

Acoustics and physical models of bird sounds

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Abstract

For humans bird song is as natural phenomena as speech or human singing. However organization and generation of bird song is not so well-known as one for speech. In this paper we take short review to the basic structures of sounds birds can produce and also to principles of sound producing mechanism in birds. Birds have unique organ for sound production among all animals in the world. Both organ itself and also sounds it can produce have large diversity between different species. We also introduce how popular speech and audio modelling methods can be used to model sound production in birds.

1. INTRODUCTION

Birds and especially sound of birds are important for humans and to our culture. For many people sound of birds is the sign for starting of the spring. Bird-watching is also popular hobby in many countries. Birds can be heard even in big cities and there they are one of the few reminders of the surrounding nature. Also many composers, poets and writers have been inspired by the song of birds.

The primary sound source in birds is syrinx, which is a unique organ to birds (King 1989). Syrinx is located at the junction of the two primary bronchi and the trachea or entirely in the trachea or in the bronchi. Syrinx resembles human vocal cords in function, but it is very different in form. Also the vocal tract, whose main parts are trachea, larynx, mouth and beak, interacts to the sound of birds (Nowicki 1987). The anatomy of the syrinx and the avian vocal tract vary considerably among different orders of birds and sometimes even in different families within the same order.

Structure of bird song has large diversity. Typical song may contain components which are pure sinusoidal, harmonic, nonharmonic, broadband and noisy in structure (Nowicki 1997). Sound is often modulated in amplitude or frequency or even both together (coupled modulation) (Brackenbury 1989). Frequency range is relatively small, typically fundamental frequency lies between 3 and 5 kHz. A well-established way to divide song into four hierarchical levels is: elements or notes, syllables, phrases and song (Catchpole & Slater 1995). Elements can be regarded as elementary building units in bird song (Anderson, Dave & Margoliash 1996) whereas phrases and songs often contain individual and regional variation. Duration of one syllable ranges from few to few hundred milliseconds.

