



Published in final edited form as:

Brain Lang. 2010 October ; 115(1): 69–80. doi:10.1016/j.bandl.2009.11.003.

Peripheral mechanisms for vocal production in birds - differences and similarities to human speech and singing

Tobias Riede and Franz Goller

Department of Biology, University of Utah, 257 South, 1400 East, Salt Lake City, UT 84112, USA

Abstract

Song production in songbirds is considered a model system for studying learned vocal behavior. As in humans, bird phonation involves three main motor systems (respiration, vocal organ and vocal tract). The avian respiratory mechanism uses pressure regulation in air sacs to ventilate a rigid lung. In songbirds sound is generated with two independently controlled sound sources, which reside in a uniquely avian vocal organ, the syrinx. However, the physical sound generation mechanism in the syrinx shows strong analogies to that in the human larynx. Differences in the functional morphology of the sound producing system between birds and humans require specific motor control patterns. The songbird vocal apparatus is adapted for high speed, suggesting that temporal patterns and fast modulation of sound features are important in acoustic communication. Rapid respiratory patterns determine the coarse temporal structure of song and maintain gas exchange even during very long songs. The respiratory system also contributes to the fine control of airflow. Muscular control of the vocal organ regulates airflow and acoustic features. The upper vocal tract of birds plays a role in filtering the sounds generated in the syrinx, but source-filter interactions may also play a role. The unique morphology and biomechanical system for sound production in birds presents an interesting model for exploring parallels in control mechanisms that give rise to highly convergent physical patterns of sound generation. More comparative work should provide a rich source for our understanding of the evolution of complex sound producing systems.

Keywords

Sound production; songbird; syrinx; larynx; respiration; vocal tract modification; biomechanics; bioacoustics

INTRODUCTION

Song production in songbirds is a widely studied animal model system for learned vocal behavior (e.g., Doupe & Kuhl, 1999; Zeigler & Marler, 2008). The most thoroughly explored parallels between the songbird model and human speech production and development involve central processing and control. For example, the songbird system has been used to investigate lateralization of vocal motor control (e.g., Nottebohm, 1971; 1977), reliance on acquired acoustic information for proper development and a distinct sequence of ontogenetic periods (e.g., Goldstein et al., 2003; reviewed in Doupe & Kuhl, 2008). These parallels in central

Address correspondence to: F.G., Department of Biology, University of Utah, 257 South, 1400 East, Salt Lake City, UT 84112, USA., goller@biology.utah.edu, Phone: 801.585.1929.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

control and behavior are contrasted by striking differences in the peripheral organs. Among terrestrial vertebrates, birds generate sound with a unique vocal organ, the syrinx, which is located at the caudal end of the trachea. The syrinx is part of a respiratory system, which also shows remarkable differences to the mammalian lung. Any analogy in central control mechanisms must accommodate these pronounced differences in the peripheral systems involved in sound generation. Remarkably, the physical process of sound generation is strikingly similar between songbirds and mammals, despite these morphological and functional differences at the peripheral level.

Understanding the role and functional aspects of the peripheral target organs for sound generation is a key aspect of deciphering central motor control and learning mechanisms. In birds and mammals the vocal organ is a complex nonlinear device, whose intrinsic behavior is controlled by neural input from central vocal control pathways. Similarly, vocal production makes use of the respiratory system whose primary functions such as gas exchange and acid/base balance may put constraints on vocal behavior. The motor systems of the upper vocal tract are also an essential part of a number of other behaviors (e.g., food manipulation, airway protection, grooming, etc.). Motor control of vocal systems therefore is a complex interplay between morphological, dynamic and physiological aspects of the peripheral systems with specific adaptations and constraints and central neural control mechanisms, which are also subject to various constraints and selective pressures.

In comparison with research on human vocal production, the exploration of peripheral mechanisms in the avian model is subject to serious technical limitations on the one hand, but offers potential for experimentation on the other. The location of the syrinx at the caudal end of the trachea makes direct observation of vibratory behavior very difficult and therefore much less information is available in comparison to studies of the human vocal folds in action. It is also difficult to obtain vocal behavior from restrained birds, thus limiting the range of vocalizations, which can be explored with endoscopic filming methods. Consequently, research on the syringeal mechanisms of sound production lags behind direct exploration of the vibratory behavior of the human vocal fold. The avian system, however, offers the possibility of experimental manipulation and chronic recording techniques, which are not possible to the same degree in human subjects. It is clear therefore that the two research efforts can benefit greatly from each other.

This review focuses on peripheral mechanisms of avian sound generation and attempts to highlight similarities and differences in peripheral structures and control mechanisms between songbirds and humans. Acoustic behavior arises from the interplay of morphological structures, biomechanics, and neural control. Understanding peripheral mechanisms is essential for elucidating central motor control of vocal behavior. While the discussion is centered on available data for songbirds, we will also emphasize areas where critical data are still missing.

MOTOR SYSTEMS AND BIOMECHANICS

Singing in birds, like human speech and singing, requires coordination of several complex motor systems. Each main motor system, respiration, vocal organ and vocal tract structures, involves a number of different muscles, whose activity must be coordinated (e.g., Suthers & Zollinger, 2008). Here we discuss each motor system including biomechanics, muscle systems and neural control at a functional level rather than providing detailed descriptions.

1. Integrating vocalization and respiration

a) Functions of syrinx and larynx—The avian syrinx and mammalian larynx share two major functions, a) regulating airflow from and to the lungs (gating) and b) modulating airflow during sound production. The avian larynx constitutes a second valve for regulation of airflow

(McLelland, 1989a) but no evidence exists in any bird group that it acts as a sound source. Although we will discuss the two main functions sequentially, it should become clear that they contribute in an integrated fashion to sound production.

b) The avian and human lung system—The avian lung consists of rigid air conduits (parabronchi), which are lined by epithelia for gas exchange. Ventilation of the lung arises from the bellows-like activity of air sacs, which attach to the posterior and anterior end of the rigid lung (Figure 1). This difference in respiratory design between birds and mammals results in different ventilatory mechanics. In birds, the pressure conditions of inspiration and expiration are always actively generated by muscles. Passive recoil forces potentially arise from the thorax, but play less of a role than recoil from the mammalian diaphragm (McLelland, 1989b). Expiration is mostly driven by activity of the abdominal muscle sheet (m. obliquus externus, m. obliquus internus, m. transversus abdominis, m. rectus abdominis) whose contraction raises the sternum, thus increasing pressure in the air sacs. Although intercostal muscles are also active during expiration (Fedde et al., 1964a) and are therefore likely to contribute to the generation of vocalizations, their role during songbird phonation has not been investigated. Inspiration involves lowering of the sternum through the activation of a set of muscles situated along the vertebral column (mm. scalenus and levatores costarum) (Wild, 2008; Wild et al., 1998) and intercostal muscles (Fedde et al., 1964a,b; McLelland, 1989b). The activation patterns of the latter during phonation have not been investigated.

Unlike in humans, the avian chest and abdominal cavity are not separated into two separated compartments by a diaphragmatic muscle (e.g., McLelland, 1989b). The two-compartment morphology in humans affects temporal patterns of breathing, speech and singing (Hoit & Hixon, 1986; 1987; Watson et al., 1989). Whereas at least the initial pressurization of the lung for expiration originates in the passive recoil of the diaphragm, the abdominal muscle sheet can contribute actively to the generation of expiratory pressure.

The passive component of the expiratory effort makes braking of the recoil by inspiratory muscles possible. Such braking has been proposed as a mechanism for fine control of expiratory pressure during phonation (Draper et al., 1959; Hoshiko 1960; Hoshiko & Berger, 1965; Sears & Newsom-Davis, 1968). In the two songbird species for which recordings of inspiratory muscles are available during song, their activity is confined to the inspirations. Fine regulation of pressure during both respiratory phases does not appear to involve braking of one phase by the opposing muscles (Wild et al., 1998).

c) Respiratory patterns and vocal temporal patterns—Song is typically generated using an expiratory airstream, although occasional inspiratory phonation has been documented (Gaunt et al., 1982; Goller & Daley, 2001; Beckers et al., 2003). Respiratory patterns of song vary greatly between species and determine the coarse temporal structure of song (e.g., Suthers & Goller, 1997; Suthers et al. 1999; Suthers & Zollinger, 2008). Silent inter-syllable intervals correspond to short inspirations (mini-breaths) if there is sufficient time for reconfiguration of the respiratory system from expiration to inspiration. These mini-breaths replenish the air used for sound production during the preceding or following syllables (Hartley & Suthers, 1989; Goller & Daley, 2001), enabling birds to sing very long songs. For example, the song of some species consists of trills that last 30 seconds to a minute (e.g., Brewer's sparrow, *Spizella breweri*; canary, *Serinus canaria*). If syllable repetition rates are very high, mini-breaths are no longer possible during the inter-syllable intervals (Hartley & Suthers, 1989), and the duration of such song elements becomes limited by the air supply. Air supply and requirements for gas exchange therefore dictate to some degree the temporal patterning of song. The highest mini-breath rate confirmed by air sac pressure recordings is 33 Hz in Waterslager canaries (Hartley & Suthers, 1989) and is lower in cardinals and other larger birds (Suthers & Goller, 1997; Suthers et al., 1994). This evidence and tutoring experiments with modified song tempo

in emberizid sparrows (Podos, 1996; Podos & Nowicki, 2004) suggest that mini-breath syllable rate is constrained by body size.

