windy conditions

that birds would sing closer to the upwind sides of their territories so as to equalize the reception in all neighboring territories.

Frequency-Dependent Attenuation

Absorption of sound by molecular vibrations in the medium results in additional attenuation. Because absorption occurs in addition to the universal attenuation from spreading, it is a form of excess attenuation. Absorption of sound by molecules in the atmosphere is complex, but the practical consequences for communication with frequencies in the range of many animals' hearing (100–10 000 Hz) are relatively simple. In this range, absorption is not significantly affected by temperature or humidity of the air. However, absorption increases monotonically with frequency in all natural environments. As a result, the lowest frequencies produced by animals propagate farthest in any natural environment.

There are two other important sources of excess attenuation. First, near a boundary layer, such as the ground, sound propagating in the atmosphere interacts with energy propagating near the boundary or reflected from the boundary. This effect is also strongly frequency-dependent in accordance with the properties of the boundary. Highly porous soil can result in a nearly 180° phase shift of the low frequencies in reflected sound, so there is nearly complete destructive interference between direct and reflected sound at these frequencies during transmission near the ground. As a result of this ground effect, many birds that forage on the ground move to higher perches when they sing.

Second, sound is absorbed and reflected by objects in the path of transmission. Large objects simply reflect sound and create a sound shadow beyond. Smaller objects absorb sound in their vibrations or refract sound away from the path of transmission in complex ways. Very small objects, those well below a wavelength in diameter, have little effect on the transmission of sound. The leaves in forests have particularly interesting effects on reverberation. Many broad leaves should refract or reflect sounds with wavelengths smaller than roughly 10 cm, corresponding to frequencies greater than 3400 Hz in air. In contrast, coniferous needles should only affect sounds with much higher frequencies (1 cm diameter would correspond to a frequency of 34 000 Hz). As expected, birds in coniferous forests use higher frequencies on average in their songs that do birds of similar size in broad-leaved forests.

Provided the air and vegetation are homogeneous in composition along the path of propagation, excess attenuation is a constant fraction of the intensity of sound for each unit of distance. Because atmospheric absorption results in constant decreases in intensity of sound with distance but spherical spreading results in exponential decreases, spherical spreading dominates attenuation at short ranges, and atmospheric absorption dominates at long ranges. As a result, we should expect to find adaptations to minimize excess attenuation in communication only at relatively long ranges. Human speech, for instance, has notably poor transmission at a distance. Presumably it has evolved for communicating lots of information rapidly at short range rather than for efficacy of communicating a few crucial messages at long range.

Reverberation and Amplitude Fluctuations

Frequency-dependent attenuation alters the spectrum of sound as it propagates by disproportionately reducing the higher frequencies in a sound. Reverberation and amplitude fluctuations also have pronounced effects on the temporal properties of sound, sometimes called degradation rather than attenuation.

Reverberation results from multiple refractions and reflections of sound from objects in the path of transmission. As a result, sound no longer arrives at the receiver along a single, direct path. Instead, it arrives from a wide angle along many paths of different lengths. Some of the sound is thus delayed, in relation to the rest, in reaching the receiver. The result is a smearing of any temporal patterns in the sound. Distinct notes at the source arrive as blurred sounds. Staccato becomes sostenuto. To the extent that shapes or timing of notes is important for a receiver's response, reverberation degrades signals. Reverberation is more severe in environments with greater density of objects in the path of transmission. Forests, for instance, produce more reverberation than open air above grasslands. As expected, birds in forests, especially broad-leaved forests, are less likely to incorporate rapid repetitions of notes at any one frequency in their songs than are birds of grasslands. Because broad leaves reflect mostly sounds with higher frequencies in the range used by many songbirds, reverberation is greater for these frequencies. Greater reverberation of higher frequencies, as well as greater attenuation, can explain why birds in forests use lower frequencies on average than do birds of open habitats.

