

Bilaterally Symmetrical Respiratory Activity during Lateralized Birdsong

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ABSTRACT: We investigated whether activity of expiratory muscles reflects lateralized activity of the vocal organ during production of birdsong. Respiration and syringeal motor activity were assessed in brown thrashers by monitoring bilateral airflow and subsyringeal air sac pressure, together with the electromyographic activity of expiratory abdominal muscles and vocal output. Activity of expiratory muscles was always present on both sides, regardless of whether song was produced bilaterally or on only one side of the syrinx. The average amplitude of expiratory EMG of one side does not change significantly, even if that side is silent

during phonation. The temporal pattern of the electromyogram (EMG) was similar on both sides. Bilateral bursts of EMG activity on both sides accompanied changes in the rate of syringeal airflow, even when these flow fluctuations were generated only by one side of the syrinx. Motor commands to the respiratory muscles therefore appear to be bilaterally distributed, in contrast to the lateralized motor control of the syrinx. © 1999 John

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Functional lateralization of motor control is a poorly understood aspect of brain evolution, even though it is widely distributed among vertebrates including humans (e.g., Arnold and Bottjer, 1985; Bradshaw and Rogers, 1993). Song production in birds became one of the first animal models of functional lateralization when left-side dominance in vocal control was discovered in several songbird species (e.g., Nottebohm, 1971; Lemon, 1973; Nottebohm and Nottebohm, 1976; Seller, 1979). Some functional laterality in the motor control of the bipartite vocal organ, the syrinx, has since been found in most species that were investigated (reviewed by Suthers, 1997). It is not known,

however, whether the motor patterns controlling the other motor components involved in song production, such as the respiratory system, exhibit lateralization similar to that of the syringeal muscles. Is the lateralization of song production limited to the vocal organ or are other song motor subsystems, such as respiration, also lateralized, thus creating functionally separate “vocal systems” on the left and right sides?

Phonation in birds requires coordinated activity of the muscles of the syrinx and respiratory muscles. Sound production is initiated by generation of a high positive air sac pressure. Elevated respiratory pressure, in combination with increased syringeal resistance, generates airflow that induces vibrations of the sound-generating structures in the syrinx (e.g., Greenewalt, 1968; Stein, 1968; Gaunt et al., 1973; Gaunt, 1987; Fletcher, 1988; Brackenbury, 1989; Suthers, 1990; Goller and Larsen, 1997). Syringeal muscles contribute to phonation by regulating the syringeal aperture and controlling the phonic structure of the sound (e.g., Vicario, 1990; Goller and Suthers, 1996a,b).

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In providing the pressure head necessary to induce phonation, respiratory muscles also determine the coarse temporal pattern of song. Measurements of respiratory motor correlates during song provide clear evidence for respiratory involvement in song patterning in all species investigated (Calder, 1970; Hartley and Suthers, 1989, 1990; Suthers, 1990, 1997; Allan and Suthers, 1994; Suthers et al., 1994). The only study in which expiratory electromyograms (EMGs) were recorded during song (Hartley, 1990) linked expiratory effort directly to activity of the abdominal muscles.

The bipartite nature of the songbird syrinx, with its ipsilateral innervation, facilitates lateralized activity at the level of the vocal organ. In songbirds, syringeal lateralization ranges from extreme unilateral dominance, in which one side of the syrinx contributes most sounds, to lateralization without dominance, where both sides contribute about equally, either by simultaneous production of different sounds or by alternating phonation between sides of the syrinx (for reviews see Suthers, 1997; Suthers and Goller, 1997).

The respiratory system of songbirds is characterized by a number of bilaterally paired air sacs as well as a medial interclavicular air sac. Inspiration and expiration are active processes, and sound is normally generated during expiration. Expiratory flow is driven by compression of the air sacs through contraction of the abdominal and some intercostal muscles (e.g., Kadono et al., 1963; Fedde et al., 1969; Gaunt and Gaunt, 1977; Hartley, 1990; Wild, 1993a). Contraction of abdominal expiratory muscles compresses mostly the ipsilateral members of the paired thoracic and abdominal air sacs, potentially providing a mechanism by which expiratory activity might be lateralized. However, connections between air sacs on the right and left sides through the unpaired, midline interclavicular air sac and possibly through direct cross connections (McLelland, 1989) lead to relatively uniform air pressure throughout the air sac system (Brackenbury, 1971, 1972, 1973; Gaunt et al., 1973). In view of this, there would seem to be no functional advantage in lateralization of respiratory muscle activity (Konishi, 1994), but it does not eliminate the possibility that it may exist (Wild, 1994a). In fact, one could argue that bilateral air sac interconnections, by equalizing pressure, reduce the necessity for bilaterally symmetrical expiratory forces. Because the air sacs of the two sides are interconnected, lateralized respiratory activity is unlikely to generate differential airflow through the two sides of the syrinx and therefore should not contribute to syringeal lateralization. There are no experimental studies on how

expiratory muscles on each side of the body are activated during unilateral or bilateral phonation.

