Tracheal Length Changes during Zebra Finch Song and Their Possible Role in Upper Vocal Tract Filtering

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Received 24 July 2003; accepted 10 September 2003

ABSTRACT: Sounds produced in the avian vocal organ may be modified by filter properties of the upper vocal tract. Possible mechanisms to actively control filter characteristics include movements of the beak, tongue, and larynx and adjustments of tracheal length. We investigated whether length changes of the trachea are a likely mechanism for adjusting upper vocal tract filter properties during song in the zebra finch (*Taeniopygia guttata*). Tracheal length was monitored at the basal end using sonomicrometry and was recorded together with subsyringeal air sac pressure and acoustic output. Tracheal shortening occurred at the onset of song bouts, and during each motif the tracheal length decreased during expiratory pressure pulses and increased during the short inspirations. A bilateral tracheal syringeal nerve cut confirmed that the initial shortening at the onset of the song bout is an active shortening of the trachea (i.e., mediated by syringeal muscle activity). The modulation of length during the motif was not affected by the denervation and is most likely driven by the pressurization of the interclavicular air sac. The absolute length change during the motif was small (<0.2 mm) and not clearly related to acoustic features of the song. For example, some high-frequency syllables, which are generated during inspiration, were accompanied by tracheal elongation. Because this elongation shifts tube resonances to lower frequencies, it is inconsistent with an active adjustment of length to enhance high frequency sounds. The small magnitude and inconsistent nature of dynamic tracheal length changes during song make it unlikely that they significantly affect vocal tract filter properties if the trachea is modeled as a rigid tube. J Neurobiol 59: 319–330, 2004

Keywords:* vocalization; trachea; resonance; air sac pressure; sonomicrometry; zebra finch; *Taeniopygia guttata

INTRODUCTION

Sound generation in birds occurs in a unique vocal organ, the syrinx, which is located in an unpaired air sac at the basal end of the trachea. Sound is typically produced by vibrations of membranes or labia (Goller and Larsen, 1997a,b; Fee et al., 1998; Larsen and Goller, 1999), which act as pneumatic valves similar to the proposed action of the mammalian vocal folds (Goller and Larsen, 2002). The resonances of the upper vocal tract are likely to affect the sounds generated in the syrinx. Because of the unique location of the syrinx at the basal end of the trachea, the trachea may also have a role in modifying vocalizations that is unique to birds.

In contrast to the recognized important role of the upper vocal tract in human speech (e.g., Kent, 1997), acoustic filter properties of suprasyringeal structures were initially viewed as relatively insignificant in birds (e.g., Greenewalt, 1968). More recently, however, experiments with birds singing in a heliox gas

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Contract grant sponsor: NIH; contract grant number: DC 04390.

DOI 10.1002/neu.10332

mixture showed more prominent upper harmonic content than in normal air, demonstrating that the vocal tract plays a role in suppressing upper harmonics, (Brittan-Powell et al., 1996; Nowicki, 1987). This suppression is present even as the fundamental frequency varies significantly between different syllables, suggesting that the filter properties are adjusted to track the fundamental frequency (Nowicki, 1987).

Filter properties of the upper vocal tract are determined by the characteristics of the trachea, larynx, mouth, nasal cavities (e.g., Nowicki and Marler, 1988; Suthers and Goller, 1997), and, possibly, the air sac system (e.g., Beckers et al., 2003). Because the vocal organ of birds is located at the basal end of the trachea or at the cranial end of the primary bronchi, the length of the suprasyringeal airways can provide an effective filter for frequencies that are typical of many bird songs. Bronchial formants have been identified to play a role in upper vocal tract filtering of calls in the oilbird (*Steatornis caripensis*) (Suthers, 1994), and enhanced tracheal length in a variety of bird groups may function to convey larger than natural body size through altered formant frequency dispersion (Fitch, 1999).

Like humans during speech, birds may be able modify the resonance characteristics of the upper vocal tract. Possible mechanisms for adjustment of filter properties are beak movements, tongue movements, glottal and laryngeal control of the airway opening, and adjustments of tracheal length. In songbirds, beak movement has received the most attention in both theoretical and empirical studies as a potential means of modifying the spectral content of song (Fletcher and Tarnopolsky, 1999; Westneat et al., 1993; Suthers and Goller, 1997; Hoese et al., 2000; Williams, 2001). Beak movements are thought to change the effective length of the tube, and, possibly the acoustic impedance at the cranial end, and thus, alter the filter characteristics of the upper vocal tract. Beak movements accompany many songs, and beak gape is positively correlated with the fundamental frequency of song syllables in swamp sparrows (*Melospiza georgiana*) (Westneat et al., 1993). Experimental manipulation of beak gape in white-throated sparrows (*Zonotrichia albicollis*), swamp sparrows, canaries (*Serinus canaria*), and cardinals (*Cardinalis cardinalis*) (Hoese et al., 2000; Suthers and Goller, 1997) leads to acoustic changes that are consistent with the hypothesis that beak movements function to modulate the filter properties of the upper vocal tract.

The other possible mechanisms for dynamically altering filter properties have not been explored experimentally. One of these possible mechanisms involves active changes of tracheal length. If approximated as a simple tube, the resonance of the upper vocal tract is determined by its length (Fletcher, 1988, 1989; Fletcher and Tarnopolsky, 1999). Contracting the tracheolateralis muscles might allow birds to dynamically adjust length during song (Goller and Suthers, 1996a,b). It is unknown whether direct changes of tracheal length also contribute to modifying the properties of the vocal tract filter.

In this study we test the hypothesis that dynamic changes in tracheal length modulate the filter properties of the upper vocal tract. We investigated this possibility by measuring tracheal length changes during song in zebra finches (*Taeniopygia guttata*). Male zebra finches sing stereotyped motifs of typically three to seven distinct syllables. Many syllables are characterized by low fundamental frequency and complex harmonic content, where upper harmonics often exceed the fundamental frequency in relative amplitude (Williams et al., 1989; Williams, 2001). Beak movements during song appear to support the idea that the effective length of the upper vocal tract is modified to adjust the filter properties. Here we show that stereotyped tracheal length changes occur during song, but that their magnitude is so small that they may not have a strong impact on upper vocal tract filtering.

METHODS

Animals

Four male zebra finches were isolated from the aviary and equipped with an elastic band around the upper thorax holding a Velcro tab on the back for later attachment of connectors and transducers. The "belted" bird was considered ready for surgery once he sang when presented with a female in a separate cage.