Amplitude fluctuations also degrade the temporal structure of propagating sounds. These fluctuations arise from turbulence in the flow of air. Even a gentle breeze, particularly near a rough surface such as the ground or the canopy of a forest, includes irregular eddies. The dimensions of these eddies (or their periodicities as they pass any one point) have an exponential spectrum with progressively decreasing representation of smaller dimensions (or smaller

periodicities). These eddies refract sound away from a direct path of transmission and thus impose fluctuations in the intensity of the sound for a receiver. Because the periods of these fluctuations are mostly long in relation to the time constants for animals' ears, they produce dropouts in sounds (periods of irregular length with lower intensity). Amplitude fluctuations affect sounds primarily in open environments, where wind is rarely absent, as opposed to, for instance, the interior of a forest. As a result, birds in open country (such as sandpipers, larks, pipits, and longspurs) often have prolonged tinkling songs (several seconds of extremely rapid notes in complex patterns). These birds appear to produce songs with high specificity in any brief part so that unpredictable dropouts in the song would not affect the possibility for recognition. Conspecific listeners might identify these songs by hearing any brief part them.

Background Sound

All natural environments include background sound, sound not relevant to communication by any one species or particular individuals. This background sound arises from physical features of the environment – wind, vegetation, and water. It also includes sounds made by other organisms – often not only different species but also other individuals of the same species. In recent centuries, especially in recent decades, human-generated noise, especially from airplanes and automobile traffic, pervades natural environments even at surprising distances from the source. These sources of irrelevant sound mask to varying degrees the sounds produced by animals for communication.

In tropical forests, insects (mostly Tettigoniidae, Gryllidae, and Cicadidae) create a nearly constant and ubiquitous band of noise with frequencies of 4–10 kHz. The tendency of birds in the interior of tropical forests to use lower frequencies in their songs than do those in open habitats might result primarily from the ceiling imposed by noise from insects and the floor imposed by the dimensions of the birds themselves. In addition, as described above, reverberation and excess attenuation of sound increase more rapidly with frequency in forests (particularly broad-leaved forests) than in the open. The combination of these features often creates a sound window for communication in these forests.

For any level of background sound, attenuation sets a distance beyond which the signal can no longer be detected in the noise. To determine the active space of a signal, we need measurements of attenuation and background energy and also experiments to find the signal–noise ratio necessary for recognition by conspecific listeners. Such investigations have shown that the signal space for birds' songs, primates' loud calls, or insects' stridulations equals approximately twice the average spacing of individuals, as expected if individuals moving around in their territories or home ranges stay in touch with all their neighbors at all times.

Minimizing or Compensating for Attenuation and Degradation

Investigation of the transmission of animals' sounds in natural environments has led to the environmental adaptation hypothesis: animals' sounds should evolve features that transmit well in the relevant habitat. Although sometimes not explicitly acknowledged, this hypothesis should apply primarily to signals used for relatively long-range communication. At short range, transmission should be dominated by spherical spreading. Only at long range should transmission be dominated by excess attenuation, reverberation, amplitude fluctuations, or background energy. Recent analyses of independent phylogenetic contrasts have often confirmed that birds in forests (especially broad-leaved forests) use lower frequencies on average and avoid rapid repetitions of notes in comparison with species in open habitats, as predicted by this hypothesis. Comparisons of different populations of the same or closely related species have often had similar results. Nevertheless, not all studies have confirmed the hypothesis.

Insects and anurans (frogs and toads) in particular have provided little support for the environmental adaptation hypothesis, perhaps because communication in these animals often occurs over relatively short distances. One study of cricket frogs *Acris crepitans* in Texas, however, did reveal two populations that differed as predicted in the frequencies of sound in their calls. The population that inhabited denser vegetation had lower-frequency calls, which propagated with less distortion in this habitat. These calls also propagated better in the more open habitat, although the difference was much less there. The tuning of the females' auditory neurons nearly matched the differences in calls between the populations. As a consequence, the auditory neurons of the population with high-frequency calls did a better job of rejecting the predominantly low-frequency noise in both habitats.

Adjustments to pervasive human influences on environments have also come under investigation recently. Birds in areas subject to intense and continual noise from traffic produce louder songs than conspecifics in quieter environments (the Lombard effect). They also produce songs with higher frequencies, which avoid overlap with most of the predominantly low-frequency noise from traffic.