We present here the first analysis of bilateral EMG activity of expiratory muscles during birdsong. These experiments were conducted in brown thrashers, which sing a loose sequence of syllables (Kroodsma and Parker, 1977; Boughey and Thompson, 1981) that may consist of independent simultaneous contributions from the two sides of the syrinx as well as individual unilateral contributions (Suthers, 1990; Suthers et al., 1994). Rapid switching of phonation from one side of the syrinx to the other is achieved by syringeal muscles, which can silence each side independently by closing it (Goller and Suthers, 1995, 1996a). Although there is no asymmetry in the contribution each side makes to sound production, thrasher song is lateralized in the sense that either side can be engaged in sound production while the contralateral side is silent. Our results indicate that bilaterally symmetrical expiratory activity accompanies lateralized syringeal function.

MATERIALS AND METHODS

Experimental Birds

Six adult male brown thrashers (*Toxostoma rufum*) were used in this study. The birds were hand-raised from the age of 5–7 days and tutored with tape recordings of conspecific song. They were then housed in individual cages in a room with other brown thrashers of mixed ages on a photoperiod that simulated normal seasonal changes in day length.

Experimental Procedures

Data were recorded from awake, freely behaving birds during spontaneously produced song. Preparation of birds for experiments, surgical procedures, and measurements of air sac pressure and bilateral bronchial airflow followed the techniques described in Suthers et al. (1994). In brief, vigorously singing birds were taken from the aviary and received a subcutaneous implant of a 3-week timed-release pellet of testosterone propionate (15 mg; Innovative Research of America). Over the next few days approximately 2000 syllables of song were recorded before we proceeded with the experiment. Birds were accustomed to wearing an elastic belt around their thorax with a self-fastening tab (Velcro) on the back for later attachment of electrical connectors. Surgical implantation of sensing devices was performed under chloropent anesthesia ($4 \mu\text{L} \cdot \text{g}^{-1}$). A flexible cannula (Silastic tubing; Dow Corning) was inserted into the posterior thoracic air sac and connected to a small piezoresistive pressure transducer (FPM-02PG; Fujikura) mounted on the back.

Next, the syrinx was approached through a midline, ventral incision in the skin and the interclavicular air sac. Flow probes constructed from microbead thermistors (0.13 mm, BB05JA202; Thermometrics) were inserted into the left and right bronchus four to five bronchial rings caudad from the syrinx. Wires were led out of the interclavicular air sac and routed subcutaneously to microconnectors on a backpack. The rate of airflow through each side of the syrinx was determined by a feedback circuit in which the current needed to maintain a heated thermistor at a constant temperature was proportional to the rate of airflow (Hector Engineering).

Electromyogram recordings were obtained from expiratory abdominal muscles which were exposed by making a lateral incision in the skin approximately 2 cm rostral of the pubic bone. Connective tissue and the outermost fascia of the thin muscle sheets were carefully dissected to expose a small area of muscle into which a bipolar stainless-steel electrode (0.025 mm, SS 304 H-ML; California Fine Wire; insulated except at the tip) was inserted. A small drop of tissue adhesive (Nexaband; Veterinary Products Laboratory) was used to secure the electrode pair to the fascia. Wires were then routed subcutaneously to the backpack, from which stronger wires led EMG and airflow signals out of the cage to signal conditioning and recording instruments. Electromyographic recordings were differentially amplified (Model 113, Princeton Applied Research, or Model EX4-400, Dagan Corporation) and bandpass filtered (150–3000 Hz).

The thin sheetlike nature of the partially overlapping abdominal muscles (George and Berger, 1966; Fedde, 1987) made it difficult to record selectively from only one muscle. The electrode insertion sites were selected to record from the two main muscles, *m. obliquus externus abdominis* and *m. transversus abdominis*, but no effort was made to confine recordings to one of these. In one bird, one pair of EMG electrodes was implanted into the left abdominal muscles; in two other thrashers two electrode pairs were implanted into the left expiratory muscles 0.6–0.8 cm apart; and in three birds separate pairs of electrodes were inserted into the left and right expiratory muscles. In one of these the flow probes were no longer functional by the time singing resumed 3 days after surgery.

Vocalizations were recorded on a Sennheiser microphone (Model MKH416 TU-3) placed in front of the cage. All data (bilateral air flow, air sac pressure, one or two EMGs, microphone recordings of song) were recorded simultaneously on an eight-channel rotary storage recorder (Model RSR512; Metrum Information Storage). Spectrograms of preoperatively recorded song were compared to experimental song to make sure that experimental manipulations did not interfere with normal sound production.

Data Analysis

All simultaneously recorded parameters were reproduced at half speed and digitized at a 20-kHz sample rate (DT-

2821-G; Data Translation) for a real-time sample rate of 40 kHz/channel. The time and frequency axes were corrected for the reduced playback speed. Between 150 and 250 syllables were digitized for each individual and analyzed using Signal v. 3.0 software (Engineering Design). Airflow measurements could not be calibrated because of the dynamically changing bronchial diameters. Whereas the response of the thermistors is not linear, that of the pressure transducers is linear for the range of pressures generated by our birds. Relative changes (voltage) of all measured parameters are presented. Unless otherwise stated, individual data points in the quantitative analysis represent averages of the respective parameter calculated for individual syllables. If changes, such as a switch from left to right airflow, occurred during a syllable, data points represent averages of parameters calculated for parts of a syllable (minimum duration 35 ms).