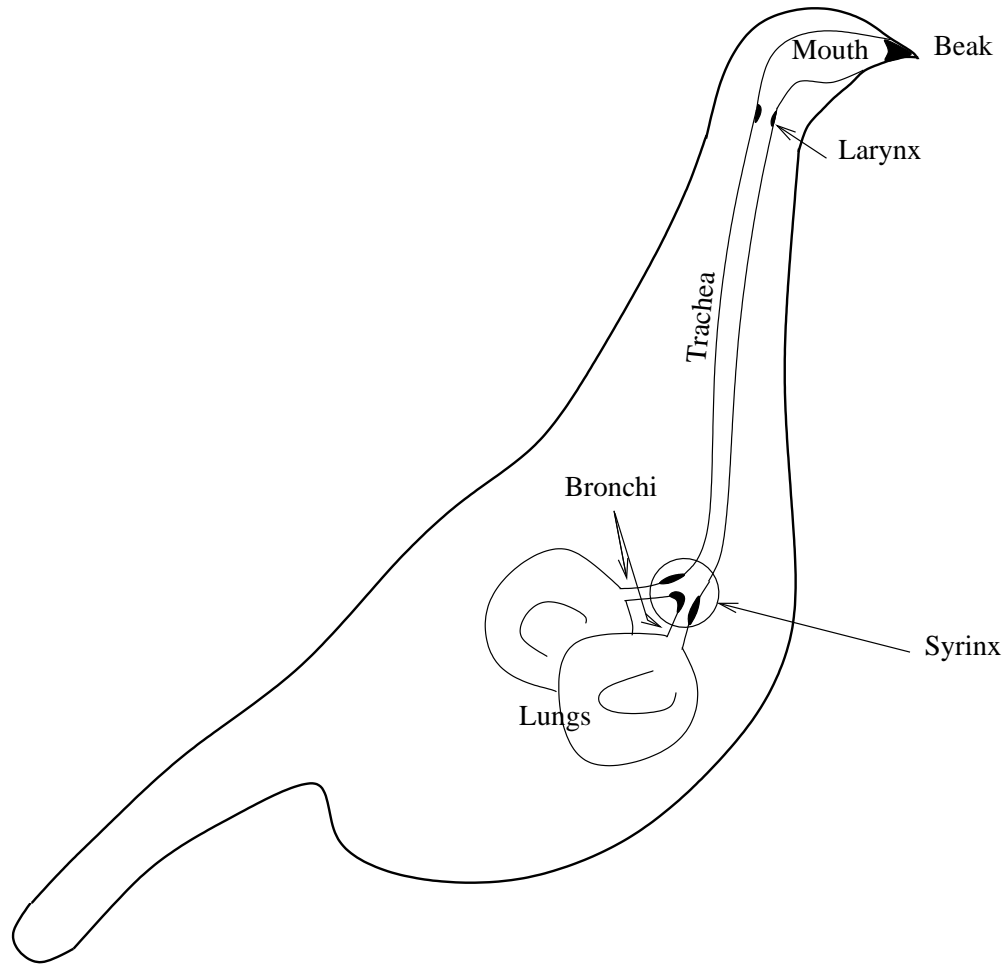


Figure 1: *Parts and organization of avian sound producing mechanism.*

The sound producing mechanism in birds resembles the one in humans. Excitation signal in birds is produced by syrinx and vocal tract can be seen as a resonator tube that modulates the signal from the syrinx. Elements of the bird song are acoustically distinct, like notes in music, and they constitute a characteristic sequence. Therefore it is natural to use methods used in speech and musical instrument modelling to model and synthesise the sound of the birds. Digital waveguides are a popular method to model many kinds of spatially distributed acoustical mechanisms and organs and it have also been used to model sound production in birds (Kahrs & Avanzini 2001) (Smyth & Smith 2002).

2. SOUND PRODUCTION MECHANISM

Main parts of sound production mechanism in birds are lungs, bronchi, syrinx, trachea, larynx, mouth and beak. Airflow from lungs travels through the bronchi to the syrinx, which is the main source of sound. Sound from syrinx is then modulated by vocal tract, which consist of the trachea, larynx, mouth and beak. In figure 1 is presented schematic view of the mechanism. Dimensions of mechanism and parts of it varies considerably among different species, but organization is rather uniform.

2.1. Syrinx

Syrinx (see Figure 2) is the most important and most extensively studied organ in the bird sound production mechanism. Besides that the organ is important in sound production, it has also provided valuable information to the taxonomy of birds because of distinction between anatomy of the organ in different species. The German anatomist Müller classified bird species by their syringeal anatomy already in 1878 (Müller 1878). Müller limited his studies to Passeriformes, but Beddard (Beddard 1898) took a wider range in his studies. Many later studies have confirmed the classification by Müller and Beddard.

Three different types of syrinx, namely tracheobronchial, tracheal and bronchial, can be found according to distinction between tracheal and bronchial elements of syrinx and topographical position of the main sound producing mechanism. When main sound production mechanism is located in the bronchi it can be in different position in the two bronchi. Tracheal elements are cartilage rings (see Figure 2), typically complete, in direct continuation with trachea. Bronchial elements are paired incomplete C-shaped cartilage rings with open ends against each other. Classification into these three classes is however difficult task because intermediate forms are common.

Songbirds (order Passeriform suborder Passeri) are the largest group of the birds, they cover about 4000 out of 9000 total number of bird species (Catchpole & Slater 1995). Songbirds and the syrinx of songbirds are most extensively studied among all birds. The syrinx of songbirds is complex in structure but relatively uniform in this group (King 1989) and it can be regarded as the prototype syrinx (Figure 2). The syrinx is located in the junction of the trachea and two bronchi and therefore it belongs to the group of tracheobronchial syrinx. When a bird is singing, airflow from lungs makes syringeal medial tympaniform membrane (MTM) in each bronchi to vibrate through the Bernoulli effect (Fletcher 1992). The membrane vibrates nonlinearly opposite to the cartilage wall. Voice and motion of the membrane is controlled by a symmetrical pair of muscles surrounding the syrinx. Membranes can vibrate independently to each other with different fundamental frequencies and modes. Membranes are pressure controlled like a reed in woodwind instruments, but membranes are blown open while the reed in the woodwind instruments is blown closed.

In contrast to the MTM theory recent studies with endoscopic imaging have shown that MTM would not be the main source of sound (Goller & Larsen 1997b). Goller suggests that sound is produced by two soft tissues, medial and lateral labia (ML and LL in Figure 2), similar to human vocal folds. Sound is produced by airflow passing through two vibrating tissues. Further evidence to this comes from a study where MTM's were surgically removed (Goller & Larsen 2002). After removal birds were able to phonate and sing almost normally. Small changes in song structure however were found, which indicates that MTM's have a function in sound production. However it is possible that birds may be able to compensate the loss of MTM.

Also, because of large diversity in structure of avian syrinx and also in sounds, it is possible that the MTM theory is correct for some species. For example Goller and Larsen limited their study only to cardinals (*Cardinalis cardinalis*) and zebra finches (*Taeniopygia guttata*). In contrast in (Gaunt, Gaunt & Casey 1982) ring doves (*Streptopelia risoria*) were studied as evidence for the MTM theory. Furthermore in (Goller & Larsen 1997a) it was found that the main source of sound in pigeons and doves is the tympaniform membrane. However this membrane is located in the trachea and not in the bronchi.