Surgical Procedure

The birds were anesthetized using isoflurane delivered in breathing air. To record air sac pressure, a flexible cannula was inserted into a posterior thoracic air sac, and connected to a miniature pressure transducer (Fujikura model FPM-02PG) attached to the Velcro tab and worn as a backpack by the bird. The response of the pressure transducer is linear within the ranges of pressures recorded during bird vocalization. Therefore, we report the pressures as output voltages, which typically correspond to a range between 8–25 cm H_2O during song.

Piezoelectric sonomicrometry crystals (0.7 mm; Sonometrics) were placed on the trachea about 6–7 mm apart at the location where the trachea enters the interclavicular air sac. The trachea was exposed by making a small longitudinal incision through the skin on the ventral base of the neck.

The ventral surface of the trachea was freed of the surrounding connective tissue, and crystals were secured using 6-0 silk suture, looped around one cartilage ring of the trachea, then further secured with a small amount of tissue cement (Nexaband). The lead wires from the piezoelectric crystals were passed subcutaneously behind the neck to the back, after leaving a single loop under the skin at the base of the neck to allow for head movement. The wound was closed using 6-0 suture and the bird was allowed to recover until it resumed singing spontaneously, usually within 2 days.

In one zebra finch, we made additional recordings of tracheal length change, air sac pressure, and acoustic output after denervation of the syrinx. The syrinx was denervated by bilaterally cutting the tracheosyringeal branch of the hypoglossal nerve (NXII). The nerve was accessed through an additional small incision approximately 1.5 to 2.0 cm above where the trachea enters the interclavicular air sac, and a segment of both nerves was removed to ensure that regeneration would not occur during the experimental period.

Sonomicrometry

We used sonomicrometry (Sonometrics) to directly measure changes in tracheal length during vocalization. Sonomicrometry uses piezoelectric crystal transducers to measure length change by recording the time for an ultrasonic sound pulse to travel from a transmitting crystal to a receiving crystal. Distance between the crystals is equal to velocity times travel time, where the velocity is the speed of sound through soft tissue (1540 $\mathrm{m \cdot s^{-1}}$), as indicated for vertebrate skeletal muscle (Goldman and Richards, 1954). This value is close to the velocity of sound through water (approx. 1525 $\mathrm{m \cdot s^{-1}}$ at 40°C). Although the crystals in this experiment were surrounded by connective tissue rather than muscle and sound velocity may have been slightly different from the assumed value, the main interest focused on relative change in distance between the crystals, rather than the precise absolute distance. Small changes in the value of sound propagation would not appreciably alter the results or main conclusions of this study.

The maximum distance over which a sonomicrometry signal can be reliably recorded from a crystal pair is limited because the intensity of the sound signal is inversely related to the squared distance from the emitting source. Due to the small diameter of the zebra finch trachea, the smallest available sonomicrometry crystals were used (0.7 mm; Sonometrics). For these crystals, reliable signals could be recorded only when the crystals were <1 cm apart. For this reason the crystals were implanted 6–7 mm apart along the basal end of the trachea, and the total length change of the trachea was estimated based on the fractional length change measured between the crystals. A similar method is commonly used in studies of *in vivo* muscle function (e.g., Biewener et al., 1998; Gillis and Biewener, 2000; Daley and Biewener, 2003).

Data Sampling and Tracheal Length Analysis

Between 10 and 20 songs were recorded from each bird over several days. The different measurements were recorded onto separate channels of a data recorder (TEAC 135T), and subsequently digitized into a computer using a sample rate of 32 kHz per channel (Data Translation 2821G) and analyzed using Signal software (version 3.1, Engineering Design). Microphone recordings were converted to spectrograms with frequency resolution of 78 Hz and temporal resolution of 12.8 ms. Average and standard deviations were calculated for respiratory pressure and tracheal length normalized to the song motif of each bird. Song duration varied little between songs for each individual, facilitating the calculation of average traces. The maximum within-song and between-song tracheal length changes were measured for each bird. We used these values to calculate the corresponding maximum change in harmonic frequency, formant frequency, and formant dispersion.

Quantitative Analysis of Tracheal Length and Frequency Characteristics

To explore the quantitative relationship between acoustic characteristics and tracheal length, we calculated average air sac pressure, tracheal length, fundamental frequency, and peak frequency for each note (i.e., acoustically distinct part of syllables). In order to pool data of the four individuals, the relative voltage values for air sac pressure and tracheal length were normalized. Measured values were divided by the difference between the maximum during the song and values during quiet respiration. Frequency values were determined from power spectra. If two simultaneous fundamental frequencies were present, we used the lower of the two frequency values for the analysis. Peak frequency of harmonic stacks was determined as the harmonic component with the highest energy. For each individual we measured notes from 5–10 motifs and entered the averages for each note in the motif into the analysis.

Linear regression analyses were performed to explore various relationships between the measured parameters (SigmaPlot 5). We excluded inspiratory notes ($n = 3$) from the data set because the subatmospheric pressure and tracheal lengthening during their production provided extreme values that masked the other relationships. All analyses including peak frequency as a variable were restricted to the notes that were classified as harmonic stacks (30 of the 34 notes). Notes with high fundamental frequency (>1500 Hz) lacking upper harmonics and notes with rapid, noisy FM were excluded.

RESULTS

Extent and Nature of Tracheal Length Change

The basal end of the trachea exhibited stereotyped patterns of length change during singing. Tracheal

