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S26-1 Respiratory dynamics and syllable morphology in songbirds

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Abstract Song in birds is produced as air flows past the vibratory structures of the syrinx typically during expiration. Whereas there is detailed information about bilateral syringeal contributions to sound production, little is known of the interactions of air sac pressure and airflow, and how these affect sound frequency and sound amplitude. We studied air sac pressure and airflow during song in brown-headed cowbirds, cardinals and zebra finches, three species with acoustically dissimilar songs. Results revealed no consistent relationship between air sac pressure and airflow during song syllables with different acoustic structure, suggesting that adjustments in syringeal resistance play an important role in airflow regulation. In cowbirds and zebra finches, high frequency sounds were produced with higher air sac pressure. In these same species, sound amplitude appears to be greater for high than low frequency sounds, suggesting greater efficiency in transforming fluid dynamic energy into acoustic energy.

Key words Air sac pressure, Airflow, Sound frequency, Sound amplitude, Acoustics

1 Introduction

Singing in birds is an acoustic behavior important for male-male and male-female communication in a reproductive context. In songbirds, learning plays a major role in song development, which is thought to enhance information content about the fitness of the sender and is therefore involved in sexual selection (e.g., Nowicki et al., 2002). A first step towards understanding the evolution of song is to explore physiological requirements for song production and possible physiological constraints on temporal and acoustic patterns of song.

Song is typically produced during a series of expiratory pressure pulses, which generate airflow past the vibratory structures of the vocal organ, the syrinx. The songbird syrinx consists of two independently controlled sound sources, creating the potential for greater acoustic complexity of song than is possible with only one source. The variable use of the bi-partite syrinx to enhance vocal complexity has been analyzed by recording physiological information about the contributions of both syringeal halves to song (Suthers and Goller, 1997).

Songbird species use their two independently controlled sound sources in various ways, presumably to enhance different aspects of song complexity. These uses range from simultaneous generation of different sounds (two-voice) to alternating emissions between the two halves, either to increase frequency range or to generate a pattern of alternating low and high frequency syllables. For example, song in brown-headed cowbirds consists of a sequence of 3–4 expiratory pulses separated by mini-breaths. The first 2–3 pulses generate notes that alternate between low-frequency left-side generated (450–1 100 Hz) and higher frequency right-side generated (1 000–4 500 Hz) notes. Syllables of very high fundamental frequency (6–12 kHz), generated entirely on the right side of the syrinx, end the song (Allan and Suthers, 1994). In cardinals, song consists of sequences of repeated syllables, and each individual bird may have repertoires of 6–16 syllable types. Most syllables are either frequency upsweeps or downsweeps. Frequencies below approximately 3.5 kHz are generated by the left side of the syrinx and higher frequencies by the right, such that a syllable covering a wide frequency range is generated by sequential use of both sides (Suthers and Goller, 1997).

Despite this detailed information on syringeal contributions, very little is known about how air sac pressure and syringeal airflow relate to sound frequency and sound amplitude. Where syllables are repeated, the sound amplitude of a syllable typically increases as air sac pressure and airflow increase (e.g., Gaunt et al., 1973; Suthers and Goller, 1997). However, it is not known whether this relationship also applies to different syllables with different frequency components. We investigated the relationship between air sac pressure and airflow for sounds of different acoustic characteristics in three songbirds whose songs vary widely in syllabic structure. The results indicate a general relationship between the frequency and amplitude of syllables that cannot be explained simply by airflow or air sac pressure conditions.

2 Methods

Experiments were performed on three adult males of each of the following three species: brown-headed cowbird (*Molothrus ater*), cardinal (*Cardinalis cardinalis*) and zebra finch (*Taeniopygia guttata*). Vigorously singing birds were selected from a holding aviary and isolated in a small cage. There they were fitted with an elastic belt around the thorax and tethered to a counterbalance arm, which permitted free movement within the cage and compensated for any additional mass added during the experiment. Once birds resumed singing, surgical implantation of the flow transducer and air sac cannula was performed under isoflurane anesthesia. The specific procedures are described in detail in Hartley and Suthers (1989) and Suthers et al. (1994), so only a brief summary is given, as follows.

