

Quantitative modelling of the biomechanics of the avian syrinx

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Abstract—We review current quantitative models of the biomechanics of bird sound production. A quantitative model of the vocal apparatus was proposed by Fletcher (1988). He represented the syrinx (i.e. the portions of the trachea and bronchi with labia and membranes) as a single membrane. This membrane acts as a valve that rapidly closes and opens during phonation. This model can be used as a basis to address comparative morphological and physiological questions. More recently, the syrinx was modelled as a simple modified oscillator. Many features of the sound were captured remarkably well. The parameter values, however, did not represent the distribution of the actual material properties of the syrinx. These models demonstrated the minimum number of parameters required to describe the essential dynamics of the sound signal. Furthermore, we address possible interesting future directions for modelling.

Keywords: Birdsong; communication; sound production; vocalisation.

INTRODUCTION

The beauty of the virtuoso singing of birds has inspired composers and scientists for centuries, but only during the last few decades has our understanding of the mechanisms and control of sound production advanced very rapidly. The avian sound source was identified 250 years ago (Hérissant, 1753) as a modification of the airway and was named the syrinx (Huxley, 1877; cited in King, 1968).

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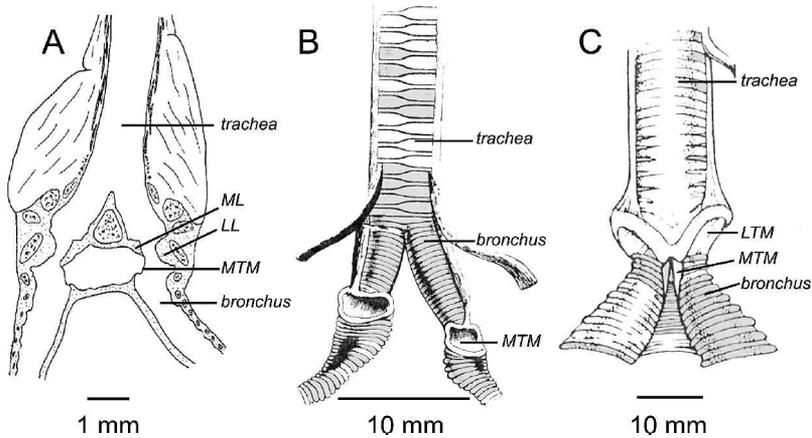


Figure 1. Variation in syrinx morphologies. **A:** Cross section through the syrinx of a Brown thrasher (*Toxostoma rufum*), which is a typical Passeriformes syrinx (modified after Suthers et al., 1999); **B:** Ventral external view of the syrinx of an oilbird (*Steatornis caripensis*; modified after King, 1989); **C:** Ventral external view of the syrinx of a cormorant (*Phalacrocorax carbo*; modified after King, 1989). *ML*: Medial Labium; *LL*: Lateral Labium; *LTM*: lateral tympaniform membrane; *MTM*: medial tympaniform membrane.

Syringeal morphology of the extant bird species varies considerably (cf. fig. 1), and the variation has been used for taxonomic classification, e.g. the distinction between songbirds (oscines) and non-songbirds (non-oscines). For reviews on syrinx morphologies see Setterwall (1901), Rüppell (1933) and King (1968). Of the over 9600 extant bird species known, almost 4000 species are non-songbirds (Pough et al., 2002).

Several qualitative models of syringeal function to explain sound generation in birds have been debated (Greenewalt, 1968; Gaunt and Gaunt, 1985; Goller and Larsen, 2002, and many references therein). Recently, Goller and Larsen (1997b, 2002) discovered, by direct endoscopic observations, that the actual sources of sound in songbirds were the vibrating labia acting as pneumatic valves. This ‘labial hypothesis’ was in contrast to the thin Medial Tympaniform Membranes (MTM) being the sound generators, as was previously hypothesised based on morphological observations. Endoscopic observations also suggested that in the pigeon (*Columba livia*) and the cockatiel (*Nymphicus hollandicus*), two non-songbird species, the Lateral Tympaniform Membranes (LTM) acted as a pneumatic valve in the trachea (Goller and Larsen, 1997a; Larsen and Goller, 1999; 2002).

Identification of the vibratory sound generators demonstrated that the physical mechanisms underlying sound production in the syrinx were similar to the mechanisms found in the larynx of most tetrapods.