Almost no research has focused on adjustments of signal perception (as opposed to signal production) to attenuation, degradation, and masking of acoustic

signals. A suggestion of the possibilities comes from one study that determined thresholds for hearing in the great tit *Parus major*, both in quiet conditions, as such measurements are usually conducted, and in the presence of noise matching natural background sound. In quiet conditions, the best frequencies for hearing were considerably lower than those in the species' songs, but in the presence of noise, there was a close match between the best frequencies for hearing and the frequencies in songs. Because the masking bandwidth for hearing decreased steadily with frequency, the optimal frequency for hearing shifted upward in the presence of noise.

Using Attenuation and Degradation to Localize Signals

Attenuation and degradation of signals could be put to good use by listeners to determine the distance to a signaler, an ability called ranging. Any change during transmission of a sound might be used for ranging. This capability is studied experimentally by playing back signals (such as birds' songs) in order to compare responses to relatively clean signals and to artificially or naturally attenuated and degraded signals. If the subjects decide the signals come from a distance, they might respond as if they came from a neighboring territory rather than from their own. A responding bird can also reveal a judgment of distance simply by overshooting or undershooting its approach to the speaker.

Overall intensity of sound (as affected, for instance, by spherical spreading) might not be a good cue for distance, at least in competitive interactions, because intensity can be manipulated by the sender. Nevertheless, experiments have shown that overall intensity is used by birds for ranging conspecific songs. However, they also use frequency-dependent attenuation and degradation by reverberations to judge distance, even when overall intensity is held constant. Furthermore, ranging can occur, at least approximately, even when the birds lack prior experience with a particular song pattern. Experience does play a role, however, because birds adjust their responses to reverberated songs depending on the season. During spring and summer in temperate forests, when more leaves are present and reverberation accumulates more rapidly with distance, Carolina wrens *Thryothorus ludovicianus* give territorial responses only to songs with more reverberation than during winter.

Acoustic Signals in Water

Sound propagates in water about 5 times faster than in air, in most natural conditions, and thus wavelengths for any frequency of sound are 5 times longer. As a consequence, reverberation in water results only from objects that are 5 times the size of objects that produce reverberation at similar frequencies in air. No studies have documented effects of reverberation on animals' signals in water. Excess attenuation as a result of molecular absorption also occurs much less rapidly with distance than in air. As a result, signal space is much greater in water. In addition, background sounds from farther away can effectively mask signals. One consequence is that human-generated sound, principally from ships' engines and propellers, pervades underwater habitats much more than it does terrestrial habitats.

A further complexity of sound in water, as a consequence of the longer wavelengths of sounds at audible frequencies, is the likely importance of wave guides. Any body of water less than a few tens of meters in depth might constitute a wave guide for sound. The practical consequences are reduced attenuation because of nonspherical spreading and dispersive transmission as a result of frequency-dependent speed of sound in wave guides. Dispersion alters the basic frequency–time structure of sound because a listener hears different frequencies in the source as they arrive at different times.

Although it is clear that sound is a major modality for communication by marine mammals, fish, and invertebrates, we know little about how transmission affects the structure of signals or responses to them. Because of the lower attenuation and longer wavelengths of sound in water, more communication occurs at ranges where spherical spreading dominates or even in the near field, where particle movement rather than pressure dominates. Nevertheless, there is evidence that some whales maintain communication over great distances in the oceans, distances at which frequency-dependent attenuation, reverberation, and dispersion during transmission could affect the structure of signals.

Visual and Olfactory Signals

Visual communication differs from acoustic communication because the source of the transmitted energy is not the signaler (except in the special cases of bioluminescence). Instead the signaler provides a surface that reflects light from the sun. Because sunlight can arrive either directly from the sun or indirectly from the atmosphere (the blue sky) and because it is also reflected and transmitted by any nearby objects, including vegetation, the light incident on a visual signal varies with the exact location of the signaler. Furthermore, the ability of a conspecific to detect a visual signal depends on its contrast with light reflected from the background as well as with diffuse

light scattered from particles in the atmosphere. In some cases at least, the colors of animals' signals, the places they choose to display these signals, and even their modifications of their immediate surroundings all serve to increase the contrast of signals with the background light as viewed by conspecific observers.

