Sound in the Animal World

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ABSTRACT: Energy relations involved in sound production by animals are examined, and it is found that different animals devote vastly different fractions of their available muscular energy to this form of communication. Typical sound energy output is found to range from a fraction of a watt for particularly noisy animals, through a typical value of around a milliwatt, and down to a microwatt or less for tiny insects. Consideration of atmospheric propagation and background noise suggests an optimal song frequency for a given available acoustic power, the preferred frequency for a power near 1mW being in the range 1 to 10kHz. Mechanical and pneumatic methods of sound production employed by animals are reviewed, and brief consideration is given to auditory systems and to the encoding of information in vocal utterances.

1. INTRODUCTION

Although vision, touch and smell are all important, the principal means of communication for most species in the animal kingdom is through sound. It is therefore interesting to examine the physical limitations to this form of communication and to see how various animals have adapted to exploit the possibilities. As we might expect, many different strategies are used, depending upon the habitat, size, and mode of life of the animal concerned, and it is not possible to mention all of these here. Examination of a representative sample, however, shows the wealth of variety that exists, and makes clear some of the physical principles involved. As we might expect, there have been many books and papers written about the subject from behavioural, anatomical and physiological points of view. The interested reader is referred to some of the more general books on the subject [1-5] which in turn lead to the more specialised literature. Not surprisingly, human hearing and speech [6-9] receive particular attention, as also does bird song [10].

2. ENERGY PRODUCTION

The amount of sound that an animal can produce is ultimately limited by its total available muscular energy, so it is useful to have an estimate of this quantity. Order-of-magnitude estimates suffice for this argument, since a few decibels more or less in sound power are not significant. For a human, the extreme of energy production is approximated in exercises such as running up stairs. In rough terms, for a 100kg adult running so as to achieve a vertical ascent rate of 1 m/s, this amounts to about 1kW, or about 10W/kg of body mass. Of course this rate can be maintained for only a short time, and a more realistic continuous rate, corresponding to walking up

an incline of about 1 in 10 at 1m/s is about 100W or 1W/kg (though a trained athlete could do rather better). For comparison, the energy production rate required simply to keep the body functioning is about 100W, so that the human machine is not a very efficient producer of continuous mechanical energy. Most vertebrates can do several times as well as this in terms of power output per kilogram of body weight, as we can see by noting that a dog or a horse can run uphill at least three times as fast as a man, though perhaps this is in part because quadrupeds use the muscles of four legs, rather than only two, when they run. We might also note that one horsepower is 746W, which is about 1W/kg for a horse, and we might presume that this level of output can be maintained throughout most of a working day. A cursory examination of insect performance suggests relative performance significantly higher than that of other active animals, so that we can estimate about 10W/kg or 10mW/g as the maximum sustainable power output in this case.

Returning to available power, it is useful to relate this to sound production. As we shall see presently, the typical efficiency with which mechanical energy can be converted to acoustic energy is only about 1 percent, though it may be a good deal lower than this for some conversion systems. Against this figure, rather surprisingly, we must put the observed fact that many animals produce a maximum sound power of around a milliwatt–quivalent to an intensity of about 80dB at 1–almost independently of size. This is certainly true of humans, dogs, birds, and noisy insects such as cicadas. A human that invests about 100mW, or only 0.1% of available energy, in sound production, while for a cicada weighing only about 1g the sound-production energy investment of about 10mW (allowing for a sound-production efficiency of nearly 10% in this case) is almost equal to the total available energy used for flying.

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3. SONG FREQUENCY

Another feature of sound communication that is, at first sight, surprising is that we can hear the known songs of nearly all animals (although this statement is itself perhaps a tautology!). Indeed it is only the echo-locating chirps of bats, typically around 60-80kHz, that lie outside our normal hearing range of around 20Hz to 20kHz. Is it that human hearing has an immensely wide frequency range, or is there some physical factor that mandates a restricted choice of frequency?

The object of sound production is, of course, to communicate, principally to members of the same species. This suggests that sound production organs and auditory organs will be similarly tuned, but does not influence the frequency band. On top of this comes the evolutionary advantage of being able to communicate over as large a distance as possible, since sound communication serves the dual roles of attracting mates and of defining territory. Large initial vocal power clearly helps here, but efficiency of sound transmission is also important.

