

S26-3 Aspects of syringeal mechanics in avian phonation

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Abstract The vocal organ of birds, the syrinx, is formed by modified cartilages of the trachea and bronchi. Recently, the use of thin, flexible endoscopes has made direct observation of the syrinx possible *in situ*. The effects of direct muscle stimulation on the syringeal aperture identified adductor and abductor muscles, confirming results from electromyographic studies. Endoscopic observations also revealed the dynamics of syringeal reconfiguration during phonation. In songbirds, phonation is initiated by rostral movement and stretching of the syrinx together with simultaneous movement of the medial and lateral labia into the bronchial lumen where they form a narrow slot. The medial tympaniform membranes play a minor role in vocalization as their removal causes only small changes to song. In the tracheal syrinx of the pigeon, sound production is initiated by almost full adduction of the lateral tympaniform membranes into the tracheal lumen, where they bulge rostrally during phonation. Endoscopic observation combined with vibration detection by laser light suggests that the avian sound generating mechanism is a pulse-tone mechanism similar to that in the human larynx, with the labia (or lateral tympaniform membranes) forming a pneumatic valve. A numerical, two-dimensional model of the pigeon syrinx is proposed.

Key words Sound production, Songbird, Pigeon, Pneumatic valve, Endoscopic technology

1 Introduction

The avian vocal organ, the syrinx, is a specialized structure located rather inaccessibly where the trachea bifurcates into the two primary bronchi. This is one of the reasons why most of our knowledge about syringeal mechanics is based on such indirect evidence as electromyography, emitted sound, and anatomy. The syrinx of different avian taxa varies in position (King, 1989), and consists of a skeletal framework comprising modified cartilage (or bony) rings, flexible membranes or soft tissue masses (labia) stretched between elements of this framework, and the syringeal muscles (Fig. 1).

Early investigations showed that sound production could be induced by airflow in an excised syrinx (Rüppell, 1933) or by injecting air into subsyringeal air sacs (Miskimen, 1951). The “classical model” of songbird sound production is based on these early studies. It states that in songbirds, sound is generated by oscillations of the edge-clamped, very thin medial tympaniform membrane (MTM) while a soft tissue mass, the lateral labium (LL), provides constriction of the syringeal lumen to induce MTM vibrations (Gaunt and Gaunt, 1985). An alternative model, the pulse-tone model, in which the labia act as a pneumatic valve, has also been proposed (Klatt and Stefanski, 1974).

Arising from theoretical difficulties in explaining how a vibration-based mechanism can generate tonal sounds (Casey and Gaunt, 1985), a third model, the “whistle

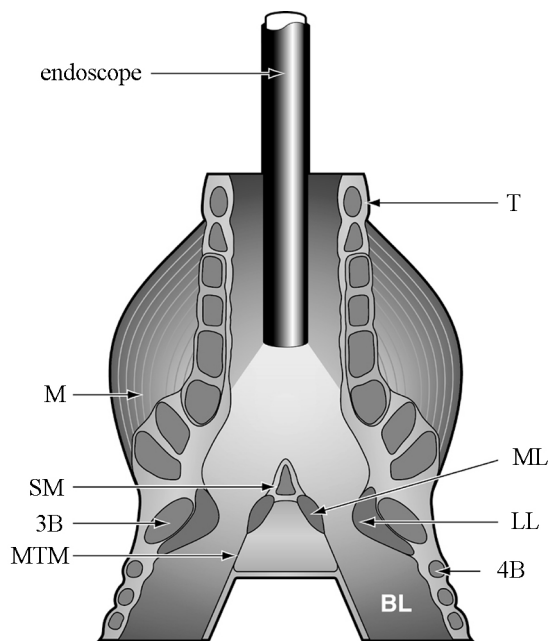


Fig.1 Vertical section through the syrinx of a typical songbird, illustrating the main morphological structures involved in sound production

Abbreviations: 3B and 4B = 3rd and 4th bronchial cartilages, BL = bronchial lumen, LL = lateral labium, M = syringeal muscles, ML = medial labium, MTM = medial tympaniform membrane, SM = semilunar membrane, T = trachea. Modified after Larsen and Goller (2002).

