

ACOUSTICAL BACKGROUND TO THE MANY VARIETIES OF BIRDSONG

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Birdsong can be broadly classified into two categories: biphonic in which two different notes can be sung simultaneously, and monophonic in which only one note is sung. Monophonic song can be further divided into rich harmonic song, single-frequency song, and chaotic song. While some of these distinctions arise from clear anatomical features of the bird, others are more subtle and pose problems for physical scientists working in collaboration with biologists. This paper provides information on the physics and acoustics underlying these differences and shows how quantitative predictions can be made.

INTRODUCTION

Birdsong is a biological phenomenon of general interest because of its variety and auditory attractiveness, a classic survey having been given in a book by Greenewalt [1] and a collection of articles edited by Kroodsma and Miller [2] and a more recent survey by Marler and Slabbekoorn [3]. In biology 'birdsongs' can be produced only by 'songbirds' which are defined to be birds with five syringeal muscles, other birds producing 'calls', or more generically 'vocalisations'. In this paper I will not be greatly concerned with this subtle distinction – I hope it will not annoy the biologists!

Some birds produce songs with individual notes or 'syllables' that are almost pure tone in some species but rich in harmonics in others, with the spectrum shaped into emphasised formant bands like the vowels of human speech. The calls of some birds such as cockatoos, however, have a truly chaotic waveform rather than simply a broad spectrum [4]. Finally, those species known as 'songbirds' are actually able to sing two different notes at the same time, a skill for which there is a simple anatomical explanation as is discussed later.

Birdsong is a field of study in which there can be great advantages in collaboration between biological and physical scientists, because both the physiology and the acoustics involved are quite complex. My own involvement in such collaborations has provided the stimulus for a detailed analysis from an acoustic viewpoint [5] which provides a quantitative model for sound production in various anatomical cases. More recent collaborations have examined various special cases, some of which will be discussed here.

BASIC SOUND PRODUCTION PHYSIOLOGY

The basic mechanism for sound production is essentially the same in all air-breathing animals – perhaps omitting those that live under water. Air stored in the lungs at an overpressure of order 1 kPa (10 cm water-gauge) is exhaled through the vocal tract which consists of two tubes, the 'bronchi', leading through a single exit tube, the 'trachea', to the mouth. The vocal tract in mammals contains an adjustable and flexible constriction, the larynx, near the top of the trachea that can be maintained in vibration by the combination of aerodynamic and elastic forces acting upon it. In some birds the anatomy is similar, but in song-birds there is one

such valve in each of the bronchial tubes rather than a single one in the trachea, as shown in Fig. 1(a).

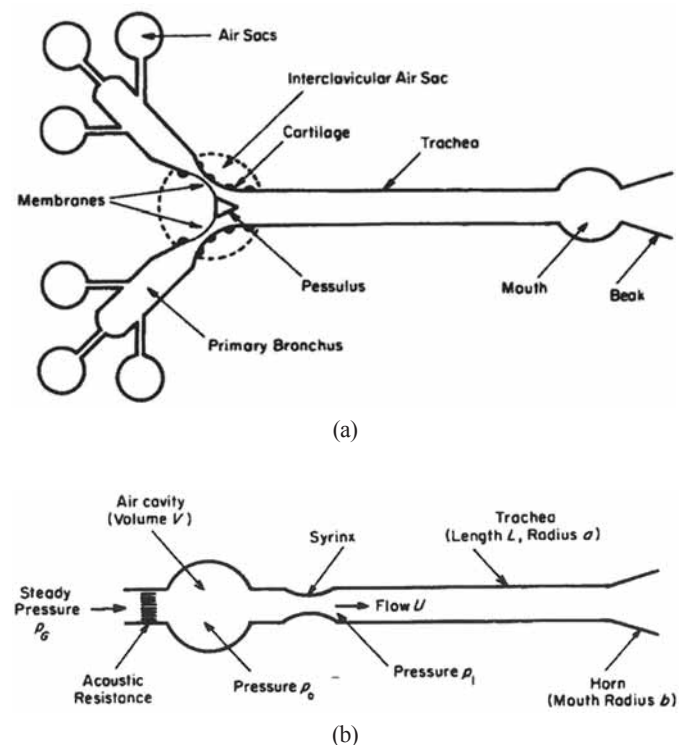


Figure 1. (a) Vocal anatomy of a songbird, showing the two valves of the syrinx. (b) A simplified single-valve model used for calculation of the behaviour. (From ref. [5]) The symbols show the quantities used in the model analysis.