In the song of the Waterslager canary, the volume of air that is exchanged during some syllables and associated mini-breaths is less than the tracheal deadspace (Hartley & Suthers, 1989). Although air supply is maintained, the low volume that is exchanged during each respiratory cycle raises the question whether adequate gas exchange is possible during long songs. Surprisingly, gas exchange appears to be maintained during even the most elaborate temporal patterns of song in canaries and zebra finches (*Taeniopygia guttata*) (Oberweger & Goller, 2001; Franz & Goller, 2003). However, the ventilation rates of song may cause hyperventilation in some individuals as indicated by marked apneic periods following song (Hartley & Suthers, 1989; Franz & Goller, 2003).

d) Respiratory contribution to airflow control—In songbirds, the ventilatory system does not only provide the driving pressure for sound generation, but it also contributes to the fine control of airflow. Modulations of airflow at frequencies below 80 Hz are correlated with air sac pressure modulations arising from changes in the activation of expiratory muscles (Hartley, 1990; Goller & Suthers, 1999; Goller & Cooper, 2004; 2008). Modulations at higher frequencies (80–250 Hz) are controlled by the faster syringeal gating muscles (Elemans et al., 2008a). It is clear therefore that fine control of airflow for song production requires intricate coordination of the respiratory and syringeal motor systems.

e) Lung pressure and vocalization—During quiet respiration subsyringeal expiratory pressure in birds is approximately 1 cm H₂O and during phonation ranges from 10–60 cm H₂O (reviewed by Brackenbury, 1989). This range is similar to that found during human speech and singing (Bouhyus et al., 1968; Holmberg et al., 1988; Plant et al., 2004). However, in addition to general pressure ranges it is of interest to study the relationship between driving pressure and sound generation. One important measurement is the minimum pressure required to initiate phonation (phonation threshold pressure - PTP). PTP is well studied in humans (Titze, 1992a). PTP values vary with the fundamental frequency of sound (Titze, 1992b; Lucero & Koenig, 2007; Solomon et al., 2007), vocal tract design (Chan & Titze 2006), and physiological parameters, such as hydration status (Verdolini et al., 1994; Roy et al., 2003), visco-elastic properties of the vocal folds (Gray et al., 1999). PTP values and their dependence on acoustic features in birds have received much less attention.

Modeling approaches of the human sound source suggest that PTP scales with size of the vocal folds (Titze, 1988). Longer vocal folds widen the glottal area, which leads to an increased force acting on the vocal folds (the force is a product of pressure and area), and therefore should require a lower PTP. If a simple scaling function were applicable, PTP should be much higher in birds, but this is not the case (Figure 2). The fact that PTP is similar in small songbirds and humans implicates other factors in affecting PTP. Among these are the viscous damping of the oscillating tissue (Titze, 1988) and vocal tract inertance. Visco-elastic properties of the human vocal folds have been investigated, but similar data for the avian labia are not available (see below). Vocal tract acoustics will be discussed below in the context of vocal tract acoustics.

2. The sound sources

a) Functional morphology of the syrinx—The morphology of the avian syrinx varies substantially between different taxa and shows a high degree of specialization in oscine songbirds (e.g., King, 1989), although little of this morphological variability can be linked to specific features of a species' vocal repertoire (Gaunt, 1983). Modified cartilages form a cylinder-like structure, the tympanum. A cartilaginous bar at the caudal end of the tympanum, the pessulus, supports the bronchial septum and the medial aspects of each sound source. Below

the tympanum there are three modified cartilaginous half-rings (A1–A3 in Figure 3) on each side. Tympanum and tracheo-bronchial half-rings constitute the skeletal framework for the syringeal muscles, the labia and the medial tympaniform membrane (MTM).

The songbird syrinx contains two sound sources, each consisting of a pair of labia (lateral and medial labium) which are located at the base of the tympanum near the tracheobronchial junction. Endoscopic images from a top view of the songbird syrinx identified the labia as the main vibrating structures during sound production (Goller and Larsen, 1997), whereas prior to this study, the MTM were seen as the main sound source (e.g., Miskimen, 1951; Greenewalt 1968; Brackenbury, 1989). In addition to the evidence from direct endoscopic imaging, surgical ablation of the MTM did not prevent sound generation (Goller & Larsen 1997; Goller & Larsen, 2002), thus providing strong support that the labia are the main sound generators.

The basic mechanism of sound generation in birds shares strong similarity with that in the human larynx. In both cases, tissue masses – labia in the songbird syrinx and vocal folds in the human larynx – are set into vibration by a passing airstream. Muscle activity sets the oscillating masses into pre-phonatory position, and the viscoelastic properties of the vibrating masses determine acoustic output. These common features justify the term aerodynamic myoelastic sound source for larynx (van den Berg, 1958) and the syrinx. In comparison to much more elaborate information on vibratory behavior and dynamics for a wide range of sounds in the human larynx, we know very few details about labial dynamics in the songbird syrinx. Especially in light of the remarkable range of frequencies present in the songs of different species, more research is needed to elucidate dynamic mechanisms for different sounds.

In contrast to human vocal folds, very little is known about the histology or elastic properties of the labia in songbirds. Measurements of the mechanical properties (compliance) in the excised syrinx of zebra finch and canary demonstrate a narrow mechanical resonance of the medial labia that is consistent with the lower frequencies of the respective normal vocal ranges of these species (approx. 700 Hz in the zebra finch, and 1.7 kHz in the canary). A small but distinct difference in lowest resonance frequency was measured between the left and right medial labium in the zebra finch (575 Hz on the left vs 830 Hz on the right), which is consistent with the general observation of differential frequency contributions by the two sources to the frequency range of song (Fee, 2002). Clearly, more research is needed in songbirds, as information on the biomechanical properties of the vibrating structures is also very important for modeling of the sound source (e.g., for review Mindlin & Laje, 2005).

Six pairs of syringeal muscles provide mechanical control in the songbird syrinx, four of which have both insertion sites on the syrinx (intrinsic muscles) (e.g., King, 1989; Larsen & Goller, 2002). Each side of the syrinx is innervated by the ipsilateral tracheosyringeal branch of the hypoglossal nerve (for review, Wild 2008). Syringeal muscles adjust the position of the labia, which act as valves regulating airflow from complete closure to active opening. The dorsal (dTb) and ventral (vTb) tracheobronchial muscles act as adductor and abductor of the lateral labium, respectively (Goller & Suthers, 1996a; Larsen & Goller, 2002). Activity in the ventral syringeal muscle (vS) is closely correlated with fundamental frequency which suggests that it regulates tension of the labia (Goller & Suthers, 1996b), but its stimulation does not cause movement of the medial labium into the bronchial lumen (Larsen & Goller 2002). The role of the medial portion of the dorsal syringeal muscle (dS) during song is not clear, but stimulation of the muscle effects an adduction of the medial labium (Larsen & Goller, 2002), which is consistent with its direct insertion on the medial labium (Fee 2002).

These interpretations from electromyographic records during song and muscle stimulation experiments reflect only a very basic picture of the muscular control of the syrinx. Very few species have been studied, and synergistic interactions of muscles have not been explored. In

zebra finches, for example, the role of the vS muscle appears to include abductive activity, as indicated by its activation during the expiratory phase during quiet respiration (Vicario, 1991; Goller & Cooper, 2004). It is therefore likely that modifications to the general picture of biomechanical control will have to be made as more data from other species become available.

Syringeal muscles are heterogeneously composed of fast oxidative and superfast fibers (Uchida et al., 2009) and display very fast *in situ* kinetics (Elemans et al., 2008a). In isolated fiber bundles positive work was generated up to 250 Hz in the gating muscles of the European starling (*Sturnus vulgaris*) and 200 Hz in the zebra finch. The rapid contraction kinetics are matched by muscle activation patterns, which are correlated with rapid modulation patterns of frequency and amplitude, suggesting that these acoustic effects are generated by these muscles (Elemans et al., 2008a).

b) Two sound generators expand the frequency range in birds—Different songbird species make use of the two sound generators in different ways. As has been reviewed elsewhere (e.g., Suthers & Goller, 1997; Suthers et al., 1999; Suthers, 2004; Suthers & Zollinger, 2008), the dual sound sources allow generation of two independent tones simultaneously, in partial temporal overlap or alternating. In all investigated species, the left sound source tends to generate lower frequencies than the right, with a varying degree of overlap in the frequency ranges. Typically both sides contribute to the vocal repertoire, but exceptional lateralization of sound production to one side has been observed as well. Particularly in the Waterslager canary more than 90% of all song syllables are generated on the left side of the syrinx (Suthers 1999). This extreme lateralization is a product of human selection for low-frequency song syllables in this strain. Domestic canaries that have not been bred for particular song features use both sound generators more evenly (Suthers et al., 2004).