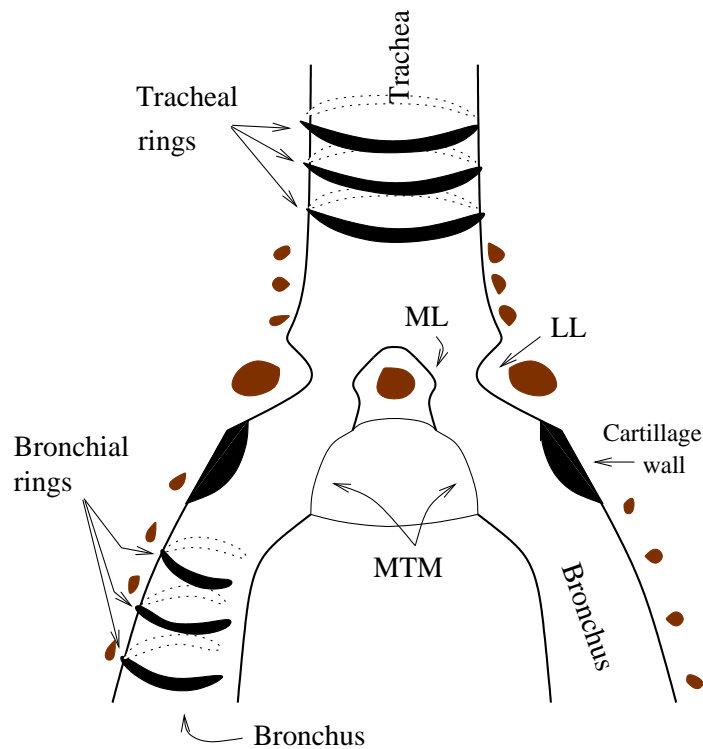


Figure 2: Schematic view of songbird syrinx. According to classical theory sound is produced by the vibrations of the medial tympaniform membrane (MTM) against the cartilage wall. Recent studies suggests that sound is produced in similar way than in the human vocal folds by the medial labia (ML) and the lateral labia (LL).

2.2. Trachea

The trachea in the birds is a tube between the syrinx and the larynx which acts as a resonator to the sound produced by the syrinx. Elements of the tube are cartilage rings, which are typically complete (McLelland 1989). The number of the tracheal cartilage rings depends on the length of the neck and it ranges from about 30 in small passerines to about 350 in long necked flamingos and cranes. However in the number of species the trachea is arranged in loops or coils so that the length of the trachea is much longer than the length of the neck. It have been argued that the tracheal loops improve transfer function so that the trachea can transfer many frequencies (Gaunt, Gaunt, Prange & Wasser 1987). In some species the trachea is joined with air sacs or bulbous expansions. In some penguins (*Spheniscidae*) and petrels (*Procellariidae*) the trachea is fragmented into two channels. These species specific features are responsible for some characteristic sounds in these species.

2.3. Larynx, mouth and beak

The larynx in the birds does not include vocal folds like in humans. Only few studies have related to the larynx in the birds and its function to sound production is controversial. The larynx seems to play only little or no role in sound production.

The mouth operates in birds as a cavity resonator like in humans. The mouth in birds is however less flexible. With the tongue birds can control the cross-sectional area of the mouth (Fletcher & Tarnopolsky 1999), but only few species can use the tongue for sound

production like humans (Patterson & Pepperberg 1994) because most of the birds have a rather stiff tongue.

Analysis of the acoustical behaviour of the beak is a difficult task because form of the beak is rather complex (Fletcher & Tarnopolsky 1999). The analysis can not be reduced into one or two dimensions without losing vital information. Another difficulty with beak acoustics is its highly dynamic nature. Beak opening and closing change acoustical properties of the beak by changing dimensions of the gape. Recent studies suggest even bigger role for the beak in sound production (Hoese, Podos, Boetticher & Nowicki 2000). Hoese et al. shows that beak opening and closing changes the effective length of the vocal tract, but effect to the vocal tract resonances is nonlinear. Birds can also change dimensions of the vocal tract by movements of the head (Westneat, Long, Hoese & Nowicki 1993).