A cannula was inserted into a thoracic air sac through a hole made into the body wall below the last rib and sutured in place. The free end of the cannula was routed to the back, where a piezoresistive pressure transducer (Fujikura FPM-02PG) was mounted on a Velcro tab on the elastic belt. Tracheal airflow was measured with a miniature thermistor bead implanted into the base of the trachea right above the syrinx. A small hole was made into connective tissue between two tracheal cartilaginous rings through which the thermistor was inserted, such that the bead was centered in the tracheal lumen. The flow probe was sutured to a tracheal ring, and the wires were routed subcutaneously to the back. Stronger wires led from the backpack to signal conditioning equipment. Airflow was determined as the voltage needed to maintain the thermistor bead at approximately 60°C (Hector Engineering). The voltage is nonlinearly proportional to airflow. Airflow data were not calibrated, so all comparisons are based on relative voltage changes.

Song was recorded with a microphone (Audiotechnica AT8356) placed approximately 30 cm from the bird. Airflow, air sac pressure and acoustic data were recorded on different channels of a multi-channel data recorder at 25 or 40 kHz sample rate (TEAC 135T or Metrum Information Storage, model RSR 512) and later played into a computer at 40 kHz per channel (Data Translation 2821G) for analysis with Signal software (version 3.1; Engineering Design). Segments of acoustic syllables with relatively constant fundamental frequency were chosen, and average air sac pressure, tracheal airflow and sound amplitude were calculated for these segments. In cardinals, short frequency sweeps were used in their entirety

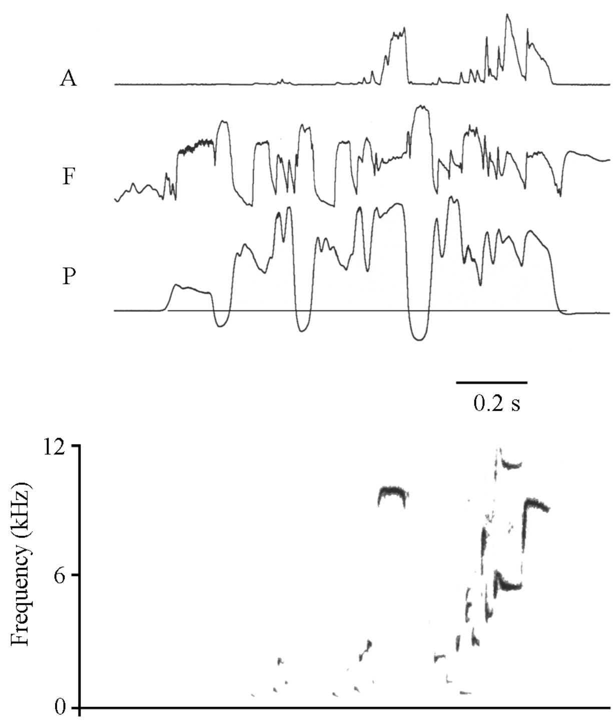

Fig. 1 Typical example of a cowbird song showing simultaneously recorded motor patterns and vocal output
Top panel: A = rectified and integrated oscillogram, *F* = tracheal airflow, *P* = subsyringeal air sac pressure pattern; bottom panel: spectrogram. The first expiratory pressure pulse results in almost inaudible sound despite the high airflow. At the beginning of expiratory pressure pulses 2 and 3, both sides of the syrinx are closed (no airflow). The significance of this silent period is not understood.