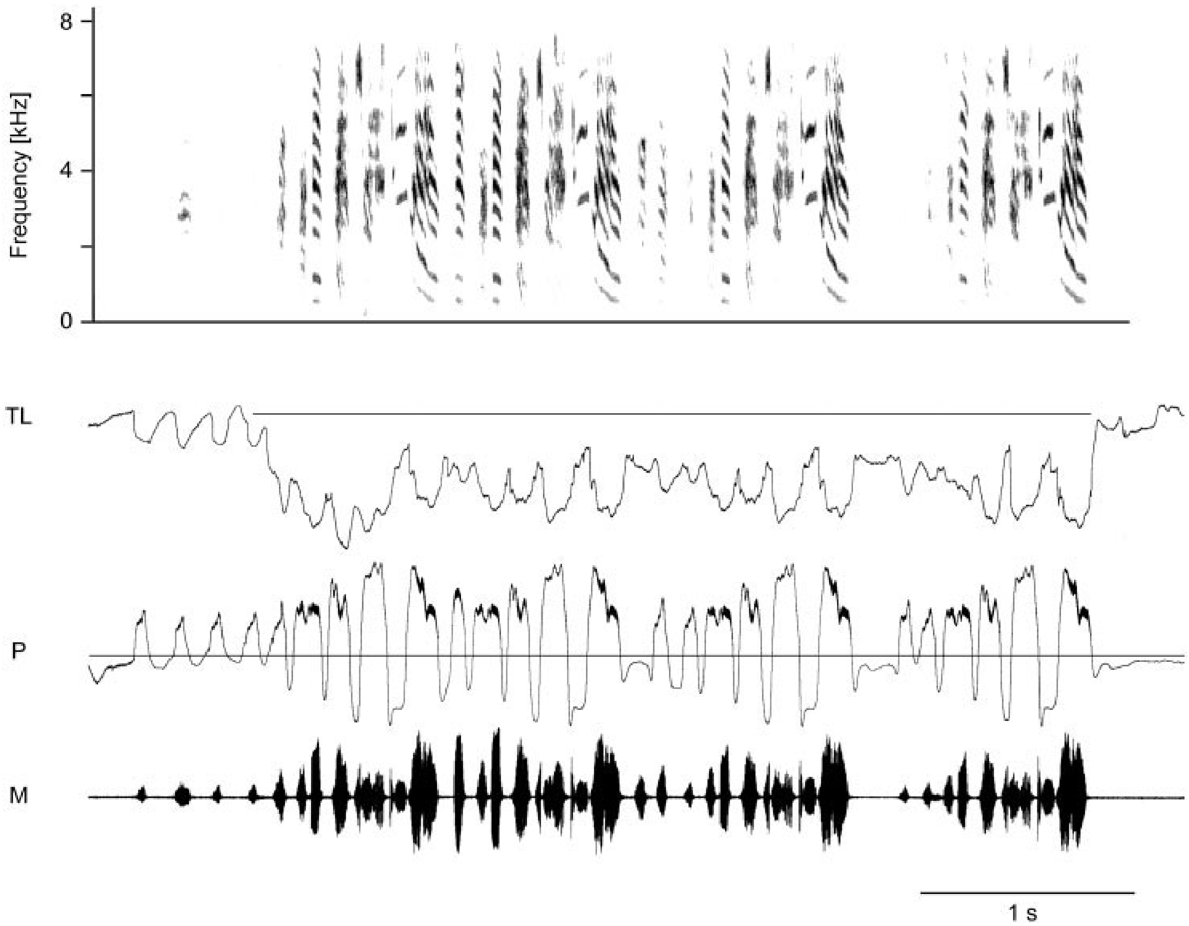

Figure 1 Zebra finch song bout (shown as oscillogram, M, and spectrographically, top) illustrating the relationship between phonation, subsyringeal air sac pressure (P; horizontal line is ambient pressure), and tracheal length change (TL). After a number of introductory notes, the trachea shortens at the beginning of the song, and only returns to presong levels at the end of the song bout. Each note in the song motif is accompanied by a highly stereotyped tracheal length change, which primarily follows changes in air sac pressure. The trachea shortens during expiration and lengthens during inspiration.

shortening occurred at the beginning of each song bout, typically at the onset of the first motif after the introductory notes. At the end of the bout, tracheal length returned to presong levels (Fig. 1). During each expiratory pulse of the song motif, the basal end of the trachea shortened, while its length increased during intersyllable inspirations (minibreaths) (Fig. 2). Within a song bout, tracheal length change correlated primarily with the pattern of air sac pressure for all individuals in the study (Fig. 3). In many cases, even small fluctuations in air sac pressure during the expiratory pulses of the motif were accompanied by corresponding changes in tracheal length. In addition, differences in air sac pressure between two similar syllables were also reflected in the pattern of tracheal length change (Fig. 4). For individual sound segments (notes) there was a significant negative linear relationship between air sac pressure and tracheal length for all individuals. As air sac pressure increased, tracheal length decreased (Fig. 5).

Although all four birds in this study showed a high degree of stereotypy in the tracheal shortening pattern within the song bout, the changes associated with any individual syllable were very small (within motif maximal 0.2 mm; Table 1). A major part of the shortening of the trachea always occurred at the beginning of the song bout (between 42 and 66% of the total observed length change). At the end of the song the trachea lengthened again to presong levels. For comparison, the length changes during a song bout are typically smaller than length changes observed during small head turning.

In addition, in the one bird where crystals were originally placed more distant from the syrinx, we