Suppose that we start with a single-frequency source with a power of 1mW, which is typical for a "loud" biological source such as a large bird singing or a human shouting. If we assume the source to radiate equally in all directions then, as shown in Fig. 1, the sound-pressure level at 1m is about 80dB, and this falls by 6dB for every doubling of the distance from the source. It makes little difference, only 3dB overall, whether we assume radiation into a sphere or, more realistically, into a hemisphere bounded by the ground. This overall inverse-square-law behaviour is, of course, independent of frequency, but this is not the whole story. On top of simple spherical spreading, we have to consider sound absorption in the air, and this is quite strongly frequency-dependent, the absorption coefficient increasing as the square of the frequency.

When we put these two effects together, as shown in Fig. 1, we see that the curves for sound of high frequency soon drop well below the inverse-square-law line. The attenuation has a quite extreme effect at ultrasonic frequencies, and such sounds can scarcely propagate beyond a few tens of metres. Conversely, sounds with frequencies below 1kHz suffer very little extra attenuation out to ranges of several kilometres. This effect is dramatically demonstrated in the case of a thunder clap, which has a very high instantaneous acoustic power level and so can be heard over very large distances. The thunder impulse has a very wide acoustic spectrum and, close at hand, gives the impression of a sharp sizzling snap. As the thunder of a kilometre or so, the snap is gone but the crash is still bright and clear. When the thunder is delayed by more than about 15 seconds after the lightning stroke, implying a distance of more than about 5km, the sound is a dull rumble with low-frequency components dominating.

In addition to these attenuation effects, which would appear to favour a very low song frequency, an animal must contend with the masking effect of background noise, largely
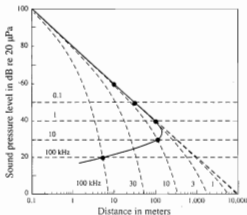

Figure 1. Propagation characteristics of sound of various frequencies (shown in kHz as a parameter) in air, from a source of power 1mW (broken curves), together with typical one-third-octave-band noise levels (about 40dB(A) overall) at the same frequencies (broken lines). The intersections of these two sets of curves (full curve) define the communication distance within which the signal-to-noise ratio is better than 0dB. (Modified from [1].)

created by wind in vegetation. This background noise will depend very much on the environment, but has the general property that its sound-pressure level rises with decreasing frequency. Indeed, natural background is one of those noise types for which the energy is approximately inversely proportional to frequency–so-called $1/f$ noise. If we consider one-third-octave bands as representing the frequency range over which background can mask a pure-tone signal, then the noise level in each of these bands increases by 10dB if the centre frequency is lowered by a factor 10. This effect clearly works in the opposite direction to the attenuation effect, since low frequencies are increasingly likely to be lost in the sea of background noise.

This situation is illustrated also in Fig. 1, where the background noise levels in one-third-octave bands of a moderately quiet environment of about 50dB(A) are shown superimposed on the propagation curves for our 1mW single-frequency source. If we follow the propagation curve for a frequency of 100kHz, then we see that the signal becomes submerged in the background noise at a distance of about 6m from the source. Distances where the signal becomes less than the noise can be similarly identified for other frequencies, and the result is the curve shown, from which it is clear that greatest audibility distance is achieved if the signal frequency lies in the range 1-10kHz, the distance then being about 200m under the noise conditions considered.

The graph in Fig. 1 was drawn for a source of acoustic power 1mW, corresponding to a human shout, a moderately loud bird, or a very noisy insect such as a cicada. For a smaller and less powerful insect, say one with an acoustic power of only 1μW, the signal propagation curves are all lowered by
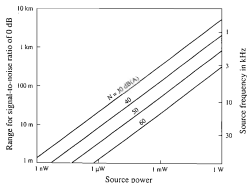
Figure 2. Optimal frequency and communication distance for a signal-to-noise ratio greater than 0dB for narrow-band sources of specified power in ambient noise of the level shown as a parameter. (The figure is not meant to be quantitatively exact. (Modified from [1].)

30dB, and the intersections suggest an optimal frequency of around 10kHz and a range of about 10m. Of course, insects are gregarious, and many individuals of the same species will be singing at once, so the effective range is very much less than this because of the enhanced background in the song-frequency band. These conclusions are summarised in Fig. 2, which gives, in approximate terms, the optimal frequency and range as functions of source power under various conditions of background noise.