Electromyogram recordings were rectified (using the ENV procedure in Signal with a time constant of 0.1 ms) for measurements and cross-correlation analyses. EMG amplitude was determined as the average of digital EMG values for the specified duration (i.e., average of area under rectified EMG trace). EMG records in figures were also smoothed by integrating with a time constant of 2 ms (using the Signal SM procedure). Cross-correlation analysis was performed for comparisons of EMG signals using the XC command in Signal, which calculates the absolute covariance of the two signals (no rotation of signals against each other was allowed). Other statistical tests were performed using SPSS v. 6.1.3 software.

RESULTS

Abdominal Muscles Have a Consistent Role in Expiration during Song

Electromyogram activity was always present in the external oblique and abdominal transverse muscles when expiratory air sac pressure was elevated during song (Fig. 1). Air sac pressure increased with increasing amplitude of EMG activity ($r = 0.54$ – 0.79 for different individuals and electrode pairs; all linear regressions were significant at $p < .0001$). The duration of the EMG burst was always highly correlated with the duration of the associated positive air sac pressure cycle ($r^2 = 0.98$ – 0.99).

Activity in Respiratory Muscles is Present Even Though the Ipsilateral Side of the Syrinx Is Silent

Electromyograms recorded simultaneously from the left and right abdominal muscles were compared to determine whether the activity of these respiratory muscles is lateralized. Thrashers produce some song syllables with only the left or right side of the syrinx,

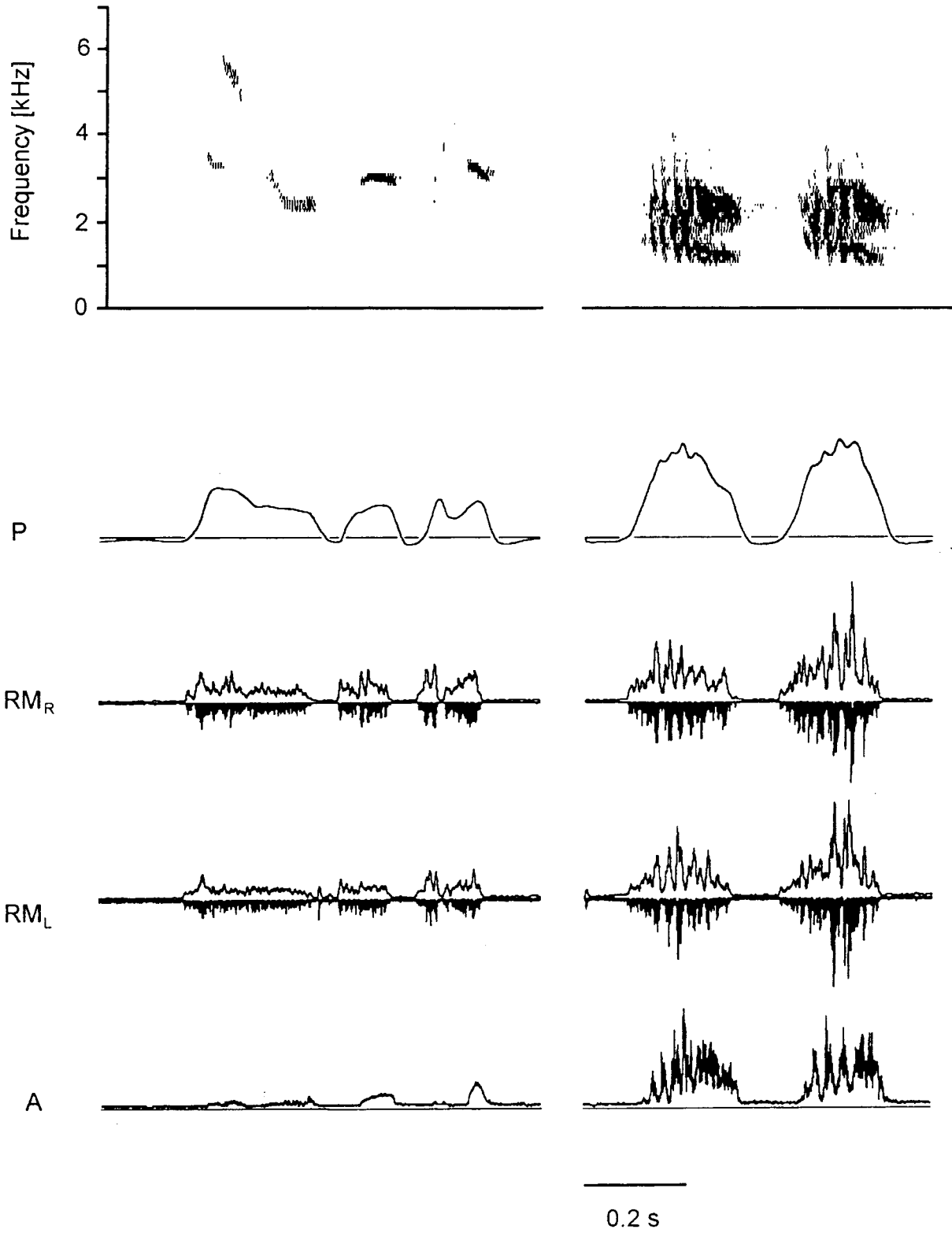


Figure 1

the lumen of the contralateral side being closed, whereas other syllables are produced with both sides of the syrinx (Suthers, 1990; Suthers et al., 1994). Both unilaterally and bilaterally produced syllables are included in this analysis of respiratory activity.