3. ORGANIZATION OF BIRD SOUNDS

Bird sounds are typically divided into two categories: songs and calls (Krebs & Kroodsma 1980). Singing is limited to songbirds, but they cover only about half of the birds. Non-songbirds use also sounds to communicate and it is not less important than for songbirds (Beckers, Suthers & ten Cate 2003). Generally songbird sounds are more complex and they have a larger repertoire than non-songbirds, because the ability to control sound production is better (Gaunt 1983).

Diversity of different sounds birds can produce is large. Characteristics of simple voiced sounds are a fundamental frequency and its harmonics. Voiced sounds in birds are closely related to the human vowel sounds in both structure and in a way they are produced. However control of the vocal tract in birds is less complex than in humans. In voiced sounds in birds fundamental frequency lies between $100Hz$ and $1kHz$ in different species. Birds can emphasize intensities of different harmonics with filtering properties of the vocal tract. Birds can also produce pure tonal or whistled sounds that does not include any harmonics. In both voiced and whistled cases sounds can be modulated in both frequency and amplitude. Amplitude modulations of the fundamental element are mostly generated by the syrinx (Beckers et al. 2003) but intensity differences between harmonics is based on the properties of the vocal tract. Frequency modulation can be divided into two categories: continuous frequency modulations and abrupt frequency jumps. Both frequency modulations are source-generated (Beckers et al. 2003) (Fee, Shraiman, Pesaran & Mitra 1998). In addition to these bird sounds can be also noisy, broadband or chaotic in structure (Fletcher 2000). Characteristic of chaotic behaviour is unpredictability in future waveform even though source and filter conditions are rather well-known. In figure 3 is examples from songs and calls from different species and it illustrates diversity of sounds birds can produce.

3.1. Two-Voice Theory

With two independently vibrating membranes in the syrinx, birds can in theory produce two totally independent carrier waves. It have been suggested that this makes possible to sing “internal duet”. Different species use two sound sources in sound production in different manner. For example Canaries (*Serinus canarius*) use only one syringeal source to sound production whereas Black-capped chickadees (*Parus atricapillus*) produce complex call notes by using both sources (Nowicki 1997). Three different methods can be found: sound can be produced by either membrane alone, by both acting together or by

