



REVIEW

Estimating the distance to a source of sound: mechanisms and adaptations for long-range communication

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Acoustic signals are used for long-range communication in many animals from insects to birds and mammals. Long-range signals are used primarily by males to advertise and defend their home ranges or territories or to attract mates. During transmission over long distances, the structure of signals becomes progressively degraded. At the position at which a receiver makes a decision to respond, the characteristics of signals can differ markedly from those at the source. This degradation impairs extraction of information coded in the signal but also allows receivers to assess the distance (range) of the signaller. Auditory distance assessment (called 'ranging') is particularly important in territorial species as the optimal initial response often depends on the distance of the signaller. Perception of distance is comparatively well studied in animals but this work is not well integrated with information from related fields such as sound perception in humans or other animals. Here we review recent advances in studies of distance estimation and relate these to fundamental issues in sound transmission and sound perception. We consider the different components of signal degradation and how they can be measured in a perceptually meaningful way. We discuss limitations on the perception of degradation and the possibility that signallers might send deceptive information about their actual distance from a receiver. By integrating studies of auditory distance perception and studies of sound perception in animals and humans, we provide a framework for understanding the evolutionary implications of sound degradation in communication.

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Long-range acoustic communication has been an excellent model for evolutionary issues in animal communication. Long-range signals serve to keep rivals at a distance or to attract mates. Because signals inevitably degrade progressively during propagation from the signaller to the receiver, selection should favour signals that transmit information efficiently by minimizing degradation during transmission (Wiley & Richards 1982; McGregor 1994; Klump 1996).

On the other hand, degradation of signals during transmission can allow receivers to extract information about the signaller's distance (called ranging). The distance of the signaller is often crucial in evaluating a signal. A signal from a rival nearby requires more attention than

one at a distance. Receivers, signallers, or even both, might benefit from a receiver's accurate assessment of its distance from the signaller. If so, selection might favour the evolution of long-range signals that allow some degradation.

Adaptations of signals for efficient propagation thus have implications for adaptations for ranging. To examine these two influences on the evolution of long-range signals, we begin this review by summarizing current knowledge of signal degradation and its consequences for ranging. We consider not only the capabilities of animals in natural habitats but also the capabilities of humans in controlled conditions. Research on auditory distance perception in humans has a long history, but it has not been incorporated into discussions of communication in other animals. In addition to summarizing information about how humans and other animals range sounds, we consider sensory capabilities that affect the perception of degradation in sound, limitations on the accuracy of

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ranging, and the possibility of deception by signallers that might benefit from misrepresenting their distance from a receiver.

ACOUSTIC AND SENSORY BASIS FOR DISTANCE PERCEPTION

For a receiver to judge the distance to a source of sound solely on the basis of the acoustic structure of a signal, it must determine how the sound has changed during propagation through the environment. To do so, it must know something both about the structure of the signal at the source and about the degradation of signals during propagation. The kinds of changes in acoustic signals during propagation are now relatively well understood for propagation at a substantial distance above the ground. There are complex ground effects, but these decrease rapidly with height. In general they have little influence on transmission of sound more than 1 m above ground. The majority of birds sing much higher above ground than 1 m, and in many species locations of singing are higher than those of other activities (Wiley & Richards 1978, 1982).

Aside from the complex ground effects, at least six processes alter the structure of sound during propagation: spherical attenuation; attenuation by atmospheric absorption; attenuation by scattering of directional sounds; accumulation of reverberation from reflections from relatively stationary objects near the path of transmission; accumulation of irregular amplitude fluctuations as a result of diffraction from nonstationary turbulence in the atmosphere; and diffraction of sound by temperature and other velocity gradients in the environment (Piercy et al. 1977; Wiley & Richards 1978, 1982; Wiley 1991). These processes produce four kinds of changes in the sound received at a distance: overall attenuation; frequency-dependent attenuation (greater attenuation of higher frequencies); reverberation; and fluctuations in amplitude. Reverberated signals are also less directional than unreverberated signals, because the indirect sound field is relatively more prominent in reverberated signals than it is in unreverberated signals.

It is possible to measure each of these four kinds of changes in sound from oscillograms and spectrograms of sound recorded at different distances from the source (Morton 1975; Marten & Marler 1977; Michelsen 1978; Richards & Wiley 1980; Waser & Brown 1986; Fotheringham & Ratcliffe 1995). For sources well above the ground, sound often spreads approximately spherically, so that energy decreases with the square of distance from the source for all frequencies (6 dB for each doubling of distance). Attenuation in forested environments often increases an additional 5–10 dB for frequencies in the range 1–10 kHz. Reverberation is usually measured as a rate of decay of energy following the termination of a pulse of sound (Waser & Brown 1986; Mershon et al. 1989; Holland et al., *in press*) or the ratio of the energy in the tail and the energy of the signal (Richards & Wiley 1980; Naguib et al. 2000). Irregular amplitude fluctuations are best measured by the variation in the amplitude of a continuous steady tone or of successive

identical pulses (Richards & Wiley 1980; Waser & Brown 1986).

Nevertheless, instead of separate measurements of the components of degradation, many recent studies of environmental adaptations in acoustic signals have adopted a single overall measure to quantify degradation in complex natural signals. These composite measures differ between studies, but all rely on cross-correlation or some other comparison of the waveform near the source and at a distance over a period of ca. 1 s. For instance, Brown & Handford (2000) computed the cross-correlation between selected 1-s intervals of the two waveforms; Gish & Morton (1981) compared the numbers of amplitude peaks at different levels in 1-s intervals of the waveforms; Dabelsteen et al. (1993) and Holland et al. (1998) compared the ratio of energy in the 'tail' of a frequency-modulated pulse to the energy in the pulse itself again in the two waveforms. Although these studies have identified interesting aspects of long-range communication, such as the effects of the receiver's height on degradation and the variation in degradation among signals at any one distance, these measures provide little insight into how changes in acoustic structure are likely to be perceived by birds or other organisms.

