

ACOUSTIC SYSTEMS IN BIOLOGY: FROM INSECTS TO ELEPHANTS*

Neville H. Fletcher

Research School of Physical Sciences and Engineering,
Australian National University, Canberra 0200, Australia

ABSTRACT Nearly all animals use sound for communication, for seeking prey, and for avoiding predators. What physical principles govern their choice of frequency? What are their mechanisms of sound production and directional hearing? Why are cicadas so loud? How do birds produce those beautiful, or sometimes not-so-beautiful, sounds? Quantitative analysis of the acoustic mechanisms involved reveals (nearly) all: the action of the sensory hairs on caterpillars, the hollow bodies of cicadas that act as resonators, the horn-shaped burrows dug by crickets and their remarkably human-like auditory anatomy, the inflatable vocal sacs used by "pure tone" songbirds and by frogs, and the chaotic structure of the shrieks of sulphur-crested cockatoos. This lecture will explore all these matters and perhaps some more.

ANIMAL COMMUNICATION

Sound signals are important for nearly all animals. They listen passively for warning sounds signalling the approach of predators, they listen carefully for sounds given out by their own prey, and they use sound actively to communicate with other members of the same species. Some animals, such as bats and dolphins, also use active sonar methods to map their environment and seek out prey. While the variety of anatomical details and habitats can explain much of the variation between the sonic activities of different species, there are certain general principles that apply to all animals, while the ancestry of evolution gives clues for anatomical similarities between animals as diverse as crickets and humans. The present paper will deal exclusively with land-dwelling animals, leaving underwater communication to other speakers.

Since the number of books and papers published on biological aspects of animal behaviour is immense, I can perhaps be forgiven for concentrating on those to which I have contributed myself, which deal with physical and acoustic aspects of the subject. One of these (Fletcher 1985) gives a brief survey of the subject, while comprehensive treatments have been given in two others (Fletcher and Thwaites 1979a, Fletcher 1992). Of course I have benefited greatly from the research of others, particularly biologists, but I have left it to my biological colleagues to filter this work into my consciousness.

Let us look first at conspecific communication and see what general rules apply. It is not unreasonable to expect that there may be a large difference in behaviour between air-breathing animals such as elephants, humans and birds, and those animals such as insects that have to produce sound by mechanical vibration of some part of their anatomy, so we first examine these air-breathers.

Since one aim of conspecific communication is to maximise the distance over which the call can be heard, and since this depends on both the acoustic power that can be produced and the frequency of the call signal, we might expect a relation between the call frequency and the size of the animal. There is indeed such a relation and it is indicated by the summary in Fig. 1. To analyse the scaling rule that might be expected requires consideration of the sound-production mechanism,

essentially air flow through a vibrating valve, sound radiation, propagation loss (which increases as the square of frequency), and auditory sensitivity. Putting these all together yields the rule that dominant frequency should be inversely proportional to the mass of the animal's body to the power 0.4 (Fletcher 2004). This is the line shown in the figure. Clearly there are some outliers in this general correlation, but the result is surprisingly consistent when the range of animal size and anatomy is considered. A similar scaling rule can be derived for the communication distance, which varies about as body mass to the power 0.6.

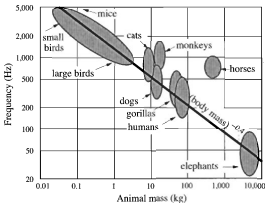


Figure 1. Distribution of dominant frequencies for a large range of air-breathing animals. The line is the calculated behaviour: frequency proportional to $(1/\text{body mass})^{0.4}$. (Adapted from Fletcher 2004)

Insect song behaviour is, as might perhaps be expected, very much less consistent because the sound production mechanism varies widely between species, but it is clear that very small insects make sounds of very high frequency. We return to this later.

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INFORMATION CONTENT

Information can be encoded in vocalisations in several ways, but the most important are the spectral structure and envelope, and the time variation of the signal. Insects generally have the simplest signals, which are essentially repeating pulses at a single frequency, the reason being that these are simply mating calls by the males of the species and need to convey nothing other than their existence and location. At the other end of the scale, humans use both time encoding (sentences, words, syllables) and frequency encoding (vowels, consonants) to construct a language with high information content. Birds are perhaps anomalous, since their songs are complex in both time and frequency but, because they are repetitive, the total information content is limited.