The left and right abdominal expiratory muscles have similar relative levels of EMG (the absolute voltage may differ between electrode pairs) activity during song regardless of which side of the syrinx is producing sound. During the song segment in Figure 2, for example, the right side of the syrinx contributes to sound production throughout the first syllable, less during the second, and very little during the last four syllables when right airflow is almost zero. However, there is clearly strong EMG activity on both sides. Moreover, the left and right abdominal expiratory muscles appear to be very similar in amplitude and temporal pattern for all these syllables. This bilateral symmetry in the amplitude and temporal pattern of expiratory muscle activity was confirmed by a quantitative analysis of over 500 different syllables.

Quantitative Analysis of Amplitude

For individual syllables (or portions of syllables if syringeal contributions changed), the amplitudes (average area under rectified EMG trace) of EMGs measured simultaneously on the left and right sides were highly correlated in all three individuals for which bilateral EMG recordings were available. Coefficients of determination (r^2) were 0.68, 0.77, and 0.89 for the three individuals ($n = 64, 141, \text{ and } 303$, respectively; all linear correlations were significant at $p < .001$) (Fig. 3). If there is a lateralization of activity in abdominal expiratory muscles during song, as there is in syringeal muscles, then the EMGs in the left and right expiratory muscles should differ depending on which side of the syrinx is producing song, but this did not appear to be the case. The mean amplitude of abdominal expiratory EMG did not differ significantly among the following three conditions of left–right interactions: (a) Only the ipsilateral side is phonating; (b) the contralateral side is phonating while the ipsi-

lateral side is fully adducted and silent; (c) both sides are open and generate song simultaneously (Table 1). Small differences in the average EMG amplitude between the conditions were consistent with corresponding changes in mean air sac pressure. Overall similarity of pressure means between the conditions excluded the possibility that significant lateral differences in the activity of the respiratory muscles might have been masked by differences in respiratory air pressure.

Fine Temporal Patterns of EMG Activity

As we have seen above, the coarse temporal pattern of respiration during song does not reflect syringeal lateralization because both sides are active during all syllables regardless of the degree to which phonation is lateralized. However, it is possible that lateralized activity may modulate some basic pattern of activity and therefore may become only evident in the fine temporal structure of expiratory EMG patterns. Although EMG signals only allow limited assessment of the fine temporal modulation of muscle contraction patterns, comparisons between rectified left and right EMG signals, using cross-correlation analysis, provide a preliminary indication of the similarity of the fine temporal patterns of the left and right expiratory muscle EMGs. The average cross-correlation coefficient between left and right EMG patterns is $r = 0.91$ (range 0.85–0.97; $n = 84\text{--}119$) for pooled data of all three individuals containing syllables with frequent lateralization of song production. This constitutes a high degree of similarity when compared to two control data sets that provide reference points for these correlation coefficients. The average cross-correlation coefficients between left and right EMGs of equal duration from two different randomly chosen syllables is $r = 0.80$ (range 0.49–0.95). Because of the onset and offset, as well as the one-dimensional nature of EMG signals, these correlation coefficients are relatively high. Nevertheless, the average r value of control comparisons is significantly lower than the average r value of left–right comparisons for the same

Figure 1 Temporal pattern and amplitude of bilateral respiratory EMG activity appears to be correlated with air sac pressure and sound amplitude during song syllables. Microphone recordings of sound are represented as rectified, integrated oscillogram (A) and spectrographically (top). EMG recordings of the left (RM_L) and right (RM_R) abdominal muscles are presented in rectified (downward) and integrated (upward) form. Horizontal line on the air sac pressure (P) trace marks zero pressure difference to atmospheric pressure. Note also the phase-delayed occurrence of amplitude modulations and peaks in EMG activity during the last two syllables and the overall similarity between left and right EMG traces.