By comparing waveforms, these studies conflate the different sources of degradation. Animals, including humans, however, perceive them separately to various degrees. The overall waveform is affected by reverberation, amplitude fluctuations, and attenuation at all frequencies in the sound. Yet all of these processes are frequency dependent (all become more pronounced at higher frequencies), and animals' ears often analyse sound in relatively narrow bands of frequency. Indeed birds' ears have nearly the same frequency selectivity that mammals' ears do (Dooling 1982). Even anurans and orthopterans, although the majority have auditory receptors tuned to distinct bands of frequencies, have relatively high frequency selectivity. This selectivity is important when analysing structural changes in sound, for two reasons: (1) frequencies are not equally affected by the majority of the processes degrading sound during propagation; and (2) changes at one frequency do not affect the changes at other frequencies.

For instance, imagine a bird or frog that produces a trill (a series of frequency sweeps) in a reverberant environment such as a dense forest. The waveform of the reverberated trill as received at a distance from the source no longer reveals the distinct pulses of the original signal which instead appears smeared. However, for a frequency-analysing receiver, the reverberation of the higher frequencies in each sweep does not affect perception of lower frequencies in the sweep. Such a receiver can thus perceive a signal with considerably less reverberation than one that analyses the waveform. Suppose each sweep lasted 10 ms with each interval between sweeps also 10 ms. A receptor tuned to a narrow band of frequencies in the sweep would sense a gap of nearly 20 ms between pulses of stimulation (Fig. 1). An imaginary receptor affected by the entire band of frequencies would sense a gap of 10 ms between the end of one sweep and the beginning of the next. Significant reverberation

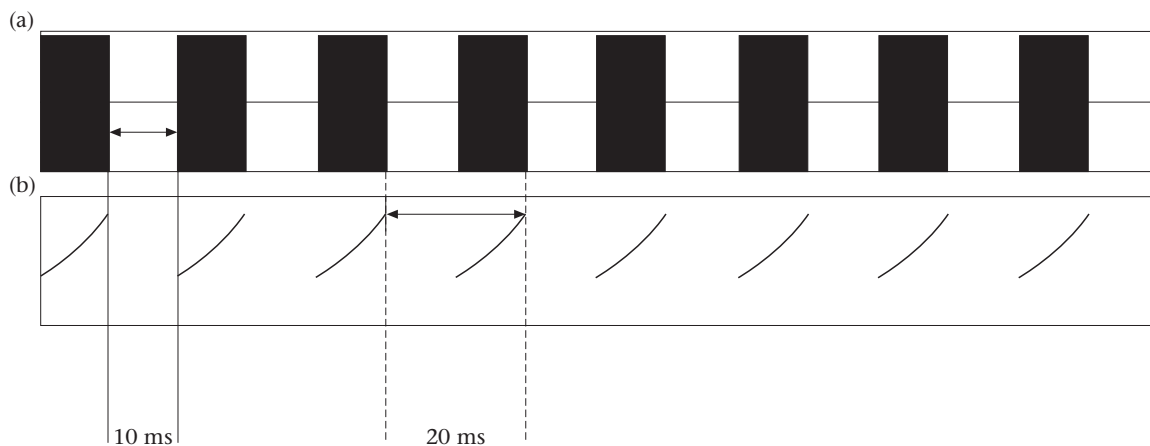


Figure 1. (a) Waveform and (b) spectrogram of a trill consisting of frequency sweeps spaced at time intervals equal in duration to each note. A receiver determining spacing of notes based on the waveform would sense silent intervals with half the duration as a receiver determining spacing of elements within separate frequency bands. Ears are frequency-sensitive receivers and would sense much longer silent intervals than analytical procedures comparing waveforms. If frequency sweeps are 10 ms in duration spaced at 10-ms intervals a receiver using the waveform would determine a 10-ms gap whereas a frequency-analysing receiver would determine a 20-ms gap.

lasting 10 ms might not have much effect on the tuned receptor's ability to resolve pulses, yet could well affect the untuned receptor's (Fig. 1).

Consequently, little can be concluded from composite measures of degradation about the perception of attenuation, reverberation, or amplitude fluctuations in acoustic signals. To take a sensory neuron's perspective, analysis of attenuation and temporal degradation should consider physiologically reasonable bandwidths of frequencies and should preserve physiologically reasonable temporal resolution. For birds and mammals, frequency resolution approximates 1–5% and temporal resolution 1–10 ms (Dooling 1982, 1989). Although no detailed studies of the perception of the various kinds of degradation in sounds are yet available, it is clear that frequency resolution by avian and mammalian ears is adequate to judge frequency-dependent attenuation and temporal resolution is adequate to judge both amplitude fluctuations and reverberation in natural environments. Indeed, each of these sources of degradation can be heard by an attentive human. To understand how sound degradation affects signal perception and ranging, future studies should separate measures of the different aspects of degradation.

Animal signals could conceivably include components that enhance the perception of degradation. Wide frequency sweeps, for instance, would assist judgments of high-frequency attenuation. A trill of similar notes might assist judgments of reverberation, as each successive note provides a standard for comparison with reverberation from the preceding note. Because trills should be obscured by reverberation more easily in forested environments than in the open, proportionately fewer forest-inhabiting species include rapid trills in their songs than species of open habitats (Handford 1981; Sorjonen 1986a, b; Wiley 1991; Tubaro et al. 1993). Nevertheless, some forest species do include trills in their long-range songs, perhaps to permit accurate judgements of reverberation decay by listeners (Wiley & Godard 1996). The temporal

spacing and number of elements in a trill would determine a distance at which individual elements could no longer be resolved.