The case of elephants is particularly interesting, since the dominant frequency of about 30 Hz could be characterised as "infrasonic", and it propagates over long distances, particularly when there is a temperature inversion in the atmosphere. It turns out, however, that other elephants cannot recognise an individual until they are able to hear the information contained in frequency components above about 100 Hz.

VOCALISATION IN MAMMALS

All mammals have very similar vocalisation mechanisms, as shown in Fig. 2(a). Air is compressed in the lungs to a pressure that does not vary greatly across species or the size range, since muscle stress is about the same and both the thickness of containing muscles and the radius of the lung sac vary in the same way with animal size. The vocal organ contains a pressure-controlled flap valve, the oscillation frequency of which, and hence that of the air flow, is controlled by muscular tension. Above the valve is a vocal tract terminated by a flexible opened mouth, and it is the acoustic resonances of the contained air column that can be adjusted to create emphasised formants in the radiated sound. The frequency of the lowest formant band is typically several times that of the valve oscillation, and the formant frequencies can be adjusted over quite a large range by variation in mouth geometry.

While this vocalisation mechanism is very flexible, it is not very efficient, typically reaching a maximum of not much more than 1% at high sound levels. Typical maximum continuous sound output is of order 10 μ W per kilogram of body mass. This amounts to about 10 mW (90 dB at 1 m) for a human and perhaps 1 W for an elephant. Birds and insects, as we shall see later, do much better.

Bats are particularly interesting animals acoustically because of their use of ultrasonic signals (around 60 to 80 kHz) for echo-location. Their vocal anatomy is similar to that of other animals except that their nasal tract often contains several cavities that appear to be matched so as to emphasise the preferred frequency. Bat calls usually consist of upward-sweeping syllables which are presumably reconstructed into sharp pulses by their auditory analysis system. This technique is reminiscent of the "chirping-dechirping" technique often used for radar signals and allows the emitted call to have high acoustic energy without requiring high peak power.

VOCALISATION IN BIRDS

The vocalisation mechanism in birds differs from that in mammals only in detail. The vocal valve, or syrinx, is duplicated in song birds and the two valves are at the upper ends of the bronchi, as shown in Fig. 2(b), rather than in the base of the trachea just above the junction of the bronchi as in mammals. Birds can thus divide the vocal effort between the two syrinx valves, using one for high and the other for low notes, or can even sing two notes at once. The valves themselves differ in structure from the larynx in mammals, and generally involve inflatable sacs that can be made to close off the airway and thus respond to pressure variations in an oscillatory manner.

The upper vocal tract is less flexible in birds than in mammals, since the beak is less adjustable than the lips and the tongue is generally narrow. Despite this, the song of birds such as ravens bears a close resemblance to human song, with adjustable formants at frequencies well above that of the fundamental (Fletcher 1988, 1992, Fletcher and Tarnopolsky 1999). This explains why parrots and cockatoos can imitate human speech, since they can reproduce the upper formants that encode the vowels, while the missing first formant below about 1 kHz simply makes the speech sound "artificial".

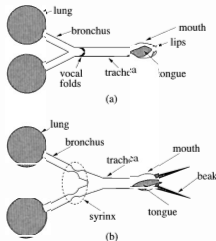


Figure 2. Anatomy of the vocal system of (a) a mammal and (b) a songbird.

Some birds can tune their vocal systems to produce nearly pure-tone songs, particular examples being the Ring Dove, which employs an inflatable sac in the vocal tract, keeping its beak closed and relying upon direct sound radiation from the vibrating sac walls to produce its 'coo' sound (Fletcher et al. 2004). Analysis shows that the resonance frequency varies by only a small amount for a moderate change in the sac inflation, since the increased compliance of the enclosed air is largely balanced by the increase in wall area.

The Northern Cardinal produces a similar effect, but with a widely adjustable frequency range, by singing with its beak slightly open and relying upon a Helmholtz resonance in an adjustable vocal cavity to tune the formants. One of the

most spectacular birdcalls is, however, that of the Australian sulphur-crested cockatoo, which produces an immensely loud shriek that can be shown by analysis to be actually a chaotic oscillation of its syrinx valve (Fletcher 2000).

Although they are not closely related, animals such as frogs use a resonant vocalisation technique that is very similar to that employed by doves. It is easily seen that most frogs inflate a large thin-walled sac below their mouth when producing sound. The sac remains inflated during the call and the mouth is closed, so that sound radiation occurs through the agency of the vibrating sac walls and the resonance frequency is not very sensitive to sac inflation.