In the case of humans and other mammals, this valve is known as the larynx and contains two opposed flaps termed 'vocal folds' which are constricted by tension in two 'vocal cords'. The fundamental vibration frequency is determined by the mass and tension of the vocal folds and is about proportional to the mass of the animal to the power -0.4 , a slight variation on simple inverse scaling with length [6]. This general rule applies to birds as well as to other animals up to the size of elephants. In the case of birds, the vocal organ is called the 'syrinx', and two different

anatomies exist, as mentioned above. This division of bird species explains why songbirds can sing two notes at once, since the two bronchial valves of the syrinx are largely independent. Operation of the songbird vocal system is essentially the same as that of other birds except for two things. Firstly, the distance from the syringeal valve to the open beak is much larger than is the case for a similar bird with the syringeal valve in the trachea. This means that the vocal tract resonances are lower in frequency for a songbird than they are for an ordinary bird of the same general size, a feature that will change the tonal properties of the sound in a way that has not yet been explored in detail. Because birds are generally small anyway, giving resonances of rather high frequency, this may give a more ‘mellow’ tone to the songbird song. Secondly, there is the possibility of acoustic interaction between the two valves through the air column. Again this has not been explored in detail, and some songbirds avoid the possible problem by singing high-pitched notes from one bronchus and low-pitched notes from the other with little temporal overlap between them.

OPERATION OF THE SYRINGEAL VALVE

A good understanding of the basic acoustics of bird song can be reached by studying the behaviour of a single syringeal valve linked to an upstream air reservoir and a downstream cylinder representing the trachea [5]. The subtleties of the influence of the tongue and beak opening upon the tracheal resonances can also be explored [7] but this is a refinement of the basic model. Examination of such valve models for the human voice has a long history, an excellent summary being given in a book by Sundberg [8]. A ‘source/filter’ approach in which the vibration of the vocal folds provides an independent source and the resonances of the vocal tract a filter appears to be adequate to explain most aspects and certainly simplifies the analysis. The first resonance of the human vocal tract is at about 500 Hz, with higher resonances near 1500 and 2500 Hz, all these frequencies being widely adjustable by changes in the mouth opening and tongue position. The fundamental voiced frequency is usually well below this so the resonances produce bands of emphasised frequencies known as formants. A particularly interesting case is that of ‘coloratura’ sopranos who can sing notes with fundamental frequency as high as 2 kHz. To achieve this, the singer changes tongue and lip configurations so that one of the vocal tract resonances matches the frequency of the note being sung, thus reinforcing it [9]. We will see later that something similar happens in the songs of some bird species.

Treating the syringeal valve as a simple isolated mechanism, it is still necessary to take account of the influence of small pressure oscillations in the upstream reservoir, since the pressure there is influenced by the flow through the valve. The valve can then be maintained in oscillation by the influence of up-stream and downstream pressure variations and their effects both through simple pressure exposure to the upstream portion of the valve and also by Bernoulli flow through the valve aperture. The general features of such behaviour are well understood [10] and apply to human vocalisation and to lip motion in the playing of trumpets as well as to birds. A detailed model [5] for the song of birds with rich-harmonic vocalisations, as sketched in Fig. 1(b), predicts results, as shown in Fig. 2, that are in good agreement with observation. For the parameter values selected, the syringeal valve is found to close completely on each cycle at a frequency of about 200 Hz and

there are emphasised formant bands near 1 kHz and 2 kHz, which correspond to resonances of the vocal tract [7]. These formants are important to sound quality but are not essential for the production of sound. The radiated sound will retain these formant features, but its waveform will be much more ‘continuous’ in structure than are the pressure and flow in the figure. Each of the two syringeal valves in the song-bird anatomy of Fig. 1(a) will function in a very similar manner.

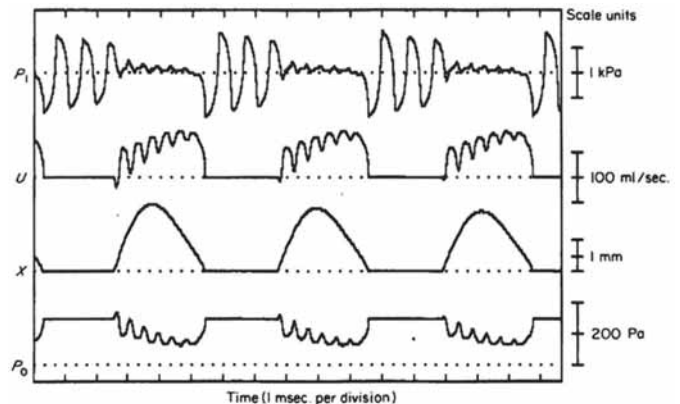


Figure 2. Calculated acoustic behaviour of a syringeal valve as in Fig. 1(b). Variable p_1 is the acoustic pressure in the trachea above the valve, U is the acoustic flow through the valve, x is the valve opening, and p_0 is the pressure in the reservoir below the valve. (From ref. [5])

PURE-TONE SONG

One puzzling feature of the model proposed for the production of normal bird song is the fact that it fails to provide an explanation for the almost pure-tone songs produced by some birds. The only way in which this can be achieved with the model is to use a very low blowing pressure so that the valve fails to close on each cycle, but this results in an extremely low sound level, which is not what is observed in practice.