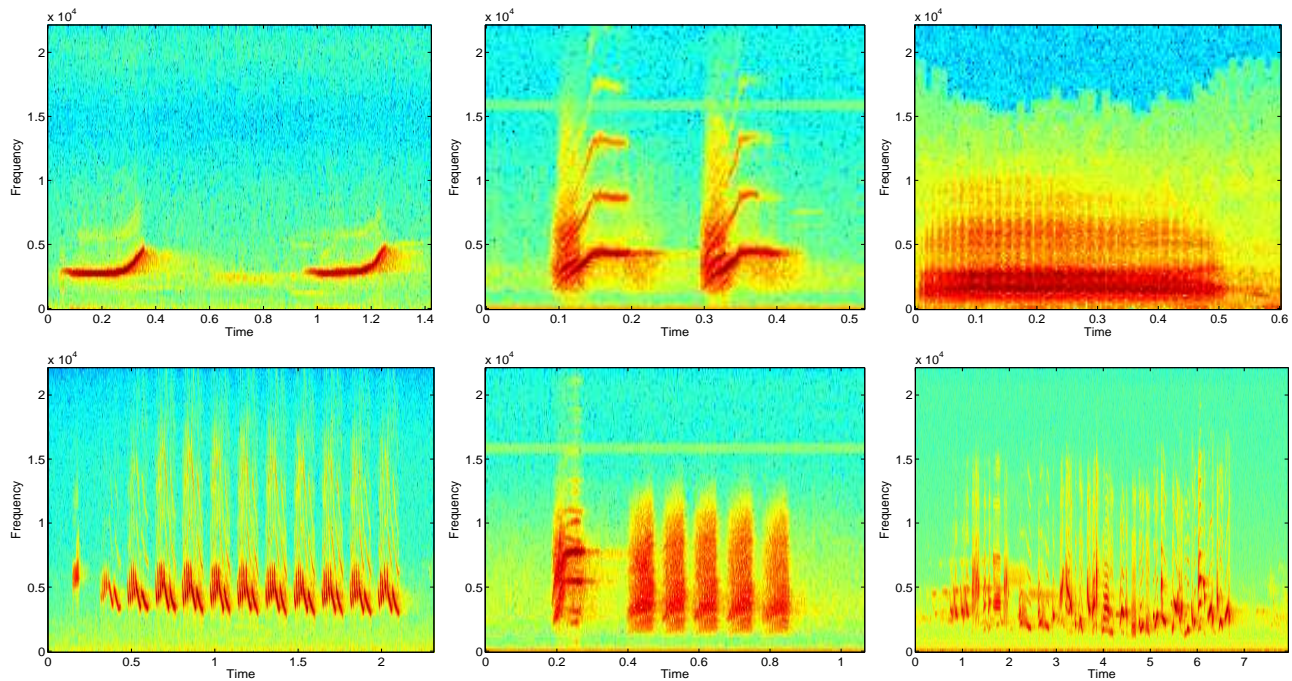


Figure 3: Examples of bird sounds from different species. In upper row from left to right Willow Warbler (*Phylloscopus trochilus*), Common Chaffinch (*Fringilla coelebs*) and Hooded Crow (*Corvus corone cornix*). In lower row Arctic Warbler (*Phylloscopus borealis*), Great Tit (*Parus major*) and Garden Warbler (*Sylvia borin*). The x and y-axis in panels represent time in seconds and frequency in Hz, respectively.

switching sound source from one membrane to other (Suthers 1990). When both membranes are active together they may generate same or different sound. It is also common for some species that they use all three methods in sound production. First syllable from call sound of great tit (*Parus major*) in the lower center panel in figure 3 represented in figure 4 is a example from sound whose generation two sound sources were used.

3.2. Bird Songs

Generally songs are long and complex vocalization produced spontaneously by males. In few species however also females sing and some species sing even duets. Female songs tend to be simpler than song produced by males. Most species sing at certain time of the year but birds have also a particular daily schedule when they sing. Best time for observing bird singing is in the breeding season at spring. Some birds do not sing at all during the rest of the year. Especially during the breeding season male bird song has two main functions. One is to attract females and the other one is to repel rival males. However in some species song used to attract females tends to be longer and more complex than song for territorial defence. Similar features and functions in female song can be found than in male song.

During the day birds have biggest activity in singing at dawn. Several explanations to this have been proposed. Feeding conditions are better after dawn and therefore birds have more time to sing at dawn. It is also best time to take over vacant territories. Female birds are most fertile at dawn and it is best time to copulate. For example it has been observed that great tit (*Parus major*) males sing at dawn until female wakes and then copulates with her (Mace 1987). One practical reason is also that conditions for sound transmission are

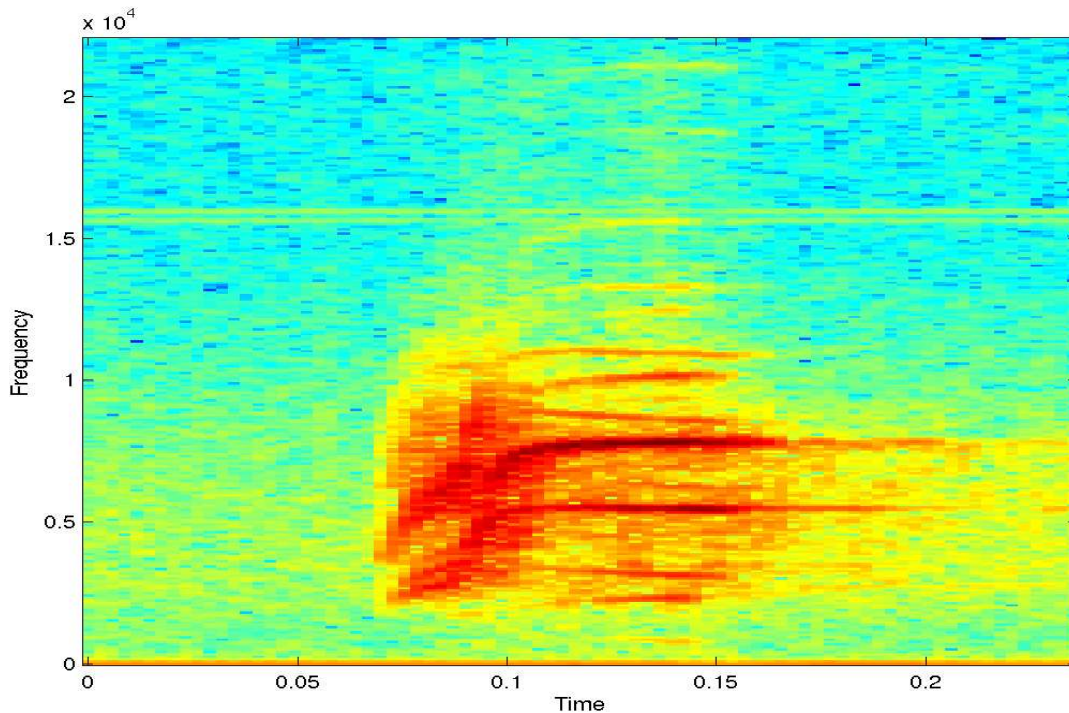


Figure 4: Call sound of Great Tit (*Parus major*). Some elements of the sound are not in harmonic ratio.

favourable at dawn, because wind and air turbulence are reduced.