SOUND PRODUCTION BY INSECTS

When we turn to consider sound production by insects, the situation is very different, for they must rely upon resonant structures vibrating in the air. Indeed this method, but with surrounding water rather than air, is also used by crustaceans. Two significantly different methods are used, as we now discuss.

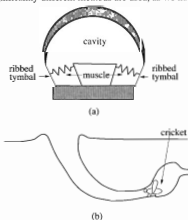


Figure 3. (a) Sound production system of a cicada. (b) Geometry of the horn excavated in the ground by a cricket.

In the first, which is characteristic of cicadas, anatomy provides a large body cavity, in the walls of which are two rather stiff deformable ribbed plates (tymbana) that can be made to vibrate by muscular action, as shown in Fig. 3(a). As the driving muscles contract, these plates deform progressively in an step-wise manner as each rib flips from one stable position to another, thus providing an acoustic displacement current with a frequency equal to the rate of individual rib collapse. Since there may be ten ribs, this mechanism multiplies the excitation frequency provided by muscle oscillation by a factor ten in this case. The body cavity volume has been tuned by evolution so that the resonance frequency of the two tymbana, backed by the cavity, is equal to the rib collapse frequency, so that there is a large resonant amplification of the excitation. Because the two tymbana move in phase, and their vibrations are closely coupled by the resonance, they act in combination as a monopole source and give highly efficient sound radiation (Fletcher and Hill 1978).

The radiated sound from a cicada thus consists of a string of consecutive identical "syllables", each one corresponding to a single

buckling motion of the tymbals and containing within it a train of oscillations at the cavity resonance frequency. The information content can be varied by changing the number of syllables in a "word" or, more usually, by varying the syllable repetition rate.

Insects as a rule devote much more of their available muscular power to sound production than do mammals. Thus a continuously singing cicada weighing less than 1 g may produce as much as 1 mW of sound energy (80 dB at 1 m), which is comparable with that produced by a human opera singer weighing some 10^3 times as much!

The second class of insects we should consider consists of those such as crickets that produce sound by drawing a toothed file of some sort across a part of their anatomy, generally a wing or wing cover, thus causing it to vibrate. As the contact is lifted and released by each tooth of the file it generates a damped vibration at the resonance frequency of the wing panel, giving a series of these vibrations for each leg stroke. This is intrinsically a much less efficient sound production mechanism than that used by the cicada, since the vibrating source is a dipole, and generally serves for short-distance communication within a fairly large population.

To overcome this inherent dipole disadvantage, a few insects such as the cricket have developed the ingenious strategy of digging a horn-like burrow with a cavity at the buried end, arranging for this structure to be resonant at their song frequency, and positioning themselves at the junction between the horn throat and the cavity so that the dipolar flow created by their vibrating wing covers drives the whole oscillation effectively (Daws et al. 1996). This arrangement is shown in Fig. 3(b).

AUDITORY AND VIBRATION SENSORS

It is a notable feature of auditory systems that most of them rely upon sensory cells with thin hairs protruding from one end (Fletcher 1978). Deflection of the hairs by fluid displacement induced by the acoustic signal opens ion channels in the cells which, in turn, leads to an electrical signal in the attached nerve channel. In the case of some insects such as caterpillars, these sensory hairs are used directly to detect close-range signals from the beating wings of predatory wasps. In the case of aquatic creatures, the hairs may be loaded with small massive otoliths so that when the bulk of the body of the fish is displaced by an acoustic signal, the inertia of the otolith deflects the sensory hair. Some fish, however, have an air-filled "swim bladder" that has the same effect, though differing in phase by 180° .

In land-dwelling animals, including humans, these sensory hair cells have often been incorporated into assemblies with some sort of frequency dispersion mechanism, generally through waves propagating on a tapered membrane, in the organ known as the cochlea, as will be discussed later.

Sensing of vibration is also important for most animals – even humans can detect quite small vibrations through their fingertips and larger low-frequency vibrations through the legs. For some insects, however, the sensing of vibration is more important than the sensing of air-borne sound. Two obvious examples are the spider in its web, and the related water-skimmer that detects surface ripples generated by insect prey caught by surface tension. Some insects have specialised detectors just below their knee-joints (and therefore called "sub-genual organs") to detect these vibrations.