Lateralized production of sounds involves active closing of the silent side (Suthers, 1990; Allan & Suthers, 1994; Suthers et al., 1994). Unilateral phonation therefore involves activation of syringeal muscles on both, the phonating and silent side. Neural control of the silent side is as elaborate as control of the phonating side, which indicates that song motor control is not organized in the same lateralized pattern as speech motor control (Goller & Suthers, 1995; 1996a,b).

Both sound sources are used for generation of very low frequencies. These low frequencies may be generated in a condition where labial vibrations arise from a different dynamical regime than during generation of sounds with higher frequency (Jensen et al. 2007; Sitt et al., 2008). The low frequency sounds in the vocal repertoires of crows (*Corvus corone cornix*), European starlings (350–800 Hz) and zebra finches (480–1100 Hz) are rich in upper harmonic content and appear to be pulse tones. Airflow recordings in the latter two species indicate that both syringeal sides are used simultaneously to generate the low-frequency sounds. Sound pulses on each side occur either synchronously, suggesting that labial opening happens at the same time, or out of phase, resulting in a doubling of the frequency. In this case each side contributes half of the sound pulses at the same frequency (Jensen et al., 2007). How these phase relationships between the pulses on the two sides are regulated is unknown.

The production mechanism for these low-frequency sounds is reminiscent of the mechanism for pulse-tone generation (vocal fry) in the human larynx (e.g., Hollien et al. 1969; Whitehead et al. 1984; Blomgren et al., 1998). High-speed images of the crow syrinx illustrate the parallels with the vocal fold dynamics during vocal fry (Jensen et al., 2007). Long closure of the syringeal valve is interrupted by short opening events, which correspond to the sound pulses. The two sound sources either are synchronized and open simultaneously or alternate in pulse generation.

Similar to human voice this dynamic regime of labial vibration gives rise to sounds with rich harmonic content. The frequency of the pulse tone is positively correlated with the driving air sac pressure. Interestingly, both sets of labia generate the same frequency in this mode, whereas the respective frequency ranges are different for higher-frequency sounds (Jensen et al., 2007).

c) Transformation of aerodynamic into acoustic energy—The process of energy transfer at the labia involves tissue movement consisting of presumably two major components. A medial-to-lateral component interrupts the air stream as the labial tissue (Goller & Larsen 1997) or vocal fold (Titze, 2006) oscillates in and out of the tracheo-bronchial lumen (Figure 4). A second, cranial-to-caudal component refers to a wave-like movement of the tissue causing an asymmetric geometry (Figure 4). This component has been demonstrated in human vocal folds (Hirano et al., 1991; Boessenecker et al., 2007). It is extremely difficult to demonstrate this movement of the labial tissue experimentally in the intact syrinx. In birds, the cranial-caudal component therefore still remains hypothetical (Fee et al., 1998; Mindlin et al., 2003; Elemans et al., 2008b).

In the human vocal fold the changing convergent and divergent geometry results from its layered structure (Figure 5) (Hirano, 1974; Hirano et al., 1982). The specific biomechanical properties of the layer structure as well as the proximity to the driving aerodynamic force gives rise to a self-oscillating system (Titze 1988).

We have a general understanding of the tissue composition of the labia in birds. The majority of the tissue is extracellular matrix sandwiched between two layers of epithelium (Setterwall, 1901; Häcker, 1900; Frank et al., 2006). However, more detailed information about the histological composition of the labia as well as imaging during phonation is needed to confirm the assumption that a convergent/divergent tissue movement of the labia is possible (Mindlin & Laje, 2005).

d) Comparison with the functional morphology of the larynx—The human larynx consists of nine cartilages that form the skeletal framework (Figure 5). Five intrinsic muscles regulate ab- and adduction of the vocal folds as well as vocal fold tension by adjusting its length (Table 1). The biomechanics of gating airflow during respiration (Bartlett et al. 1973) and regulating fundamental frequency (e.g., Atkinson, 1978; Hirano et al., 1969; Gay et al., 1972; Shipp & McGlone, 1971) have been described in detail. The specific roles of laryngeal muscles in controlling a range of acoustic features in human vocalizations give a detailed picture of synergistic activity (Honda, 1983; Whalen et al., 1999). Humans modulate fundamental frequency of phonation primarily by vocal fold length changes (Hollien & Moore, 1960). Elongation of the vocal folds causes increased tension (i.e., force per cross-sectional area in the tissue), leading to an increase in fundamental frequency. It is important to note that only 2–3 superficial layers of the vocal fold oscillate. Each layer of the vocal fold responds with a different stress to elongation, thereby making it difficult to predict the overall tension and the amount of the tissue that will be recruited into oscillation. This mechanism of variable use of tissue may explain the observation that elongation patterns of the vocal folds for achieving a certain fundamental frequency or a frequency change are individual-specific (Nishizawa et al., 1988).

Laryngeal muscles for which data are available are characterized as very fast (Alipour et al., 2005; Hast, 1966; 1967), but do not reach such high contraction/relaxation rates as syringeal muscles in songbirds (Elemans et al., 2008a). Bird motor systems for song production appear to be specialized for high temporal performance with comparatively high respiratory and syringeal modulation rates. Small size most likely facilitates extremely fast kinetics.

Comparative data for the mammalian laryngeal muscles indicate less specialization for speed but instead for highly differentiated tension control (Sanders et al., 1998, Hoh, 2005).

The passive components of the vocal fold (i.e. the visco-elastic properties of the various layers, in particular the three layers of the *lamina propria* and the epithelium) support a differentiated tension pattern. The *lamina propria* in humans is further differentiated into a superficial, an intermediate and a deep layer (Figure 5), and the visco-elastic properties vary between layers (Chan et al. 2007). The physical characteristics relevant for sound generation are determined by the relative amounts of extracellular matrix components (collagen, elastin, hyaluronic acid) as well as the specific orientation of the fibrous elements (Gray et al., 1999).

e) Syrinx and larynx are nonlinear sound sources—The avian syrinx and mammalian larynx are sound sources that represent intrinsically nonlinear systems (syrinx: Fee et al., 1998; Mindlin & Laje, 2005; Elemans et al., 2008b; larynx: e.g. Herzel et al., 1994; Jiang et al., 2001). These nonlinear devices therefore provide sources for complex acoustic features without requiring equally complex neural control. Acoustic consequences of this nonlinearity have been documented for birds (e.g., Zollinger et al., 2008) and mammals (Riede et al., 1997; 2007; Tokuda et al., 2002) including humans (Titze et al., 2008).

Modeling approaches were most successful when considering concepts of nonlinear dynamics to simulate labial or vocal fold vibration. Two biomechanical conceptualizations that have successfully reproduced certain aspects of oscillatory behavior of human vocal folds and avian labia are the two-mass model (syrinx: Fee et al., 1998; Elemans et al., 2008b; larynx: Ishizaka & Flanagan, 1972; Steinecke & Herzel, 1995) and the flapping plate model (syrinx: Mindlin & Laje, 2005; larynx: Liljencrants, 1991) (Figure 4). In order to explain more detail, the models must include more of the biomechanical complexity of the natural organ, for example by increasing the number of oscillating masses (Tokuda et al., 2007) or by a conceptually different approach, the finite element models (see Titze, 2006 for a review and mathematical background on vocal fold modeling).

Exploration of the low-frequency, pulse-like sounds of the zebra finch yielded insight into how variable harmonic content may be generated at the sound source. Modeling the origin of vibrations indicates that the full spectrum of pulse-tone like sounds can be better described with a Saddle Node Limit Cycle model (SNLC) than with the Hopf bifurcation model. Upper harmonic content of song elements in the zebra finch is high in the pulse-tone like syllables, whereas high-frequency syllables are more tonal. This pattern can be replicated when the SNLC model is incorporated (Sitt et al., 2008; Amador & Mindlin, 2008). These findings suggest a physical underpinning to the distinction of vocal registers, whose definition remains controversial in the human speech literature.

3. Modifying sound by vocal tract properties and movements

The sound source (syrinx or larynx) produces a primary acoustic signal, which is then filtered as it passes through the vocal tract (source-filter theory) (Fant, 1960). The vocal tract of birds and humans comprises air spaces above and below the respective sound source, which in addition to filtering the sound may also be important in interacting with the sound source (Klatt, & Klatt, 1990; Titze, 2008).