PERCEPTION OF AUDITORY DISTANCE BY HUMANS

The research by psychologists on auditory distance perception in humans (Gamble 1909; von Békésy 1938, 1960; Coleman 1963; Mershon & King 1975; Mershon et al. 1981) provides much information relevant to other animals. In particular this research has focused on the mechanisms of sound perception and on the accuracy of distance perception, issues difficult to study in animals under field conditions. The mechanisms of distance perception are in turn important for understanding evolutionary issues in animal communication.

Experiments on humans have asked subjects in well-controlled laboratory conditions to judge the apparent distance of loudspeakers. Such studies have revealed that they can use different cues in auditory distance perception: reverberation (von Békésy 1938; Mershon & King 1975; Mershon & Bowers 1979; Butler et al. 1980; Mershon et al. 1989); relative intensity of high frequencies (Coleman 1962; Butler et al. 1980; Little et al. 1992); and relative amplitude (Mershon & King 1975). When the sound source is not in midline of the ears, humans also seem to use binaural cues (Coleman 1963; Gulick 1971) but since the usefulness of this cue is more controversial we do not discuss it further. These experiments also indicate that only one cue is necessary to judge the distance of a sound source. The different cues are thus processed separately. Although accuracy is influenced by the kind of signal and the subjects' experience with the signal and with the acoustic properties of the environment, under the best conditions humans can detect a change of 5–6% in the distance to a sound source (Strybel & Perrot 1984). It is also known that subjects underestimate the perceived distance of novel sounds

(McGregor et al. 1985; Little et al. 1992) and that perceived auditory distance is not independent of visual cues. Sounds of equal amplitude at the subjects' ears were perceived as louder when a 'dummy' loudspeaker was placed further from them than when it was placed closer to them. (Mershon et al. 1980, 1981). Moreover, expectations of the distance of a sound source also affect the perceived auditory distance of the source (Mershon et al. 1980).

Cues for Distance Perception

Psychologists often make a distinction between absolute cues, which provide information about the absolute distance of a sound source, and relative cues, which provide information on relative distance of a source (is one sound nearer or further than another; Gogel 1968; Mershon & Bowers 1979).

Reverberation can serve both as a relative cue for distance (Maxfield 1931; von Békésy 1960; Mershon & King 1975; Mershon & Bowers 1979; Mershon et al. 1989) and as an absolute cue (Mershon & King 1975). Humans consistently judge reverberated sounds as more distant than similar unreverberated sounds. Sounds in a reverberant environment were judged as more distant than sounds in an anechoic environment, even on first exposure to the sounds (Mershon & King 1975). Mershon & Bowers (1979) used five different distances of loudspeakers in a reverberant environment and equalized the overall sound levels at the subject's position for the different distances. Thus reverberation was the only cue available for judging distance to the loudspeakers. Even on first presentations, before they could compare the features of sounds from different distances, subjects perceived sounds from further away as being more distant.

Overall amplitude is also a strong cue for auditory distance perception (Gamble 1909; von Békésy 1949; Coleman 1963; Gardner 1968; Mershon & King 1975; Little et al. 1992). As expected, signals with lower amplitude are perceived as originating from a source further away than signals with higher amplitude. Furthermore, in their discussion of studies by Ashmead et al. (1990) and Strybel & Perrott (1984), Little et al. (1992) concluded that changes in sound pressure level as small as 0.5 dB are sufficient to produce a perceived change in distance. Unlike reverberation, however, overall amplitude is used as a relative and not as an absolute cue. On first presentations, subjects who heard a more intense stimulus did not perceive it as coming from a different distance than subjects who received a stimulus 20 dB lower in amplitude. Subjects' performance increased over repeated trials, an indication that experience with the range of amplitudes and the acoustic properties of the environment improve distance assessment (Mershon & King 1975).

Relative intensities of high frequencies can also be used as an auditory distance cue by humans (von Hornborstel 1923; von Békésy 1938; Coleman 1968; Butler et al. 1980; Petersen 1990; Little et al. 1992). Sounds with less energy at higher frequencies are systematically perceived as more distant than sounds with more energy at higher frequencies. Like sound amplitude, spectral cues serve as a

relative cue but not as an absolute one. On first trials, subjects did not perceive systematic differences in distances between stimuli differing in high frequency content. Subjects' accuracy in judging distances, however, increased markedly in successive trials as they gained experience with the signal and the test environment (Little et al. 1992).

In addition to the preceding cues which result from changes in the properties of a signal, background noise has been shown to affect perceived auditory distance, at least in reverberant environments (Mershon et al. 1989). Humans judge the same sound as being closer under noisy conditions than they do in the absence of background noise. Since noise masks those parts of the signal that are low in amplitude, it masks the indirect weaker sound field (primarily reverberation) more than the louder direct sound field. This difference leads to a relative emphasis of the direct sound field. The sound source is perceived as being closer under noisy conditions presumably because the receiver cannot detect the full extent of reverberation. Note that the influence of background noise on perceived distance is not a consequence of the lower relative amplitude of the signal. If the relative amplitude of the signal under noisy conditions were a cue, then masking by noise should have led to an increase in perceived distance and not to a decrease.

Effects of Experience on Distance Perception

Use of most auditory cues in distance perception requires prior information on the acoustic properties of the transmission path and the properties of the signal at the source. When these properties are not known, a subject must extrapolate or generalize information from other signals and environments. How well a subject can predict the properties of an unknown signal at the source depends on variation in the characteristics of similar known signals. Although the effects of experience with the signal and with the environment have not been fully separated, the effects of experience with one or the other are clear.

The reason why reverberation is such a reliable distance cue even without prior experience with the test signal (Mershon & King 1975) is hardly discussed in the psychological literature. A possible reason is the nearly ubiquitous absence of features like reverberation in natural signals. In addition, in many habitats, subjects routinely experience reverberating sounds from various distances. Humans thus combine the general absence of reverberation in signals at the source and their experience with reverberant environments to judge the absolute distance even of novel sounds.