DIRECTIONAL HEARING IN INSECTS

It is usually important for an animal to be able to detect the direction from which an auditory signal arises, and for this reason nearly all animals have two symmetrically paired auditory organs. In the case of mammals, as for example humans, the two ears are very nearly separate from an acoustic point of view and comparison of the signals received by each is a task for the neural system. Each ear does, however, have a certain amount of directional sensitivity. In reptiles, birds, and insects there is actually a direct acoustic coupling between the two ears.

As with the sound production mechanism, the simplest auditory systems rely upon a diaphragm backed by a cavity and connected mechanically to some sort of neural transducer. Such a system can be tuned to produce a resonance, and thus maximum auditory sensitivity, at the conspecific call frequency of the animal concerned.

Two such tympana opening into the same volume are able to create a system with high directional sensitivity. This is despite the fact that the whole process relies upon the phase difference between the sound signals at the two ears, which is typically only about 30° (Fletcher 1992, chap 9). The auditory anatomy of a female cicada, shown in Fig. 4(a), thus looks like a smaller version of the male sound production system shown in Fig. 3(a), the males being the sound producers and the females the listeners. The auditory response of such a system for ipsilateral (I) and contralateral (C) sound incidence is shown in Fig. 4(b) for a particular set of parameter values. While there is no pronounced resonance for the ipsilateral ear, there is a marked decrease in response for the contralateral ear at the tuned frequency. The directional response at this frequency has a cardioid form with a directivity of more than 20 dB, as shown in Fig. 4(c).

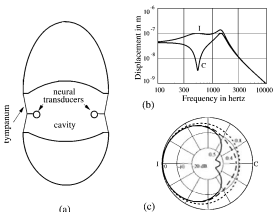


Figure 4. (a) Sketch of the auditory anatomy of a female cicada. (b) Calculated frequency response of the ipsilateral (I) and contralateral (C) ears for a particular set of parameter values. (c) Polar plot of the directional response for the two ears for several frequencies, shown as a parameter.

Some insects, however, have much more complex auditory systems. An example is the cricket, which has auditory tympana located one on each foreleg near the knee joint. Each tympanum is backed by a small cavity which is connected by a rather long flaring tube to an exit port (spiracle) on the thorax that serves to allow the ingress of air to maintain the life of the insect. The two tubes leading from tympana to spiracles are connected by a thin membrane or septum within the thorax, as shown in Fig. 5 (Fletcher and Thwaites 1979b, Fletcher 1992 chap. 11).

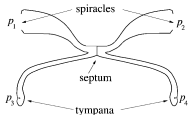


Figure 5. Schematic drawing of the anatomy of the cricket auditory system. The topology should be compared with that of the human auditory system

HEARING IN REPTILES AND BIRDS

The auditory sensitivity of birds is comparable with that of humans and generally extends over a similar frequency range, though biased towards higher frequencies as one would expect from the plot in Fig. 1. The same is true of small mammals such as mice.

Surprisingly, the auditory system of the frog (which eats cicadas if it can!) is very similar, with two simple ears opening into the mouth cavity. The presence of two small vents for the nostrils shifts the auditory sensitivity pattern somewhat away from the direct transverse direction. Since the mouth cavity is also employed to produce vocalisations, there must clearly be a mechanism for decoupling the neural transducers of the ears during song production.

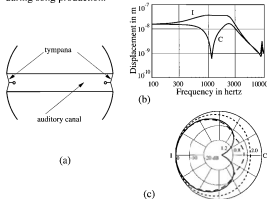


Figure 6. (a) Sketch of the geometry of the auditory system of a bird or lizard. The two tympana are connected by a simple tube. (b) Response of the ipsilateral (I) and contralateral (C) ears as a function of frequency for a particular set of parameter values. (c) Polar plot of directional response at various frequencies for this same set of parameter values.

Lizards and birds also possess auditory systems with acoustic coupling between the two ears. Instead of a simple cavity, however, they generally have a nearly straight canal to perform the connection, as shown in Fig. 6(a). With a typical canal length of say 20 mm, and appropriate values of the other parameters, such a system can give a cardioi response pattern for each ear with best separation at a frequency of around 1000 Hz, and a directionality of as much as 30 dB as shown in Fig. 6(b) and (c) (Fletcher 1992, chap. 11).