The songbird vocal tract—The caudal location of the syrinx reduces subsyringeal areas to just a few millimeters of tube-like bronchial space before the primary bronchi fan into the parabronchi. It is not known whether the subsyringeal space affects the sound source or the generated sound. The main suprasyringeal resonance cavities are the tracheal tube and the oropharyngeal-esophageal cavity (OEC). Whereas the potential for adjusting tracheal length

is limited, the volume of the OEC can vary substantially through active adjustment. In addition, movements of the beak are prominent during song in many species.

Cardinals (*Cardinalis cardinalis*) and white-throated sparrows (*Zonotrichia albicollis*) adjust the volume of the OEC dynamically during song such that its primary resonance closely matches the fundamental frequency of sound (Riede et al., 2006; Riede & Suthers, 2009). In the cardinal, the estimated volume of the OEC ranges from 0 to 2 cm³. This matching of resonance to frequency may not only provide a mechanism for generating tonal sounds (Fletcher et al., 2006; Riede & Suthers, 2009), but also reduce attenuation of sound amplitude by upper vocal tract structures. It is also possible that the actively adjusted resonance may reinforce the sound generator. Whereas such a mechanism could explain how a small sound source can generate very high sound amplitudes (e.g., up to 100 dB in a 69 g song thrush, *Turdus philomelos*, and 90 dB in a 10 g winter wren, *Troglodytes troglodytes*; Gaunt, 1987), this hypothesis remains untested. In other species, as for example in the zebra finch, song syllables exhibit rich harmonic structure, and the resonances of the vocal tract cavity presumably reinforce certain upper harmonics rather than the fundamental frequency.

The discovery of an effective, actively controlled supra-syringeal filter in songbirds illustrates another strong parallel to human speech and therefore strengthens the potential usefulness of birdsong as an animal model in which to investigate vocal mechanisms relevant to speech production. The OEC in birds is formed by anatomical structures some of which are homologous to those used by humans for adjusting the geometry of the oral and pharyngeal cavity. These structures include the hyoid skeleton, the muscles of the mouth floor, the tongue, and the strap muscles. Unlike in humans, pharyngeal constrictors (superior pharyngeal constrictor muscle, inferior pharyngeal constrictor muscle, middle pharyngeal constrictor muscle) are missing in birds (Homberger & Meyers, 1989; George & Berger, 1966), which enables them to form a wide-spaced, expandable connection from the oropharyngeal space into the esophagus. X-ray images of cardinals and white-throated sparrows suggest that the cranial third of the esophagus becomes part of the cavity that is formed during the production of low-frequency syllables, thus providing a lower resonance (Riede et al., 2006; Riede & Suthers, 2009).

The motor pattern used by birds to manipulate the size of the OEC probably originates from a phylogenetically old motor pattern, associated with ventilation. This buccal pumping is still used by reptiles for respiratory purposes (Owerkowicz et al., 1999). The hyoid skeleton in birds represents the mechanical framework for expansion of the oral and pharyngeal cavity such that muscle shortening is converted into abduction of the skeletal elements (Homberger, 1986; Homberger & Meyers, 1989). Morphological studies suggest that at least 12 different muscles are involved in this movement (George & Berger, 1966; Homberger, 1986), however their role has only been studied during feeding (Zweers, 1974) and not during phonation.

Beak gape adjustments are another prominent behavior associated with singing. Whereas beak gape is positively correlated with fundamental frequency, the strength of this correlation varies between individuals and species (Riede & Suthers, 2009). There appears to be a beak-gape-threshold beyond which its acoustic effects remain constant (Fletcher & Tarnopolski, 1999; Nelson et al., 2005). The major acoustic role of the beak is that of a radiating device or orifice for transfer of sound to the free air space, and its role as an effective component of the vocal tract is limited.

Other potentially important upper vocal tract structures are the tongue and glottis. The songbird tongue is relatively immobile and its role in adjusting upper vocal tract resonances is poorly investigated. Glottal opening may also play a role in adjusting acoustic impedances for sound radiation, but it is not known whether the glottal valve is used in this way during singing.

The human vocal tract—The human vocal tract has often been modeled as a series of cylindrical tubes of different diameters and lengths, which are added to determine total vocal tract length. The filter properties for any vowel can be approximated by a 2-tube or a 4-tube model (Fant, 1960, Stevens, 1972). Whereas such basic models capture the perceptually relevant main features of vowels, more sophisticated approaches incorporating more detail of the vocal tract are necessary for reproducing individual-specific features of a speaking or singing voice or subtle features such as context specificity. Interestingly, any given set of formants can be produced by more than one shape of the vocal tract (Atal et al., 1978; Bonder, 1983; Boë et al., 1989; Schwartz et al., 1997; Story et al., 2001).

The human sublaryngeal vocal tract consists of the tracheal space (approx. 13 cm long and 2 cm wide), which appears to have strong interactive effects on the sound source (reviewed by Titze, 2008). The supra-laryngeal vocal tract consists of various spaces that have already been studied anatomically (e.g. Story et al., 1996; Vorperian et al., 2009) and acoustically. It includes a 2 to 3 cm long intralaryngeal non-flexible space, the epilaryngeal tube (Sundberg, 1974), the pharyngeal and oral cavity, the nasal cavity (Pruthi et al., 2007) and various pocket-like extensions, like the piriform fossa (Dang & Honda, 1996) or the lateral laryngeal ventricle (Finnigan & Alipour, 2009). All of these structures can play a critical role in source filter interactions (Titze & Story, 1997).

Linear versus nonlinear source-filter interaction—The linear source-filter theory has been widely used to explain sound production in human speech (Fant, 1960; Titze, 1994) and birdsong (Rüppell, 1933; Nowicki, 1987). This model predicts that the oscillations of the sound source are independent of the filter properties of the upper vocal tract. However, growing evidence suggests that linear and nonlinear source filter interactions play a role in voice quality adjustments for speaking and different styles of singing (Titze, 2008; Titze et al., 2008). Nonlinear source-filter interaction has also been explored theoretically for the avian syrinx (Laje and Mindlin, 2005), but experimental evidence for source-filter interactions is still missing. The basic idea of a nonlinear interaction is that relative areas or lengths of the lower supra-laryngeal vocal tract (i.e. epilarynx, the pharynx, the piriform sinuses) and the nasal tract are varied in such a way that the spectrum of the source signal, the glottal waveform, and the phonation threshold pressure are affected (Titze & Story, 1997). These adjustments of the vocal tract filter properties generate resonance effects that can either increase or decrease the efficiency in transforming fluid dynamic energy into sound.

CONCLUSIONS

The vocal organs and respiratory systems of birds and humans are very different in their functional morphology. Despite these differences however, strong convergent patterns emerge. The basic physical sound generating mechanism in both systems involves soft tissue masses that form an aerodynamic, myoelastic sound source. Based on this basic design of sound generation, neural control targets, such as regulation of airflow and sound frequency are also shared, although detailed patterns of motor gestures are subject to the biomechanical circumstances of each vocal organ. Vocal tract filtering involves in part homologous structures in birds and mammals, but morphological differences again determine specific mechanisms of adjusting resonances. Central neural control of vocal behavior must therefore accommodate these pronounced differences in peripheral mechanisms, limiting the possibility for strong parallels at that level to more general neural processing mechanisms.

The exploration of human speech physiology has a much longer tradition than research on the sound producing mechanisms in birds. Consequently, a much more detailed picture is available, including functional morphology, biomechanics, physiology and acoustics. Physiological research on songbirds is impeded by their small size and related technical difficulties. In

addition, investigation of vocal production in songbirds has focused research effort on a different aspect of physiology, namely the foundation of vocal diversity within and between species. More detailed information about the biomechanical system in songbirds is needed to make the comparison with the human vocal system more fruitful. The ability to perform experimental manipulations in birds will then enable us to explore general aspects of sound generating systems. This combined approach will help to further unravel proximate mechanisms for producing complex vocal behavior but also shed light on the evolutionary forces underlying these mechanisms.

Acknowledgments

We thank Kanako Omichi for the artwork. The authors' research has been supported by NIH DC 04390 and DC 06876 to F.G., a subaward to T.R. (NIH DC 008612) and a Postdoctoral fellowship by the 'Deutsche Akademie der Naturforscher Leopoldina' (BMBF-LPD 9901/8-127) to T.R.