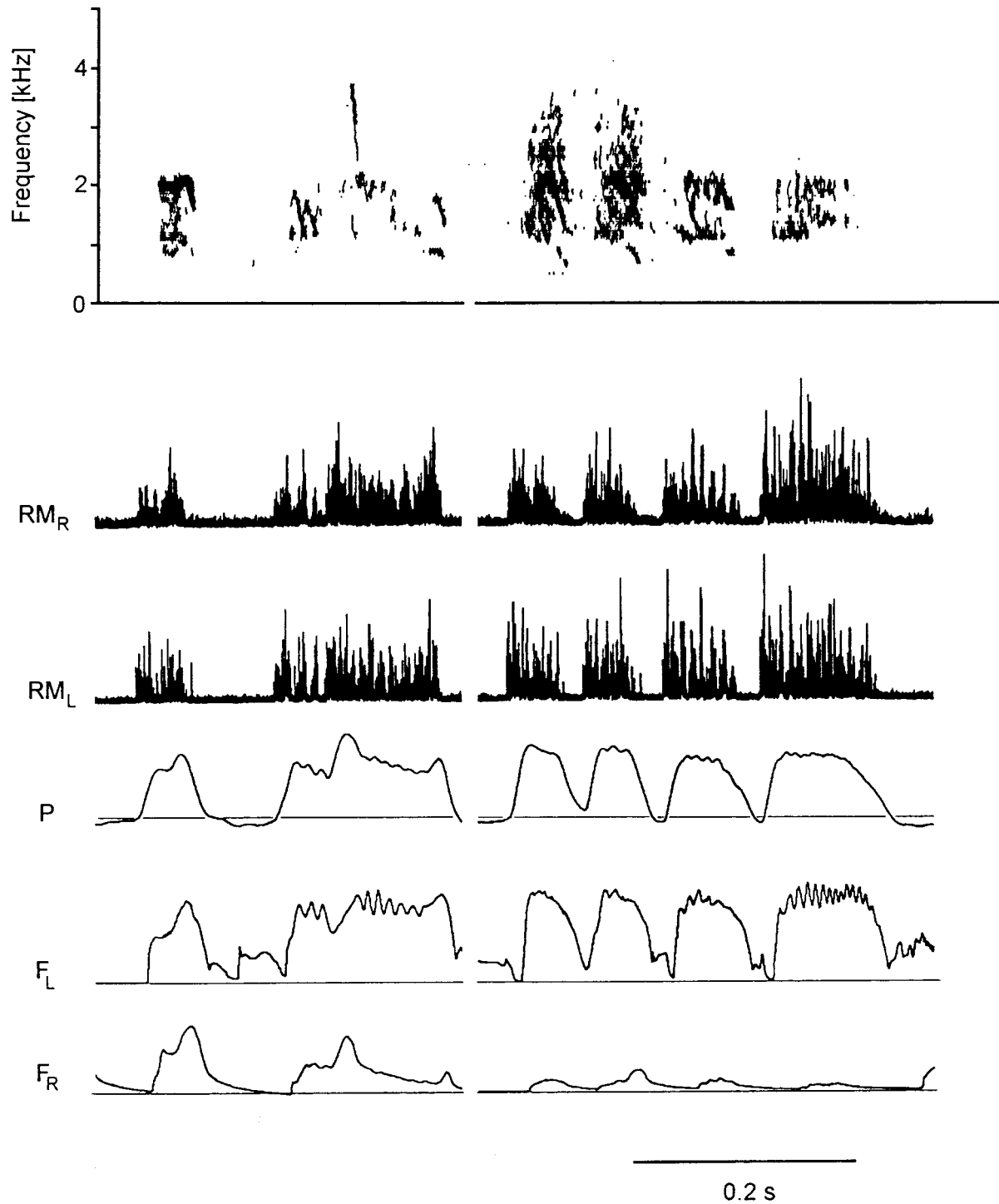


Figure 2 Activity of abdominal muscles is not lateralized. EMG activity in left and right abdominal muscles (RM_L and RM_R) is similar regardless of which side of the syrinx contributes to song. Six syllables are generated with varying contributions by the right side, as indicated by airflow through the right bronchus (F_R). Airflow through the right side is prominent during the first syllable, relatively low during the second, and almost zero during the last four syllables. Horizontal lines mark zero flow on left and right airflow panels and atmospheric pressure.

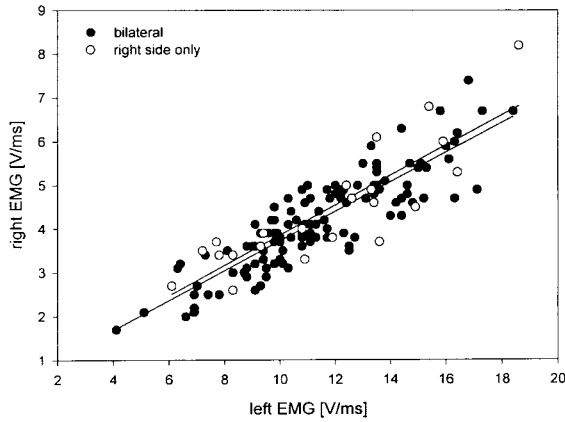


Figure 3 Electromyogram amplitudes of left and right expiratory muscles are correlated. Representative example of data from one individual showing that variations in average EMG amplitude in the right abdominal expiratory muscle follow those in the left. Individual dots represent whole syllables or segments of syllables if the respective contributions of the left and right side of the syrinx changed. The regression equation for bilaterally generated sounds (full circles, lower line) is $\text{right EMG} = 0.32 + 0.34 * \text{left EMG}$ ($r^2 = 0.77$). The equation for sounds generated on the right side only (open circles, upper line) is $\text{right EMG} = 0.40 + 0.34 * \text{left EMG}$ ($r^2 = 0.73$). Neither slopes ($t = 0.545, p > .5$) nor intercepts ($t = -0.83, p > .2$) of the two regressions are significantly different. Note that the absolute voltage values for the two sides depend on electrode position and amplification parameters, making it possible to compare only relative changes between syllables.