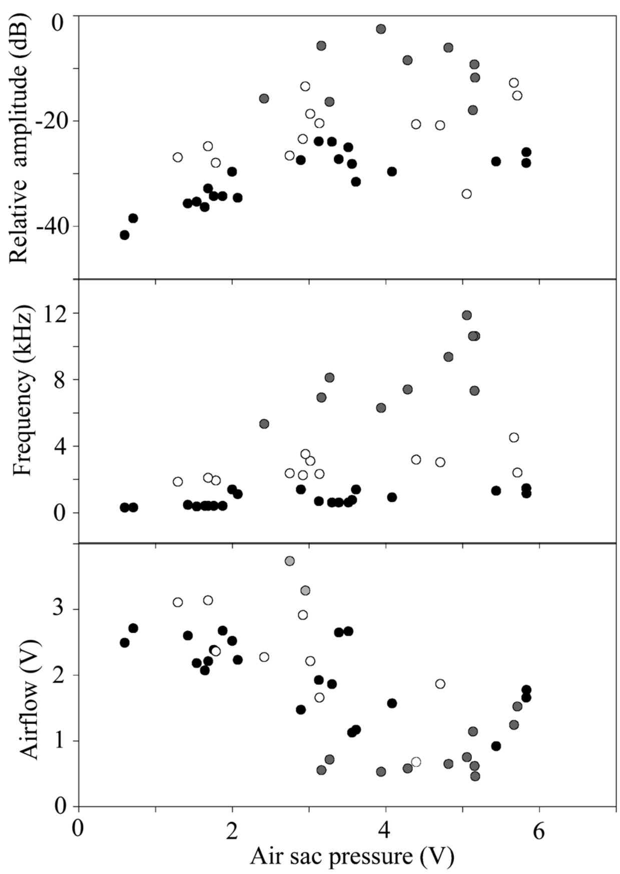

Fig. 2 Relationships between air sac pressure, airflow, and sound frequency and amplitude in cowbird song
The relationships are not simple. Mean values are plotted for individual notes in the introductory note clusters according to the side of the syrinx on which they are produced: left = black circles, right = open circles. All notes in the final whistle (gray circles) are produced on the right side. Side of production was inferred from Allan and Suthers (1994). The only two-voice segments are characterized by the highest airflow (light gray circles in the bottom panel). Data represent measurements taken from 3 songs of each of 3 song types sung by one individual.

to calculate average values for all measured parameters. The measurements were then analyzed for relationships between the various physiological and acoustic parameters.

3 Results

Patterns of airflow and air sac pressure, and corresponding acoustic parameters, are illustrated in cowbird song in Fig. 1. Airflow during inspiration is higher than during phonation, which occurs during the expiratory phase. Airflow during various parts of the song also varies and does not follow air sac pressure. This pattern is clearly illustrated by quantitative analysis in Fig. 2.

3.1 Air sac pressure and airflow

The relationship between air sac pressure and airflow varied between the three species. Whereas there was a general increase in airflow with increasing air sac pressure in cardinals and zebra finches, cowbirds showed an overall weak declining trend (Figs. 2–4). As expected, the rate of airflow during two-voice syllables, in which both sides of the syrinx are phonating, is high compared to unilaterally produced syllables, when one side of the syrinx is closed (Suthers, 1999; Suthers and Goller, 1997). In all cases, however, there was substantial variation in the pressure/airflow relationship between syllables with different acoustic structure.

3.2 Air sac pressure, airflow and frequency

The air sac pressure/flow relationship varied with the fundamental frequency of the sound in all three species. High-frequency sounds in the zebra finch and the final whistle in the cowbird were produced with higher air sac pressure than low-frequency sounds. Despite higher air sac pressure, airflow during high-frequency sounds was nevertheless generally lower than during low-frequency sounds (Figs. 2, 4). In cardinals, airflow tended to increase with air sac pressure, and in one individual it also increased with increasing fundamental frequency of sonation.

3.3 Frequency and sound intensity

Sound intensity can only be estimated from our recordings because orientation of birds towards the microphone may have varied during and between songs. However, the amplitude of high frequency syllables was 15–25 dB greater than for low-frequency sounds in all three species. Such a difference in amplitude cannot be attributed to higher airflow; but high-frequency sounds are typically associated with high air sac pressure.

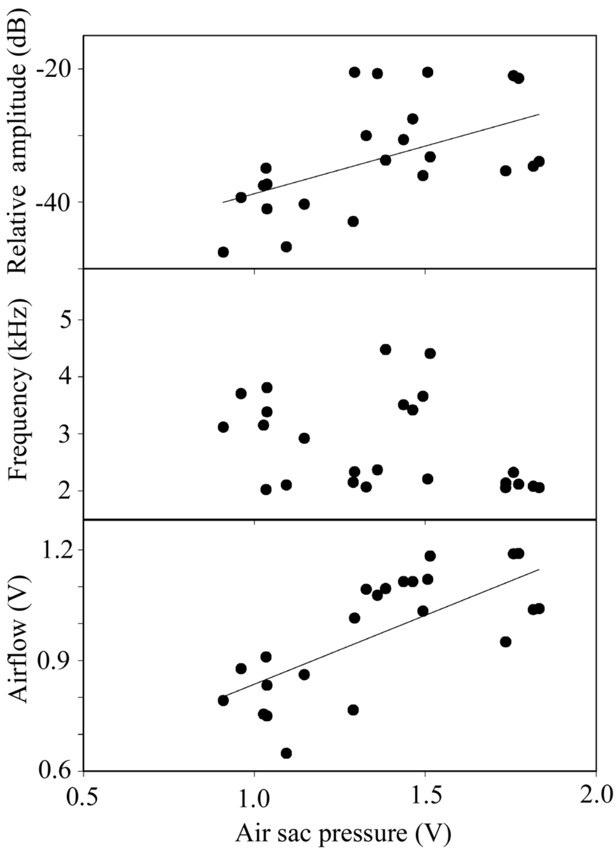

Fig. 3 Relationships between air sac pressure, airflow, and sound frequency and amplitude in cardinal song

Air sac pressure and airflow show a positive relationship (r^2=0.49), although sound frequency is not tightly correlated with air sac pressure in this individual. Amplitude generally increases with increasing air sac pressure (r^2=0.28). Data points represent measurements from 7 syllable types of one individual.