References

- Alipour F, Titze IR, Hunter R, Tayama N. Active and passive properties of canine abduction/adduction laryngeal muscles. *J Voice* 2005;19:350–359. [PubMed: 16102663]
- Allan SE, Suthers RA. Lateralization and motor stereotypy of song production in the brown-headed cowbird. *J Neurobiol* 1994;25:1154–1166. [PubMed: 7815070]
- Amador A, Mindlin GB. Beyond harmonic sounds in a simple model for birdsong production. *Chaos* 2008;18:043123. [PubMed: 19123633]
- Ames, PL. Peabody Museum of Natural History. Yale University; 1971. The morphology of the syrinx in passerine birds. Bulletin 37.
- Atal B, Chang J, Mathews M, Tukey J. Inversion of articulatory-to-acoustic transformation in the vocal tract by a computer sorting technique. *J Acoust Soc Am* 1978;63:1535–1556. [PubMed: 690333]
- Atkinson JE. Correlation analysis of physiological factors controlling fundamental voice frequency. *J Acoust Soc Am* 1978;63:211–222. [PubMed: 632414]
- Bartlett D, Remmers JE, Gautier H. Laryngeal regulation of respiratory airflow. *Respir Physiol* 1973;18:194–204. [PubMed: 4730751]
- Beckers GJL, Suthers RA, ten Cate C. Pure-tone birdsong by resonance filtering of harmonic overtones. *Proc Natl Acad Sci USA* 2003;100:7372–7376.
- Blomgren M, Chen Y, Ng ML, Gilbert HR. Acoustic, aerodynamic, physiologic, and perceptual properties of modal and vocal fry registers. *J Acoust Soc Am* 1998;103:2649–2658. [PubMed: 9604359]
- Boë LJ, Perrier P, Guérin B, Schwartz J-L. Maximal vowel space. *Eurospeech* 1989;89:281–284.
- Boessenecker A, Berry DA, Lohscheller J, Eysholdt U, Doellinger M. Mucosal wave properties of a human vocal fold. *Acta Acust Acustica* 2007;93:815–823.
- Bonder LJ. Equivalency of lossless n-tubes. *Acustica* 1983;53:193–200.
- Bouhyus A, Mead J, Proctor DF, Stevens KN. Pressure-flow events during singing. *Ann NY Acad Sci* 1968;155:165–176.
- Brackenbury, JH. Functions of the syrinx and the control of sound production. In: King, AS.; McLelland, J., editors. *Form and function in birds*. London: Academic Press; 1989. p. 193-220.
- Chan RW, Titze IR. Dependence of phonation threshold pressure on vocal tract acoustics and vocal fold tissue mechanics. *J Acoust Soc Am* 2006;119:2351–2362. [PubMed: 16642848]
- Chan RW, Fu M, Young L, Tirunagari N. Relative contributions of collagen and elastin to elasticity of the vocal fold under tension. *Ann Biomed Eng* 2007;35:1471–1483. [PubMed: 17453348]
- Dang J, Honda K. Acoustic characteristics of the piriform fossa in models and humans. *J Acoust Soc Am* 1996;100:3374–3383. [PubMed: 8914318]
- Doupe A, Kuhl P. Birdsong and human speech: common themes and mechanisms. *Ann Rev Neurosci* 1999;22:567–631. [PubMed: 10202549]

- Doupe, A.; Kuhl, P. Birdsong and human speech: common themes and mechanisms. In: Zeigler, HP.; Marler, P., editors. *Neuroscience of birdsong*. Cambridge: Cambridge University Press; 2008. p. 5-31.
- Draper MH, Ladefoged P, Whitteridge D. Respiratory muscles in speech. *J Speech Hear Res* 1959;2:16–27. [PubMed: 13655288]
- Elemans CPH, Mead AF, Rome LC, Goller F. Superfast vocal muscles control song production in songbirds. *PLoS ONE* 2008;3:e2581. [PubMed: 18612467]
- Elemans CPH, Zaccarelli R, Herzog H. Biomechanics and control of vocalization in a non-songbird. *J Royal Soc Interface* 2008;5:691–703.
- Fant, G. *Acoustic theory of speech production*. The Hague: Mouton; 1960.
- Fedde MR, Burger RE, Kitchell RL. Electromyographic studies of the effects of bodily position and anesthesia on the activity of the respiratory muscles of the domestic cock. *Poult Sci* 1964a;43:1119–1125.
- Fedde MR, Burger RE, Kitchell RL. Anatomic and electromyographic studies of the costopulmonary muscles in the cock. *Poult Sci* 1964b;43:1177–1184.
- Fee MS. Measurement of the linear and nonlinear mechanical properties of the oscine syrinx: implications for function. *J Comp Physiol A* 2002;188:829–839.
- Fee MS, Shraiman B, Pesaran B, Mitra PP. The role of nonlinear dynamics of the syrinx in the vocalizations of a songbird. *Nature* 1998;395:67–71. [PubMed: 12071206]
- Finnegan EM, Alipour F. Phonatory effects of supraglottic structures in excised canine larynges. *J Voice* 2009;23:51–61. [PubMed: 17400425]
- Fletcher NH, Tarnopolsky A. Acoustics of the avian vocal tract. *J Acoust Soc Am* 1999;105:35–49.
- Fletcher NH, Riede T, Suthers RA. Models for vocalization by a bird with distensible vocal cavity and open beak. *J Acoust Soc Am* 2006;119:1005–1011. [PubMed: 16521762]
- Frank T, Walter I, Probst A, Koenig HE. Histological aspects of the syrinx of the mallard (*Anas platyrhynchos*). *Anat Histol Embryol* 2006;35:396–401. [PubMed: 17156094]
- Franz M, Goller F. Respiratory patterns and oxygen consumption in singing zebra finches. *J Exp Biol* 2003;206:967–978. [PubMed: 12582139]
- Gaunt AS. An hypothesis concerning the relationship of syringeal structure to vocal abilities. *Auk* 1983;100:853–862.
- Gaunt, AS. Phonation. In: Seller, TJ., editor. *Bird respiration*. Boca Raton: CRC Press; 1987. p. 71-94.
- Gaunt AS, Gaunt SLL, Casey RM. Syringeal mechanics reassessed: evidence from *Streptopelia*. *Auk* 1982;99:474–494.
- Gay T, Strome M, Hirose H, Sawashima M. Electromyography of intrinsic laryngeal muscles during phonation. *Annals of Otolaryngology and Laryngology* 1972;81:401–410.
- George, JC.; Berger, AJ. *Avian Myology*. Academic; New York: 1966.
- Goldstein MH, King AP, West M. Social interaction shapes babbling: Testing parallels between birdsong and speech. *Proc Natl Acad Sci USA* 2003;100:8030–8035. [PubMed: 12808137]
- Goller F, Cooper BG. Peripheral motor dynamics of song production in the zebra finch. *Ann NY Acad Sci* 2004;1016:130–152. [PubMed: 15313773]
- Goller, F.; Cooper, BG. Peripheral mechanisms of sensorimotor integration during singing. In: Zeigler, HP.; Marler, P., editors. *Neuroscience of birdsong*. Cambridge: Cambridge University Press; 2008. p. 99-114.
- Goller F, Daley MA. Novel motor gestures for phonation during inspiration enhance the acoustic complexity of birdsong. *Proc Roy Soc Lond B* 2001;268:2301–2305.
- Goller F, Larsen ON. A new mechanism of sound generation in songbirds. *Proc Natl Acad Sci USA* 1997;94:14787–14791. [PubMed: 9405691]
- Goller F, Larsen ON. New perspectives on mechanisms of sound generation in songbirds. *J Comp Physiol A* 2002;188:841–850.
- Goller F, Suthers RA. Implications for lateralization of bird song from unilateral gating of bilateral motor patterns. *Nature* 1995;373:63–66.
- Goller F, Suthers RA. Role of syringeal muscles on gating airflow and sound production in singing brown thrashers. *J Neurophysiol* 1996a;75:867–876. [PubMed: 8714659]