syllable ($p < .0001, t$ test; the distributions of r values in Figure 4 differed at $p < .001$ for all individuals; homogeneity test after Kolmogorov and Smirnov) (Sachs, 1984). In addition, in two individuals EMG patterns were recorded with two electrodes in the same sheet of expiratory muscle. The average cross-correlation coefficient for EMG patterns within the same muscle was $r = 0.94$ (range 0.86–0.98) and therefore only slightly but significantly ($p < .001, t$

test) higher than bilateral comparisons. Furthermore, in the two individuals with bilateral flow recordings, cross-correlation coefficients between left and right EMG patterns of unilaterally and bilaterally generated sounds did not differ significantly. In thrasher 52, $r = 0.898 \pm 0.03$ for bilaterally and $r = 0.90 \pm 0.03$ for unilaterally generated sounds respectively ($p = .37; n = 100; t$ test). In thrasher 41, $r = 0.918 \pm 0.02$ (unilateral) versus $r = 0.916 \pm 0.02$ (bilateral) ($p = .62, n = 97$).

This quantitative result is further illustrated by qualitative observations. Thrashers frequently generate sounds with oscillatory fluctuations of the rate of airflow through one or both sides of the syrinx (Suthers et al., 1994). These modulations arise when activity of the syringeal muscles changes the aperture of the ipsilateral half of the syrinx (Goller and Suthers, 1996a). During such syllables, EMG activity in the expiratory muscles exhibits distinct bursts that appear to coincide with airflow modulations, suggesting a compensatory activity to maintain air sac pressure as syringeal resistance changes (Fig. 5). Whereas in the first syllable of Figure 5 airflow is modulated on both sides of the syrinx, flow modulation is prominent on only the right side in the second syllable. The left expiratory EMG activity, however, shows bursts in both cases indicating that the lateralized flow modulation at the level of the syrinx is not reflected in equally lateralized activity of the expiratory muscles (see also Fig. 2).

DISCUSSION

The motor control of song production in songbirds provides an opportunity to investigate whether the functional lateralization of a behavior generated by the coordinated activity of distinct and separately innervated groups of muscles involves lateralized activity of all the contributing motor components.

Table 1 Mean Respiratory EMG Amplitude and Air Sac Pressure during Unilaterally and Bilaterally Generated Song

Bird	EMG* (V)			Pressure (V)		
	Left Phonation	Right Phonation	Bilateral Phonation	Left Phonation	Right Phonation	Bilateral Phonation
44	2.1 ± 0.53 (34)	2.4 ± 1.01 (27)	2.3 ± 0.7 (60)	0.57 ± 0.11	0.67 ± 0.18	0.64 ± 0.18
52	4.5 ± 2.0 (9)		4.2 ± 1.1 (132)	0.93 ± 0.25		0.84 ± 0.26
41	4.6 ± 1.53 (6)		4.3 ± 1.35 (59)	0.35 ± 0.05		0.36 ± 0.05
30		8.14 ± 2.6 (14)	9.3 ± 2.4 (57)		0.40 ± 0.07	0.41 ± 0.06
RY	3.1 ± 0.54 (45)	3.3 ± 0.65 (31)	3.3 ± 0.61 (47)	0.63 ± 0.1	0.7 ± 0.1	0.68 ± 0.1

* Measurements are from the left abdominal muscles; means ± 1 S.D.

