

# Peripheral Control and Lateralization of Birdsong

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**ABSTRACT:** Recent studies on several species of oscine songbirds show that they achieve their varied vocal performances through coordinated activity of respiratory, syringeal, and other vocal tract muscles in ways that take maximum advantage of the acoustic flexibility made possible by the presence of two independently controlled sound sources in their bipartite syrinx (vocal organ). During song, special motor programs to respiratory muscles alter the pattern of ventilation to maintain the supply of respiratory air and oxygen to permit songs of long duration, high syllable repetition rates, or maximum spectral complexity. Each side of the syrinx receives its own motor program that, together with that sent to respiratory muscles, determines the acoustic properties of the ipsilaterally produced sound. The acoustic expression of these bilaterally distinct, phonetic motor patterns de-

pends on the action of dorsal syringeal adductor muscles that, by opening or closing the ipsilateral side of the syrinx to airflow, determine the amount each side contributes to song. The syringeally generated sound is further modified by muscles that control the shape of the vocal tract. Different species have adopted different motor strategies that use the left and right sides of the syrinx in patterns of unilateral, bilateral, alternating, or sequential phonation to achieve the differing temporal and spectral characteristics of their songs. As a result, the degree of song lateralization probably varies between species to form a continuum from unilateral dominance to bilateral equality.

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## INTRODUCTION

In birdsong, as in human speech, an appropriate vocal output can be achieved only through the integrated activity of diverse muscle groups. The muscles essential for song production are not limited to those of the vocal organ, but also include muscle groups having primary functions in nonvocal behaviors, such as the control of respiratory or craniomandibular movements. The coordinated action of at least four separate groups of muscles is particularly important in song production. The respiratory muscles generate the driving force necessary for vocalization by creating the respiratory pressure needed to move air through the avian vocal organ, the syr-

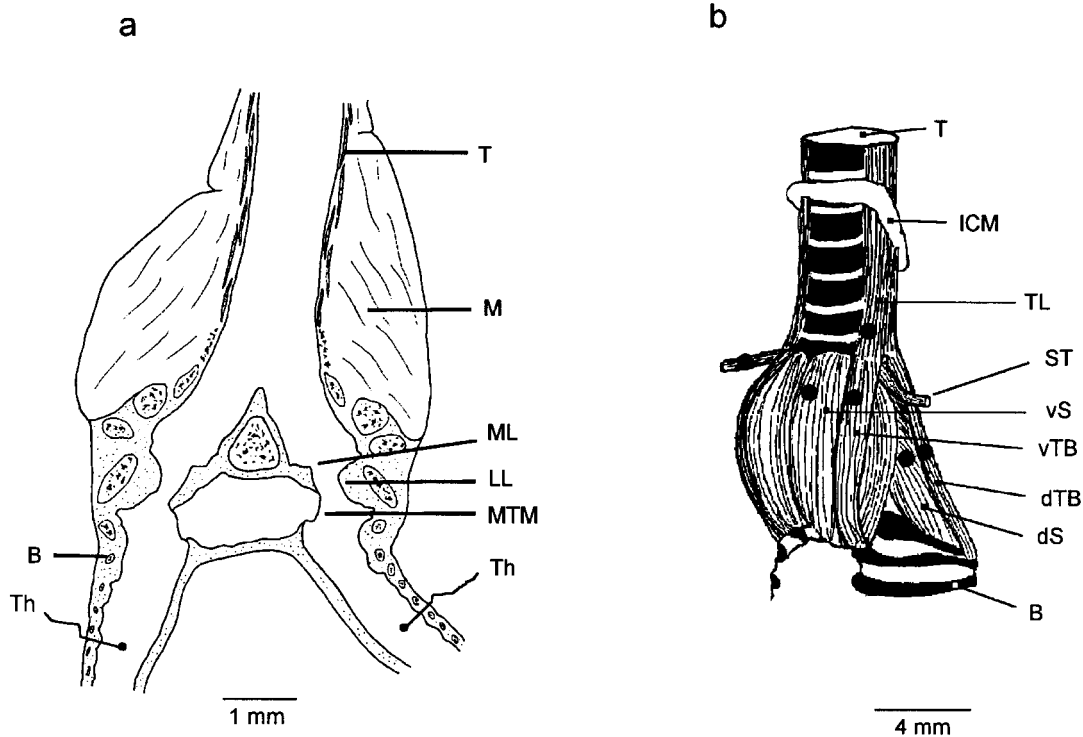
inx. Separate sets of muscles on the left and right side of the syrinx independently control sound production on each side of this organ. From a functional point of view, the two sides of the syrinx are treated here as separate muscle groups, although Wild (1997) combined them when considering neural pathways controlling song production. Finally, the sound generated in the syrinx may be modified by cranial and other muscles which control the configuration of the vocal tract.

This article summarizes some of the recent advances that contribute to a better understanding of song production. For additional background information, the reader is referred to reviews by Gaunt (1987), Brackenbury (1989), Nowicki and Marler (1988), Nottebohm (1991), Vicario (1991b), Suthers (in press), and Suthers and Goller (1997). Current knowledge of the neural pathways that control song production, and by which these groups of muscles are connected, is reviewed by Wild (1997).

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**Figure 1** The oscine syrinx is a bipartite structure containing two sound sources. (a) Frontal section through a brown thrasher syrinx. Th = position of microbead thermistor to measure rate of airflow through each side of syrinx. See Suthers et al. (1994) for detailed methods and surgical procedures. (b) Ventrolateral external view of a thrasher syrinx depicting syringeal muscles. Black dots indicate for one side the approximate location where bipolar wire electrodes were placed. T = trachea; M = syringeal muscle; ML = medial labium; LL = lateral labium; MTM = medial tympaniform membrane; B = bronchus; ICM = membrane of the interclavicular air sac; TL = M. tracheolateralis; ST = M. sternotrachealis; vS = M. syringealis ventralis; vTB = M. tracheobronchialis ventralis; dTB = M. tracheobronchialis dorsalis; dS = M. syringealis dorsalis. (Modified from Goller and Suthers, 1996a.)

## FUNCTIONAL ANATOMY OF THE VOCAL SYSTEM

The oscine syrinx is suspended in the interclavicular air sac, where it is formed from modified cartilages of the caudal end of the trachea and the cranial ends of the two primary bronchi (Fig. 1). The cranial end of each bronchus contains a medial tympaniform membrane (MTM) and a pair of labia composed of connective tissue. The medial labium is located at the cranial edge of the medial tympaniform membrane and opposes the more prominent lateral labium. The configuration of these structures is controlled by about half a dozen bilaterally paired syringeal muscles which envelop the external surface of this organ. The left and right members of each muscle pair are separately innervated by the ipsilateral tracheosyringeal branch of the hypoglossal nerve (King, 1989).

The means by which sound is generated in the

syrinx has been the subject of debate (e.g., Gaunt et al., 1982; Casey and Gaunt, 1985). Setterwall (1901) assigned this role to the medial and lateral labia, which he referred to as the inner and outer vocal cords, respectively. However, Miskimen (1951) provided experimental evidence that seemed to implicate the medial tympaniform membranes as the vibratory sound source, and this hypothesis has been widely accepted (e.g., Greenewalt, 1968). Recent endoscopic observations of syringeal configuration during phonation (Goller and Larsen, unpublished observation) provide new evidence that sound is generated by the labia, rather than the MTM, thus vindicating Setterwall's earlier assumption. Goller and Larsen observed that the medial and lateral labia are adducted and meet in the middle of the syringeal lumen prior to phonation. During phonation they bulge cranially owing to the increased respiratory pressure, and both labia vibrate as air escapes through a thin slitlike opening be-

tween them. The role of the MTM remains to be determined, but it is well positioned to influence the motion of the medial labium.