The association between low power and high optimal communication frequency has other interesting implications. Within a given family of animals, we expect smaller species to have less power available and hence to be able to produce only quieter songs. At the same time, their lighter bodies and smaller size are better adapted to produce higher-frequency sounds, and high frequencies will tend to maintain the radiation efficiency.

When we examine the songs of typical animals, we see that they fit well into this framework. Humans have fundamental speech frequencies in the range 100-300Hz and song frequencies up to about 1000Hz, but most of the speech information is carried in the "voiced" vowels, which have formant bands–resonances of the vocal tract–in the range 500-2500Hz, and in the consonants, which are essentially wide-band noise with some formant shaping, extending up to about 5kHz and so, in some cases accompanied by a voiced component. Operatic singers have learned to produce a further vocal formant, centred at about 3kHz, which makes their voices particularly recognisable against an orchestral background. The human auditory system, quite naturally, has evolved to match the range of the human voice, with maximum sensitivity in the range 500-5000Hz. The "singer's formant" lies close to the frequency of maximum sensitivity of the human auditory system, and so is particularly effective.

Birds have fundamental song frequencies in the range 500-2000Hz, and vocal formants extending up to about 8kHz,

depending on the size of the bird. Their auditory systems have similar range to the human ear, though extending to somewhat higher frequencies. Insects, on the other hand, generally have a song consisting of a modulated pure tone. The loud cicada has a song frequency of about 3.5kHz, which explains its particular insistence to human hearing, while smaller cicadas and other insects have song frequencies around 5kHz.

The one apparent exception to this scheme is the bat, which uses echo-locating calls with frequencies typically in the range 60-100kHz, depending upon the species. The animal's purpose, however, is not communication with other bats but rather the sonar location of obstacles and flying insects. For these purposes a range of 5-10m is all that is required, and a short wavelength λ is also necessary, since the echo strength varies as $1/\lambda^4$.

We could carry out a similar analysis for aquatic animals such as whales, seals and dolphins, though the results would be different because of the different propagation properties of the ocean. Two things enter here. Firstly, for long distances the ocean is essentially 2-dimensional rather than 3-dimensional, partly because of its limited depth, but also because of its layered thermal and haline structure. The attenuation due to spreading with distance is therefore only 3dB for a doubling of distance rather than the 6dB characteristic of the atmosphere. Secondly, although the attenuation of propagating sound in sea water increases roughly as the square of the frequency, as it does in air, the actual attenuation is very much less, the figures at 1000Hz being about 5dB/km for air and only 0.05dB/km for water. This, in turn, raises the background noise level very greatly. Aquatic mammals therefore have rather different acoustic problems to overcome, but generally adopt frequencies not too different from those of land-living animals of similar size. The exception, once again, is the high frequencies of the sonar clicks used for echo-location by dolphins, and this for similar reasons. Crustaceans also make high-frequency sounds, rather like insects.

4. SOUND PRODUCTION

Sound production mechanisms in animals can be divided into two classes. Insects, which have no lungs but absorb oxygen by simple diffusion through a tube-like spiracle system, necessarily make sound by mechanical means, while animals with lungs and associated muscles generally use pneumatic generation. Let us consider these in turn.

Insects have a stiff outer cartilage exoskeleton, membranous wings, and stiff wing covers, all of which can be induced to vibrate at their mechanical resonance frequency by rubbing one part against another. While simple friction might suffice, the mechanism generally involves scraping a file across a pic, or vice-versa, the tooth spacing and speed being adjusted to give mechanical resonance. While this simple mechanism is widely used, it is not very efficient, because the vibrating surface is small and acts as a dipole radiator. A simple estimate suggests an efficiency of order 0.01%, and
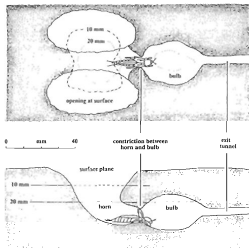
Figure 3. The mole cricket singing burrow. (From [11].)

Figure 4. Simplified model of the avian vocal system, as used for calculation of acoustic performance. (From [13].)

indeed the sound energy produced is generally in the microwatt range.