Two alternative mechanisms for pure-tone song production have been identified. In the first case [11], which applies to birds such as the Northern Cardinal *Cardinalis cardinalis* which are able to produce sweeping whistle-like sounds over a 1–8 kHz frequency range in a single ‘syllable’ of song, the mechanism relies upon a tuneable resonant cavity near the junction of the trachea and the mouth as shown in Fig. 3(a). The cavity itself is actually in the oesophagus, which leads to the stomach, and is referred to as an ‘oropharyngeal esophageal cavity’ or OEC. This cavity can be stretched over a wide volume range by attached muscles. The bird then essentially tunes this vocal tract resonance to match the frequency of the note being sung, in much the same way as do human coloratura sopranos and with the same result, though with different anatomical features. A model for this vocalisation using the electric network analog shown in Fig. 3(b) is able to produce good agreement with observations [12].

The second mechanism, which applies to the ‘coo’ sound of doves, is quite different, since doves, particularly Ring doves, sing with their beaks closed. The ‘coo’ itself is a rather short syllable, lasting not much more than one second, and typically has a frequency around 600 Hz that remains almost steady. Observations show that the dove expands a sac in its

neck when producing the call, and this sac expands somewhat during the call since the bird is exhaling into it. Once again it is possible to devise a theoretical model [13] to accommodate this anatomy and behaviour, though this model is rather different from that for the Cardinal since the beak is closed and air is simply transferred from the lungs to the vocal sac, which is once more located in the oesophagus near its junction with the mouth. The resonance of prime importance in this case is almost that of a Helmholtz resonator comprising the sac and the tubular connection through the glottis between it and the trachea, though this has to be modified to allow for vibration of the thin walls of the sac. The great difference between the dove and the Cardinal is that the dove's beak is closed, so that sound radiation is not through the beak but directly from the vibrating thin walls of the inflated oesophageal sac. Surprisingly, perhaps, the resonant frequency changes very little as the sac expands, because the decrease in the mass per unit area of the walls nearly compensates for the increase in sac volume. The song therefore maintains a nearly constant pitch.

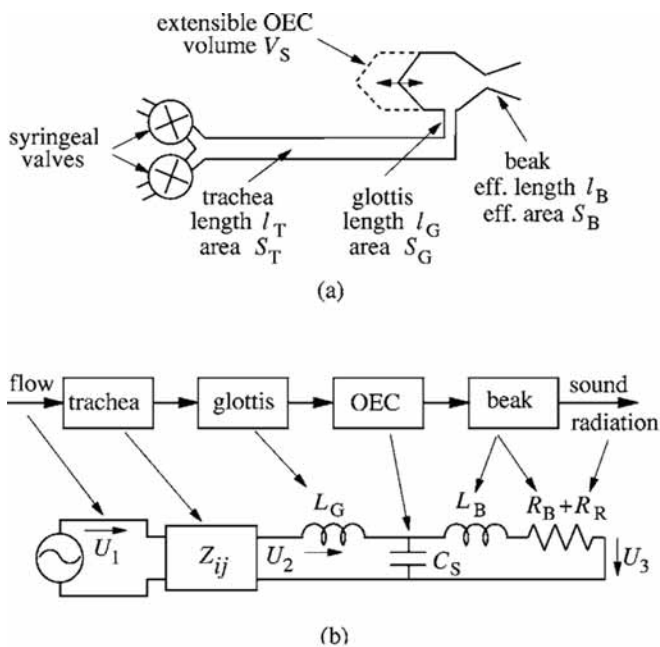


Figure 3. (a) Anatomy of the vocal tract of a pure-tone songbird such as the Cardinal. (b) Simple electrical network model used to analyse the vocal tract behaviour. The bird adjusts the resonance of the OEC and beak aperture to match the frequency of the air flow produced by the syringeal valves. (From ref. [12])

CHAOTIC VOCALISATION

The third type of song of interest can be termed chaotic song, because the waveform is genuinely chaotic rather than being just random noise [4] and typically has a Lyapunov exponent of 0.28 ± 0.06 and a correlation dimension in the range 3.2 to 3.8, values that are comparable with those for standard computed chaotic signals. Australian birds with this type of song are mostly cockatoos, the most prominent being the sulphur-crested cockatoo *Cacatua galerita*, which is also known for its beautiful appearance and its destructive behaviour when a group flies into a tree and pulls off any

flowers and new shoots, or even when they attack the rubber gaskets in street lights. The cry of these cockatoos is also very loud – about 80 dB at a distance of 10 metres, which corresponds to a radiated power of about 100 mW. The spectral distribution of the sound is broad, with a maximum near 2.5 kHz and a 10 dB bandwidth from 1 to about 3.5 kHz, so that it sounds very loud and ‘harsh’ to human ears. An example of the waveform and spectrum is shown in Fig. 4.