This experimental approach to syringeal function has been supplemented by the development of theoretical models. The most successful quantitative acoustic model of the syrinx was developed by Fletcher (1988, 1989), based on the raven (*Corvus mellori*). Although this model assumes sound is generated by the MTM, it predicts the spectral structure of voiced oscine sounds, but is not able to produce pure tones that predominate in whistled song.

Airflow through the syrinx is driven by the abdominal and thoracic respiratory muscles, which are innervated by branches of various cervical, thoracic, and lumbar spinal nerves. Birds lack a diaphragm. All the abdominal and several thoracic muscles are expiratory. Six other thoracic muscles are responsible for inspiration (Fedde, 1987). Together, these muscles ventilate the relatively small, inelastic lungs by alternately compressing and expanding the air sacs. Air sacs on opposite sides of the body are connected by the midline interclavicular sac containing the syrinx. Pressure differences between air sacs during normal respiration (Brackenbury, 1971, 1972, 1973; Scheid and Piiper, 1989) or during distress calls (Gaunt et al., 1973) are very small. Respiratory pressure on the two sides of the syrinx during song are probably also similar.

## RESPIRATORY MOTOR PATTERNS DURING SONG

### Respiration during Song

The respiratory dynamics during spontaneous song have been studied by measuring the rates of airflow through the primary bronchi or trachea with chronically implanted microbead thermistors, while monitoring respiratory pressure through an air sac cannula attached to a piezoresistive pressure transducer. Bronchial thermistors can also detect near-field sound generated in the ipsilateral side of the syrinx by responding to flow oscillations produced by the vibrating labia (Suthers, 1990).

During song, the normal respiratory pattern is modified to meet the special needs of sound production. Sound is produced during expiration. Respiratory pressure is increased and controlled during vocalization to maintain the appropriate rate of airflow across the adducted, sound-generating structures of the syrinx. Air sac expiratory pressure in the brown thrasher (*Toxostoma rufum*), for example, increases

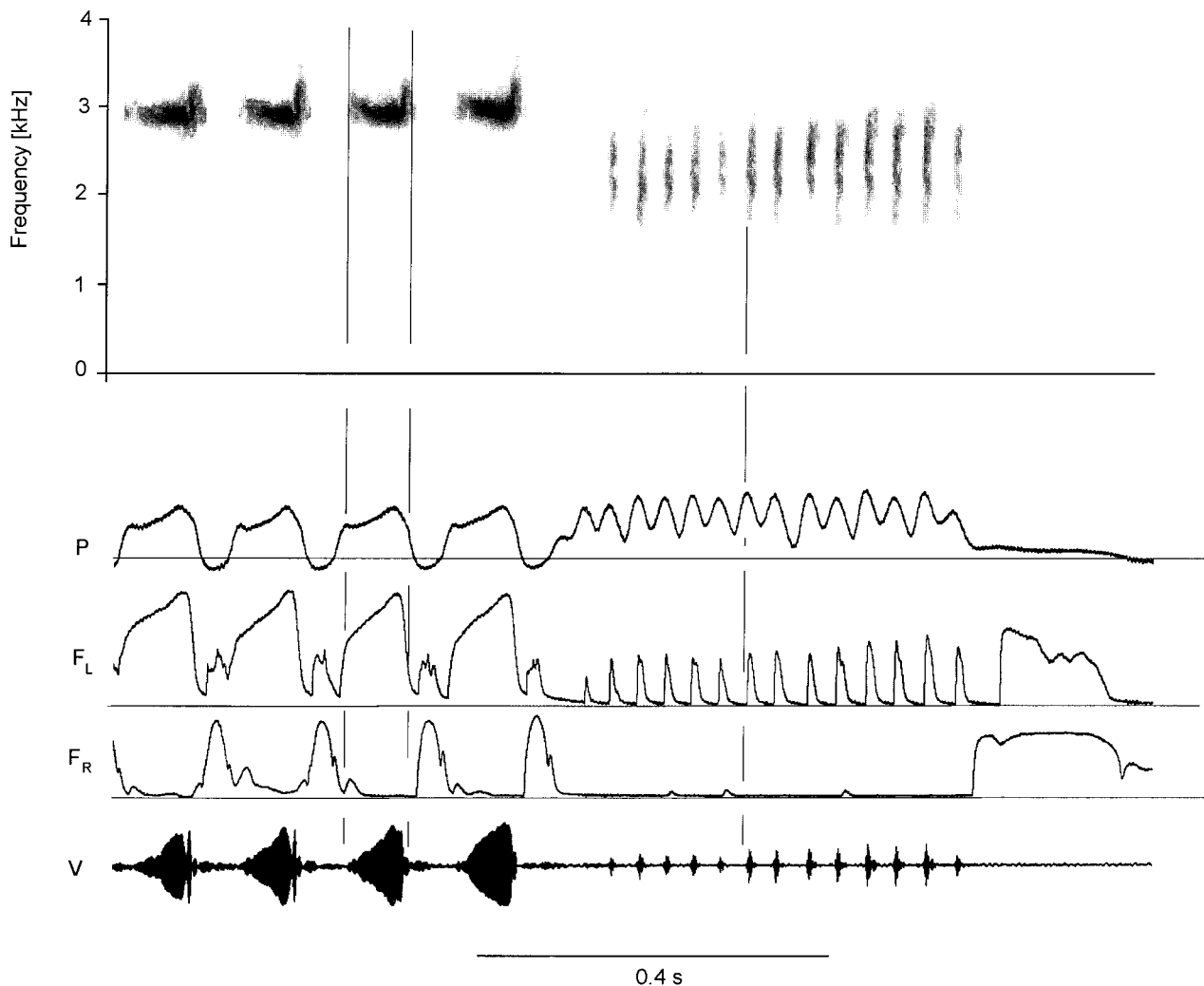
an average of 16-fold (with a maximum increase of 50-fold) during song compared to that during quiet respiration (Goller and Suthers, unpublished observation). The respiratory rhythm of a singing bird also increases in frequency and complexity. The inspiratory phase is shortened and the duration of the expiratory phase that accompanies vocalization is sometimes increased. These changes have an important role in determining the temporal pattern of the song (Hartley, 1990; Vicario, 1991a; Suthers and Goller, 1997).

Respiratory adjustments to singing depend on the tempo of the song (Suthers and Goller, 1997). Birds which sing at a relatively slow rate of a few syllables per second, such as gray catbirds (*Dumetella carolinensis*) and brown thrashers, are able to inhale enough air between each syllable to meet the needs of pulmonary gas exchange, as well as replace the volume of air needed for the next vocalization (Suthers et al., 1994). However, songs sung at a rapid tempo place greater demands on the respiratory ventilation and require precise coordination of respiratory and syringeal motor activity. Domesticated canaries (*Serinus canaria*) of the Belgian waterslager strain, for example, may sing continuously for more than 30 s. The song is divided into phrases consisting of repetitions of a single syllable type (Brenowitz et al., 1997). The syllable repetition rate within a phrase ranges from a few per second to more than 40/s, depending on the duration of the syllable (Calder, 1970; Nottebohm and Nottebohm, 1976; Hartley and Suthers, 1989).