Prior experience with a signal has more pronounced effects when overall amplitude or relative intensities of high frequencies are the only cues for ranging. In the absence of reverberation as a cue, humans are very inaccurate in judging the distances to sounds on first trials and become increasingly accurate with subsequent trials (Coleman 1962; see also Little et al. 1992). Evidently, in these conditions, experience with the test signal in the test environment is important for accurate

distance perception. When a sound was unfamiliar, subjects consistently tended to underestimate the distance. The overall amplitude of a sound at its source and relative intensity of high frequencies are much more difficult to predict than reverberation. Many sounds can be produced with different amplitudes so that, without direct information about the amplitude at the source, it is difficult to use amplitude as a distance cue. The situation is similar for the relative intensities of high frequencies. Frequencies of sounds can cover a broad range so that without some prior information about the spectral structure of the sound at the source, it is difficult to use high-frequency attenuation as a distance cue. Furthermore, overall amplitude and spectral composition of signals can vary along a continuum, whereas the majority of natural signals lack features like reverberation, so that predictions of the source are more reliable for the latter.

Special Capabilities for Distance Perception of Human Speech

Speech for humans is the analogue for song in birds. Both are signals evolved for intraspecific communication, to which listeners could have evolved special mechanisms for response. Even without experience with the particular words or speaker, humans might well use their experience with the general properties of speech to judge the distance to a speaker (Brungart & Scott 2001). Even high-frequency attenuation and overall attenuation could provide cues for ranging of speech. Speech has limited variation in these features so that the general properties could be used as a standard for particular cases. In fact when presented with speech, subjects were more accurate in their assessment of distance than when presented with artificial signals (Gardner 1968). The subjects also made adjustments for the usual contexts of different kinds of speech and thus underestimated the distance of whispered speech and overestimated the distance of shouted speech (Gardner 1968; Mershon 1997). Whispered speech of course is normally used at close range whereas shouting is used at long range (or for close-range aggression). The special possibilities for ranging speech are emphasized by a report that humans can judge the distance of normal speech but not of speech played backwards (McGregor et al. 1985). Evidently subjects had more difficulty assessing degradation in backward speech because they failed to retrieve their expectations for the source properties of speech. Since species-specific communicatory signals always have some predictable properties, perception of distance is likely to require less prior experience with these signals than with artificial signals.

EXPERIMENTAL DEMONSTRATIONS OF DISTANCE ASSESSMENT IN SONGBIRDS

In the first demonstration of ranging in songbirds, Richards (1981) showed that Carolina wrens, *Thryothorus ludovicianus*, responded less strongly to playbacks of songs degraded by broadcast and rerecording over a distance of 50 m than to playbacks of undegraded songs.

Subsequent studies confirmed that songbirds often respond less intensely to degraded songs, as if they were perceived to come from a more distant rival (McGregor et al. 1983; McGregor & Falls 1984; McGregor & Krebs 1984; Shy & Morton 1986). One problem with these early experiments, as recognized by Richards (1981), is the possibility that degraded songs are more difficult to detect, so that they evoke responses less often or with longer latencies. If for any reason degraded songs have less salience for conspecific listeners, then the interpretation of reduced responses becomes problematic. Are the degraded signals judged to be more distant or are they just less noticeable or interesting? Recent studies have answered this question by using more direct measures of ranging.

Methods to Study Distance Assessment in the Field

Direct experimental demonstrations of ranging require procedures that simulate a rival but prevent subjects from obtaining direct information about the location of the loudspeaker (Naguib 1996a). In addition, procedures must include a direct measure of the subject's judgement of distance. By presenting brief playbacks or terminating playback as soon as the subject approaches, the first objective is achieved. By observing the distance that subjects subsequently move towards or even beyond the loudspeaker, the second objective is achieved. Recent studies on ranging have followed these procedures (Naguib 1996b, 1997a, b; Wiley & Godard 1996; Nelson & Stoddard 1998; Naguib et al. 2000; Nelson 2000; Holland et al. 2001). When playback is terminated before the subject approaches the loudspeaker, the subject cannot obtain direct close-range experience with the source. As a consequence, subjects often make unambiguous flights beyond the loudspeaker and subsequently search in areas beyond the loudspeaker in response to playback of degraded songs. These responses have provided direct evidence that birds range songs by degradation.

Another methodological problem is that subjects of playback experiments usually experience conflicting messages about the distance to the source. If only one cue or one set of cues for ranging is provided, then different subjects might value the conflicting information differently. For instance, an experimental signal with reverberation but not high-frequency attenuation presents several options for the subject. It might use only reverberation or only high-frequency attenuation to range the signal or it might average the difference. The best demonstration of the consequences of such conflicting messages comes from a tendency for subjects to fly either to the virtual distance simulated by the degraded songs or to the actual distance of the loudspeaker (Nelson & Stoddard 1998). In this case, subjects seem not to have averaged the conflicting messages about distance but instead focused on one or the other cue. Birds that flew to the simulated distance (overflew the loudspeaker) presumably focused on features affected by experimental degradation of the broadcast signal. Those that flew to the actual position of the loudspeaker perhaps used some

feature not affected by experimental degradation, such as the directionality of the received sound, to locate the source.

Cues for Distance Perception

Studies of birds in natural conditions have shown that reverberation, the relative intensities of high frequencies and overall amplitude can all be used as distance cues. Furthermore, birds can use each of these cues separately. Birds thus use the same cues for ranging as humans.