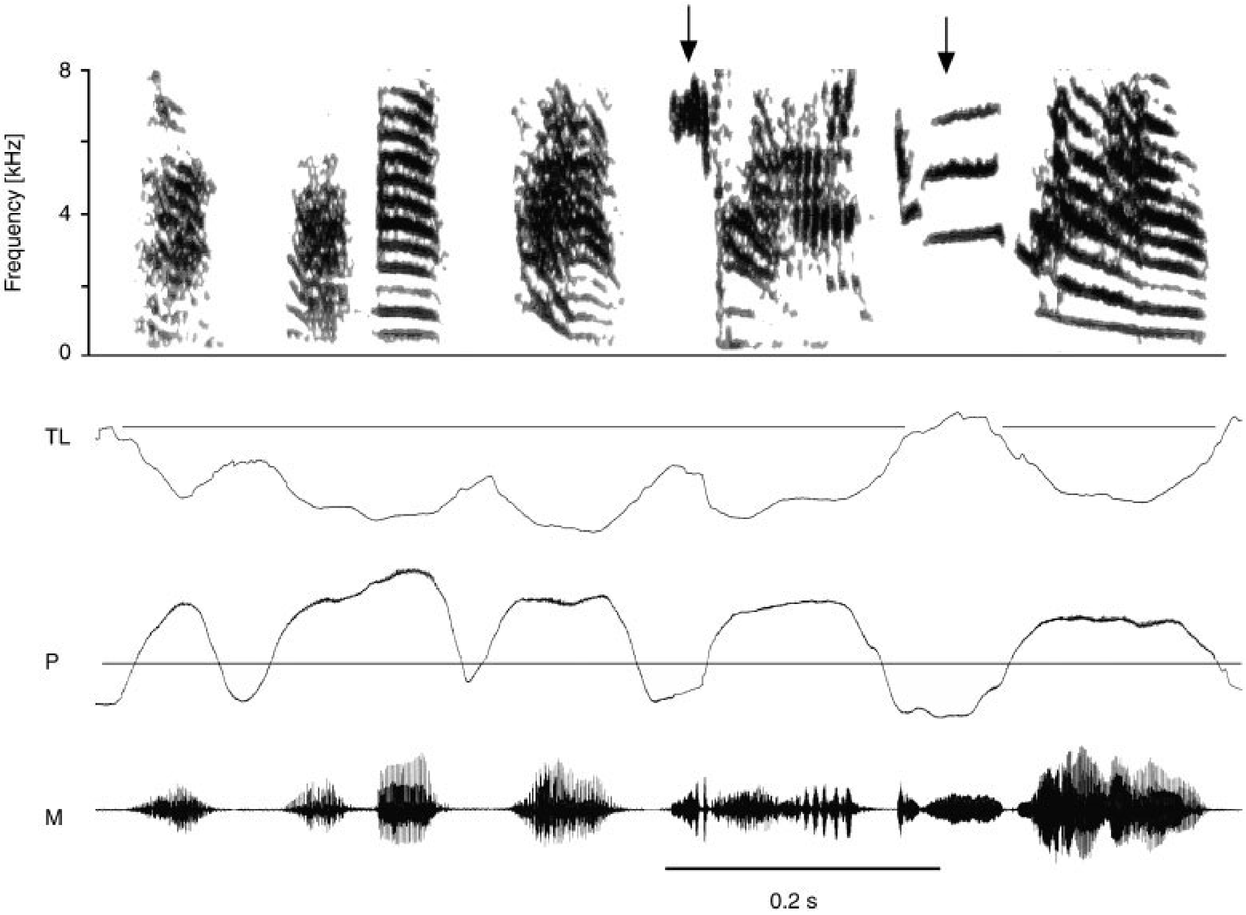

Figure 2 Tracheal length (TL) and subsyringeal air sac pressure (P) relate inversely within the song motif. The trachea shortens with increased air sac pressure during expiration and lengthens with negative air sac pressure during inspiration. Note that tracheal lengthening occurs during silent intersyllable inspirations as well as during inspiratory syllables (arrows).

observed a pattern of occasional shortening and even lengthening during the song (data not displayed). In this experiment the crystals were positioned on the segment of the trachea that runs from a lateral, right position to the medial position relative to the neck. This section is most affected by head turning, making it difficult to distinguish among tracheal length changes related to air sac pressurization, tracheolateralis muscle activity, and head movement.

Are Length Changes Related to the Acoustic Structure of Notes?

We found no significant relationship between tracheal length and fundamental frequency of notes (linear regression, $F = 0.832, p = 0.37, R^2 = 0.03$). Moreover, the highest frequency syllables in the song of ZFY16 were sung during minibreaths with tracheal length being at its maximum for the song (Fig. 2). Within harmonic stacks, peak frequency decreased with increased tracheal length [Fig. 5(a)]. However, tracheal length is also related to subsyringeal air sac pressure [Fig. 5(b)]. We accounted for this relationship by regressing peak frequency onto residual tracheal length (TL × P) [Fig. 5(c)]. Peak frequency of harmonic stacks still showed a significant negative relationship to the residuals from the regression analysis of tracheal length and air sac pressure [Fig. 5(c)]. This suggests that tracheal shortening greater than expected from the relationship with air sac pressure was associated with a shift of harmonic emphasis to higher frequencies. However, the explained variance dropped to 16%, confirming the important role of the relationship between tracheal length and air sac pressure.