### Minibreaths

How does a canary, which has a resting respiratory rate of about 1.5 breaths/s and tidal volume of 0.3–0.5 mL, sustain song at high syllable repetition rates for such a long period of time? Changes in thoracic volume (Calder, 1970) and measurements of respiratory pressures and tracheal airflow (Hartley and Suthers, 1989) during song show that in phrases with syllable repetition rates below about 30/s, a small inspiration, or minibreath, occurs after each syllable (Fig. 2). On average, each minibreath replaces the volume of air exhaled to produce the syllable. Minibreaths are a respiratory-syringeal motor strategy that allows birds to sustain song at a rapid tempo without running out of air for vocalization.

Minibreaths may also provide oxygen to the lungs. Long syllables expend more air and are followed by longer inspirations than short syllables. For example, canary syllables having a duration of 119 ms use 0.25 mL of air and are sung at a repeti-



**Figure 2** Segment of a waterslager canary song. First four syllables are sung by left syrinx and each is followed by a minibreath. During phonation, a positive air sac pressure drives expiratory air through left syrinx but not through the right, which is therefore closed. During minibreaths, air sac pressure is negative and air flows through both sides of the syrinx, with the flow rate being greatest on the right side. The trilled phrase is accompanied by pulsatile expiration. The left syrinx opens briefly to produce each syllable with a puff of expiratory air. The right side remains closed. Air sac pressure remains positive throughout the trilled phrase despite transient drops during each expiration. Both sides of the syrinx open at end of trill to exhale remaining air before inspiration.  $P$  = cranial thoracic air sac pressure. Horizontal line is ambient pressure (zero gradient);  $F_L$  and  $F_R$  = rate of airflow through left and right sides of syrinx, respectively. Horizontal lines equal zero flow. Inspiratory and expiratory flow are distinguished by sign of the pressure.  $V$  = oscillographic representation of vocalizations shown in top panel as spectrograms. Vertical lines align events during sound production.

tion rate of 6.5/s, whereas syllables having a duration of 11 ms expel between 0.007 and 0.05 mL of air at a repetition rate of 30/s (Hartley and Suthers, 1989). In canaries, the minibreaths associated with long syllables have a volume larger than that of the tracheal dead space. Although the volume of minibreaths associated with short syllables is less than the tracheal dead space, even these may con-

tribute to pulmonary gas exchange, since there is evidence that dead space air mixes at high respiratory rates with that reaching the lungs (Bech et al., 1988). Abbreviated inspirations similar to minibreaths are also prominent features of song in other species studied, including brown thrashers and gray catbirds (Suthers et al., 1994), northern cardinals (*Cardinalis cardinalis*) (Suthers and Goller, 1997),

brown-headed cowbirds (*Molothrus ater ater*) (Alan and Suthers, 1994), and zebra finches (*Taeniopygia gutta*) (Wild et al., 1997), suggesting they are a widespread motor adaptation for singing.

The production of minibreaths involves a complex sequence of motor acts requiring accurate coordination between the two sides of the syrinx and respiratory muscles. Waterslager canaries, for example, generate most syllables in their left syrinx (Nottebohm and Nottebohm, 1976; Suthers, 1992) by closing the right side during each sound-producing expiration. During each syllable, a motor program controlling sound production must be sent to the muscles of the left syrinx while other motor commands keep the right side closed. As soon as the syllable is completed, the right side opens to provide a low-resistance pathway for inspiratory airflow during the minibreath (Suthers, 1992). At syllable repetition rates approaching 30/s, these motor programs must be timed to arrive at the periphery via their respective spinal or cranial nerves with an accuracy of several milliseconds, relative to each other.

### Pulsatile Expiration

There is an upper limit in syllable repetition rate, beyond which the interval between syllables is too short to allow a minibreath. This limit is probably determined by the mechanical properties, e.g., mass and compliance, of the thoracic and abdominal structures that must oscillate at the frequency of ventilation. Canaries reach this limit at about 30 syllables/s, whereas in cardinals, which are larger, it occurs at about 16 syllables/s, yet, canaries and cardinals can sing trills containing up to about 70 or 30 syllables/s, respectively (Hartley and Suthers, 1989; Hartley, 1990; Suthers and Goller, 1996).

The air exhaled during phonation is not replaced between syllables at these high repetition rates. Instead, the minibreath motor pattern is abandoned in favor of a pattern of pulsatile expiration (Fig. 2) in which expiratory muscles maintain a positive respiratory pressure and the timing of each syllable is determined by micropuffs of air which are allowed to escape through the labia. During pulsatile expiration, the abdominal expiratory muscles of the canary exhibit either rapid bursts or continuous electrical activity, depending on the syllable repetition rate (Hartley, 1990). Although pulsatile expiration permits very high syllable repetition rates, the duration of such song phrases is limited, since neither the respiratory volume nor the pulmonary oxygen is replenished.

### Activity of Respiratory Muscles

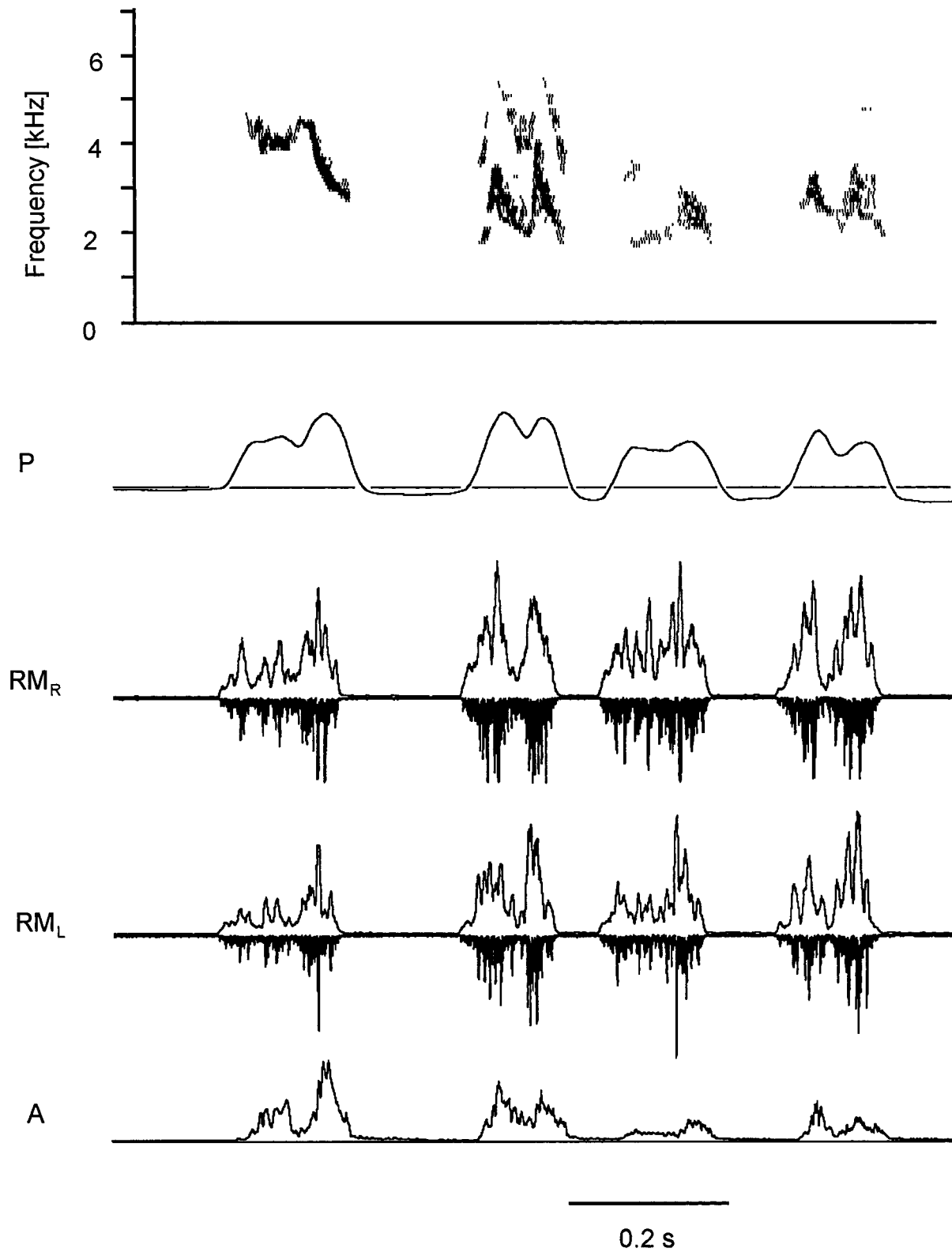
The muscular control of respiratory ventilation is thus a challenging motor task associated with song production. Electromyograms (EMG) of respiratory muscles, recorded simultaneously with respiratory pressure and airflow, show a marked increase in the activity of abdominal expiratory muscles during phonation in canaries, brown thrashers, and zebra finches (Hartley, 1990; Goller and Suthers, 1995a; Wild et al., 1997). The amplitude of this expiratory muscle EMG is positively correlated with the air sac pressure and with the amplitude of the vocalization (Goller and Suthers, 1995a) (Fig. 3). Minibreaths between syllables are accompanied by contraction of inspiratory muscles. In zebra finches and brown-headed cowbirds, each minibreath is accompanied by high-amplitude bursts of activity in the inspiratory muscles *M. scalenus* (Fig. 4) and *Mm. levatores costarum*, which originate on the transverse process of the vertebrae and insert on the ribs (Wild et al., 1997). The respiratory muscles thus actively contribute in a reciprocal, alternating pattern to both expiration and inspiration during song.