Kentucky warblers, *Oporornis formosus* (Wiley & Godard 1996) and Carolina wrens (Naguib 1995, 1997b) can use reverberation alone to judge the distance to a source of conspecific songs. In both cases, birds responded differently to short playbacks of undegraded and reverberated songs. Closer approach towards the loudspeaker (Naguib 1995) and, most importantly, flights beyond the loudspeaker (and subsequent strong responses beyond the loudspeaker) in response to reverberated songs (Wiley & Godard 1996; Naguib 1997b) provided unambiguous evidence that reverberation alone can serve to range songs.

Carolina wrens can also use the relative intensities of high frequencies for ranging (Naguib 1995, 1997b). Subjects overflowed the loudspeaker and responded significantly more strongly beyond the loudspeaker when songs contained less energy in their high frequencies than they did in response to undegraded songs. Other studies on Carolina wrens and chaffinches, *Fringilla coelebs*, have confirmed these findings with a combination of reverberation and frequency-dependent attenuation (Naguib 1996b; Naguib et al. 2000).

Overall amplitude varies more with weather than reverberation or frequency-dependent attenuation, and signallers can often vary the source amplitude. As a consequence, overall amplitude provides less reliable information about the distance of a vocalizing conspecific. Nevertheless, receivers can often obtain some information about distance, provided singers are consistent. Thus it is not surprising that Carolina wrens can use overall amplitude as a relative cue for ranging conspecific songs (Naguib 1997a). When a retreating rival was simulated by a decrease in amplitude from the first to a second playback, birds overflowed the loudspeaker more often and responded behind the loudspeaker more than when an approaching rival was simulated by an increase in amplitude. Other species also use overall amplitude for ranging (Nelson 2000).

Although these experiments have shown that songbirds can use these cues separately, the advantages of integrating the information from multiple cues are clear. First, depending on the habitat and the weather conditions, not all cues are equally available. Birds that can use multiple cues would be able to range songs in different situations and under different acoustic conditions of the habitat. In addition, use of multiple cues could increase the accuracy of ranging since each cue has its own uncertainties (Naguib 1995, 1997a). By pooling information, birds might compensate in part for the uncertainties associated with each cue.

The way birds process degraded sounds thus relates to wider issues in processing sensory information. Use of multiple cues is common in other tasks for which different cues are not always equally available and each cue is associated with a different kind of uncertainty. Ranging presents challenges similar to visual depth perception or orientation during long-distance migration. Humans use multiple cues in visual depth perception (Davies & Green 1993) and migratory animals use multiple cues for orientation (Wiltschko & Wiltschko 1993). In both these cases, an individual's performance is likely to improve when more cues can be used. For ranging, it will be interesting to see if cues have hierarchical relationships, as has been shown in studies on animal orientation during long-distance migration.

Experience with Particular Sound Patterns

To judge the distance of a sound source, two kinds of prior information are necessary, as discussed in the section on distance perception in humans: information on the structure of the signal at the source and information on the acoustic properties of the habitat. With these two sorts of information, a listener can judge the degree of degradation in a signal and the relationship between this degradation and distance of propagation. Since species-specific songs (indeed the majority of bird songs) have some predictable properties, such as the absence of reverberation-like structures, listeners might use these general properties to estimate the characteristics of the source for comparison with a received signal.

Estimating relative distance is a less demanding task than estimating absolute distance. Without much information about the signal or the environment, a bird should be able to judge changes in distance when listening to consecutive songs sung by a rival. If the properties of successive songs change, a listener must assess if these are due to changes in distance or in the signaller's behaviour, such as changes in the direction of singing or use of different song patterns, or environmental changes, for example in the wind. Changes in song types are often accompanied by changes in spectral features and possibly overall amplitude. Changes in direction can also affect the properties of signals, because songs are not broadcast omnidirectionally (Witkin 1977; Hunter et al. 1986; Larsen & Dabelsteen 1990). A change in the direction a singer faces can thus affect overall amplitude, reverberation and spectral properties of songs heard by a listener. Nevertheless, birds often sing the same song type with some consistency of intensity and direction but empirical studies on intra- and interindividual variation of song amplitude are clearly needed. If so, changes in overall amplitude, reverberation, or spectral properties in the absence of wind are likely to result from changes in distance. Thus, in many cases, birds should be able to assess relative changes in distance without experience with the habitat or the signal.

Absolute distance is likely to be more difficult than relative distance for a listener to determine as has been shown to be the case in humans. A listener needs more information about the properties of the signal at the

source and about the acoustic properties of the habitat. Nevertheless, field experiments have shown that general information about species-specific features of songs is enough to permit birds to judge the distance of a singing rival. Kentucky warblers discriminated between undegraded and reverberated songs they were unlikely to have heard previously (Wiley & Godard 1996). The same result was found in Carolina wrens regardless of whether the cue for ranging was reverberation or attenuation of high frequencies (Naguib 1997b).

Some earlier studies reported differences in responses to undegraded and degraded songs only when subjects had previously heard the song type in question. These findings at the time were interpreted as evidence that familiarity based on prior experience with the song is essential for ranging (McGregor et al. 1983; McGregor & Falls 1984; McGregor & Krebs 1984; Shy & Morton 1986). However, as the experimental procedures allowed subjects to obtain close-range experience with the loudspeaker, the evidence for ranging is not as clear (Naguib 1998; Wiley 1998). In a more detailed discussion of his early findings, McGregor (1994) also weakened his earlier conclusions and suggested that lack of prior experience with the song type may not prevent ranging when unfamiliar song types share phonological elements with familiar song types. The comparison of the different studies is complicated by the different species and the different kinds of degradation used. McGregor and his colleagues degraded the songs over open/semiopen habitats so that primarily spectral cues were provided for ranging. In addition, the indirect measures for ranging do not as clearly rule out other interpretations. European robins, *Erithacus rubecula*, for instance responded strongly to familiar undegraded songs, unfamiliar degraded and undegraded songs, but weakly to familiar degraded songs (Brindley 1991; McGregor 1994). These results might have resulted from habituation, as territorial males hear familiar degraded (distant) songs most frequently and thus might habituate to them.