The capacity of songbirds to generate more variable songs than non-songbirds does not necessarily imply that the sound elements generated by non-songbirds exhibit less complexity. Signal classifications used in the literature, such as tonal sounds, harmonic stacks and chaotic signals (Fitch et al., 2002; Wilden et al., 1998)

can be found in both songbirds, e.g. in zebra finches (Fee et al., 1998), and in non-songbirds, e.g. parrots (Fletcher, 2000). The most likely cause of the generation of the more variable songs in songbirds is their neuromuscular control of the syrinx (Laje and Mindlin, 2002) and proximal structures (beak, tongue), and learning capabilities (Brainard and Doupe, 2000; Suthers et al. 1999; Wild, 1997).

Until about 1990, only a few attempts were made to describe the physics quantitatively (Brackenbury, 1979; Casey & Gaunt, 1985; Fletcher, 1988). The issue has since aroused new interest as a result of direct endoscopic observations in birds carried out by Goller and Larsen. Recently, the efforts of physiologists and physicists have led to a new quantitative approach to the mechanisms underlying songbird sound production by presenting models based on human vocal fold models (Fee et al., 1998; Fry, 1998; Fee, 2002; Gardner et al., 2001; Laje and Mindlin, 2002; Laje et al., 2002). However, the morphology of the sound system has been either largely ignored or greatly simplified. To answer biological questions, physicists often use powerful quantitative tools that are unknown to biologists. Models can teach us a lot about a system, despite their conceptual, mathematical or physical limits. Not all models are equally suited to answer a given question, so it is of paramount importance to choose a model that can deliver meaningful answers.

In this paper, we discuss the status quo of quantitative modelling of the biomechanics of bird sound production. We consider the strengths and limitations of these models and their applicability to biological questions. It is, however, not our aim to explain the mathematical details of the models.

REVIEW OF MATHEMATICAL SYRINX MODELS

In order to provide a clear overview, it is essential to define some terms on the concepts of modelling. A physical model, or mechanical model, is a real object. A mathematical model is a purely mathematical construct. A conceptual physical model is the geometry and the physical principles on which the mathematical model is based. A computational model is the implementation of a mathematical model in a computer program with which simulations can be made for a selected range of values of the input parameters.

Several mathematical syrinx models are compared in table 1. The models use the concept that the sound sources in birds are the MTM (Brackenbury, 1979; Fletcher, 1988) or labial masses (Fee et al., 1998; Fry, 1998; Fee, 2002; Gardner et al., 2001; Laje and Mindlin, 2002; Laje et al., 2002). To our knowledge, there is no model specifically constructed based on LTM vibrations. All models aim to explain the signal properties (e.g. spectral composition) of the radiated sound from the dynamics of either vibrating membranes or two paired labia in the syrinx. Currently, only one model can account for both the production of pure tone sounds and complex harmonic sounds (Fry, 1998).

The related literature on so-called ‘collapsible tubes’ is vast. Knowledge and classification of the phenomenon of collapsible tubes, such as blood vessels, is

Table 1.

Comparison of models in literature. **A.** Brackenbury (1979b); **B.** Fletcher (1988); **C.** Fee et al. (1998); **D.** Fry (1998); **E.** Gardner et al. (2001); **F.** Laye et al. (2002); **G.** Fee (2002). ¹ SD; Spring Damper model, ² TM; Tympaniform Membrane.

Model type	Aero-acoustical		Modified oscillators				
Model	A	B	C	D	E	F	G
<i>Aim of model development</i>							
Neuromuscular control			•	•	•	•	
Morphology							
General mechanism	•	•					•
<i>Bird to validate model</i>							
Songbird		•	•	•	•	•	•
Non-songbird	•						
<i>MTM modelled by</i>							
Moving piston	•						
Edge clamped drum		•					
<i>Labia modelled by</i>							
One/two mass SD ¹			•	•	•	•	
Multiple mass SD ¹							•
<i>Input parameters</i>							
Bronchial pressure	•	•	•	•	•	•	
Complex pressure wave		•					
Labial / membrane stiffness		•		•	•	•	•
Gating of flow						•	
<i>Model output tested</i>							
Generation sounds	•	•	•	•	•	•	
Power output	•	•		•			
Amplitude modulation				•			
Pressure gradient over TM ²		•					

extremely relevant for modelling birdsong production in the near future. We would like to refer to Bertram and Pedley (1982), since it is beyond the scope of this review to include this subject.