There is one very interesting and efficient modification of this system, adopted by the mole cricket [11]. This insect digs a burrow in moist earth, the shape being roughly that of a curved exponential horn, terminated at its narrow end by a hollow bulb, as shown in Fig. 3. The cricket positions itself in the constriction between the horn and the bulb, and there vibrates its wings to produce its song. The dimensions of the horn (length about 45mm, throat diameter about 10mm and effective mouth diameter about 35mm) and of the bulb (length about 25mm and diameter about 17mm) are such that the cricket song at about 3kHz is resonant with the second horn-and-cavity mode, to which the cricket wings couple efficiently. The whole burrow gives an increase of nearly 20dB in radiated power over that of the insect in free air.

The cicada has developed a much more efficient singing mechanism, but at the expense of evolving a specialised sound production organ. The essential feature is an abdominal cavity, closed by two rather stiff ribbed membranes, called timbals, which can be flexed inwards by attached muscles, thus generating a train of pulses at the resonance frequency of the loaded cavity. This is an efficient radiator, since it is a monopole rather than a dipole source, and also since the resonator has a fairly high Q value. Calculations suggest an overall efficiency as high as 10%. One species of cicada, the green bladder cicada found on the coast and tablelands of Eastern Australia, has taken sound production to an extreme by evolving a huge abdominal bladder for the resonator. This has allowed it to use a much lower song frequency, around 800Hz, but the penalty is that the male, which is the singing partner, is scarcely able to fly. The reason why the low song frequency has been adopted is not clear.
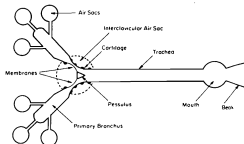
When we come to animals with lungs, the sound production mechanism becomes pneumatic—air is forced between two membranes or folds of cartilage in the larynx in such a way as to cause them to vibrate at very nearly their mechanical resonance frequency [12]. The tube of the vocal tract between the larynx and the mouth opening acts as a resonator but, since its lowest resonance is generally at a frequency many times that of the vocal valve oscillation, the resonant pressure feedback does not greatly assist the oscillation but simply increases the relative level of harmonics lying close to this resonance. This is distinct from the situation in the otherwise similar case of playing brass instruments such as the trumpet, where the lip vibration frequency is tuned by the player to match a prominent resonance of the instrument horn. This distinction results in a lower acoustic conversion efficiency, which is typically less than 1% for vocal systems, compared with a value that can approach 10% for the trumpet.

There are many minor variants of this sound-production mechanism. In humans and other mammals, the symmetrical vocal folds of the larynx lie in the trachea above its junction with the two bronchi carrying air from the lungs. Some birds have a similar positioning of the vocal organ, or syrinx, but the folds are replaced by membranes that are made to protrude into the airway by means of air pressure in a surrounding sac. So-called song birds, on the other hand, have two of these vocal membranes located one in each bronchus just below its junction with the trachea, as shown in Fig. 4. Some birds use only one syrinx membrane in singing, but some use both and are able to produce two tones simultaneously, though they generally do so only on isolated notes of the song. In some birds, such as the familiar sulphur-crested cockatoo, the syringeal oscillation is actually chaotic, producing a loud raucous screech.

It is interesting to examine the energy input to the vocal organ. In ordinary human speech, the pressure below the vocal valve is of order 300Pa (3cm on a water manometer) and the flow rate is about 300ml/s, making a total pneumatic power input of about 100mW and giving an acoustic power output of about 0.1mW, the conversion efficiency is thus about 0.1%.

For a trained singer, the lung pressure may be about 1kPa and the flow rate about 500ml/s, giving an input power of about 500mW and an output power that may be as high as 10mW, implying an efficiency of about 2%. Similar calculations can be made for birds [1,13], which may use rather higher pressures and, because of their smaller size, smaller flow rates. Birds such as cockatoos and domestic roosters can achieve peak acoustic outputs of more than 100mW with an efficiency of around 10%, but for most species the output is less than 1mW and the efficiency less than 1%.