Because the wavelengths of visible light are so small in comparison with those of audible sound, reverberation and attenuation of visual signals over relatively short distances in the atmosphere are minor. Instead, the problem in environments with dense vegetation is assuring direct line-of-sight paths to the potential receiver. Indeed, animals communicating over large distances in the interiors of forests make little use of visual signals and correspondingly prominent use of acoustic signals.

In water, light attenuates much more rapidly than in air, and the frequency dependence within the visual spectrum is much more prominent. Long wavelengths of light attenuate more rapidly than short wavelengths, so that even at modest depths in water, red light is largely absent. Red objects near the surface appear black at depths of a few meters. Although many fish and other animals that live in relatively shallow water have conspicuous visual signals for communication, we know little about how these signals are perceived by conspecifics.

Olfactory communication often takes one of two extreme forms. Either a chemical, often one with low diffusion in the atmosphere, is deposited on the substrate to await an occasion when a receiver might pass nearby, or a chemical is released into the atmosphere for propagation by wind and diffusion to a distant receiver. Communication can thus occur over long distances in relatively short times, as in acoustic or visual communication, but also over long times but short distances. In both cases, environmental conditions affect the duration or distance of potential communication.

The dispersal of an odor in the atmosphere depends on both diffusion in the air and movement of the air. Because movement of air is turbulent, the process is complex. As a result of eddies in the atmosphere, the concentrations of an odorant at even a few meters from a source can vary substantially over distances of centimeters, a situation that complicates any calculation of the distance at which an odor can be detected by a receiver.

Errors and the Evolution of Communication

The attenuation and degradation of signals during transmission and the possibilities for masking by background energy make it clear that a signal rarely if ever arrives at its intended receiver in the form that it left the signaler. As much of the attenuation and degradation of signals and the generation of background energy depends on random turbulence and heterogeneities in the environment, every signal arrives at a receiver with some unpredictable properties. This situation raises the issue of errors in communication.

Signal detection and decision theory provide a way to understand the consequences of errors in communication. In these conceptualizations of communication, every time a receiver checks its receptors for a signal, there are four possible outcomes: a correct detection (if the receiver performs an appropriate response to the signal, one that in evolutionary terms tends to increase the spread of its genes in the population by increasing its survival or reproduction), a correct rejection (if the receiver fails to respond when there is in fact no signal present), a missed detection (if the receiver fails to respond when a signal is in fact present), and a false alarm (if the receiver responds when there is in fact no signal present). These four possibilities are the logically exhaustive set of two possibilities for response (present or absent) for each of two possibilities for the occurrence of a signal (present or absent).

Signal detection theory has had only minor application to animal communication so far, but its implications suggest that it should receive more attention. A fundamental insight is that, in realistic conditions, a receiver cannot simultaneously minimize its probability of false alarms and its probability of missed detections. Raising its threshold for response, for instance, reduces false alarms but also increases missed detections. Lowering its threshold for response has the opposite effects. Complex criteria for response likewise cannot avoid an inevitable trade-off between false alarms and missed detections. In the real world, a receiver cannot usually avoid errors. It can only adjust its criterion for response (either by evolution or by learning) to optimize its expected utility. The expected utility is a function of the probability that a signal will occur and the probabilities and the consequences of each of the four possible outcomes listed above.

An optimal threshold for response thus depends critically on the probabilities and consequences for errors. For instance, if false alarms are more costly than missed detections, then with all else equal, a high threshold would be optimal. Choosing a suitable mate might fit these conditions. In this case, an optimal receiver would behave as if it were choosy, often passing up suitable mates in order to avoid choosing an unsuitable one. This case can be called adaptive fastidiousness. As a consequence, signalers should evolve more exaggerated signals in order to surpass the high thresholds of optimal receivers. From the

perspective of signal detection theory, exaggeration and redundancy of signals evolve to increase the detectability of signals by fastidious receivers.

Alternatively, if missed detections are more costly than false alarms, then with all else equal, a low threshold would be optimal. Responding to alarm calls for predators might fit these conditions. In this case an optimal receiver would behave as if it were error-prone, often responding to false alarms in order to avoid missing an actual signal. This case can be called adaptive gullibility. As a consequence, some signalers might evolve deceptive signals to take advantage of the low thresholds of optimal receivers. There are several cases among primates and birds of such deceptive alarm calls that, for instance, occasionally allow a subordinate to scare a dominant away from food or a potential mate.