In the absence of activity by the respiratory muscles, the thorax assumes a resting position in which the sternum is about halfway between that achieved at the peaks of inspiration and expiration (McLelland, 1989). Wild (1997) pointed out that inspiratory muscles do not appear to actively brake expiration at the end of a song syllable. Passive elastic recoil of the thorax, however, opposes both inspiratory and expiratory displacements of the sternum. Assuming the ventilatory movements during song are centered around the resting position of the sternum, elastic recoil may facilitate rapid oscillation of the body wall during minibreaths by passively braking both the inspiratory and expiratory phases and by initially accelerating body wall movement in the reverse direction at the onset of the opposite respiratory phase.

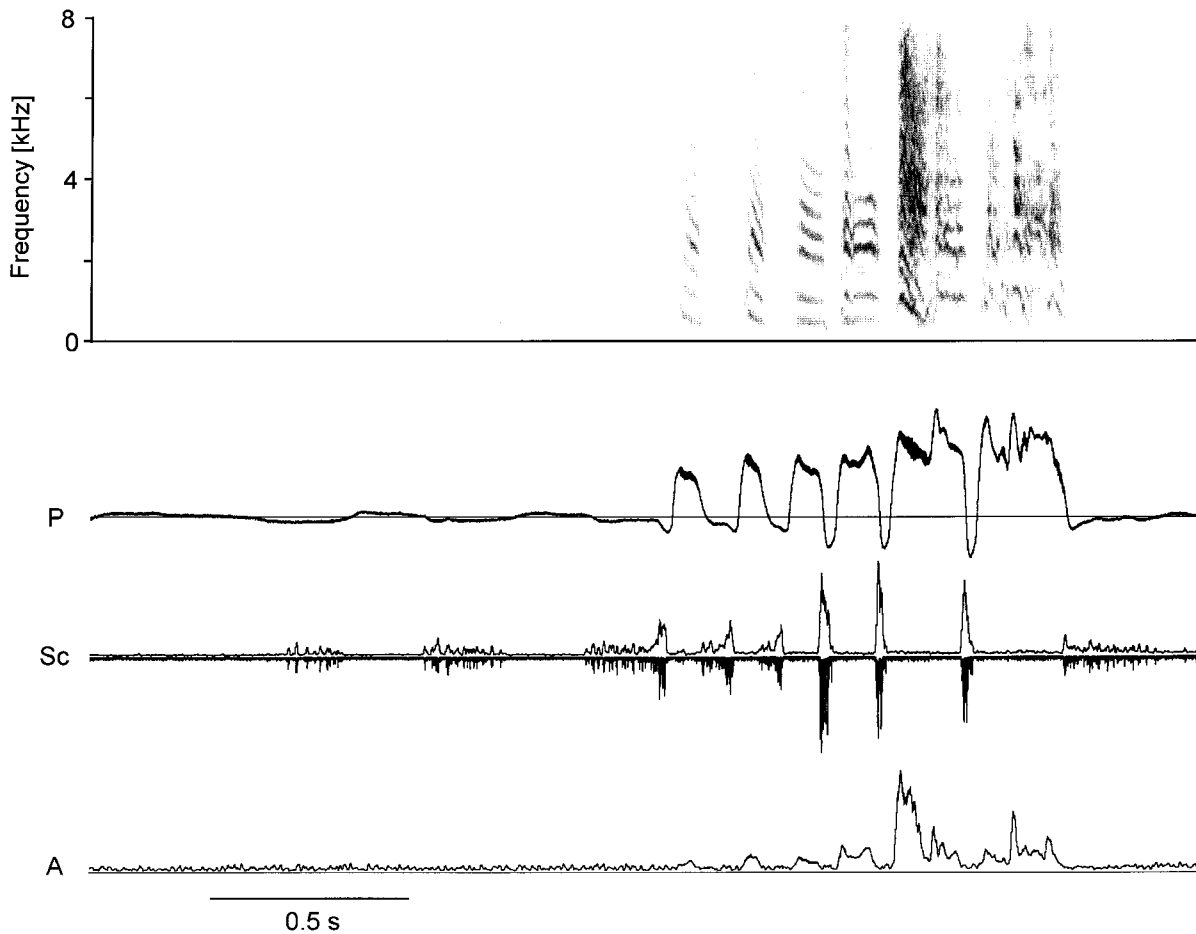
### SYRINGEAL MOTOR PATTERNS DURING SONG

#### Lateral Independence

The oscine syrinx is functionally two vocal organs, each separately innervated by the ipsilateral side of the brain. Many important parameters of song, including the timing of sound production and fundamental frequency, are controlled independently by separate motor programs sent to muscles on each side of the syrinx. These motor programs are reproduced in a similar way each time the same syllable



**Figure 3** Activity of abdominal expiratory muscles of a singing brown thrasher is not lateralized but is correlated with air sac pressure and the amplitude of vocalization. RMR and RML = right and left abdominal expiratory muscle EMG (integrated = upward; rectified = downward). A = rectified envelope of microphone recording. Other abbreviations as in Figure 2. (Goller and Suthers, unpublished observation.)