Transmission conditions are important otherwise also and those set limitations to the structure of sound. Two fundamental phenomena that affect the transmission of sound are attenuation and degradation, which is a problem especially in the dense environments. Sound propagation properties are different in different environments and also at different heights in a specific environment. Bird sounds adapt to environmental conditions so that sound is transmitted to receiver optimally. Optimality condition depends on the function of the sound and it does not always mean maximal distance.

Hierarchical levels of bird song are phrases, syllables and elements or notes. Elementary building unit of bird song is called element, which is the smallest separable element in spectrogram (see Figure 5). Elements are building blocks of syllables, that may be produced by one or more elements or notes. The structure on syllables varies a lot and therefore also the number of elements in syllables. Series of syllables that occur together in a particular pattern is called a phrase. Syllables in a phrase are typically similar to each other, but they can also be different like in the last phrase (end phrase) in figure 5. A song is constructed of a series of phrases. When a bird changes the order or types of the phrases in the songs the bird is said to have different types of songs and a repertoire of song types. Repertoire size varies typically from few to several hundred song types in different species.

3.3. Bird Calls

Bird calls are usually short and simply, but they can also be complex and can sometimes be confused to the simple songs, especially when series of call sounds are connected. Calls typically occur in specific context and carry some function and they are produced by both

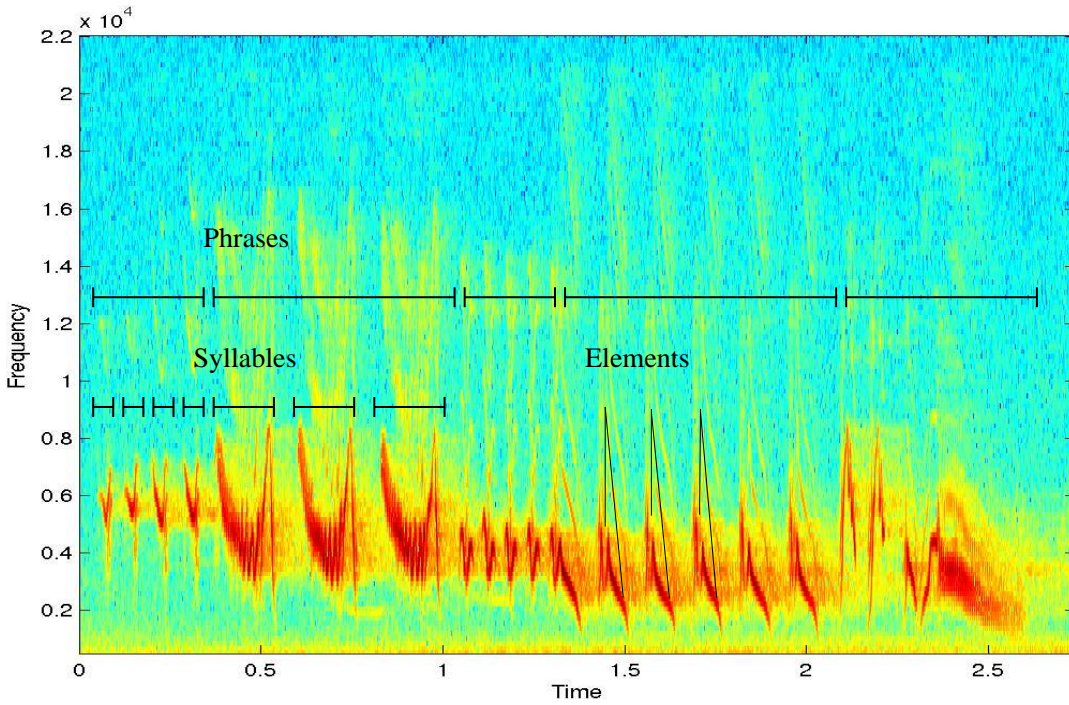


Figure 5: Hierarchical levels of common chaffinch (*Fringilla coelebs*) song. The y-axis represents frequency in Hz and x-axis time in seconds.

sexes through the whole year. Calls have a large functionality and at least 10 different call categories (e.g. alarm, flight and feeding call etc.) can be found. Furthermore some birds have more than one call for one category and some use very similar calls for different meaning. Call sounds are important for songbirds also and generally they have greater repertoire of call sounds than non-songbirds.