Aero-acoustic models

The prime examples of this type of model are those of Brackenbury (1979) and Fletcher (1988). Brackenbury (1979) calculated the amplitude of the vibrating syrinxal membranes to estimate the radiated power output for crows of a cockerel (*Gallus domesticus*). However, unrealistically large membrane amplitudes of several millimetres were required for the model to produce the measured power levels. The discrepancy probably stems from the physical assumptions that were made to describe the system mathematically. Brackenbury modified a model of Ffowcs Williams and Lovely (1975) and used their theoretical discussion on a vibrating

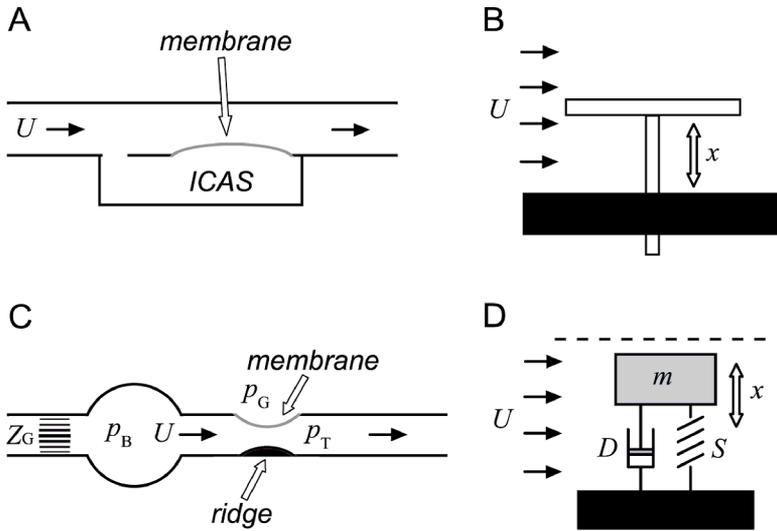


Figure 2. Schematic representation of some conceptual physical models used in the literature. **A:** Brackenbury's model illustration in Brackenbury (1979); **B:** The model used for calculations in Brackenbury (1979) based on Ffowcs Williams and Lovely (1975); **C:** The model used for calculations in Fletcher (1988). The horn is not shown; **D:** Basic mass-spring-damper model used in Fee et al. (1997), Fry (1998), Gardner et al. (2001), Laje et al. (2002), Laje & Mindlin (2002). Dotted line indicates line of symmetry. Black arrows indicate flow direction in the models. *D*: damper, *ICAS*: interclavicular air-sac, *m*: mass, p_B , p_G , p_T : pressures, *S*: spring, *x*: displacement, *U*: flow, Z_G : impedance.

surface panel exposed to a semi-infinite uniform tangential fluid flow. Ffowcs Williams and Lovely (1975) assumed that the moving panel had no influence on the bulk flow. As pointed out by Fletcher (1988), Brackenbury's geometrical representation (redrawn in fig. 2A) did not in fact correspond to the conceptual physical model used by Ffowcs Williams and Lovely (1975), represented by the drawing shown in fig. 2B. Contrary to Brackenbury's assumptions, pressure waves are produced in the syrinx as a result of the mutual influence of the membranes or labia and the flow.

Fletcher's model of the avian syrinx (Fletcher, 1988) was essentially a quantification of proposals by Greenewalt (1968). It described sounds induced by moving surfaces, and combined solid mechanics and fluid dynamics. A similar approach had been previously used to model reed-driven woodwind instruments. Fletcher modelled the geometry of the vocal system as a serial array of acoustic elements: an air-sac with driving pressure p_G , a certain acoustical resistance (or impedance, assumed to be low with respect to the resistance of the syrinx), a proximal reservoir (representing a bronchus), a syrinx portion modelled as a short tube with a single moving membrane in the wall opposite a ridge, a tube representing the trachea, and a horn (representing mouth and beak, fig. 2C). In birds, this geometry is three-dimensional, but for simplification the components of the model were one- or two-dimensional.

To model the pressure and flow, Fletcher used a force balance between the dynamic pressure forces, the acceleration of the moving membrane and the forces on the membrane due to the difference between the external pressure in the air-sac and the bronchial pressure (resp. p_G and p_B in fig. 2C).

The syrinx itself was modelled as a tube with one moving membrane and a stiff opposite wall. The longitudinal extension of the membrane was assumed to be much smaller than the length of the trachea. To simplify the calculation of the forces on the membrane, the calculation was split into a downstream and an upstream half. The aerodynamic forces on the membrane due to pressure were calculated only for the upstream half. For the downstream half, the pressure was assumed to equal the pressure in the proximal trachea (p_T). The pressure on the outer side (p_G ; representing air-sac pressure) of the membrane was prescribed and was also used to drive the system at the tube entrance.

The trans-membranous pressure difference was the difference between the local pressure inside the tube and the (relatively) steady air-sac pressure. The pressure in the bronchus varied and depended on impedance Z_G , the flow out of the syrinx U , and the pressure differential over the impedance (see fig. 2C). Nevertheless, quasi-steady flow and incompressibility of the air was assumed: at each time instant, the steady Bernoulli equation was applied to relate pressure and velocity (ignoring friction). The membrane in Fletcher's model closed off the tube in its resting position and acted as a valve that rapidly closed and opened during phonation.