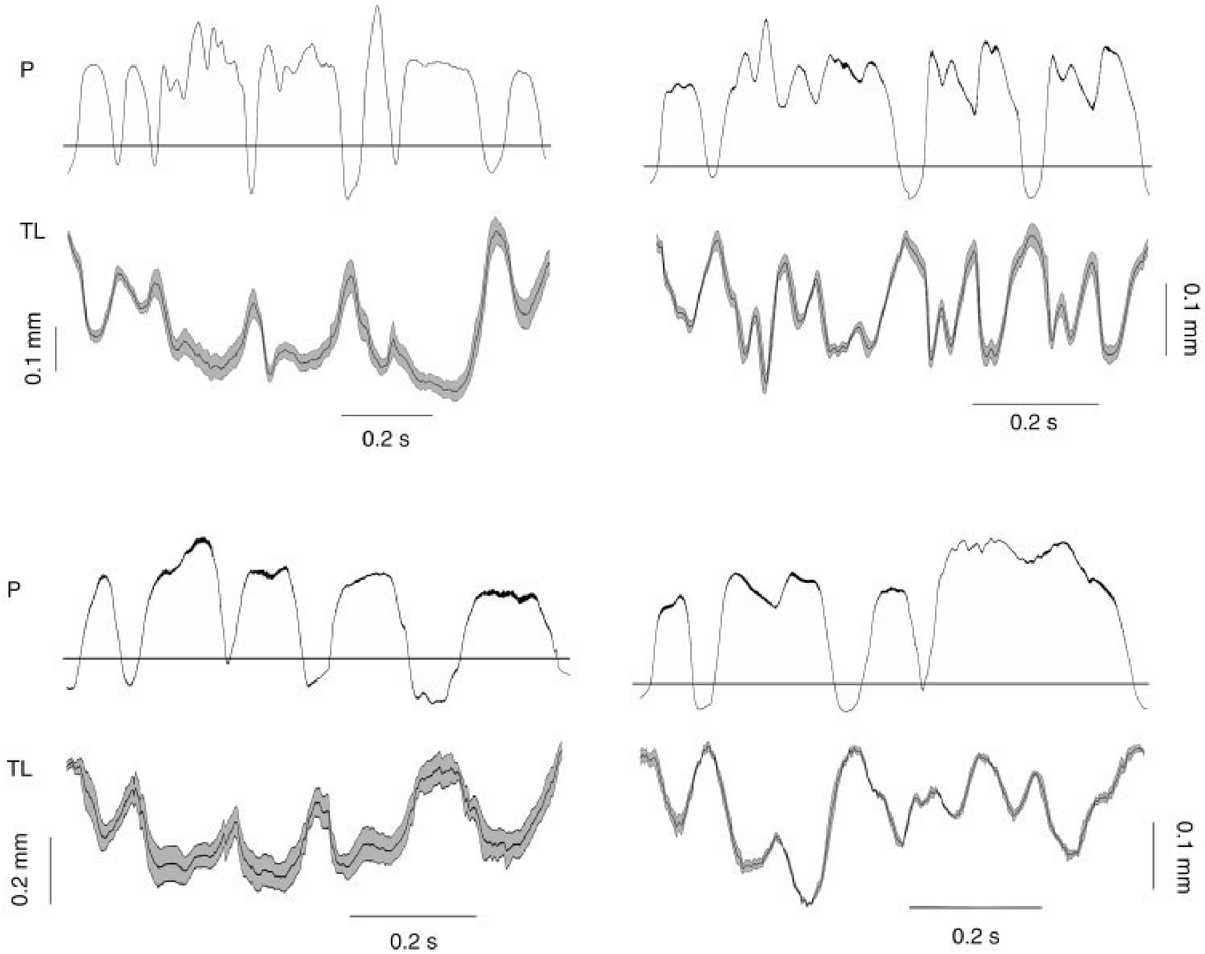

Figure 3 Within song, tracheal length changes correlate with air sac pressure for all individuals. Mean air sac pressure (P) and mean ± standard deviation tracheal length change (TL) during the song motif are shown for the four zebra finches in this study. Tracheal length changes within the song motif are highly stereotyped but small (<0.22 mm) and largely follow air sac pressure. The trachea shortens with expiration and lengthens during intersyllable inspirations. Note that the variation in tracheal length change within the song motif differs substantially among individuals and may be greater the more cranially the sonomicrometry crystals were placed along the trachea.

Length Change after Denervation of the Syrinx

Denervation of the syrinx eliminated only the rapid length change of the trachea associated with the beginning and the end of the song bout (Fig. 6). This elimination of shortening caused an overall decrease in total shortening of the trachea. However, the tracheal shortening and lengthening associated with the respiratory pattern of the song motif were still present after the nerve cut (Fig. 7).

Change in Vocal Tract Filtering due to Length Change

In order to determine the likely acoustic effects of the observed tracheal length change, we estimated the length change of the entire trachea that would result if the tracheal strain was uniform along its length. This assumption is necessary because only the basal 6–7 mm region of the trachea was measured due to the limited range of sonomicrometry transducers (see Methods). It is also unlikely that active tracheal shortening by contraction of the m. tracheolateralis can exceed the shortening observed at the basal end, because this muscle is much more prominently developed at the basal end than at higher tracheal regions. Tracheal cartilage rings are evenly spaced along the length of the trachea and no drastic changes in tracheal elasticity were apparent.

We therefore calculated the fractional change measured within the 6–7 mm region cranial to the interclavicular air sac and multiplied this fractional strain

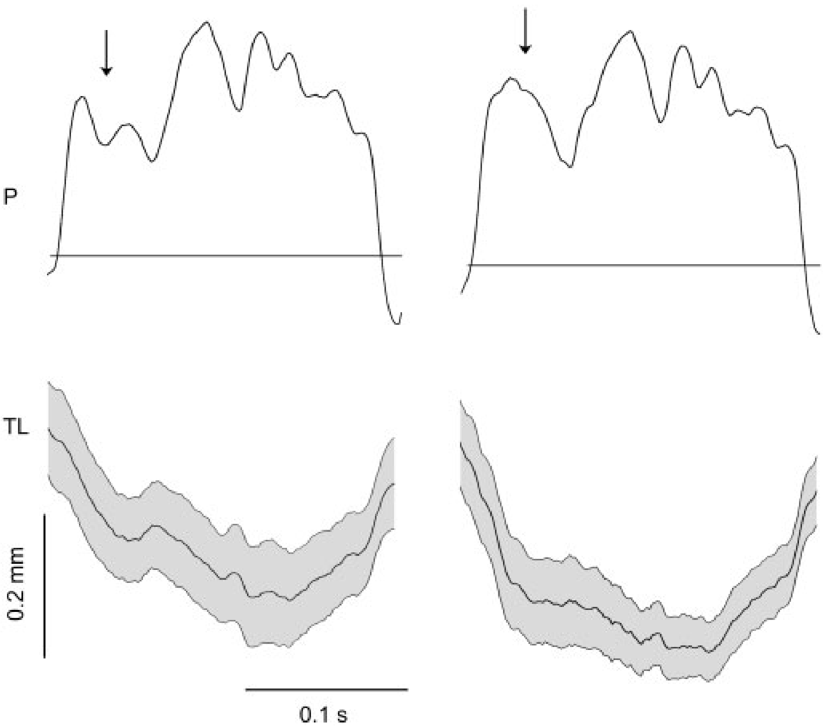

Figure 4 Tracheal length (TL; mean ± SD) and air sac pressure (P; mean) for two similar song syllables. In many cases, changes in tracheal length accompanied even small fluctuations in pressure. Furthermore, patterns of tracheal length change reflected small differences in air sac pressure between otherwise similar syllables.

between crystals by the length of the trachea to obtain the length change of the entire trachea. This estimate is likely to be an over-estimate of the actual length change. If the bird holds its head in a fixed position, thereby keeping the trachea fixed at the cranial end, shortening of the trachea at the caudal end via m. tracheolateralis activity could actually stretch the upper portions of the trachea. Shortening in the caudal end of the trachea may result in lengthening at the cranial end, thus, the shortening observed could be regional. Nevertheless, assuming uniform tracheal strain provides a reasonable estimate of the maximal frequency changes that would result from the measured length change.

Using the above reasoning, the maximal tracheal length change within a song is estimated to be approximately 3% of its length, resulting in a change of 1.0 mm for a 3.3 cm trachea. Using this value, we calculated the expected change in resonance frequency of the trachea approximated as a tube (Suthers, 1994), as well as the formant band frequencies and dispersion (Fitch and Giedd, 1999). The use of the following equations also assumes a uniform tube diameter. This assumption is reasonably met by the zebra finch trachea, as there are no striking changes in tracheal diameter from the basal end to the caudal end of the larynx.