HEARING IN MAMMALS

Referring back to insect hearing, one of the interesting features of Fig. 5 is the topological similarity between this insect auditory system and that of mammals such as humans. To see this, compare the drawing with that of a human auditory system if we were to drag our ears, and the Eustachean tubes connecting them to the nasal passages, down to our elbows! Whatever the evolutionary significance of this observation, the two systems are acoustically very different, since the human Eustachean tubes are so narrow that very little acoustic energy can flow along them, while in the cricket system the acoustic connectivity contributes significantly to the overall behaviour.

The auditory systems of mammals generally possess an "outer ear" consisting of an obliquely truncated horn, the "pinna", leading to the tympanum through an auditory canal. Even a simple conical horn has directional properties, with the direction of maximum signal response corresponding to the symmetry axis. At very low frequencies the response is not notably directional, but becomes increasingly so at higher frequencies where the sound wavelength is comparable with the diameter of the open end of the horn.

Most pinnae, however, do not have this simple shape. The most obvious variation is that the horn is obliquely truncated so that the open end faces more nearly along the line of sight, and maximum sensitivity is achieved close to this direction (Fletcher and Thwaites 1988). Many animals, such as kangaroos but not humans, are able to rotate their pinnae to maximise high frequency sound and thus locate the direction of the source, even using just one ear. In humans the shape of the pinnae is rather convoluted and this leads to additional response peaks at particular transverse resonance frequencies that may assist in directional location.

Because of the much larger size of mammal heads in relation to the significant frequencies being detected, there are clear "shadowing" effects of the head, leading to reduction of the signal at the contralateral ear. This effect, together with pinna directionality and signal phase differences provides sufficient information for the mammal to detect the general direction of a sound signal. Timing differences are probably of equal importance if the signal has sharp amplitude variations, as with a sequence of clicks.

Since the encoding of information in the complex vocal signals used by mammals depends greatly upon variation in the frequencies of vocal formants, their hearing systems have evolved to be able to discriminate frequency variations to high precision. The major frequency-dispersive element is the basal membrane in the fluid-filled cochlea. Deflection of this membrane is achieved by injecting the signal to a membrane-covered port (the "oval

window") situated on one side of the membrane and providing a pressure-relief port (the "round window") on the other side. The basilar membrane is tapered, as also are the fluid filled channels on each side of it, and this gradation tunes the local membrane resonance to progressively lower frequencies as distance from the oval window increases. The result is a wave that propagates with small amplitude through the high frequency resonances near the input, reaches a maximum displacement in the resonant section, and is then exponentially attenuated over the remainder of the membrane length. Hair cells situated along the membrane detect the local oscillations and thereby communicate a spectrally resolved signal to the auditory nerve.

This mechanism, proposed some fifty years ago by Georg von Békésy, explains the general behaviour of the ear but provides a frequency discrimination that is much less than is found in experiment. It is known, however, that in addition to the single row of "inner hair cells" that provide the signal to the auditory nerve, there are three parallel rows of outer hair cells, and it has been proposed that these constitute in some way a "second filter" to sharpen the tuning provided by the basilar membrane itself. One such mechanism, proposed by Bell and Fletcher (2004), involves generation of a particular form of transversely propagating waves on the membrane that are able to produce standing-wave resonances between the outer hair cell rows, with sharply tuned leakage propagation to the inner hair cells. Since the effective mass of the inner hair cells is much less than that of the basilar membrane and associated liquid, the quality factor Q -values of the two mechanisms are effectively multiplied together to produce the observed very sharp tuning.

CONCLUSION

This has been a short and selective treatment of a very wide subject that has interested researchers for more than a century. My purpose has been to show that, by applying the straightforward principles of acoustics to admittedly idealised versions of the sound production and hearing systems of a wide variety of animals it is possible to achieve a reasonably detailed understanding of at least those stages of the vocalisation and hearing systems that are closest to the environment. Of course this leaves a great deal to be dealt with in other ways: the electrophysiology of neural transduction, the encoding and decoding of information in the brain, and the active control of vocalisation and hearing systems through some of the muscles involved. These subjects all lie more clearly within the realms of biophysics and psychophysics and have attracted the attention of many researchers within those fields. I am sorry that I do not know enough of these achievements to be able to present an adequately clear and detailed summary, but must leave this to someone else.

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