The position of the membrane was limited to mimic a collision by setting the damping constant of the membrane κ to a much higher value in the motion equation, when the membrane touched the opposite wall. Brackenbury (1979) assumed a non-linear elasticity to avoid unrealistically large oscillations of the membrane. However, Fletcher (1988) found this to cause unspecific "undesirable effects" and, instead, chose to nonlinearly increase the so-called effective mass of the membrane.

To describe the forcing term in the equation of motion of the membrane, Fletcher summed the forcing terms for the first two dominant modes. This resulted in a harmonically complex driving force for the membrane. The force that drove the oscillation did not simply increase bronchial pressure as measured in birds. It should be noted, however, that the pressure measurements *in vivo* were generally frequency limited.

The tension effects of muscle activity were included in the tension parameter T . In the model, the final tension in the membrane is determined by two factors: the trans-membranous pressure, and muscles pulling on the membrane. Active gating of flow by muscle activity was not implemented.

With this model, Fletcher (1988) produced sounds with a rich harmonic spectrum (or 'voiced' sounds) consisting of integer multiples of the membrane oscillation frequency of about 200 Hz. The power spectrum of the evaluated tracheal pressure exhibited formants around the open- and closed pipe resonances.

The power output of the model was within an order of magnitude of the actual measured values by White (pers. comm. to Fletcher) from an Australian raven

(*Corvus mellori*), which had ‘typical values’ for anatomical and physiological parameters. Ravens belong to the Passeriformes and thus are songbirds. In fact, the raven syrinx, like that of the American crow (Goller and Larsen, 1997b), probably contains labial masses, which — as in the crow — are the likely sound sources, while the modelled thin membranes play a different (not yet established) role in vocalisation. Little is known about the actual mechanical properties of the tissues in the syrinx (Fee, 2002), in contrast to the overall morphology. However, Fletcher’s model is constructed such that it can easily be extended (Fletcher, 1989).

Modified oscillator models

Another distinct group of mathematical models can be summarised as modified oscillator models (Fee et al., 1998; Fry, 1998; Gardner et al., 2001; Fee, 2002; Laje and Mindlin, 2002; Laje et al., 2002). These models were not designed to include an accurate morphology of the syrinx and its associated air-sacs and muscles, but were developed to understand how simple neural activation patterns can lead to complex (sound) signals (Laje and Mindlin, 2002) in songbirds. The sound production system of songbirds served as a biological model system for human sound production and its control.

In these modified oscillator models, a labial mass was represented by one- or two coupled non-linear oscillating masses (fig. 2D). The flow in these systems was not modelled directly, but the flow induced a pressure force which drove the oscillators. These models had a relatively small number of free parameters that could still simulate the different classes of signals, ranging from pure sine waves to complex non-linear effects such as harmonic stacks, and period doubling (Fee et al., 1998).

The model proposed by Fry (1988) was based upon the line model of acoustic tubes by Kelly and Lochbaum (1962), which has formed the basis of a class of human speech synthesisers (Flanagan, 1972). The syrinx was represented as two sound sources, the two bronchi, each with one mass combined with a spring and a damper. This syrinx model was integrated in a high-parameter system of interconnected acoustical tubes representing the air-sacs and the trachea. Pure tones were produced when the masses did not occlude the bronchus during vibration, whereas harmonic stacks were produced when the labia in one bronchus collided. This model captured many features of birdsong, but was purely descriptive.

Several one- or two-mass models have been published (Fee et al., 1998; Fry, 1998; Gardner et al., 2001; Fee, 2002; Laje and Mindlin, 2002; Laje et al., 2002) based on classic human vocal fold models (Ishizaka and Flanagan, 1972; Titze, 1988). The motion equation of the oscillator in the model by Gardner et al. (2001), for instance, includes a non-linear dissipation term that kept the motion of the mass in the model within set boundaries (c.f. theory of relaxed oscillation, see Arnold et al., 1999, cited in Gardner et al., 2001). The non-linear term was modified in the even simpler successive model (Laje et al., 2002). Laje et al. (2002) and Laje and Mindlin (2002) included active opening and closing of the labia in their model by introducing a force that controls the stationary position of the mass. With simple sweeps of two

control parameters — the stiffness of the oscillator and the bronchial pressure — they could mimic the song of the Chingolo (*Zonotrichia capensis*). The values for stiffness, however, did not represent the distribution of the actual material properties of the syrinx.