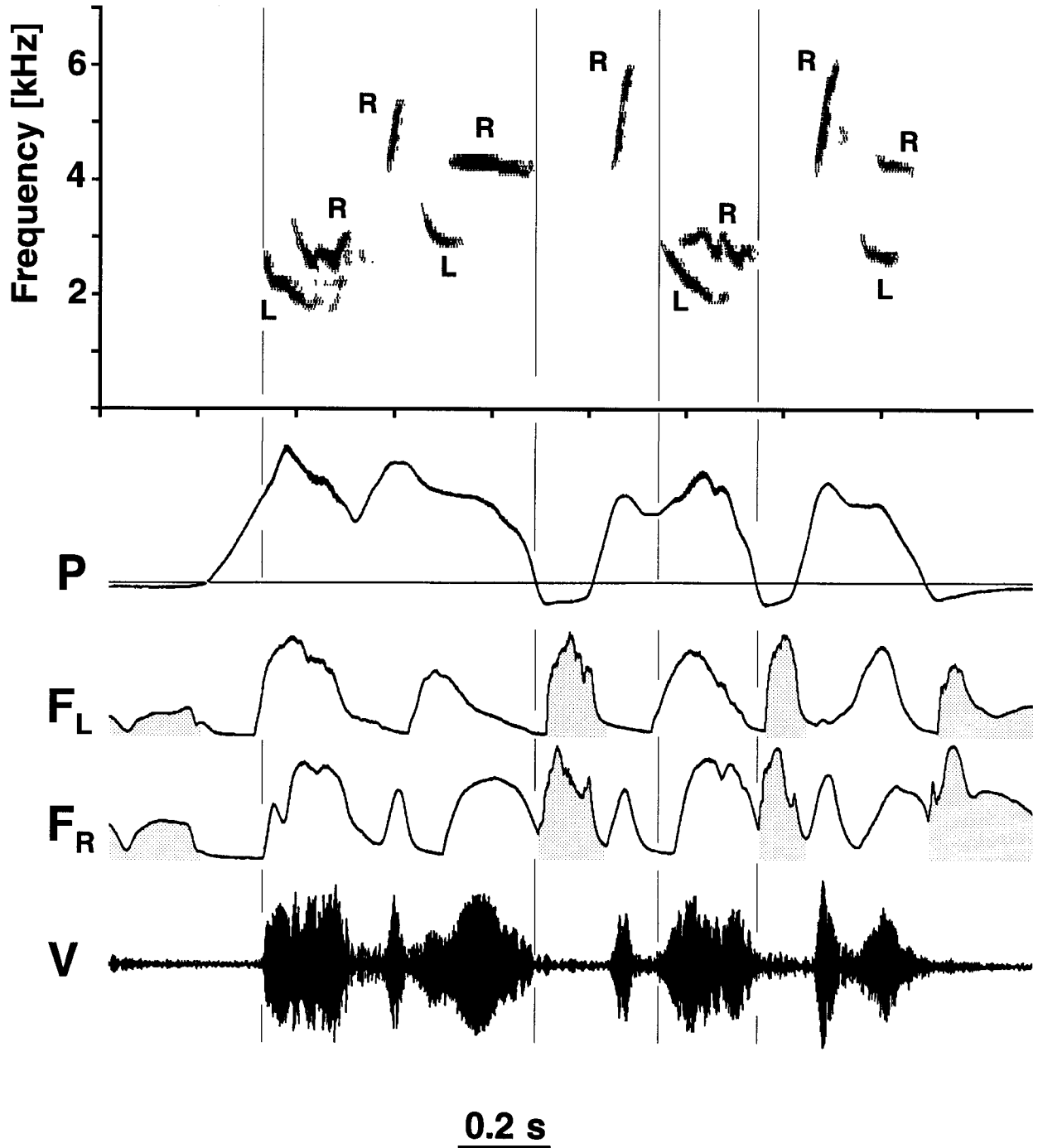
**Figure 4** Activity of thoracic inspiratory muscle, *M. scalenus*, in a zebra finch during quiet respiration and song. Muscle contraction coincides with negative pressure and inspiratory airflow (not shown) during minibreaths that accompany periods of negative air sac pressure between syllables. Note increase in EMG during minibreaths, compared to quiet respiration. Sc = EMG of scalenus muscle. Other abbreviations as in Figure 2. (Wild, Goller and Suthers, unpublished observation.)

type is repeated (Suthers et al., 1996b). This motor and acoustic stereotypy may continue in adult song of some species even in the absence of auditory feedback (Nordeen and Nordeen, 1997), suggesting that the motor programs for song production, like those that control a number of other simpler rhythmic motor patterns of other animals (Marder and Calabrese, 1996), may originate in central pattern generating circuits in the brain (Konishi, 1985; Vu et al., 1994; Yu and Margoliash, 1996).

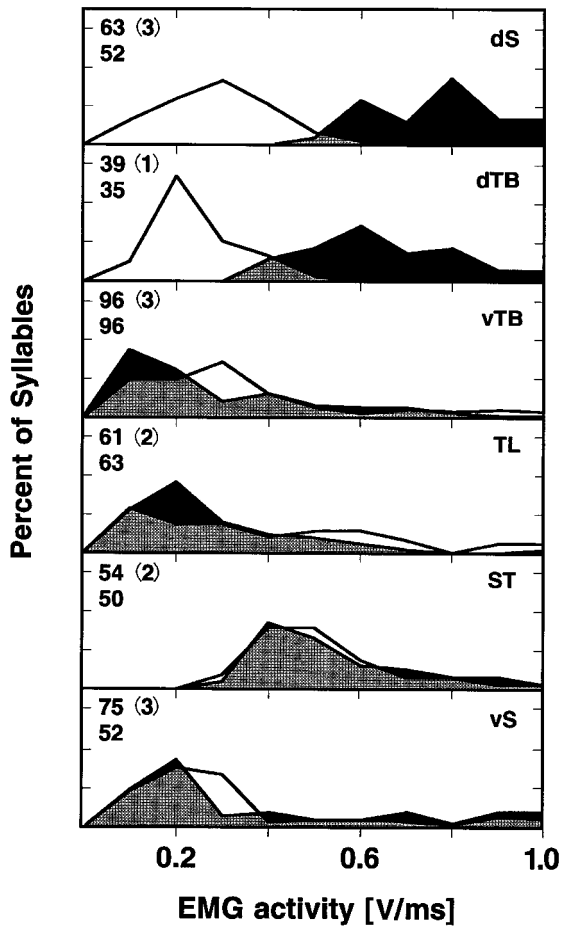
**Dorsal Muscles Control the Time of Phonation.** A fundamental aspect of song production is the ability to use the two sides of the syrinx as independent sound sources: to rely on one or the other, or switch back and forth between sides to achieve greater vocal diversity. The mechanism that determines which side produces sound is thus of critical importance

in song production. Studies on brown thrashers (Fig. 5), gray catbirds, brown-headed cowbirds, northern cardinals, and canaries show that both sides of the syrinx contribute to song unless one is closed, preventing air from flowing through it (Suthers, 1990, 1992; Allan and Suthers, 1994; Suthers et al., 1994, 1996b). The contribution each side makes to song is thus determined by muscles that control the medial and lateral labia in the cranial end of each bronchus which act as valves regulating airflow through each side of the syrinx (Fig. 1).

Electromyography of syringeal muscles in singing brown thrashers shows that two dorsal muscles, *M. syringealis dorsalis* and *M. tracheobronchialis dorsalis* (Fig. 1), are responsible for adducting the labia and closing the ipsilateral syrinx, preventing phonation (Fig. 6). These are the only syringeal muscles in which EMG activity is consistently cor-



**Figure 5** Segment of brown thrasher song showing four two-voice syllables with independent frequency modulation of the left- and right-side contributions. These are separated from each other by shorter upward sweeping syllables produced by airflow through the right syrinx while the left side is closed, and therefore silent. Note how vocal production switches between sides of the syrinx with the vocal register of the right side being higher than that of the left. R and L in spectrogram indicate contributions from right and left side of syrinx; inspiratory airflow (minibreaths) is stippled. Other abbreviations as in Figure 2. (From Suthers et al., *J. Neurobiol.* 25:917–936, © 1994, John Wiley & Sons, Inc., reproduced with permission.)