Using the equations for simple resonances in a uniform tube:

$$F1 = (1/4L) \times 20.1\mathrm{sqrt}(T_A) \qquad (1)$$

Table 1 Length Changes of the Trachea (avg ± 1 sd) during Song Bouts and within the Motif

	Bird			
Length Change	ZFY3	ZFY20	ZFY16	ZFR36
Total for bout (mm)	0.47 ± 0.07	0.24 ± 0.07	0.37 ± 0.09	0.50 ± 0.12
Within song (mm)	0.16 ± 0.06	0.14 ± 0.08	0.20 ± 0.09	0.21 ± 0.07
Within song (% of total)	34.0	58.3	54.0	42.0

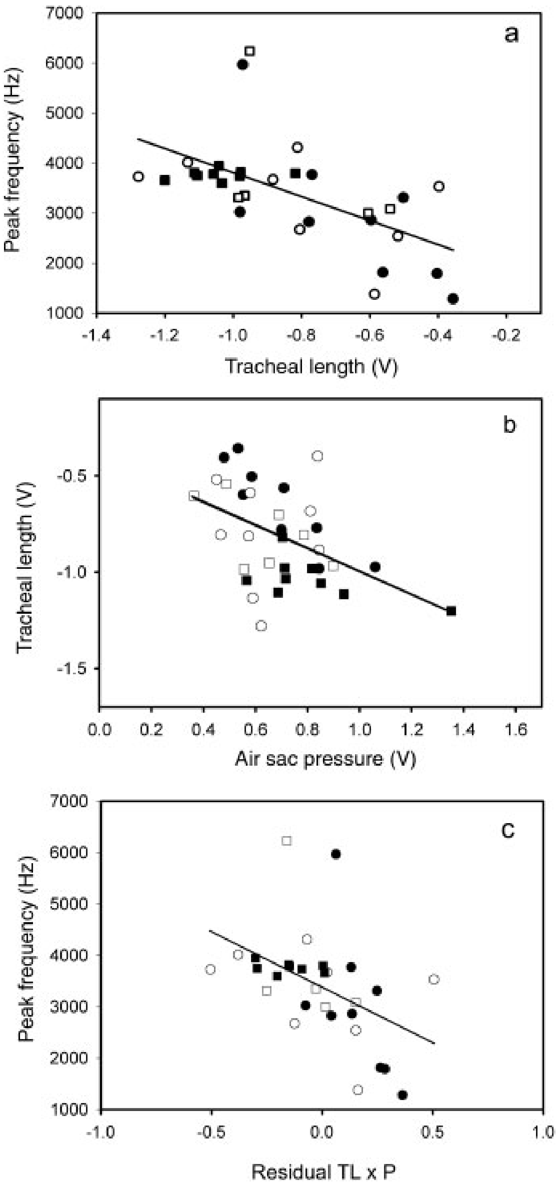

Figure 5 (a) Peak frequency of harmonic stack notes decreases with increasing tracheal length. Zero voltage is resting tracheal length. Different symbols denote data points from different individuals. Linear regression analysis: $F = 15.29$, $p = 0.0005$, $R^2 = 0.34$. (b) Increasing air sac pressure is accompanied by greater tracheal shortening. Data points represent normalized average voltage values for each individual (different symbols). Linear regression analysis: $F = 9.157$, $p = 0.005$, $R^2 = 0.25$. (c) Peak frequency of harmonic stacks is higher if tracheal length is less than expected from the linear relationship with pressure. The horizontal axis shows the residuals (P × TL) from the linear regression displayed in (b). Different symbols are data points from different individuals. Linear regression: $F = 5.34$, $p = 0.03$, $R^2 = 0.16$.

tube stopped at one end and

$$F1 = (1/2L) \times 20.1\,\mathrm{sqrt}(T_A) \qquad (2)$$

tube stopped at both ends where $F1$ is the frequency, L is the tube length in meters, T_A is the temperature in Kelvin, assumed to be body temperature (40°C), results in a resonance change of 84 and 168 Hz for a tube stopped at one or both ends, respectively. Formant dispersion is an acoustic cue inversely correlated with vocal tract length, and is equal to the average distance between adjacent formant frequencies. A longer vocal tract has more closely spaced formants. The extrapolated 3% length change would also result in a proportional shift of 3% in the formant frequency and formant dispersion (Fitch and Giedd, 1999).

DISCUSSION

This study is the first to experimentally test the hypothesis that songbirds actively change tracheal length to modify the filter properties of the upper vocal tract during vocalization. The tracheolateralis muscle could play an active role in shortening the trachea during phonation to adjust the acoustic properties of the vocal tract. However, the results of this study support earlier suggestions that direct changes in tracheal length have little effect on the filtering properties of the upper vocal tract (Greenewalt, 1968; Fletcher, 1988). Addressing whether or not the resonance changes are large enough to be perceptually significant to the bird is outside of the scope of this study. However, it does not appear that the length changes during the motif are actively controlled and therefore accomplish active tuning to enhance specific sound characteristics. Thus, actively controlled tracheal length change is unlikely to represent an important means for acoustic modulation during vocalization in the zebra finch.

Extent and Nature of Tracheal Length Change

Changes in tracheal length during song are generally small, and these changes can be put in perspective by comparison to length changes resulting from other behavior. For example, the length changes during song are smaller than those elicited by slight head turning. Thus, in spite of the stereotypy of the observed changes, their small amplitude suggests that direct change in tracheal length plays only a minor role in modulation of the acoustic filtering of vocalization, if any. Furthermore, tracheal length change