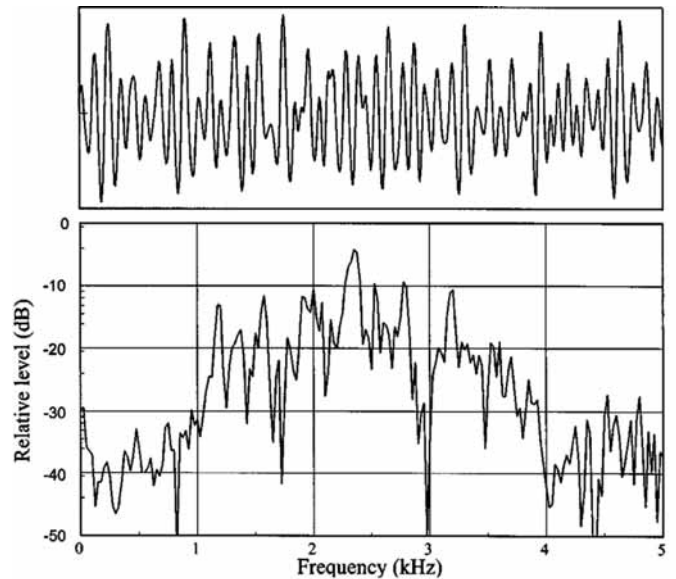


Figure 4. Waveform and spectrum of a short sample of the call of a sulphur-crested cockatoo *Cacatua galerita*. Plots for the gang-gang cockatoo are very similar. (From ref. [4])

Modelling of the production of such a sound is difficult because of lack of information about the detailed anatomy of the vocal valve in these birds. The standard model described above, however, in which the restoring force on the valve membranes under pressure is proportional to its deflection but there is a large increase in both restoring force and damping when the two membranes come into contact, does show some chaotic behaviour when the lung pressure is made very high so that the nonlinearity is emphasised [4]. This suggests that an extended model in which a nonlinear term is added to the membrane restoring force might adequately reproduce the observed chaotic behaviour at lower lung pressures. It is easy to suggest the origin of such a nonlinear term because biological structures are rarely linear in behaviour once the stretching or bending becomes nontrivial. This is because the structures are complex assemblies of cells with quite different elastic properties. To date no anatomical data on this question has been available.

SONG STRUCTURE AND MIMICRY

Setting aside the detailed acoustics of sound production in birds, there is a wealth of information encoded in the songs that has provoked great interest among behavioural biologists. While the information content of vocalisations can be formally defined and measured [14], there is much more interest in the structure of the ‘conversation’ of birds, conveying information to each other, and

in the way in which some species are adept at imitating the calls of birds or animals of other species, or even the sounds of non-biological sources such as chainsaws.

Various species of parrots and cockatoos have been known for a very long time to be able to imitate human speech by tuning the formants and articulation patterns to match human phrases such as "Pretty Polly". This is perhaps not surprising from an acoustical point of view, since the vocal formants, except perhaps the first, can be appropriately tuned by varying tongue position and beak opening [7], and there are generally clear rewards provided by their human hosts for those birds that excel at this imitation.

Of particular interest is the vocal behaviour of several species of Australian birds, particularly the lyrebird *Menura novaehollandiae*, which is adept at imitating a huge variety of birdsongs from other species as well as mechanical and other sounds [15], the pied butcherbird [16] and the magpie [17]. A true understanding of the reasons for this mimicry behaviour involves physiology and psychology as well as acoustics [18] and is outside the scope of this review.

CONCLUSIONS

Birdsong is one of the most interesting and varied forms of vocalisation produced by any animals and almost rivals human speech and song in complexity. Even the acoustics of sound production by birds is complex and varied, as has been summarised here. Collaborative studies between many biological and physical scientists have now achieved a basic understanding of the subject, but there is an immense field of research available on the information content and 'cultural' background involved as well as on the vocal anatomy and physiology of individual bird species.

REFERENCES

I must apologise for the fact that the reference list given below is largely restricted to studies with which I have had a personal involvement. The biological literature on birdsong is very large and I cannot hope to refer to it adequately here. References 1-3 have extensive citation lists. I am grateful to one of the Referees for drawing my attention to several additional recent publications.

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