4. PHYSICAL MODELS

Sound production models in birds were first studied by Greenewalt (Greenewalt 1968), whose work has constituted the basis to the studies on the classical model of bird sounds. A similar source-filter model can be used to model avian sounds than is used in speech or wind instrument modeling. A difference to speech production is that birds may have two independent sound sources in the syrinx. Sound from the syringeal source is then filtered by the vocal tract. Two different models of avian sound production system are presented in figure 6.

4.1. Models of sound source

In the classical model of the syrinx tympaniform membrane is assumed to be the main source of oscillation. Vibration is driven by membrane's natural frequency and air column resonance in bronchi. Membrane motion against the cartilage wall changes the cross-section area of bronchi causing a nonlinear change in pressure and air flow. The pressure at tracheal side of the syrinx depends on pressure at the bronchial side of the syrinx p_0 , air density ρ , displacement of the membrane x , radius of the bronchus a and air flow through syrinx U and is given in (Fletcher 1988) as

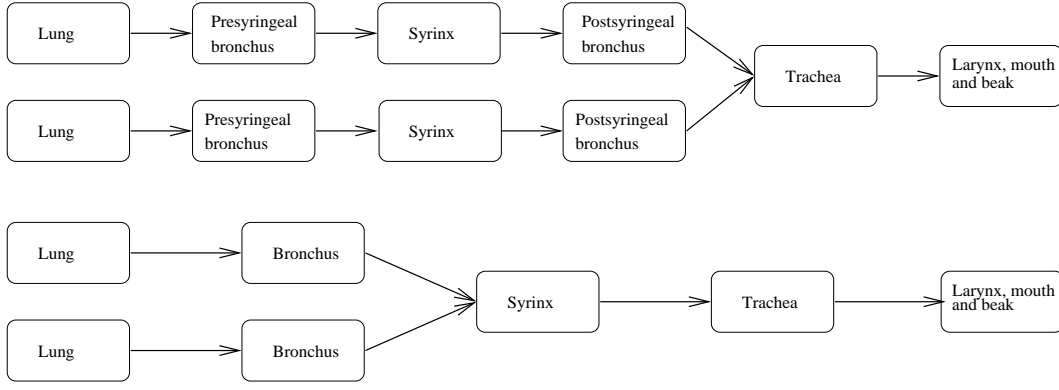


Figure 6: *Two models of avian vocal tract*

$$p_1 = p_0 + \frac{\rho}{2} \left[\left(\frac{U}{2ax} \right)^2 + \frac{1}{\sqrt{2ax}} \frac{dU}{dt} \right] \quad (1)$$

The airflow U from lungs varies in time as a bird is breathing. Membrane can be modeled as a simple taut membrane, whose displacement can be calculated as function of driving force F against the membrane as:

$$m \left[\frac{d^2x}{dt^2} + 2\kappa \frac{dx}{dt} + \omega^2(x - x_0) \right] = \epsilon F \quad (2)$$

where ω is the mode frequency, κ is the damping coefficient, m is the effective mass of the membrane associated to the mode and x_0 is position of the membrane at rest. Coefficient ϵ is small constant term, which is referred to the coupling between F and the mode. For the driving force in (2) Fletcher gives

$$F \approx 2Aah \left(\frac{p_0 + p_1}{2} - \frac{\rho U^2}{\sqrt{ax^3}} \right) \quad (3)$$

where A is constant term order of unity.

The model is successful with voiced sounds but incapable to produce whistled or tonal sounds. A one string model to model also tonal sounds was suggested in (Casey & Gaunt 1985). In this model the membranes in former model are stretched into the shape of a string. The string model is capable to produce sound with one fundamental and its harmonics. In (Doya & Sejnowski 1995) these two models were mixed so that the string model produces tonal harmonic sounds and a mixture of sound from both models produce noisy components.

As mentioned earlier, recent studies have suggested that the sound of birds is produced by the tissue folds similar to the human vocal folds (Larsen & Goller 1999). Also recent models of bird sound production have been build on models of the human vocal folds (Gardner, Gecchi & Magnasco 2001). Gardner's two-mass model is a simplification to geometrical dimensions of the folds. In the model it is assumed that the folds are controlled by bronchial pressure p_0 . Averaged pressure at tracheal side of the folds can be calculated as a function of bronchial pressure and position of the folds:

$$p_1 = p_0(1 - a/b) \quad (4)$$

where a and b are calculated in terms of phenomenological constant τ and position of the center of the folds x as:

$$a = a_0 + x + \tau \frac{dx}{dt} \quad (5)$$

$$b = b_0 + x - \tau \frac{dx}{dt} \quad (6)$$

Position of x can be calculated as given in (Laje, Gardner & Mindlin 2002):

$$\frac{d^2x}{dt^2} - (cx^2 - b) \frac{dx}{dt} - bx - F_0 = 0 \quad (7)$$

where k is the restitution constant, c is the dissipation constant, b is the driving pressure and F_0 is constant force term of the vibrating labia.