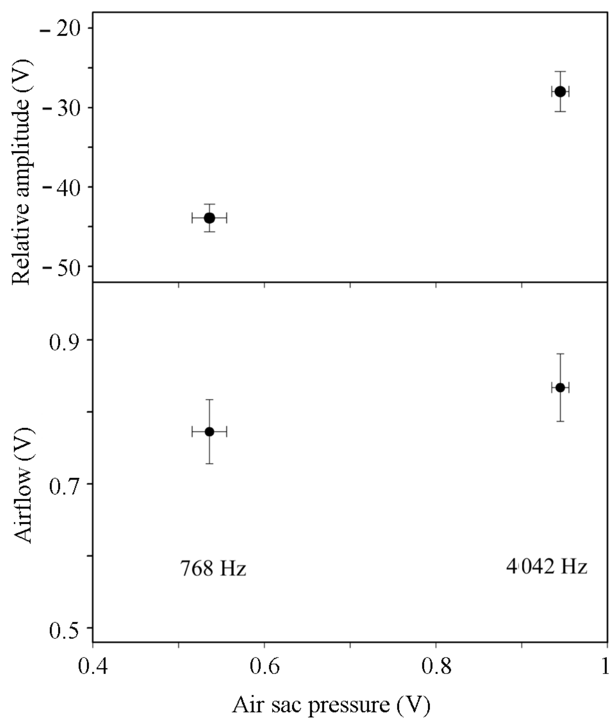

Fig. 4 Relationships between air sac pressure, airflow, and sound amplitude in zebra finch song

High-frequency syllables are generated with higher air sac pressure than low frequency syllables, but airflow is similar for both (Means ± 1 *SE*; bottom panel numbers indicate the mean frequency of included sound segments). The amplitude of high frequency sounds is substantially greater than that of low frequency syllables. Values include data from 3 motifs of each of three individuals.

4 Discussion

The inconsistent relationship between air sac pressure and airflow indicates a complex regulation of airflow by adjustments of airway resistance. The most likely structures involved in regulating airflow are the syringeal valves. The presence of two independently controlled labial valves probably allows more elaborate regulation of airway resistance. However, because no clear relationship was apparent for most individuals, even for unilaterally generated sounds, a complex interplay of sound characteristics must be postulated to account for the absence of direct dependence between air sac pressure and airflow.

A possible explanation lies in the amplitude of labial movements during low versus high-frequency vibrations. High frequency sounds are generated with more tightly adducted labia and smaller amplitude movements of the vibrating labia than low-frequency sounds (Goller and Larsen, unpubl. results). Increased activity in the gating muscles during high-frequency sound is consistent with this interpretation (Goller and Suthers, 1996). The evidence together suggests that syringeal resistance is higher for generation of high-frequency sounds.

The frequency dependence of sound intensity is somewhat surprising. In all species, and particularly zebra finches and cowbirds, high-frequency sounds were substantially greater in amplitude. Greater amplitude occurred even though airflow was consistently lower than for low frequency syllables, despite high air sac pressure. This suggests that the small aperture associated with high syringeal resistance enables the vibrating labia to convert more of the fluid dynamic energy in the expiratory air stream into acoustic energy, increasing the efficiency of producing high frequency over low frequency vocalizations. It is also possible that the filtering properties of the upper vocal tract generally favor higher frequencies. In cardinals, for example, low frequency sounds are sung with very little opening of the beak. When the beak is held open experimentally during song, the fundamental frequency of low-frequency sounds is drastically reduced in amplitude relative to upper harmonics (Suthers and Goller, 1997).

It appears that production of low frequency sounds at high intensity may be difficult for songbirds within the size range of the species used in this study. Although the lowest fundamental frequencies of zebra finch song are exceptional for a small bird, the harmonic content of the radiated sound is shifted upward in favor of higher harmonics.

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