**Figure 6** Frequency distributions of the normalized amplitude of EMG activity in syringeal muscles of brown thrashers during full adduction while the contralateral side generates sound (black area) and during ipsilaterally produced syllables (white area). The overlapping area of the two distributions is shaded. The difference in distributions is highly significant for dS and dTB ( $p < 0.001$ ), marginal for TL ( $p < 0.05$ ), and not significant for all other muscles ( $p > 0.05$ ). In each panel the number of syllables measured during adduction (upper number) and phonation (lower number) is indicated, together with the number of individuals contributing to data sets for each muscle (parentheses). See Figure 1 for names and location of muscles. (Reprinted from *Nature*, Goller and Suthers, "Implications for lateralization of bird song from unilateral gating of bilateral motor patterns," 373: 63–66, © 1995 Macmillan Magazines Limited, reproduced by permission.)

related with full ipsilateral adduction which prevents airflow despite a positive air sac pressure (Fig. 6) (Goller and Suthers, 1995b, 1996b). In addition to their unique role in turning ipsilateral sound production on and off, the dorsal syringeal muscles are also active to a lesser degree during phonation when they partially adduct the labia into a phonatory con-

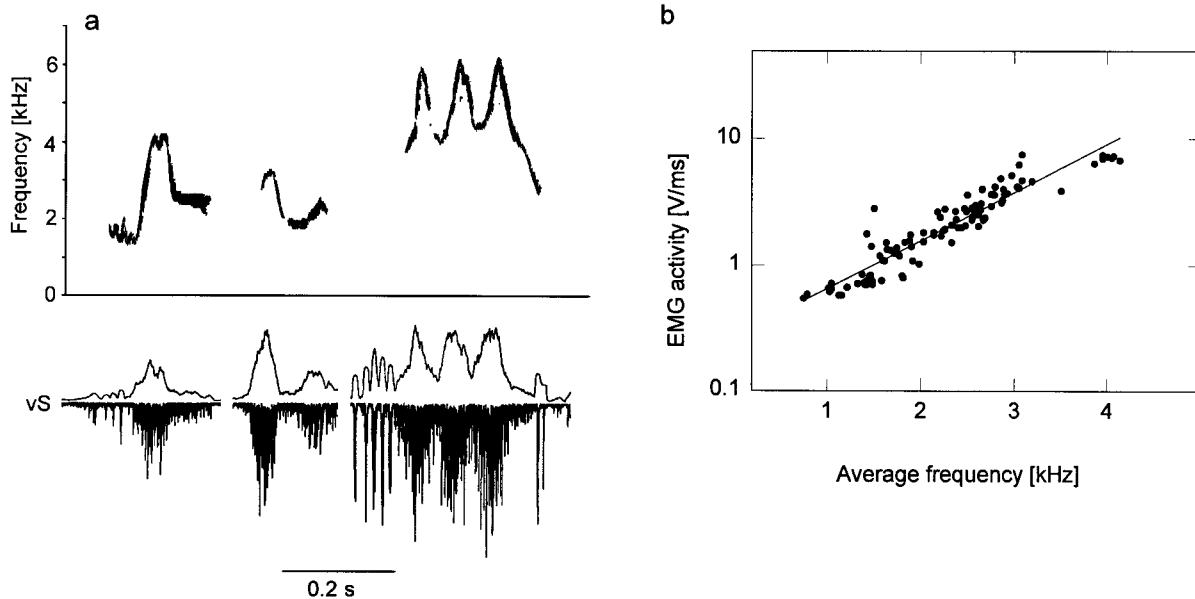
figuration. These dorsal muscles appear to have a similar function in northern cardinals (Goller and Suthers, unpublished observation) and brown-headed cowbirds (Allan and Goller, 1995).

**Control of Fundamental Frequency.** Other syringeal muscles have a major role in determining the spectral properties of song. The fundamental frequency is regulated independently on each side by the ipsilateral ventral syringeal muscles, *M. syringalis ventralis* (Fig. 1). In brown thrashers, the amplitude of the EMG in this large muscle increases exponentially with the fundamental frequency of sound generated by the ipsilateral syrinx (Goller and Suthers, 1996a). These ventral muscles are also the only muscles in which activity is strongly correlated with frequency modulation (FM). The amplitude of their EMG increases with rising FM and decreases during falling FM components of a syllable (Fig. 7). When the two sides of the syrinx produce different sounds, both ventral muscles are active but the amplitude pattern of their contractions differ depending on the frequency pattern of their respective sounds (Goller and Suthers, 1996a).

Independent activation of the left and right ventral muscles is essential in enabling a bird to generate two-voice syllables, i.e., syllables which contain simultaneous or overlapping contributions from the left and right syrinx that are not harmonically or acoustically related (Greenewalt, 1968; Stein, 1968) (Fig. 5). Two-voice syllables require that different motor programs be simultaneously transmitted to the left and right ventral muscles. It would be interesting to know if the spectral complexity which two voices add to song has special perceptual significance in vocal communication (Suthers and Goller, 1997).

Spectral diversity of song is further enhanced by the fact that the left and right syrinx have somewhat different vocal registers and generate syllables with fundamentals in different though overlapping frequency bands. The right syrinx in all cases covers a higher frequency range than the left, but in most species there is considerable overlap between sides (Nottebohm and Nottebohm, 1976; Allan and Suthers, 1994; Suthers et al., 1994; Goller and Suthers, 1996a). It is not clear whether these differences reflect lateral differences in motor control, e.g., the firing rate or recruitment of motor neurons, or anatomical asymmetries in the vocal organ, e.g., in the dimensions or mass (Luine et al., 1980) of sound-generating structures in the syrinx.

Not all frequency shifts are under direct muscular control. Fee et al. (1996) noted that sudden transitions in fundamental frequency and offsets in adja-



**Figure 7** Role of ventral syringeal muscles in the control of sound frequency by brown thrashers. (a) Amplitude of EMG activity is positively correlated with frequency modulation of sounds produced on the ipsilateral side. (b) Amplitude of EMG activity is exponentially correlated with the fundamental frequency of ipsilaterally generated sounds. EMG activity was averaged over segments of syllables having a relatively constant frequency. vS = EMG of *M. syringealis ventralis*. See Figure 2 for explanation. (From Goller and Suthers, *J. Neurophysiol.* **76**:287–300, © 1996, American Physiological Society, reproduced with permission.)

cent spectral components of zebra finch song can occur in <1 ms, too rapidly to be under neural control. They suggest these abrupt changes, which are not unique to zebra finches, depend instead on the intrinsic nonlinear dynamics of the syrinx, so that small changes in control parameters lead to large spectral changes, such as period doubling, in which the fundamental frequency and therefore the spacing between harmonic components, suddenly halves.

**Lateralization of Amplitude Modulation.** A third important aspect of song, its amplitude or intensity, depends on a number of factors involving both respiratory and syringeal muscles. Some mechanisms for producing amplitude modulation (AM) are primarily respiratory and affect both sides of the syrinx. Vocal intensity, for example, is positively related to the air sac pressure during vocalization (Goller and Suthers, 1995a; Suthers et al., 1996a) and to the strength of contraction by expiratory muscles (Goller and Suthers, 1995a) (Fig. 3). Some birds, such as thrashers, often include elements in their song with prominent, rapid AM. In some cases, amplitude modulation within syllables is accompanied by cyclical fluctuations in air sac pressure pro-

duced by respiratory muscles (Goller and Suthers, unpublished observation).