4.2. Models of vocal tract

Relatively little has been done on modeling of the bird vocal tract although its essential role in sound production has been discovered for example in (Nowicki 1987) and (Brittan-Powell, Dooling, Larsen & Heaton 1997). In (Fletcher & Tarnopolsky 1999) the acoustics of the vocal tract of Oscine birds has been studied. Although Fletcher studies limits only to song birds, models can be easily modified to correspond to many other birds. In model both syringeal sound sources are first connected to the bronchial tube that leads to the trachea. Both bronchi and trachea are modeled with an acoustical impedance matrix whose coefficients can be calculated by

$$Z_{11} = Z_{22} = -j \frac{\rho c}{S} \tan kl \quad (8)$$

$$Z_{12} = Z_{21} = -j \frac{\rho c}{S} \csc kl \quad (9)$$

where ρ is the air density, c is the speed of sound, S is the cross-sectional area of the tube, l is the length of the tube and $k = \omega/c + j\alpha$, $\omega = 2\pi f$ is the wavenumber. f is the frequency in Hertz and α is the attenuation coefficient for sound propagating in tube. The input impedance for the system that includes two bronchi and the trachea is given by

$$Z_{in} = B_{11} - \frac{B_{12}^2 (B'_{11} T_{22} + T_{11} T_{22} - T_{12}^2)}{B'_{11} (B_{22} T_{22} + T_{11} T_{22} - T_{12}^2) + B_{11} (T_{11} T_{22} - T_{12}^2)} \quad (10)$$

where B and B' refer to the two bronchi and T refers to the trachea.

Fletcher presents also a models for the larynx, mouth and beak. The larynx is modeled by a simple series impedance $L = j\omega\rho l/S$, where l is length and S is cross-sectional area of the larynx. The mouth can be modeled in a similar way that is used for models of the human mouth. Fletcher considers the mouth as a short tube, with varying cross-sectional area controlled by raising and lowering of the tongue.

For the beak Fletcher provides a simplified conical model. The main motivation in this model is that it can be solved analytically

$$K(f, g) = j \frac{\rho c}{S_B} \left[\frac{\csc^2(k\delta/2)}{\cot(k\delta/2) - k\delta/2} - \cot\left(\frac{k\delta}{2}\right) \right] \quad (11)$$

where $k = 2\pi f/c$ and S_B is cross-sectional area of peak base. δ is end correction based on measurements with a light sheet-metal beak model and it is given by terms of length of the peak l , frequency f and tip gape g as

$$\delta \approx 0.05l + 10^{-5}fl^2/g \quad (12)$$

Mixing all elements to a network Fletcher gives the final input impedance as

$$Z_{in} = T_{11} - \frac{T_{12}^2(M_{22} + K)}{(T_{22} + M_{11} + L)(M_{22} + K) - M_{12}^2} \quad (13)$$

where T , L , M and K refer to input impedances of the trachea, larynx, mouth and the beak, respectively.

5. SUMMARY

Primary sound source, namely syrinx, in birds is located in most of the species in the junction of the bronchi and the trachea. There exists two competing theories to sound producing mechanism in the syrinx. Classical theory profess that sound is produced by vibrations of the tympaniform membrane. According to later theory sound is mainly produced by two soft tissues similar to human vocal folds. Diversity in structure of the syrinx is large and it is possible that either theory holds for some species. The vocal tract consist of the trachea, larynx mouth and beak. The function of the vocal tract is as a transfer channel and a resonator tube to the open air.

Spectrum of different sounds birds can produce is large. Sounds fluctuate from pure tonal sounds to noisy sounds. Modulations in amplitude and frequency are common. Bird sounds can be divided into two groups, songs and calls, with different function. Songs are produced mainly by males in the breeding season and main functions of songs are to attract females and to compete with other males. Calls are produced by both sexes through the whole year. Calls occur always in some particular context with some function.

Models of bird sound producing mechanism are usually reproduced models from human or instrument models. Generally two models are used to model sound production in syrinx. In context of classical theory on sound production a membrane model is used. Recent studies models sound production in syrinx with two mass model. Main parts of the vocal tract excluding the beak are modeled as a tube resonator. For beak simplified analytical model have been used.

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