- Goller F, Suthers RA. Role of syringeal muscles in controlling the phonology of bird song. *J Neurophysiol* 1996b;76:287–300. [PubMed: 8836225]
- Goller F, Suthers RA. Bilaterally symmetrical respiratory activity during lateralized birdsong. *J Neurobiol* 1999;41:513–523. [PubMed: 10590175]
- Gray SD, Titze IR, Chan R. Vocal fold proteoglycans and their influence on biomechanics. *Laryngoscope* 1999;109:845–854. [PubMed: 10369269]
- Greenewalt, CH. *Bird song: Acoustics and physiology*. Washington D.C: Smithsonian Institution Press; 1968.
- Häcker, V. *Der Gesang der Vögel und seine anatomischen Grundlagen*. Jena, Germany: Gustav Fischer; 1900.
- Hartley RS. Expiratory muscle activity during song production in the canary. *Respir Physiol* 1990;81:177–187.
- Hartley RS, Suthers RA. Airflow and pressure during canary song: direct evidence for mini-breaths. *J Comp Physiol A* 1989;165:15–26.
- Hast MH. Mechanical properties of the cricothyroid muscle. *Laryngoscope* 1966;76:537–548.
- Hast MH. Mechanical properties of the vocal fold muscle. *Pract Oto-rhinolaryng* 1967;29:53–56.
- Herzel H, Berry D, Titze IR, Saleh S. Analysis of vocal disorders with methods from nonlinear dynamics. *J Speech Hear Res* 1994;37:1008–1019. [PubMed: 7823547]
- Hirano M. Morphological structure of the vocal cord as a vibrator and its variations. *Folia Phoniatr Basel* 1974;26:89–94. [PubMed: 4845615]
- Hirano M, Ohala J, Vennard W. The function of the laryngeal muscles in regulating fundamental frequency and intensity of phonation. *J Speech Hear Res* 1969;12:616–628. [PubMed: 5811852]
- Hirano M, Kikita Y, Ohmaru K, Kurita S. Structure and mechanical properties of the vocal fold. *Speech Lang* 1982;7:271–297.
- Hoh JFY. Laryngeal muscle fiber types. *Acta Physiologica Scandinavica* 2005;183:133–149. [PubMed: 15676055]
- Hoit J, Hixon J. Body type and speech breathing. *J Speech Hear Res* 1986;29:313–324. [PubMed: 3762095]
- Hoit J, Hixon J. Age and speech breathing. *J Speech Hear Res* 1987;30:351–366. [PubMed: 3669642]
- Hollien H, Moore GP. Measurements of the vocal folds during changes in pitch. *J Speech Hear Res* 1960;3:157–165.
- Hollien H, Damste H, Murry T. Vocal fold length during vocal fry phonation. *Folia Phoniatr* 1969;21:257–265.
- Holmberg EB, Hillman ER, Perkell JS. Glottal airflow and transglottal air pressure measurements for male and female speakers in soft, normal and loud voice. *J Acoust Soc Am* 1988;84:511–529. [PubMed: 3170944]
- Homberger, DG. *The lingual apparatus of the African grey parrot, Psittacus erithacus Linne (Aves: Psittacidae): Description and theoretical mechanical analysis*. Washington, D.C: The American Ornithologist's Union; 1986.
- Homberger DG, Meyers RA. Morphology of the lingual apparatus of the domestic chicken, *Gallus gallus*, with special attention to the structure of the fasciae. *Am J Anatomy* 1989;186:217–257.
- Honda, K. Variability analysis of laryngeal muscle activity. In: Titze, IR.; Scherer, R., editors. *Vocal fold physiology: Biomechanics, acoustics, and phonatory control*. Denver: Denver Center for the Performing Arts; 1983.
- Hoshiko MS. Sequence of action of breathing muscles in speech. *J Speech Hear Res* 1960;3:291–297. [PubMed: 14403292]
- Hoshiko MS, Berger KW. Sequence of respiratory muscles activity during vocal attack. *Speech Monogr* 1965;32:185–191.
- Ishizaka K, Flanagan JL. Synthesis of voiced sounds from a two-mass model of the vocal cords. *Bell Syst Tech J* 1972;51:1233–1268.
- Jensen KK, Cooper BG, Larsen ON, Goller F. Songbirds use pulse tone register in two voices to generate low frequency sound. *Proc R Soc Lond B* 2007;274:2703–2710.

- Jiang JJ, Zhang Y, Stern J. Modeling of chaotic vibrations in symmetric vocal folds. *J Acoust Soc Am* 2001;110:2120–2128. [PubMed: 11681389]
- King, AS. Functional anatomy of the syrinx. In: King, AS.; McLelland, J., editors. *Form and function in birds*. London: Academic Press; 1989. p. 105-192.
- Klatt DH, Klatt LC. Analysis, synthesis and perception of voice quality variations among male and female talkers. *J Acoust Soc Am* 1990;87:820–856. [PubMed: 2137837]
- Larsen ON, Goller F. Direct observation of syringeal muscle function in songbirds and a parrot. *J Exp Biol* 2002;295:25–35. [PubMed: 11818409]
- Liljencrants, J. Speech Transmission Laboratory Quarterly Progress and Status Report 1. Royal Institute of Technology; Stockholm: 1991. A translating and rotating mass model of the vocal folds; p. 1-18.
- Lucero JC, Koenig LL. On the relation between the phonation threshold lung pressure and the oscillation frequency of the vocal folds. *J Acoust Soc Am* 2007;121:3280–3283. [PubMed: 17552679]
- McLelland, J. Larynx and trachea. In: King, AS.; McLelland, J., editors. *Form and function in birds*. London: Academic Press; 1989a. p. 69-103.
- McLelland, J. Anatomy of the lungs and air sacs. In: King, AS.; McLelland, J., editors. *Form and function in birds*. London: Academic Press; 1989b. p. 221-279.
- Mindlin, GB.; Laje, R. *The physics of birdsong*. Berlin: Springer Verlag; 2005.
- Mindlin BG, Gardner TJ, Goller F, Suthers RA. Experimental support for a model of birdsong production. *Phys Rev E* 2003;68:041908.
- Miskimen M. Sound production in passerine birds. *Auk* 1951;68:493–504.
- Nelson BS, Beckers GJL, Suthers RA. Vocal tract filtering and sound radiation in a songbird. *J Exp Biol* 2005;208:297–308. [PubMed: 15634849]
- Nishizawa, N.; Sawashima, M.; Yonemoto, K. Vocal fold length in vocal pitch change. In: Fujimura, O., editor. *Vocal Physiology: Voice Production, Mechanisms and Functions*. New York: Raven Press; 1988. p. 75-82.
- Nottebohm F. Neural lateralisation of vocal control in a passerine bird. *I Song J exp Zool* 1971;177:229–262.
- Nottebohm, F. Asymmetries in neural control of vocalization in the canary. In: Harnard, S.; Doty, RW.; Goldstein, L.; Jaynes, J.; Krauthammer, G., editors. *Lateralization of the nervous system*. New York: Academic Press; 1977. p. 23-44.
- Nowicki S. Vocal tract resonances in oscine bird sound production: evidence from birdsongs in a helium atmosphere. *Nature* 1987;325:53–55. [PubMed: 3796738]
- Oberweger K, Goller F. The metabolic cost of birdsong production. *J Exp Biol* 2001;203:3379–3388. [PubMed: 11606611]
- Owerekowicz T, Farmer CG, Hicks JW, Brainerd EL. Contribution of gular pumping to lung ventilation in monitor lizards. *Science* 1999;284:1661–1663. [PubMed: 10356394]
- Plant RL, Freed GL, Plant RE. Direct measurement of onset and offset phonation threshold pressure in normal subjects. *J Acoust Soc Am* 2004;116:3640–3646. [PubMed: 15658714]
- Podos J. Motor constraint on vocal development in a songbird. *Anim Behav* 1996;51:1061–1070.
- Podos, J.; Nowicki, S. Performance limits on birdsong. In: Marler, P.; Slabbekoorn, H., editors. *Nature's music: The science of birdsong*. New York: Elsevier Academic Press; 2004. p. 318-342.
- Pruthi T, Epsy-Wilson CY, Story BH. Simulation and analysis of nasalized vowels based on magnetic resonance imaging data. *J Acoust Soc Am* 2007;121:3858–3873. [PubMed: 17552733]
- Riede T, Arcadi AC, Owren MJ. Nonlinear acoustics in pant hoots and screams of common chimpanzees (*Pan troglodytes*): Vocalizing at the edge. *J Acoust Soc Am* 2007;121:1758–1767. [PubMed: 17407912]
- Riede T, Wilden I, Tembrock G. Subharmonics, biphonations, and frequency jumps, common components of mammalian vocalization or indicators for disorders. *Zeitschr Säugetierkunde* 1997;62 (Suppl 2):198–203.
- Riede T, Suthers RA, Fletcher NH, Blevins WE. Songbirds tune their vocal tract to the fundamental frequency of their song. *Proc Natl Acad Sci USA* 2006;103:5543–5548. [PubMed: 16567614]
- Riede T, Suthers RA. Vocal tract motor patterns and resonance during constant frequency song: the white-throated sparrow. *J comp Physiol A* 2009;195:183–192.