Experience with a particular song pattern might accrue even within a bout of song. Presentations of a single song, for instance, seem unlikely to result in ranging as accurate as presentations of a series of similar songs, even if we can be sure that the listener does not use the extra time to obtain direct information about the location of the speaker. One response to hearing degraded signals is to move upward instead of to approach (Mathevon et al. 1996). Sound transmission experiments have suggested that differences in degradation are more pronounced at higher positions in the vegetation (Dabelsteen et al. 1993; Mathevon & Aubin 1997; Holland et al. 1998). Thus by changing locations and assessing additional songs, birds might improve their estimates of distance.

Although birds, like humans, seem able to range conspecific sounds without previous experience with the particular patterns, it is likely that experience would improve performance. More detailed information about the structure of a song pattern at the source should increase the accuracy of judging degradation (McGregor 1994; Wiley & Godard 1996; Naguib 1997b, 1998), an idea that has yet to be tested experimentally.

Experience with Transmission Characteristics of a Habitat

While conspecific songs always have some predictable properties, the situation is more complex for the acoustic properties of the transmission path. For a bird to associate a particular level or kind of degradation with a distance, it must have some experience with the acoustic properties of its habitat. In addition, birds in deciduous forests have to deal with changes in the acoustic properties of their habitat as the density of vegetation changes from season to season and with differences in vegetation structure at different locations within their territory at the same time of the season. In the only study that has addressed this problem, Carolina wrens compensated for seasonal changes in the acoustic conditions of their territories before and after leaves emerged fully (Naguib 1996b). These wrens can apparently use their recent experience with the acoustic conditions of their habitat to recalibrate the association of perceived degradation with propagation distance, when environmental conditions change. Apparently birds more or less regularly update their assessment of the acoustic conditions of their habitat.

Accuracy of Distance Assessment

The changes in acoustic structure during propagation will often provide only rough information about the distance to the source. Changes in atmospheric conditions from hour to hour and in vegetation from place to place even in any one habitat make much precision difficult to achieve.

To determine the accuracy of ranging by territorial birds, an experiment would have to present at least three levels of degradation, to assess capabilities for differentiating at least two levels. Instead experiments on ranging by birds have usually compared only two sets of stimuli (undegraded and degraded). Information on the accuracy of ranging thus comes from only a few studies. Carolina wrens discriminated between three levels of song degradation (Naguib 1996b) and chaffinches discriminated between five levels of degradation and tended to overfly the speaker more the more degraded the song was. The latter study in particular suggests that birds can make graded discriminations in ranging, but it also shows limits at which birds did not respond differently to differences in degradation of rivals' songs (Naguib et al. 2000). Eastern towhees, *Pipilo erythrophthalmus*, are also capable of fairly accurate assessments of distance to playbacks of the species-specific call (Nelson & Stoddard 1998).

A difficulty for field experiments on ranging is that at close range visual cues might dominate acoustic cues, so it will be a challenge to design further tests of the accuracy in discriminating levels of degradation and distance in the field. Conditioning techniques under laboratory conditions can be used to examine perceptual limitations on discriminating degradation (Phillimore et al. 1998), and more information from such experiments is needed as background for discussions on the accuracy of ranging. It is also possible that accuracy is

related to the natural spacing of competitors or territory sizes so that birds might be particularly sensitive to degradation over a particular range of distances.

DEVELOPMENT OF CAPABILITIES OF DISTANCE ASSESSMENT

The preceding sections emphasize that ranging requires some information about the structure of a signal at its source. Evidence suggests that species-specific characteristics of signals can provide enough general information to allow birds and humans to range, at least approximately, even previously unfamiliar signals. Nevertheless, more accurate information about the structure of signals at the source should improve the accuracy of ranging. These considerations raise questions about how individuals might acquire information about the properties of species-specific signals at the source.

To perceive a sound accurately, a listener might also have to be able to produce it. Morton (1982) thus suggested that a bird has to incorporate a song pattern into its own repertoire before it could judge its distance when sung by others (Morton 1982, 1986, 1998). At about the time this proposal was first made, it was discovered that neurons in a passerine's brain respond selectively to the individual's own song pattern (Margoliash 1986). These neurons seemed like the ideal comparator for ranging: the more degraded a song the less it might stimulate these own-song neurons. Experiments have never determined how degradation affects the responses of own-song neurons, so this particular hypothesis has never been tested directly. Nevertheless, evidence that young Carolina wrens discriminate between undegraded and degraded songs before they themselves sing (Morton et al. 1986) so far suggests that neither production nor experience with a specific song is required to determine whether it is degraded.

The analogy with theories of production-based perception of human speech (Willams & Nottebohm 1985; Nottebohm et al. 1990; Nottebohm 1991; Margoliash 1997) no doubt fostered interest in this idea (Margoliash 1986). Even if this theory is applied to human language, it does not seem directly applicable to ranging. Speech perception involves many highly complex discriminations of sequences of sound, whereas ranging requires discriminations of a few parameters of a sound, its overall spectrum, intensity, or reverberation, as discussed above.

Experimental evidence and theoretical considerations suggest that birds can range songs with at least coarse levels of accuracy when they have only general information about the structure of songs at the source. The possibility of production-based perception could still apply. Perhaps perception of the general properties of species-specific song requires a capability for producing, if not specific song types, at least normal songs. Thus production-based perception might operate at different levels of specificity. Although the field experiments indicate that production of particular song patterns is not required for coarse levels of ranging, it might still be the case that production of species-specific song and perception of its general properties are linked. So far, however,

there is no reason to suppose that general perceptual experience is not enough to achieve accuracy in ranging. Motor experience with a particular song seems unnecessary for ranging in principle and so far has no empirical support.