PERSPECTIVES

Mathematical modelling is required to elucidate the mechanisms of sound production and to interpret the experimental data and overwhelming structural complexity found in birds. Modelling can also help to direct experimental research. Keeping the number of parameters low considerably simplifies the exploration of the parameter space. Some of the aforementioned models have relatively few parameters (Fee et al., 1998; Gardner et al., 2001; Laje and Mindlin, 2002; Laje et al., 2002), with only one or two oscillating masses. These basic models provided fundamental insights into how a grossly simplified system operates and could be controlled. They also provide the minimum number of parameters required to describe the essential dynamics of the sound signal. The one- or two-mass models are not primarily designed or suitable for including the diverse morphologies and physiological parameters found in bird species. The approach by Fletcher (1988) seems to be more suitable for extending by workers interested in these areas. Extensions of his model can be made in various directions. The model calculations were quasi-steady, thus it was assumed that the pressure terms associated with local variations in U (dU/dt) are small and could be ignored. Also, viscosity of the flow was ignored (although viscous losses were included in the membrane). While this may be a valid assumption outside the syringeal region, it seems hard to defend for the tiny slit between the membrane and the opposing wall. High velocities are expected, and high velocity gradients are bound to occur during the short moments of slit opening. Thus, friction may indeed play an important role during the most critical phase of phonation as found with physical models of the human larynx (Deverge et al., 2003). Fletcher's model could be extended to account for these effects.

The air-sac pressure external to the vocal membrane was assumed to be identical to the driving pressure of the system. In fact, rapid pressure fluctuations do occur in the interclavicular air-sac as was recently demonstrated for pigeons (Beckers et al., 2003). Membrane motion is likely to be a combined effect of driving pressures, membrane properties and acoustical properties of the vocal tract. The first two vibrational modes of the membrane were prescribed in Fletcher's model, thereby restricting a priori the motion of the membrane. The validity of this assumption is supported by measurements on the properties of the medial labium in zebra finches and canaries (Fee, 2002).

Identifying the role of different parts of the vocal apparatus is relevant for solving important morphological and evolutionary questions. This requires an integrative modelling approach. Isolated measurements on different parts cannot provide definite answers to their role in the vocal system. Recently, the role of the

medial tympaniform membranes (MTM) and the labia during sound production in songbirds have received much attention (Goller and Larsen, 2002). Correspondence in fundamental frequency between labial vibrations and sound does not necessarily exclude a fundamental role in the system of the MTM. For instance, the compliance of the MTM may be essential for the deformation of the syrinx during phonation. Combined measurements and modelling are needed to shed light on this issue.

The distinction made between membranes and labia in songbirds is artificial and actually comprises a continuum of different tissues with a varying mass and stiffness distribution. Based on this idea, Fee (2002) modelled the continuum of labia and adjacent membranes (the MTM) as a matrix of 121 interconnected masses. In fact, this represents a numerical-experimental approach that estimates material parameters of this complex system. This model has not yet been implemented into a syrinx model.

A quantitative model aimed at comprehending the sound-producing system must consider the fluid dynamics and solid dynamics of the system as inseparable. Numerical modelling of the tissues of the syrinx and the vocal tract, combined with Computational Fluid Dynamics (CFD) modelling of the flow of air as used in human phonation research (de Vries et al., 2003), could be a step towards a more realistic dynamic model that addresses the architectural complexity found in birds. CFD models have the advantage of allowing complex morphologies and material properties to be included. The obvious disadvantages are the large number of required parameters and the computational costs of such a model. It is impossible to explore the parameter space of high-parameter models exhaustively because the number of parameter combinations is too high and, although theoretically finite, quickly becomes practically infinite. Nevertheless, to understand the diversity and evolution of syrinx morphology present in birds, high-parameter models would be worth exploring. A numerical approach could also be used to explore the significance of asymmetries in the vocal system.

Physical models have been used in bird-song research only rarely. To our knowledge, in one study only (Brittan-Powell et al., 1997) simple plastic tubes with latex membranes were used as syrinx models to investigate source-resonator coupling. In human phonation research, physical modelling is often used to test the validity of model assumptions (Hofmans et al., 2002; Deverge et al., 2003) or to develop prosthesis (Lous et al., 1998; de Vries, 2000).

On the one hand, advances in transducer technology and surgical procedures provide more accurate experimental data of bird song. On the other hand, the continuous increase in computational power facilitates the exploration of relatively complex parameter spaces. Only by combining experimental work with quantitative modelling are we able to answer the many open questions and to make significant progress in understanding the mechanisms by which birds produce sound and control their song.

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