- Roy N, Tanner K, Gray SD. An evaluation of the effects of three laryngeal lubricants on phonation threshold pressure. *J Voice* 2003;17:331–342. [PubMed: 14513956]
- Rüppell VW. Physiologie und Akustik der Vogelstimme. *J Ornithol* 1933;81:433–542.
- Sanders I, Han YS, Wang J, Biller H. Muscle spindles are concentrated in the superior vocalis subcompartment of the human thyroarytenoid muscle. *J Voice* 1998;12:7–16. [PubMed: 9619974]
- Schwartz JL, Boë LJ, Vallée N, Abry C. The dispersion-vocalization theory of vowel systems. *J of Phonetics* 1997;25:255–286.
- Sears TA, Newsom Davis J. The control of respiratory muscles during voluntary breathing. *Ann NY Acad Sci* 1968;155:183–190.
- Setterwall, CG. PhD dissertation. University of Lund; Sweden: 1901. Studier öfver syrinx hos polymyoda passerer; p. 133
- Shipp T, McGlone R. Laryngeal dynamics associated with voice frequency change. *J SpeechHear Res* 1971;14:761–768.
- Sitt JD, Amador A, Goller F, Mindlin GB. Dynamical origin of spectrally rich vocalizations in birdsong. *Phys Rev E* 2008;78:011905.
- Solomon NP, Ramanathan P, Makashay MJ. Phonation threshold pressure across the pitch range: Preliminary test of a model. *J Voice* 2007;21:541–550. [PubMed: 16753281]
- Steinecke I, Herzog H. Bifurcations in an asymmetric vocal fold model. *J Acoust Soc Am* 1995;97:1874–1884. [PubMed: 7699169]
- Stevens, KN. The quantal nature of speech: Evidence from articulatory-acoustic data. In: David, EE.; Denes, PB., editors. *Human communication: A unified view*. New York: Mc Graw Hill Book Co; 1972. p. 51-66.
- Story B, Titze I, Hoffman E. Vocal tract area functions from magnetic resonance imaging. *J Acoust Soc Am* 1996;100:537–554. [PubMed: 8675847]
- Story BH, Titze IR, Hoffman EA. The relationship of vocal tract shape to three voice qualities. *J Acoust Soc Am* 2001;109:1651–1667. [PubMed: 11325134]
- Sundberg J. Articulatory interpretation of the singing formants. *J Acoust Soc Am* 1974;55:838–844. [PubMed: 4833080]
- Suthers RA. Contributions to birdsong from the left and right sides of the intact syrinx. *Nature* 1990;347:473–477.
- Suthers, RA. The motor basis of vocal performance in songbirds. In: Hauser, MD.; Konishi, M., editors. *The design of animal communication*. Cambridge: MIT Press; 1999. p. 37-62.
- Suthers, RA. How birds sing and why it matters. In: Marler, P.; Slabbekoorn, H., editors. *Nature's music: The science of birdsong*. New York: Elsevier Academic Press; 2004. p. 272-295.
- Suthers, RA.; Goller, F. Motor correlates of vocal diversity in songbirds. In: Nolan, V., Jr ; Ketterson, E.; Thompson, CF., editors. *Current Ornithology*. New York: Plenum Press; 1997. p. 235-288.
- Suthers, RA.; Zollinger, SA. From brain to song: the vocal organ and vocal tract. In: Zeigler, HP.; Marler, P., editors. *Neuroscience of birdsong*. Cambridge: Cambridge University Press; 2008. p. 78-98.
- Suthers RA, Goller F, Hartley RS. Motor dynamics of song production by mimic thrushes. *J Neurobiol* 1994;25:917–936. [PubMed: 7964705]
- Suthers RA, Goller F, Pytte C. The neuromuscular control of birdsong. *Philos Trans Roy Soc Lond B* 1999;354:927–939. [PubMed: 10382225]
- Suthers RA, Vallet EM, Tanvez A, Kreutzer M. Bilateral song production in domestic canaries. *J Neurobiol* 2004;60:381–393. [PubMed: 15281075]
- Titze IR. The physics of small-amplitude oscillation of the vocal folds. *J Acoust Soc Am* 1988;83:1536–1552. [PubMed: 3372869]
- Titze IR. Phonation threshold pressure, a missing link in glottal aerodynamics. *J Acoust Soc Am* 1992a; 91:2926–2935. [PubMed: 1629485]
- Titze IR. Acoustic interpretation of the voice range profile (phonetogram). *J Speech Hearing Res* 1992b; 35:21–34. [PubMed: 1735970]
- Titze, IR. *The myoelastic aerodynamic theory of phonation*. Denver: The National Center for Voice and Speech; 2006.

- Titze IR. Nonlinear source-filter coupling in phonation: Theory. *J Acoust Soc Am* 2008;123:2733–2749. [PubMed: 18529191]
- Titze IR, Story BH. Acoustic interactions of the voice source with the lower vocal tract. *J Acoust Soc Am* 1997;101:2234–2243. [PubMed: 9104025]
- Titze IR, Riede T, Popollo P. Vocal exercises to determine nonlinear source-filter interaction. *J Acoust Soc Am* 2008;123:1902–1915. [PubMed: 18396999]
- Tokuda I, Riede T, Neubauer J, Owren MJ, Herzel H. Nonlinear analysis of irregular animal vocalizations. *J Acoust Soc Am* 2002;111:2908–2919. [PubMed: 12083224]
- Tokuda IT, Horacek J, Svec JG, Herzel H. Comparison of biomechanical modeling of register transitions and voice instabilities with excised larynx experiments. *J Acoust Soc Am* 2007;122:519–531. [PubMed: 17614509]
- Uchida AM, Green J, Ahmad S, Goller F, Meyers RA. Sexual dimorphism of syringeal muscles in songbirds. *Integr Comp Biol* 2009;49:e318.
- Van den Berg J. Myoelastic-aerodynamic theory of voice production. *J Speech Hear Res* 1958;1:227–243. [PubMed: 13576514]
- Vicario DS. Contributions of syringeal muscles to respiration and vocalization in the zebra finch. *J Neurobiol* 1991;22:63–73. [PubMed: 2010750]
- Verdolini K, Titze IR, Fennell A. Dependence of phonatory effort on hydration level. *J Speech Hearing Res* 1994;37:1001–1007. [PubMed: 7823546]
- Vorperian HK, Wang S, Chung MK, Schimek EM, Durtschi RB, Kent RD, Ziegert AJ, Gentry LR. Anatomic development of the oral and pharyngeal portions of the vocal tract: An imaging study. *J Acoust Soc Am* 2009;125:1666–1678. [PubMed: 19275324]
- Watson PJ, Hoit JD, Lansing RW, Hixon TJ. Abdominal muscle activity during classical singing. *Journal of Voice* 1989;3:24–31.
- Whalen DH, Gick B, Kumada M, Honda K. Cricothyroid activity in high and low vowels: exploring the automaticity of intrinsic F0. *J Phonet* 1999;27:125–142.
- Whitehead RL, Metz DE, Whitehead BH. Vibratory patterns of the vocal folds during pulse register phonation. *J Acoust Soc Am* 1984;75:1293–1297. [PubMed: 6725780]
- Wild, JM. Birdsong: anatomical foundations and central mechanisms of sensorimotor integration. In: Zeigler, HP.; Marler, P., editors. *Neuroscience of birdsong*. Cambridge: Cambridge University Press; 2008. p. 136-151.
- Wild JM, Goller F, Suthers RA. Inspiratory muscle activity during bird song. *J Neurobiol* 1998;36:441–453. [PubMed: 9733078]
- Zeigler, HP.; Marler, P. *Neuroscience of birdsong*. Cambridge: Cambridge University Press; 2008.
- Zollinger SA, Riede T, Suthers RA. Two-voice complexity from a single side of the syrinx in northern mockingbird *Mimus polyglottos* vocalizations. *J Exp Biol* 2008;211:1978–1991. [PubMed: 18515729]
- Zweers GA. Structure, movement, and myography of the feeding apparatus of the mallard (*Anas platyrhynchos* L.): A study in functional anatomy. *Netherlands J Zoology* 1974;24:323–467.

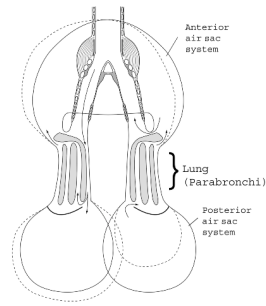


Figure 1.

Schematic view of the avian respiratory system, illustrating the lung-air sac system. Air sacs are functionally separated into an anterior and posterior set (although each set is comprised of at least 2 anatomically separate air sacs) and attach to the cranial and caudal end of the lung, respectively. Airflow during inspiration is driven by expanding air sacs (right) and expiration by compression of air sacs (left) as indicated by arrows and stippled boundaries. The lung is a set of rigid tube-like parabronchi through which oxygenated air flows during both respiratory phases.

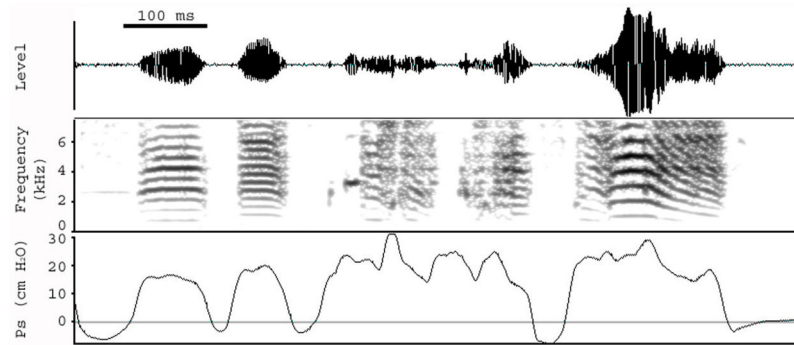


Figure 2. Example of a song motif from a zebra finch (top, oscillogram and middle, spectrogram) with subsyringeal air sac pressure (cm H₂O; ambient pressure is zero indicated by gray horizontal line). Pressure conditions for sound onset are near 10 cm H₂O and silent periods during song correspond to short inspirations, mini-breaths.