We might imagine two stages in the development of the ability to perceive species-specific sounds for purposes of ranging. In stage I, young birds might have innate (independent of specific experience) information about at least some of the species-specific characteristics of its songs or acquire this information early in life. This general information might include the overall spectrum of songs and the types of notes included. Some evidence suggests that the types of notes in songs is a much smaller set than the song patterns produced from these notes (Marler & Peters 1977; Marler & Pickert 1984; Payne 1996) and that the set of note patterns might be recognized without prior experience in some species (Marler & Peters 1977). As soon as a young bird can hear, it might begin to acquire additional information about the general properties of species-specific song. Thus at an early stage they could have information about the normal spectrum of songs and the most frequent structures of notes. Even with such rudimentary information about songs, an individual would be able to judge the approximate distance to the source of a typical song of its species.

No doubt experience with the detailed structure of a song pattern and the habitat would improve the ability to range its source. Thus stage II in the development of ranging abilities might involve experience with the habitat and particular songs. Thus a two-stage (or a continual) process for the development of ranging leaves room for both innate information and experiential information at different levels of specificity. Kentucky warblers and Carolina wrens that can range songs without prior experience with the particular song pattern show that birds need only rudimentary information about species-specific songs in order to range them (stage I). Carolina wrens that adjust to seasonal changes in the density of vegetation suggest refinements based on experience with particular conditions (stage II). Future studies using direct measures of ranging could explore the possibility that experience with a particular song type improves the accuracy of assessing distance.

LIMITS ON DISTANCE ASSESSMENT AND IMPLICATIONS OF SIGNAL ADAPTATION FOR DISTANCE ASSESSMENT

The precision, as opposed to accuracy, of ranging raises questions about the physiological limitations on comparisons of the perceived signal and the subject's internal standard, whether innate or experiential. The just-noticeable difference (JND) in degradation determines the JND for distance to the source (Fig. 2a, b). Assessing degradation, as discussed above, requires assessing or comparing the intensities of sound in particular bands of frequency in a signal or periods of time in the tail of a signal. The JND for degradation thus depends on the JND for these discriminations of intensity. Because overall attenuation and reverberation do not accumulate linearly

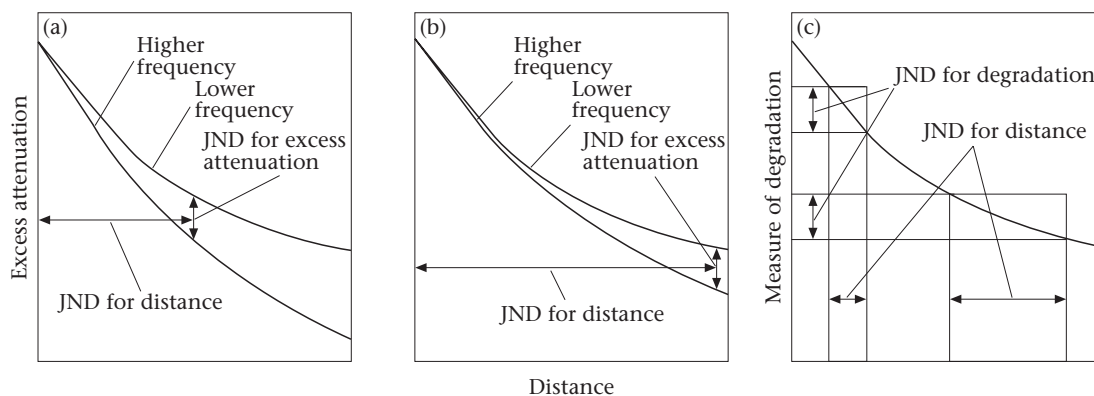


Figure 2. Ranging by attenuation of higher frequencies relative to lower frequencies. Excess attenuation (as a result of atmospheric absorption and scattering) is a linear function of distance (absorption/m remains constant), but higher frequencies (within the range of avian and human hearing) are absorbed at a higher rate than lower frequencies. To judge the distance of a source, a listener could compare the intensities of two frequencies at the source and the destination. The magnitude of the difference in excess attenuation of the two frequencies determines the precision of ranging. For any JND (just-noticeable difference) for a change in the intensity difference between the two frequencies, there is a corresponding JND for distance of the source (a). If signals evolved to concentrate energy in those frequencies with least excess attenuation, then the precision of ranging would decrease (b). On the other hand, concentration in frequencies with less excess attenuation would increase the distance at which these frequencies remained above the level of background sound (a consequence of attenuation by spherical spreading in addition to excess attenuation), so the maximal distance for ranging would increase. A fixed JND for degradation in combination with exponential changes in degradation with distance will result in smaller JND for distances at shorter range than at longer range (c).

with distance (Wiley & Richards 1982), the JND for degradation corresponds to a larger JND for distance at longer range (Fig. 2c).

The precision of discrimination depends on the variability of propagation as well as the limitations of perception. Studies using composite measures of degradation have so far suggested considerable variation of degradation at any one distance (Dabelsteen et al. 1993; Holland et al. 1998) but composite measures make it difficult to assess the variation in degradation of physiologically relevant features. Experimental transmission of sounds in natural environments might in the future measure the variation as well as the trend in degradation in physiologically relevant frequency bands such as the rates of decrease of reverberation, as discussed above.

Information about the pertinent JNDs and the variability in degradation should eventually allow calculation of the zone within which ranging of sound is possible. The standard deviations (or root mean square variation) in intensities relevant for judging distance are likely to increase with distance, as the mean intensities decrease. At some distance, the variation will become so large in relation to the mean that no further judgements of distance would achieve enough accuracy to make the effort worthwhile. Even before reaching this distance, the subject's JND for the relevant intensity discriminations will set a maximal distance beyond which judgements of distance are impossible. Both relative and absolute ranging must occur within these limits. Ranging thus has an active space, as does more straightforward detection of a signal. We might thus expect that the active space of ranging is linked to the natural spacing of communicating individuals or their territory sizes.