hypothesis”, was formulated (Nottebohm, 1976; Gaunt et al., 1982). Recent mathematical models of the songbird syrinx confirm, however, that generation of tonal sounds by vibration of one or both labia in combination with upper vocal tract filtering is theoretically possible (Gardner et al., 2001). Testing the different models experimentally is difficult. Indirect methods, such as analyses of song generated in a helium-oxygen atmosphere (Nowicki, 1987; Ballintijn and ten Cate, 1998), did not support the “whistle hypothesis” but could not distinguish between the “classical model” and the “pulse-tone model” either.

These problems generated a need to visualize the syrinx during phonation *in situ*. We therefore developed techniques that allowed direct visualization of the intact phonating syrinx by filming it during sound generation through fine endoscopes (Goller and Larsen, 1997a,b; Larsen and Goller, 1999, 2002). These experiments provide support for a pulse-tone model of sound production in which labia (songbirds) or lateral tympaniform membranes (pigeons) form an oscillating pneumatic valve. We also tested the role of the MTM in songbirds (Goller and Larsen, 1997b, 2002), and attempted a mathematical simulation of the acoustic behavior of the simple pigeon syrinx from first principles.

2 Materials and methods

We inserted a fine endoscope (Olympus angioscope AF14, 1.4 mm outer diameter) into the trachea of anesthetized birds through a small opening in the neck area and advanced it to a suitable position above the bronchial partition (Fig. 1). To visualize muscle function we inserted bipolar 0.025 mm stimulation electrodes into different syringeal muscles near their rostral insertion and stimulated them one by one.

We induced phonation in anesthetized birds by electrically stimulating a song control nucleus in the brain (HVC) in three songbird species: brown thrasher (*Toxostoma*

rufum), northern cardinal (*Cardinalis cardinalis*), and hill myna, (*Gracula religiosa*); the DM of the brain was also stimulated similarly in experimental pigeons (*Columba livia*). A tame crow (*Corvus brachyrhynchus*), with angioscope inserted, was allowed to recover from anesthesia as well, and its spontaneous calls were recorded. The endoscopic images of the syrinx together with sound recordings were stored on a videocassette recorder. For a detailed description of all endoscopic procedures and laser vibration detector equipment, see Goller and Larsen (1997a, b) and Larsen and Goller (1999, 2002).

In ablation experiments we directly tested the idea that the MTM is the principal sound generator in songbirds (Fig. 2; details of procedures and analysis in Goller and Larsen, 1997b, 2002). Song was recorded on cassette tape from each of five individual zebra finch males (*Taeniopygia guttata*) prior to manipulation. We opened the membrane of the interclavicular air sac, destroyed the MTM with fine forceps, and carefully closed the air sac membrane with tissue adhesive. Recording of song started one day after MTM removal and continued daily for 4–7 weeks. In most individuals, some MTM regeneration was noticed after a few weeks; but after removal of regenerated tissue, the MTM stayed fully ruptured to the end of recordings. Syllable similarity between song bouts was quantified with software developed by Tchernichovski et al. (2000). For pre- and post- comparisons of song recovery we normalized each similarity score.

Our two-dimensional numerical model of the pigeon syrinx consisted of an infinitely stiff air tube, with two symmetrically positioned elastic membranes enclosed in an air space to simulate the air sac enclosing the syrinx (Fig. 3). To calculate flow-induced sound, we applied Newton’s second law of motion to obtain the Navier-Stokes equation and made a numerical approximation of the latter. This was coupled with a solid mechanics model of membrane vibra-