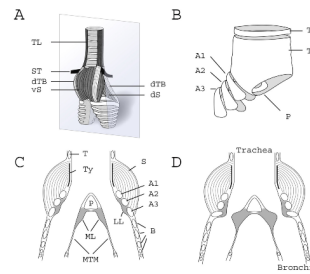


Figure 3.

The syrinx is a complex structure composed of a cartilage framework which contains the vibratory tissue and provides attachment for 6 pairs of syringeal muscles. **A.** The schematic external ventral view of the excised organ illustrates the syringeal muscles, which cover the cartilage framework of the syrinx, the tympanum. **B.** The cartilage components (schematic view modified after Ames, 1971) consists of the tympanum (Ty) and free specialized tracheo-bronchial semi-rings (A1–A3), which provide attachment sites for syringeal muscles. The tympanum contains in its caudal end a dorso-ventral bar (P, pessulus), which spans the lumen of the trachea and forms the separation from trachea into the primary bronchi. The pessulus is an important attachment for the medial labium. **C:** Schematic of a cross section of the syrinx. (Ty, tympanum; T, tracheal ring; P, pessulus; ML, medial labium; LL, lateral labium; A1–A3, tracheo-bronchial semi-rings; B, bronchial rings; **D:** schematic of the adducted position of the labia. The gray plane in A. indicates the level of sectioning in C. and D.

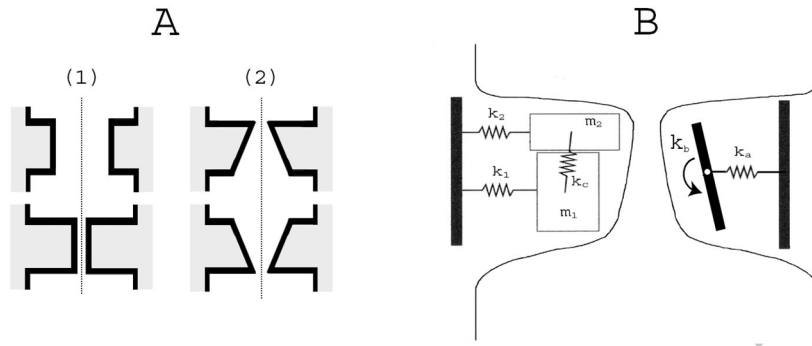


Figure 4.

A. Schematic cross sectional view through an aerodynamic myoelastic sound source. The vibrating tissue masses (portions of lateral and medial labia in the case of a songbird, vocal folds in the human case) undergo two major components of movement, one latero-lateral component and a cranio-caudal component. During the movement the shape of the vibrating tissue presumably changes between a convergent and divergent cross-sectional profile. This out-of-phase movement of the upper and lower part of the tissue produces larger asymmetries in the forces that act on it during the opening and closing phase of the oscillation than would be the case if only an in- and outward movement of a tissue portion occurred. Such a pattern results in a positive pressure on the tissue during the opening phase and a net energy input to the tissue maintaining a self-sustained oscillation.

B. Sound sources have been modeled as two-mass models (left side) or as flapping-plate like models (right side).

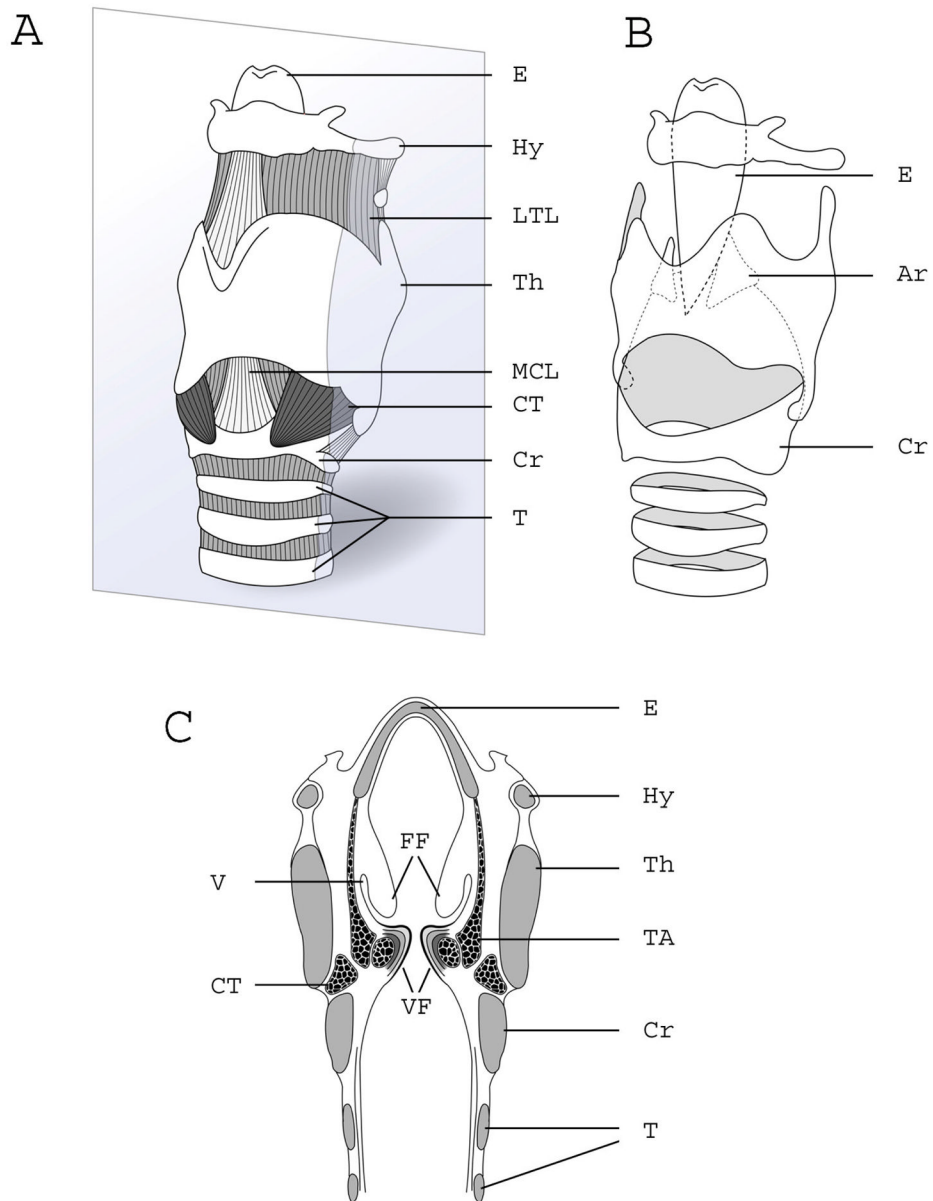


Figure 5.

The larynx is composed of a cartilage framework which contains the vocal folds. **A.** The schematic external ventral view of the excised organ. **B.** The cartilage components are the epiglottis (E), the thyroid cartilage (Th), the cricoid cartilage (Cr), the arytenoid cartilages (Ar). The hyoid bone (Hy) provides attachment for the muscles of the mouth floor, the tongue and the larynx. The thyrohyoid membrane (ThM) or median cricothyroid ligament (MCL) are among the ligamentous structures supporting the framework of cartilages and bones. **C.** Schematic of a cross section of the larynx. (T, tracheal rings; CT, cricothyroid muscle; TA, thyroarytenoid muscle; V, lateral laryngeal ventricle; FF, ventricular or false folds; VF, vocal folds). Note that the vocal fold consists of various layers. The gray plane in A. indicates the level of sectioning in C.

Table 1

The morphology of the avian and human sound source.

	Syrinx	Larynx
Cartilage framework	Tympanum with pessulus; 3 tracheo-bronchial half-rings	Thyroid cartilage; Cricoid cartilage 2 arytenoids cartilages Epiglottis 2 corniculate cartilages 2 cuneiform cartilages
Oscillating soft tissue	Two sets of medial and lateral labia, one in each primary bronchus.	Left and right vocal fold. Specific singing styles also make use of the ventricular folds.
Intrinsic muscles		
Adductors	dS dTb	LCA* IA TA
Abductors	vTB, portions of vS (in zebra finch)	PCA
F0 (pitch) modulation	vS, dS(?) synergistic contributions from other muscles (?)	CT TA

* LCA, lateral cricoarytenoid muscle; PCA, posterior cricoarytenoid muscle; IA, interarytenoid muscle; TA, thyroarytenoid muscle; CT, cricothyroid muscle.