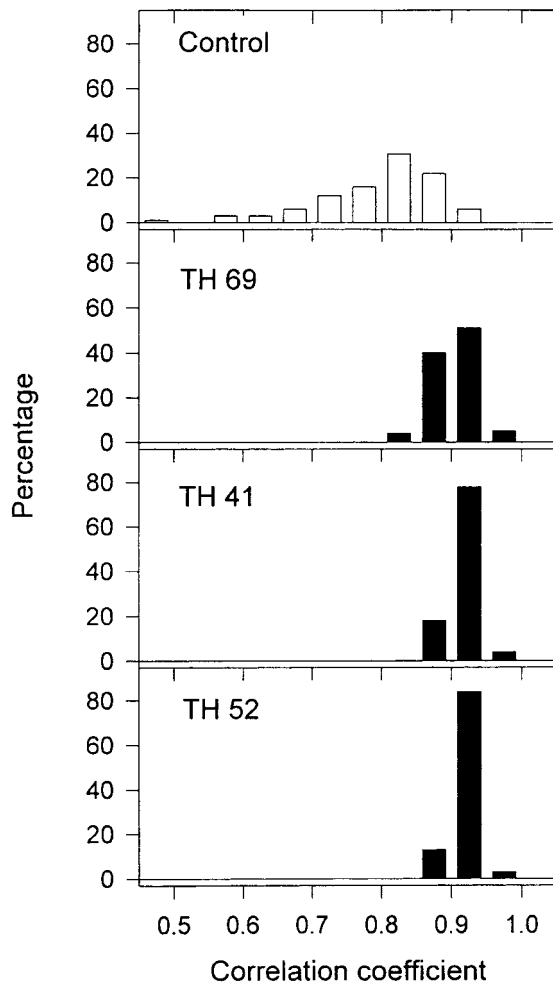


Figure 4 Temporal patterns of left and right expiratory EMGs are similar. Normalized frequency distributions (bin size 0.05) of cross-correlation coefficients (r) in comparisons of simultaneous EMG activity in the left and right abdominal muscles. Each data set contains cross-correlation coefficients for between 86 and 120 syllables. A representative control distribution (control) reflects EMG correlation coefficients of randomly chosen, equal duration segments of song syllables when EMG on one side is compared with an EMG for a different syllable on the other side.

Some degree of syringeal lateralization of sound production has been postulated in a number of song birds based on the different effects on song of left and right denervation of the vocal organ (e.g., Nottebohm, 1971; Lemon, 1973; Nottebohm and Nottebohm, 1976; Seller, 1979; Williams et al., 1992; Williams and McKibben, 1992). All songbirds from which bilateral flow through a normally innervated syrinx has been recorded during song show left–right differences in the respective contribution each side makes to phonation (Suthers, 1990, 1992, 1997; Suthers et al., 1994; Allan and Suthers, 1994; Goller and Suthers,

1995; Suthers and Goller, 1996). In brown thrashers, song is lateralized in the sense that sound generation is frequently switched from one side to the other, although both sides contribute about equally to song (Suthers, 1990; Suthers et al., 1994; Goller and Suthers, 1995). This poses the question of whether independent motor action on each side of the thrasher syrinx is accompanied by lateralized activity in the respiratory muscles during unilateral phonation (Wild, 1994a).

Our data indicate that abdominal muscle activity in brown thrashers is not lateralized and therefore does not share the functional asymmetry of syringeal motor activation during song. Expiratory muscles are always active on both sides, even if one side of the syrinx does not contribute to phonation. Furthermore, mean amplitudes of EMG bursts in the abdominal muscles of either side do not differ significantly, regardless of whether sound is generated unilaterally (on the ipsilateral or contralateral side) or bilaterally (Table 1). Nor could we detect difference in the fine temporal pattern of the EMG activity that is associated with lateralized syringeal function between expiratory muscles on both sides. Although direct data on muscle contractions are not available, we conclude from the EMG recordings that lateralized activity of the expiratory muscles during lateralized song production is unlikely, even on a fine temporal scale.

The high degree of similarity at all levels of analysis thus implies that comparable descending motor commands are distributed to the expiratory muscles on both sides. Such bilateral distribution of respiratory motor commands might occur at several levels and is in marked contrast to the mostly ipsilateral motor control of the syringeal muscles (e.g., Wild, 1997). Premotor neurons in nucleus retroambiguus (RAM) appear to project bilaterally to the motor neurons innervating the abdominal expiratory muscles (Wild, 1993a, 1994). There are also cross connections between the dorsomedial nuclei of the intercollicular complex (DM) (Striedter and Vu, 1997) and contralateral projections of descending pathways from DM to RAM and weak projections from nucleus robustus archistriatalis (RA) to contralateral RAM (Vicario, 1993; Wild, 1993a,b; Wild et al., 1997). In contrast, descending connections in the syringeal motor system are predominantly ipsilateral. No prominent direct contralateral connections from RA (premotor nucleus) to the motor nucleus nXII are known. Indirect cross connections are thought to provide bilateral feedback for interhemispheric coordination, but do not directly effect bilateral distribution of syringeal motor commands (Striedter and Vu, 1998). These anatomical differences in regard to the prominence of cross con-