Higher rates of amplitude modulation—up to 125 Hz in thrashers—are produced by the unilateral action of syringeal muscles which repeatedly open and close one side of the syrinx to modulate vocal intensity, by either producing sound or shunting air from the contralateral phonating side, to reduce sound intensity (Suthers et al., 1994; Goller and Suthers, 1996b). This kind of AM is nearly always generated by the right syrinx through repetitive activation of the dorsal syringeal adductor muscles *M. tracheobronchialis dorsalis* and *M. syringealis dorsalis*, sometimes in alternation with the syringeal abductor *M. tracheobronchialis ventralis* (Goller and Suthers, 1996a). The smaller mass of the syringeal labia, compared to the thoracoabdominal wall, is probably a factor making it possible for the syringeal muscles to achieve higher rates of AM than the respiratory muscles.

### Lateral Interactions

Although the left and right syrinx often act independently to produce song, in some ways the two sides are interdependent. Acoustic interactions may oc-

cur: For example, when slightly different frequencies are generated at a similar intensity on each side, the acoustic pressure waves may interact in the trachea to produce a combination tone. Linear bilateral interactions may give rise to a difference tone, or beat note, at a frequency equal to the difference between the frequency of the component emanating from each side of the syrinx. Greenewalt (1968) cited evidence for beat notes in the song of the Lapland longspur (*Calcarius lapponicus*). Beat notes are also prominent features of some syllables in brown thrasher song (Suthers et al., 1994; Goller and Suthers, 1996a). Beat notes make it possible to produce prominent amplitude modulation at a higher modulation rate than is attainable using syringeal muscles.

The properties of song may also be affected by complex nonlinear bilateral interactions. The spectrum of the “dee” syllables of the black-capped chickadee (*Parus atricapillus*) song is not the sum of that produced by the left and right sides after contralateral denervation, but is predicted if the two sides of the syrinx interact in a nonlinear process involving multiplication of the harmonic series generated on each side (Nowicki and Capranica, 1986a,b). This could give rise to a series of sum and difference frequencies. This bilateral coupling may be due to direct physical interaction between the two syringeal oscillators or to mechanical feedback through the structure of the syrinx itself. It is assumed that unilateral denervation of the syrinx does not alter the sound generated by the intact side. Bilateral interactions of the kind described here have not yet been observed in larger songbirds.

### Interactions between Syringeal and Respiratory Muscles

The motor patterns sent to syringeal and respiratory muscles must be coordinated during song to achieve the appropriate vocalization. If a change in syringeal resistance or expiratory effort affects syringeal airflow and pressure, it is likely to alter the sound being generated.

Syringeal resistance changes abruptly during song when a bird switches from unilateral to bilateral phonation, or vice versa, in the middle of a syllable. This phenomenon occurs frequently in the songs of thrashers and catbirds, as well as in other species. Some brown thrasher syllables show evidence of respiratory adjustment for syringeally generated changes in resistance that would otherwise alter the flow and pressure across the syrinx, and thus change the acoustic properties of the vocalization (Suthers et al., 1994). An example is shown

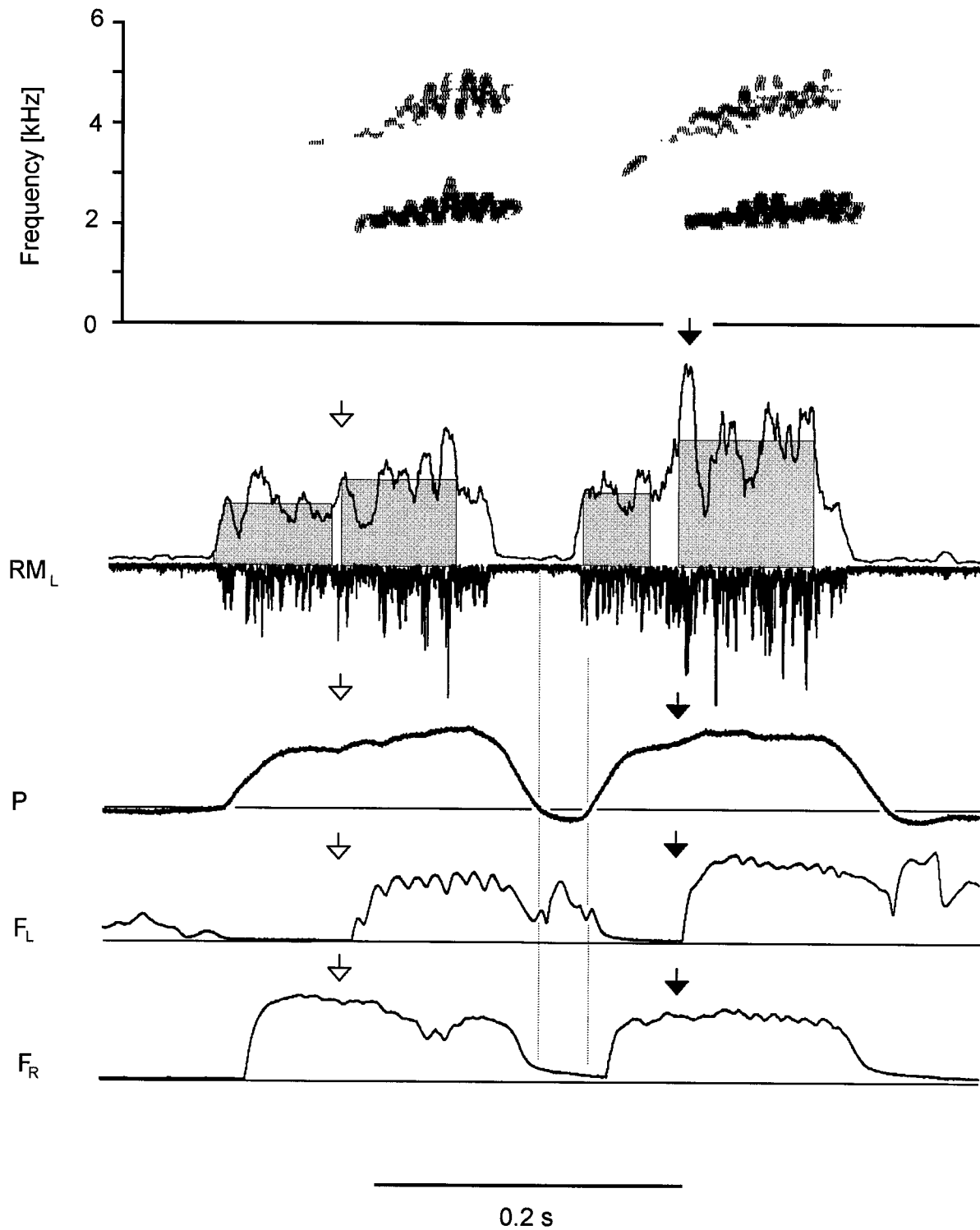
in Figure 8, in which the left syrinx opens suddenly in the middle of a syllable. The reduction in syringeal resistance that accompanies this switch to bilateral airflow should result in a drop in expiratory pressure, but pressure remains almost constant owing to an increase in the contraction of abdominal expiratory muscles, evident in the mean amplitude of their EMGs when both sides are open to flow (Goller and Suthers, 1995a).

In other experiments, the possible role of feedback on the stereotypical motor patterns of crystallized adult cardinal song have been investigated by suddenly increasing air sac pressure during song by injecting a small volume of air into the cranial thoracic air sac via a cannula (Suthers et al., 1997). Elevation of respiratory pressure by air injection early during a syllable is accompanied by a compensatory decrease in the amplitude of the EMG in abdominal expiratory muscles during the remainder of that syllable. Air injection during trilled phrases alters airflow during the normally inspiratory intervals between syllables but does not affect the temporal respiratory rhythm or the rate of airflow during phonation. It appears that even during normally stereotyped, crystallized song, the motor program is modified by either mechanoreceptive or auditory feedback to stabilize the rate of syringeal airflow during phonation, but not during the intervening minibreaths. This response to changes in respiratory pressure is consistent with the hypothesis that minibreaths are generated by the oscillating output of central pattern-generating networks. The basic rhythm of central pattern generators in other animals can be modulated, to varying degrees, by sensory feedback (e.g., Harris-Warrick and Johnson, 1989; Bianchi et al., 1995).