It is interesting to compare these figures with those for musical wind instruments, although, as remarked above, the resonance conditions are quite different from those of vocal tracts. Maximum power output for flutes, clarinets, oboes and bassoons is just a few milliwatts, and the conversion efficiency is around 1%. For brass instruments such as trumpets, maximum power output approaches a watt, and the conversion efficiency can be as high as 10%. These figures are thus surprisingly similar to those for natural pneumatic vocal systems.

When we come to consider aquatic mammals such as seals, dolphins and whales, the sound production mechanism is rather similar to that for land-based mammals, except that the air may be exhausted from one body cavity to another through the vocal folds, rather than being expelled. This works because of the good acoustic impedance match between body tissue and the surrounding water, which allows efficient radiation from body vibrations, a mechanism that is subject to a 30dB impedance mismatch loss in the case of animals in air. This air-conservation strategy has obvious advantages for animals that dive deeply.

5. HEARING

The varieties of hearing mechanism that have developed in various animals have been discussed in some detail before in this journal [14], as well as in other publications [1-5], and we therefore deal with this topic rather briefly. In all cases, the hearing mechanism is based upon the deflection of hairs embedded in sensory cells. Deflection of the hair by an amount comparable to an atomic diameter opens ion channels in the cell membrane, which allows it to depolarise and send a pulse along its axon towards the brain. In insects and crustaceans these hair cells on the outer parts of the body are often the primary means by which motion of the surrounding air or water is detected. Being velocity or displacement sensors, they give information about sound direction as well as about frequency and amplitude. If the hairs are tuned elastically, then they respond primarily to a limited bandwidth.

In higher animals, though also in many insects such as flies or crickets, there are additional specialised auditory organs consisting essentially of a membrane covering a cavity and conveying its vibrations through a mechanical link to an auditory capsule in which the hair cells are embedded. The appreciable area of the diaphragm improves the auditory sensitivity, while its mechanical properties tune the system response. It is, of course, basically a pressure sensor, and is so not sensitive to sound direction. A pair of such ears can, however, be coupled acoustically by means of a common cavity or by interconnecting tubes to give a cardioid response and thus good directional sensitivity. In the case of humans and other mammals, the acoustic connection between the two ears is, however, essentially inoperative because of the small tube size, and sound direction must be determined by neural analysis of the outputs from the two ears. There are also clues from the frequency-dependent directionality of the external ear [15].

The auditory capsule, for its part, may also perform a frequency analysis by means of some sort of tuning of its component hair cells. In the case of the human auditory capsule, the cochlea, this analysis function is carried out with the aid of a tapered and fluid-loaded membrane, the basilar membrane, to which the hair cells are attached.

The threshold sensitivity of most diaphragm-based animal ears is not very different, ranging from about 10dB to 30dB sound-pressure level at the frequency of maximum sensitivity. Simple insect ears, such as those of the fly or cicada, have a frequency range of less than an octave, to match the song of their species, while the range of efficient human hearing is around two decades or about 6 octaves. Animals such as dogs have somewhat wider hearing range, and bats, of course, have specialised hearing in a narrow range around their ultrasonic cry frequency.

6. CODING AND INFORMATION

The purpose of producing sounds is, of course, to convey information, and for this purpose the song or message must be coded in some way. In the case of human speech, we are familiar with the coding of speech sounds that we classify as vowels and consonants. These differ in their spectral properties in characteristic ways, and feature detectors in the brain are able to recognise and decode the patterns. The fundamental voice frequency plays rather a small role in most languages, serving principally to express emotion, though there is an exception to this in the tonal languages of Asia, where variations in the fundamental pitch of vowel sounds are a primary encoder of meaning.

Birds also have songs that may be very complex, involving both rapid pitch variation, formant changes and other articulations. It is unlikely that these features have much information to convey, and they probably serve simply as markers of status or experience on the part of the singer, attracting a mate and advertising the ownership of territory.

Animals such as frogs, cows, and even dogs, have a very limited vocal repertoire, and presumably do not rely upon vocal utterances to convey detailed meaning to other members of the species. Insects, too, have very stylised songs, coded by carrier frequency and repetitive time pattern, which serve largely to broadcast the presence of a male of the species.

7. CONCLUSION

In this brief survey it has been possible to mention only a few of the fascinating features of animal acoustics. My purpose in doing so has been to emphasise that physical acoustics has a useful role to play in providing a quantitative framework to underpin the studies of biologists.

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