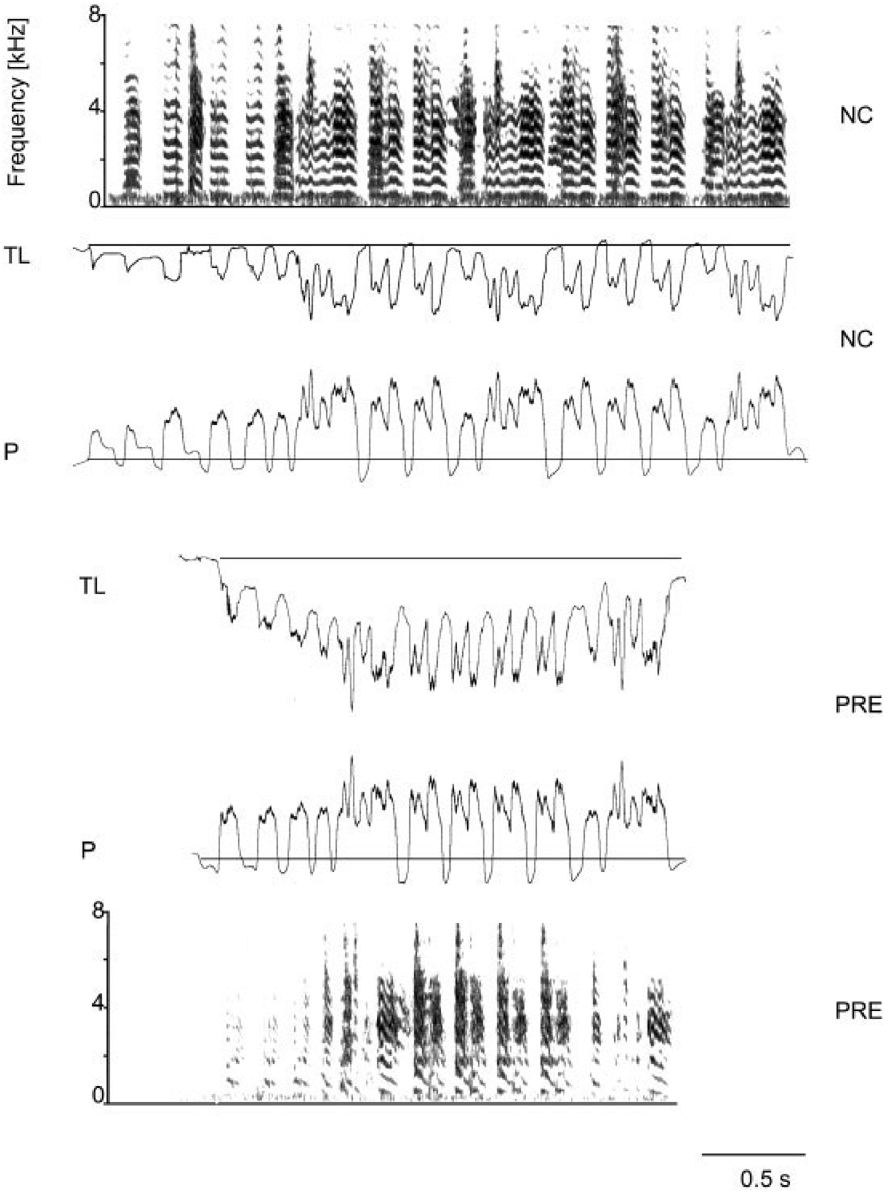

Figure 6 Zebra finch song (shown spectrographically), air sac pressure (P), and tracheal length change (TL) before (PRE) and after (NC) bilateral resection of the tracheosyringeal nerve. Denervation of the syrinx eliminated only the rapid length change of the trachea associated with the beginning and end of the song bout. The tracheal length changes associated with the air sac pressure were similar before and after denervation.

primarily correlates with air sac pressure. Most syllables are produced during expiration, and accompanied by shortening of the trachea in association with increased air sac pressure. In contrast, inspiratory syllables, which are of high fundamental frequency (arrows, Fig. 2; Goller and Daley, 2001), are accompanied by tracheal lengthening in association with subatmospheric air sac pressure. Furthermore, a bilateral denervation of the syringeal muscles did not abolish the dynamics of length change. Because the innervation pattern for the tracheolateralis muscle is not known in zebra finches, it is possible that segments cranial to the nerve section (1–1.5 cm) were not affected by our nerve cut. However, at least two-thirds of the muscle was denervated, and the disappearance of tracheal shortening at the beginning of song is consistent with successful denervation. Therefore it is unlikely that the rapid tracheal length changes that remained after the nerve cut were caused by m. tracheolateralis activity. These results strongly suggest

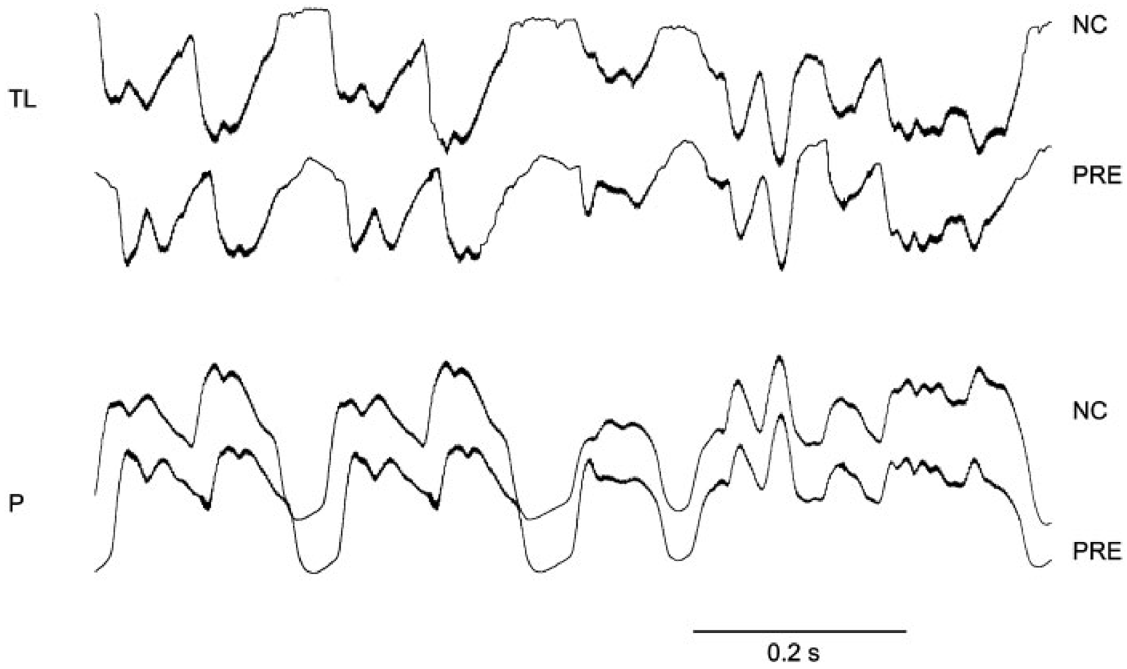

Figure 7 Tracheal length change (TL) and air sac pressure (P) recordings during single song motifs before (PRE) and after (NC) denervation of the syrinx. The tracheal shortening and lengthening associated with the respiratory pattern of the song motif remained largely unchanged after the nerve cut. The two motifs were aligned using peak pressure of the last expiratory pulse. A slight temporal offset at the beginning of the motif is the result of a slight difference in song tempo between the two motifs and is also reflected in the tracheal length pattern.

that the dynamic length changes during song are primarily caused by the pressure conditions of the air sac system. We measured tracheal length changes at the basal end of the trachea near the attachment of the membrane of the interclavicular air sac. As pressure changes in this air sac, its attachment on the trachea will result in a translation of the pressure change into movement of the basal end of the trachea. Increased expiratory pressure will push the trachea in a rostrad direction, thus causing shortening; inspiratory pressure will pull the trachea downward causing a lengthening.