Similar considerations show that adaptations of signals for efficient transmission in a particular environment

should increase the distance at which signals can be ranged (Fig. 2a, b). By using frequencies that accumulate reverberation or amplitude fluctuations less rapidly or by avoiding high frequencies subject to rapid attenuation, signals should remain above ambient background noise at greater distances from the source and thus allow ranging at greater distances. Because the accumulation of degradation is spread over a greater distance, the precision in ranging should decrease at any particular distance (a greater difference in distance should be required to produce the JND in degradation). Thus adaptations for efficient transmission of signals should extend the distance over which ranging is possible but should reduce the precision of ranging at any particular distance. Less well-adapted signals can be ranged accurately over a short distance but, once a signal is strongly degraded, resolving different distances will be difficult, whereas well-adapted signals will reach this limit at a much greater distance. Maximizing the active space for detection of song by evolutionary adaptations to minimize degradation is also likely to maximize the active space for ranging.

CAN SIGNALS PROVIDE DECEPTIVE DISTANCE INFORMATION?

Could animals make their vocalizations sound further or nearer than expected by adjusting their acoustic structure? If so, is there any evidence that they might?

Any deceptive signal would presumably have to fit the requirements for stable deception. Often these requirements would include relatively infrequent use (Wiley 1983, 1994; Dawkins & Guilford 1997; Hughes 2000). Deceptive signals might thus either be produced by relatively few individuals or by individuals relatively

infrequently. In the latter case, individuals might have both typical and degradation-mimicking forms of signals in their repertoires.

An overall decrease in intensity would result in a signal with one of the salient features of greater range, but it would leave discordant cues from reverberation and high-frequency attenuation. Decrease in intensity might also serve to reduce eavesdropping by inappropriate receivers (McGregor & Dabelsteen 1996; Naguib & Todt 1997) or simply to save energy by the signaller (Dabelsteen et al. 1998). Decreases in overall intensity would thus require careful study to provide clear cases of deceptive range.

Singers might make their songs sound further away, in a more convincing manner, if they incorporated features that mimicked reverberation or frequency-dependent attenuation. These possibilities would involve eliminating or attenuating the normal high-frequency end of the spectrum of typical songs. Individuals' repertoires often include variant vocalizations that differ in spectral properties. It has been suggested that vocalizations emphasizing lower frequencies might have advantages by mimicking a larger source (Fitch 1999). A song with a marginally lower distribution of frequencies might also mimic a more distant source, at least for listeners that had not yet acquired experience with the particular song. If true, these effects would somewhat dilute each other, as an individual bluffing a lower-pitched source would sound both larger and more distant to an inexperienced receiver.

Individuals could avoid this conflict by adding apparent reverberation to their vocalizations, by extending the termination of each note (prolonging the release time). One case in which this sort of deception might occur involves howling monkeys, *Alouatta palliata* (Whitehead 1987). Groups of these monkeys occupy overlapping ranges. When they detect others nearby, they howl and grunt. Playbacks have shown that groups usually withdraw from each other after such interactions. In particular a group near the centre of another's range is likely to withdraw. Such an invading group might conceivably buy time for further feeding by uttering deceptively distant grunts. Howling monkeys in fact have such grunts in their repertoire; on spectrograms and to the ear they sound like carelessly produced grunts with prolonged release times. Playbacks suggest that nearby groups are less likely to respond to these grunts than to cleaner ones.

Individuals might also produce deceptively close signals by adding high-frequency pre-emphasis and by using unusually quick release times of notes. Such a signal might mimic an approach without having to risk an engagement with the rival. The few reports available suggest that individuals might lower the frequency of their vocalizations as encounters become imminent, rather than raise them, apparently to mimic larger size rather than closer range. Perhaps the possibility of mimicking proximity has not yet been considered by investigators. The advantages of mimicking proximity might also accrue at some distance from a rival, whereas the advantages of mimicking larger size might have greatest urgency when encounters are imminent.

Although it would presumably be difficult to reduce reverberation by changing the structure of songs, it might nevertheless prove possible to mask it. Notes that trailed off gradually, for instance, would provide little chance to judge reverberation and yet might end so gradually that no possibility of mimicking natural reverberation would arise. The gradual onset and release of the hawk-alarm calls of many passerines might provide an example (Marler 1955). Such notes would not allow rapid changes of intensity or frequency, however, and thus could not encode complex information rapidly.

CONCLUSIONS AND PERSPECTIVES

The consequences of sound transmission over long distances have been fairly well framed by experimental studies. Theories in animal communication still struggle to incorporate the diversity found in how signals are adapted to the transmission characteristics of the habitat and how signal degradation affects receiver perception and decision rules.

Some general mechanisms underlying distance perception have now been determined in birds and humans, although much remains to be learned. We know that receivers can attend separately to different kinds of degradation. Yet few studies of sound transmission have measured the components of degradation in ways that reveal how it might be perceived by a receiver. The effects of degradation on responses by receivers are often striking, but we still do not know how receivers integrate the different kinds of information. We can make predictions about the active space for ranging, but we still know little about the accuracy and precision of ranging. We also know little about the circumstances in which animals use ranging, nor about adaptations in signals that might promote or impede ranging by listeners or even mislead listeners.

Recent experiments have introduced new procedures that permit more definitive and precise studies of ranging and thus open possibilities for further work on these questions. The issues raised by ranging of conspecific signals are related to issues in other forms of complex perception and to basic issues in the evolution of territorial behaviour and the coevolution of signaller and receiver strategies. Like other complexities of animal communication, we are beginning to see the possibilities.

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