Conclusion

An understanding of the alteration and masking of signals as they pass from the signaler to the receiver is necessary for an understanding of evolutionary adaptations in communication. It is the possibility of error arising from the attenuation, degradation, and masking of signals that leads to predictions for the optimal behavior of receivers and thus for the optimal behavior of signalers.

See also: Animal Communication: Honesty and Deception; Audiovocal Communication in Bats; Communication in the Honeybee; Facial Expression in Primate Communication; Localizing Signal Sources; Multimodal Signaling in Animals; Pheromones and other Chemical Communication in Animals; Primate Communication: Evolution; Sexual Selection and the Evolution of Animal Signals; Signal Design Rules in Animal Communication; Social Communication in Whales and Dolphins; Visual Signaling in Animals; Vocal Communication in Birds.

Further Reading

Brenowitz EA (1982) The active space of red-winged blackbird song. *Journal of Comparative Physiology A* 147: 511–522.

Brown CH (1989) The active space of the blue monkey and grey-cheeked mangabey vocalizations. *Animal Behaviour* 37: 1023–1034.

Brumm H and Slabbekoorn H (2005) Acoustic communication in noise. *Advances in the Study of Behavior* 35: 151–209.

Endler JA (1993) The color of light in forests and its implications. *Ecological Monographs* 63: 1–27.

Gerhardt HC and Huber F (2002) *Acoustic Communication in Insects and Anurans.* (pp. 370–379, 431–438). Chicago, IL: University of Chicago Press.

Gerhardt HC and Klump GM (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.

Kime NM, Turner WR, and Ryan MJ (2000) The transmission of advertisement calls in Central American frogs. *Behavioral Ecology* 11: 71–83.

Klump GM (1996) Bird communication in the noisy world. In: Kroodsma DE and Miller EH (eds.) *Ecology and Evolution of Acoustic Communication in Birds*, pp. 321–338. Ithaca, NY: Cornell University Press.

Langemann U and Klump GM (2001) Signal detection in amplitude-modulated maskers: I. Behavioral auditory threshold in a songbird. *European Journal of Neuroscience* 13: 1025–1032.

Naguib M and Wiley RH (2001) Estimating the distance to a source of sound: Mechanisms and adaptations for long-range communication. *Animal Behaviour* 62: 825–837.

Slabbekoorn H (2004) Singing in the wild: The ecology of birdsong. In: Marler P and Slabbekoorn H (eds.) *Nature's Music: The Science of Birdsong*, pp. 178–205. Amsterdam: Elsevier.

Warren PS, Katti M, Ermann M, and Brazel A (2006) Urban bioacoustics: It's not just noise. *Animal Behaviour* 71: 491–502.

Waser PM and Brown CH (1986) Habitat acoustics and primate communication. *American Journal of Primatology* 10: 135–154.

Wiley RH (1991) Associations of song properties with habitats for territorial oscine birds of eastern North America. *American Naturalist* 38: 973–993.

Wiley RH (1994) Errors, exaggeration, and deception in animal communication. In: Real L (ed.) *Behavioral Mechanisms in Ecology*, pp. 157–189. Chicago, IL: University of Chicago Press.

Wiley RH (2006) Signal detection and animal communication. In: Brockman HJ (ed.) *Advances in the Study of Behavior,* vol. 36, pp. 217–248. San Diego, CA: Elsevier.

Wiley RH and Richards DG (1978) Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology* 3: 69–94.

Wiley RH and Richards DG (1982) Adaptations for acoustic communication in birds: Sound propagation and signal detection. In: Kroodsma DE and Miller EH (eds.) *Acoustic Communication in Birds*, vol. 1, pp. 131–181. New York: Academic Press.

Witte K, Farris HE, Ryan MJ, and Wilczynski W (2005) How cricket frog females deal with a noisy world: Habitat-related differences in auditory tuning. *Behavioral Ecology* 16: 571–579.

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

Wollerman L and Wiley RH (2002) Background noise from a natural chorus alters female discrimination of male calls in a neotropical frog. *Animal Behaviour* 63: 15–22.