Even small deviations from a length change pattern driven passively by air sac pressure do not necessarily indicate an active regulation of tracheal length for specific acoustic characteristics. Activity of syringeal muscles related to the acoustic structure of syllables may change the compliance of the airways near the syrinx and therefore alter the effects of pressure changes on tracheal length. The passive effect of pressurization on tracheal length may also decrease after the initial shortening, such that higher pressures no longer cause a proportional shortening of the trachea. In addition, the courtship dance of zebra finches includes head movements (Williams, 2001), which, as indicated above, may influence tracheal length substantially. Because head movements are not stereotyped during the courtship dance of the zebra finch, they are an unlikely alternative mechanism for adjusting tracheal length (Williams, 2001; F. Goller, unpublished observation).

The only length change inconsistent with such a passive mechanism is the shortening that occurred at the beginning of the song bout. Because this shortening and the associated relengthening at the end of the song bout were abolished by the denervation, it is likely that it constitutes an active shortening mediated by syringeal muscles. The most likely muscle to effect such a length change is the m. tracheolateralis, which runs from the syrinx laterally alongside the trachea. A rostrad movement of the syrinx was reported at the onset of brain stimulated and spontaneous vocalization in songbirds (Goller and Larsen, 1997b, 2002). This rostrad movement may contribute to the shortening of the trachea at the onset of the song bout. It is, however, also possible that a postural change (Williams, 2001) contributes to the tracheal shortening before song.

Length Changes and Resonance Shift

The observed shortening of 0.1–0.2 mm at the basal end of the trachea represents maximally a 3% length change for the segment studied with the sonomicrometry crystals. This length change at the basal end may not be representative of an equivalent length change over the full length of the trachea. Several observations indicate that the observed changes are at least partially restricted to the basal end. The length change driven by pressurization of the interclavicular air sac encompasses approximately 50% of the total observed length change. It is unlikely that the strain could evenly progress over the entire length, thus this passive length change is likely restricted to the basal end of the trachea. Furthermore, the presumed active contribution was no longer present in the one experiment where the crystals were placed further away from the syrinx.

Nevertheless, if we assume that the length change at the basal end can be extrapolated over the entire length of the trachea, providing a maximal estimate of its effect, a 3% length change still only results in a small shift in tube resonance of 85–170 Hz. The lowest fundamental frequency of zebra finch syllables is 500–600 Hz. The observed and extrapolated length change would therefore result in resonance shifts that are substantially less than the frequency steps between harmonics.

While the dynamic tracheal length changes during song likely have little effect on upper vocal tract filtering when the trachea is modeled as a rigid tube, more complex interactions between the trachea and syringeal structures, such as changes in compliance and shape, may substantially alter sound production. Both passive pressurization and syringeal muscle activity could alter the compliance of vocal tract tissues and the coupling between the syrinx and upper vocal tract. Such changes could profoundly influence sound production due to the nonlinear intrinsic dynamics of the syrinx (Fee et al., 1998; Fee, 2002). Shape change resulting from tracheal length change could also alter acoustic dynamics. It is unlikely that tracheal length changes affect the diameter of the trachea because tracheal rings are typically complete and partially ossified (McLelland, 1989). However, if the geometry of the inner surface of the trachea changes even slightly, aspects of resonance and airflow may be affected in a more complex fashion (Fletcher and Tarnpolski, 1999). It is therefore possible that although simple tube resonance may not be altered substantially, resonance properties of the trachea might be affected by small changes in the tracheal lumen resulting from length changes. Such effects may contribute to the observed relationship between peak frequency of harmonic stacks and tracheal shortening patterns.

Neural Control

Many of the complexities of vocalization are controlled by coordination between the respiratory system as a driving force and the syringeal muscles in gating and tension control (e.g., Gardner et al., 2001; Goller and Daley, 2001; Goller and Suthers, 1996a; Suthers et al., 1999; Wild et al., 1998). It is interesting that this respiratory-syringeal control also passively drives much of the tracheal length change observed in this study. The possible active component is most likely effected by the m. tracheolateralis, an extrinsic syringeal muscle innervated by the tracheosyringeal branch of the hypoglossal nerve.

The respiratory-syringeal neural pathways therefore play a major role in controlling tracheal length. However, head movements during the courtship dance may influence tracheal length more than the length changes investigated here. Because movements of the dance appear to be coordinated with vocal gestures (Williams, 2001), these different motor systems must be coordinated with vocal systems. In addition, the control of other upper vocal tract mechanisms, such as beak movements, involves yet other neural pathways. The integration of these different motor systems clearly adds complexity to the task of vocal motor control, but the neural pathways and mechanisms of integration of these accessory motor systems are not well understood.

In conclusion, both theoretical and experimental evidence suggests that changes in beak opening during vocalization have a much greater effect on harmonic content of song syllables than changes in tracheal length of the magnitude measured in this study (e.g., Williams, 2001; Goller et al., 2004). This finding in zebra finches is consistent with results in other species. In addition, experimental tests confirm the role of beak movements. For example, impeding beak movements in canaries results in a considerable increase in the amplitude of the second harmonic, sometimes resulting in a shift of highest acoustic energy to the second harmonic, whereas the energy is concentrated in the fundamental during normal singing (Hoese et al., 2000). Similar results were found in zebra finches (Goller et al., 2004), in which upper harmonic content appears to play a much larger role than in other investigated species. Compared to this shift in emphasis of 2–4 kHz, the 85–170 Hz change expected from tracheal strain as measured in the current studies seems inconsequential. However, we cannot rule out the possibility that complex acoustic interactions may allow these small changes to be important. Further, the active shortening of the trachea at the beginning of the song does appear to be important for moving the syrinx into phonating position.

We thank Anooshka Jansen for help with data collection.

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