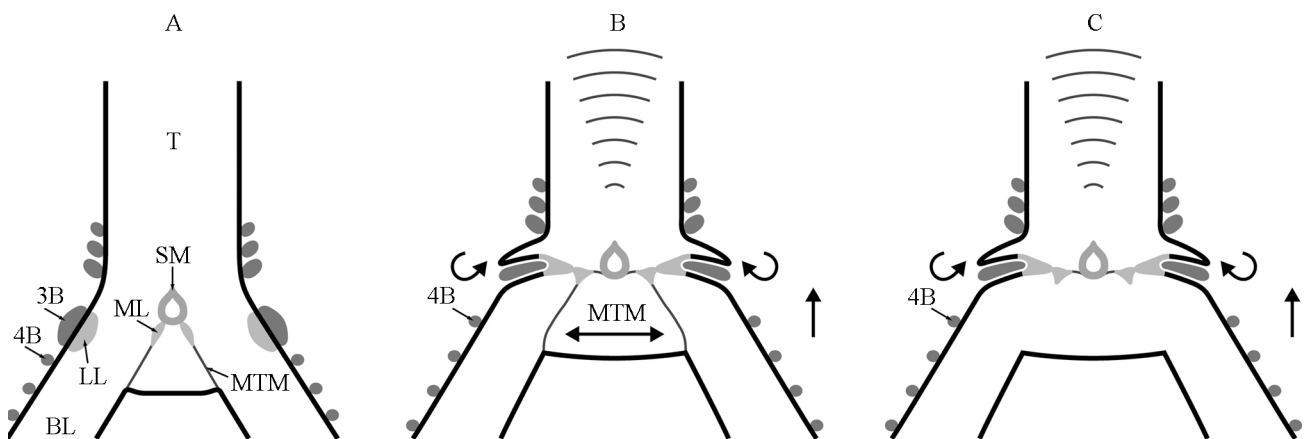


Fig. 2 Schematic interpretation of the songbird syrinx in quiet respiratory position (A), phonatory position (B), and with the medial tympanic membrane (MTM) removed (C)

The typical phonatory position, according to endoscopic evidence, involves a stretching of the bronchi and the medial tympaniform membrane as the syrinx is moved upward, accompanied by closure of the syringeal lumen by the labia to form a narrow vibrating slot that acts as a pneumatic valve. Removal of the MTM (C) does not prevent sound production; abbreviations as in Fig. 1. Redrawn from Goller and Larsen (1997b).

tion and implemented in a computer program written in MatLab.

3 Results

3.1 Syringeal muscle function in songbirds

Electrical stimulation and endoscopic observation show that contraction of the dorsal tracheobronchial muscle constricts the syringeal lumen by rotating and translating the third bronchial cartilage such that the medial edge is drawn inward, thereby pushing the lateral labia (LL) into the bronchial lumen (Figs. 1, 2a, b).

This rotation is probably facilitated by syringeal geometry, since artificial stretching of an excised syrinx causes the third bronchial cartilage to move somewhat into the lumen. The medial portion of the dorsal syringeal muscle appears to be involved in moving the medial labia (ML) into the lumen, but the mechanics of this movement are not understood. Activity in the ventral tracheobronchial muscle enlarges the syringeal lumen, as upon its contraction, the LL is rotated out of the lumen. Contraction of the prominent ventral syringeal muscle does not result in observable movement but seems to tense the ML and is correlated with the frequency of emitted sound.

3.2 Dynamics of syringeal sound production

Observations from the four songbird species, including the spontaneously vocalizing crow, indicate that phonation proceeds in three steps: a repositioning of the syrinx in preparation, tissue vibrations closely correlated with emitted sound, and a return to the syringeal resting position upon cessation of sound. External observations show that prior to phonation there is a vigorous upward movement of the whole syrinx, which leads to a stretching of the anchored bronchi, including substantial stretching of the MTM (note the position of 3B and 4B in Figs. 2a and b). Sound is produced when the syrinx is in its uppermost position, after which it drops back to its resting position.

Internal observations show that syringeal stretching coincides with movement of ML and LL into the bronchial lumen (Figs. 2a, b). The LL covers approximately two thirds of the bronchial lumen in the fully adducted state as it comes

into close contact with the ML. Here ML and LL form a narrow slot in the airway and appear to vibrate during phonation. A detailed video analysis of the vibrations is not possible because we filmed at 30 frames per second. However, measurements with a custom-built laser vibrometer in the trachea show that the vibration wave shape closely matches that of the emitted sound. A similar sequence of events is observed in the tracheal syrinx of the pigeon where the cranially bulging lateral tympaniform membranes form the narrow slot during phonation.