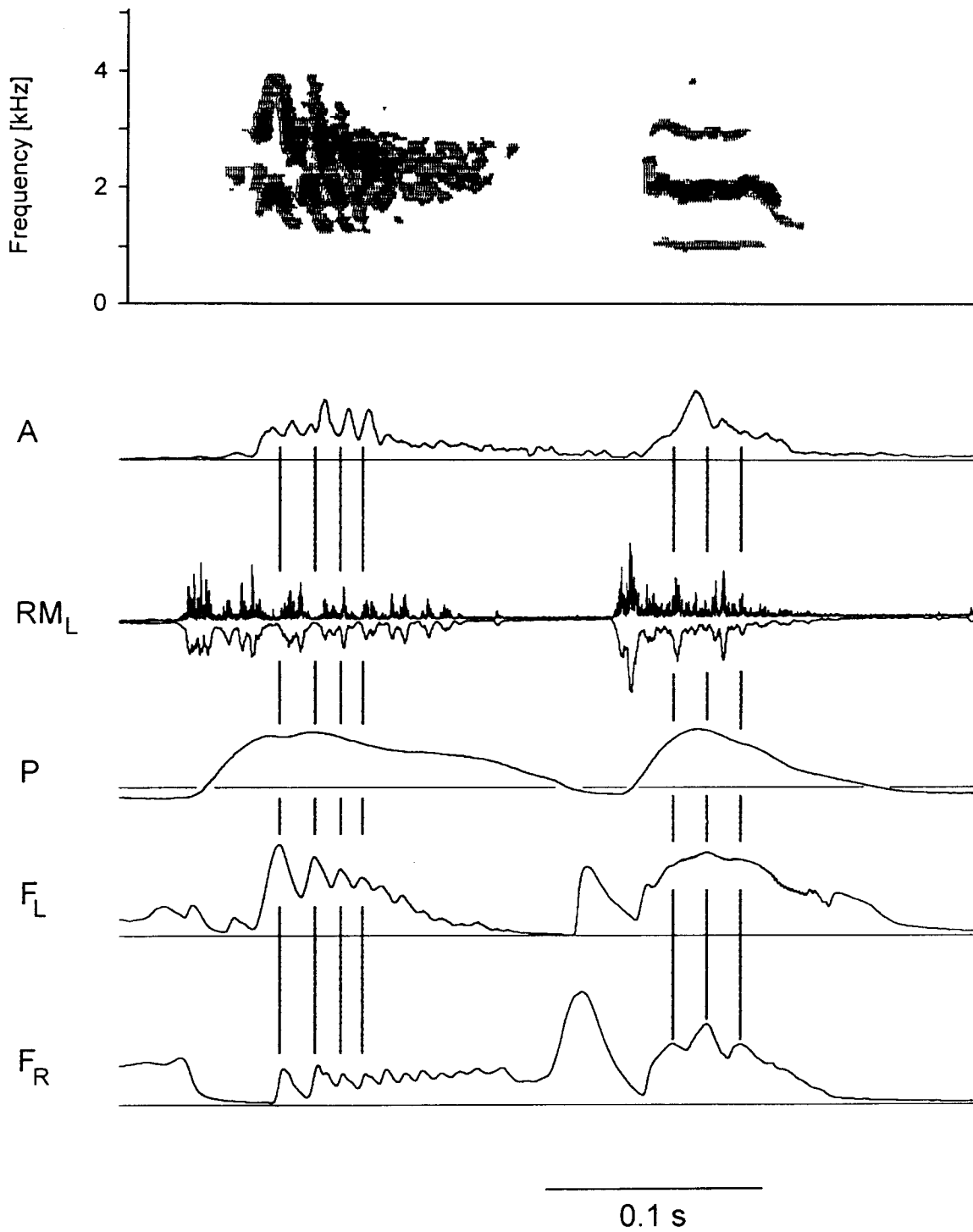


Figure 5 Expiratory EMG activity during syllables with oscillatory flow modulation occurs in bursts that appear aligned with the modulation. Bursts in the left expiratory muscles occur regardless of whether airflow through the left side is modulated (right flow is modulated in both syllables). Abbreviations as in Figure 1.

nections between syringeal and respiratory motor pathways support our interpretation that bilateral distribution of respiratory activity may be the normal pattern for phonation.

The nucleus robustus archistriatalis is directly or indirectly connected to all motor systems involved in song production and probably plays a major role in coordinating respiratory and syringeal activity during song (Vicario, 1994). Most functional aspects of the motor integration are not known (Vu et al., 1994; Yu and Margoliash, 1996; Margoliash, 1997; Wild, 1997), but data on peripheral motor patterns provide some basic information about motor coordination during lateralized birdsong.

Lateralization of song production may have evolved to make maximal use of the two independent sound sources and valves of the syrinx for generation of spectrally and temporally complex acoustic signals (Suthers, 1997; Suthers and Goller, 1997). The evolutionary pressures may therefore have been quite different from those leading to lateral dominance in the central control of human speech (Goller and Suthers, 1995). Not only is respiratory activity not lateralized, but even at the level of the syrinx song lateralization is not accompanied by inactivity of syringeal muscles on the silent side. The silent side of the syrinx is fully adducted, owing to strong activity in the adductor muscles, and the other ipsilateral syringeal muscles of the closed side are activated in a phonatory pattern that produces sound whenever the adductors relax and permit air to flow (Goller and Suthers, 1995). However, in contrast to the bilaterally similar activity of expiratory muscles during unilateral and bilateral phonation, the pattern and amplitude of various syringeal muscles differ on either side, since both sides very rarely generate the same sound in thrashers (Suthers et al., 1994). Thus, lateralized song production is achieved through concurrent independent unilateral activation of syringeal muscles in combination with bilaterally similar activation of expiratory abdominal muscles. Because the syringeal patterns during lateralized song production in species with pronounced dominance, such as the canary, are similar to those in thrashers (Goller and Suthers, unpublished observations), we suspect that lateralized respiratory motor control is also absent in those species. This aspect of respiratory-vocal motor coordination may be common to most or all oscine songbirds despite species differences in the syringeal lateralization of song production.

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