3.3 Role of the medial tympaniform membrane (MTM)

The “classical model” of songbird sound production predicts that ablation of the MTM will silence the bird. Male zebra finches with MTM removed, however, sang readily on their first post-operative day. Song structure had changed somewhat in all individuals, most likely because of the destruction of the MTM and not because of post-operative effects. Over time, song structure improved in all individuals and, at the end of the experiment, was either qualitatively indistinguishable from control song or at least much improved over initial post-operative song. Quantitative similarity scores gradually improved over time as well and, after approx. 25 days, pre- and post- syllable comparisons approached nearly 100%. So, the MTM is not required for song production in zebra finches, but may play a role in adjusting tension of the labia.

3.4 Numerical simulation

We calculated fluid flow through a model of the relatively simple pigeon syrinx (Fig. 3) by numerical solution of the Navier-Stokes equation. The simulation predicted two-dimensional variation in air pressure (Fig. 3), velocity, and vorticity as a function of time. The model also predicted a fundamental sound frequency of about 500 Hz, as well as sudden jumps in sound intensity and fundamental frequency, but included more high frequency components than are present in real pigeon vocalizations.

4 Discussion

Our direct endoscopic observations largely confirm conclusions based on indirect evidence (Suthers et al., 1999) that, in songbirds, the labia are moved by indirect action of intrinsic syringeal muscles. Even though the biomechanics of the songbird syrinx has been described (Klatt and Stefanski, 1974), the precise mechanism of how muscle force effects movement of the third bronchial cartilage is not sufficiently clear, even from our endoscopic observations.

From our experiments, we conclude that the principal sound generating mechanism in the songbird syrinx involves vibration of the medial and lateral labia, and that sound production is not dependent on the presence of the MTM. This “labial hypothesis” suggests that the physical mechanism of phonation in songbirds is very similar to that in the human larynx. Calculations based on models of human vocal fold vibration can also describe sound generation in songbirds (Gardner et al., 2001; Laje et al., 2002).

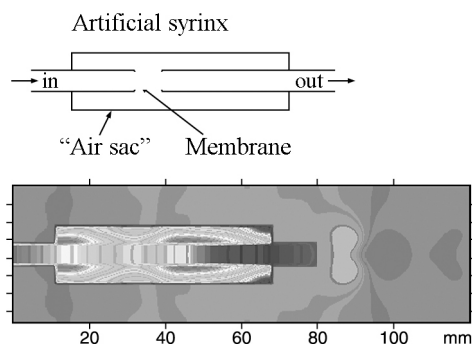


Fig. 3 The two-dimensional model of the pigeon syrinx (upper panel) and the predicted sound pressure distribution in the model after 200 ms (lower panel)

The stretching of the syrinx may facilitate repositioning of the labia. This event preceded sound production in all endoscopic observations of the phonating syrinx (Goller and Larsen, 1997a,b; Larsen and Goller, 1999, 2002). The repositioning makes generation of a pressure differential across the syrinx possible, between bronchi BL and trachea T (Fig. 2b). Such a differential causes increased velocity of airflow inducing Bernoulli forces, which act on the labial tissue forming the constriction and pull it towards the center of the lumen. The interplay between Bernoulli forces and elastic recoil forces acting on the labia is thought to constitute a self-oscillating system, a pneumatic valve, which generates and sustains the labial vibrations that modulate the airflow. Although the labial hypothesis describes the basic model of sound production in songbirds (Goller and Larsen, 1997b) and some non-songbird groups (Larsen and Goller, 1999), it is likely that multiple mechanisms and intermediate states are employed for some sounds.

Surprisingly, even a simple two-dimensional model of the pigeon syrinx produces basic features of pigeon vocalization, such as the correct fundamental frequency and nonlinear phenomena. Clearly it should be extended to a 3-dimensional model and compared to a physical model with known mechanical and acoustic properties. Such work is now in progress (Elemans et al., 2002).

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