## CRANIAL MOTOR ACTIVITY DURING SONG

### Acoustic Role of the Vocal Tract

The sound generated in the syrinx is modified during its passage through the vocal tract before it is emitted as song. Frequency-dependent acoustic interactions determined by the dimensions or shape of the vocal tract may significantly change the amplitude spectrum of the vocalization by allowing some frequencies to pass, but attenuating others. The extent to which this occurs can be assessed by comparing the spectrum of song in air with that in a light gas mixture which increases the velocity of sound, and therefore correspondingly increases its wavelength. A light gas mixture of 80% helium



**Figure 8** Two brown thrasher syllables showing the EMG of abdominal expiratory muscles during an abrupt switch from unilateral (right side) to bilateral phonation in midsyllable (arrows). Shaded boxes indicate average EMG amplitude during unilateral and bilateral phonation. Increased amplitude of EMG during bilateral sound production may maintain a constant pressure and airflow despite the decrease in total syringeal resistance to airflow. Vertical dotted lines indicate minibreath.  $RM_L$  = left abdominal expiratory muscle EMG. See legend of Figure 3 for explanation. (Goller and Suthers, unpublished observation.)

and 20% oxygen (heliox) increases the velocity of sound about 74% compared to air, so that the wavelength of the second harmonic in heliox will be nearly equal to that of the fundamental in air. Nowicki (1987) found that when songbirds sing in heliox, the second harmonic appears in the song at a much greater amplitude than normal, providing evidence that the vocal tract in air is tuned to preferentially transmit the fundamental and attenuate the second harmonic of the syringeally produced waveform. This is not always the case, however, since measures of bronchial sound in catbirds and thrashers singing in air show that they sometimes suppress the fundamental rather than a harmonic (Suthers, 1990).

Of particular interest in Nowicki's experiments is the finding that in the species tested, it is always the second harmonic that is enhanced in heliox, regardless of its absolute frequency, which in a low-frequency syllable might be similar to that of the fundamental in a high-frequency syllable (Nowicki, 1987). Nowicki interpreted this to mean that these songbirds are normally able to adjust the tuning of their vocal tract as they sing so that it matches or tracks the fundamental frequency of each syllable. The means by which this is accomplished is unknown, although a variety of factors including changes in tracheal length by elevation of the syrinx or changes in the glottal aperture should affect vocal tract acoustics.

### Role of Beak Movements during Song

The prominent beak movements that often accompany song may also affect the acoustic properties of the vocal tract. Westneat et al. (1993) tested this hypothesis by reconstructing patterns of beak opening from video films of singing swamp sparrows (*Melospiza georgiana*) and white-throated sparrows (*Zonotrichia albicollis*). In most of the note types analyzed, the opening, or gape, was positively correlated with sound frequency, but not strongly correlated with sound amplitude. A similar correlation of beak gape with song frequency has also been reported in Bengalese finches (*Lonchura domestica*) (Moriyama and Okanoya, 1996).

Suthers et al. (1996a) extended these experiments by using a magnetosensitive chip and small magnet attached to the upper and lower mandible, respectively, to continuously measure beak gape in singing cardinals. Beak gape in these birds is also positively correlated with fundamental frequencies below about 3.5 kHz, but not at higher frequencies. When gape is artificially fixed at a large opening, the magnitude spectrum of the fundamental is not

greatly affected, but at fundamental frequencies below about 3.5 kHz, the magnitude of the second harmonic increases significantly relative to the fundamental. This is consistent with the hypothesis that in adult cardinals, beak opening is normally adjusted to suppress the harmonics of fundamentals in this frequency band.

Beak gape motor patterns and tonality develop in young song sparrows (*Melospiza melodia*) after the acoustic structure of the song becomes adultlike. In song sparrows, tonality is achieved in late plastic song, which is also about the time that beak movements, though still small, begin to be correlated with fundamental frequency (Podos et al., 1995).

## LATERALIZATION OF SONG PRODUCTION

### Evidence for Lateral Dominance in Birdsong

Lateralization of neural function was first described for human speech, for which it was shown that damage to the left cerebral cortex often produced aphasia, whereas a similar insult to the right cortex did not affect speech (Broca, 1861). For some time, cerebral dominance was widely assumed to be a uniquely human attribute related to human linguistic ability. Despite the realization that functional lateralization is a relatively widespread and fundamental feature of various kinds of motor and cognitive processes, little is known about either the underlying neural mechanisms or their evolutionary significance (e.g., Arnold and Bottjer, 1985; Hellige, 1993; Kimura, 1993).

In songbirds, the lateralization of song production appears to be limited to syringeal motor control. There is no evidence of lateralization in respiratory motor activity during song. The timing, temporal pattern, and amplitude of EMGs in the left and right abdominal expiratory muscles are similar in brown thrashers, regardless of which side of the syrinx is producing sound (Goller and Suthers, 1995a) (Fig. 3). Since the air sacs on each side of body are interconnected through the interclavicular and certain other air sacs, it is doubtful that unilateral activation of respiratory muscles, should it occur, would be an effective way of varying pressure or flow through the two sides of the syrinx.

Little is known in songbirds about motor activity which might change the configuration, and hence the acoustic properties, of the upper vocal tract. Lemon (1973) reported that unilateral section of the lingual branch of the hypoglossal nerve, which

innervates intrinsic muscles of the tongue, had no obvious effect on song in white-throated sparrows. The beak gape of cardinals is correlated with fundamental frequency over the vocal register of the left syrinx, but there is no consistent correlation with frequencies produced by the right syrinx (Suthers et al., 1996a). It is not clear if this lateralized correlation reflects a preferential access by circuits controlling the left syrinx to those controlling beak gape, or if it is due to wavelength-dependent acoustic interactions in the vocal tract.

### Exploiting Song Lateralization for Vocal Diversity

The songs of oscine birds encompass a tremendous range of acoustic diversity (Brenowitz et al., 1997). The few species in which song production has been studied show important differences in the way they use the two sides of their syrinx. These interspecific variations in syringeal use have apparently evolved to produce the different characteristic acoustic properties of species-specific song.

**Unilateral Dominance.** Unilateral dominance was first reported by Nottebohm (1970, 1971a, 1972) in chaffinches (*Fringilla coelebs*) and waterslager canaries (Nottebohm and Nottebohm, 1976). These studies demonstrated that paralysis of the left side of the syrinx by cutting the ipsilateral tracheosyringeal branch of the hypoglossal nerve results in a much greater deficit in postoperative song than when the same operation is performed on the right side. Right nerve cuts have only a modest effect on song in these birds, but after left hypoglossal neurotomy, only about one-third (chaffinches) or one-tenth (canaries) of the original song elements are retained. The effect of left neurotomy on canary song, compared to chaffinch song, is greater than these fractions suggest, since in canaries lost syllables were usually replaced by silence or brief clicklike noises, but in chaffinches they were often replaced by distorted, noisy syllables or simple modulated notes.

McCasland (1987) suggested that left hypoglossal dominance in canaries may be due to peripheral rather than central lateralization and arise from differences in the size or strength of the two sides of the syrinx. The muscle mass of the left syrinx is about 14% greater than the right (Luine et al., 1980). In support of his hypothesis, McCasland (1987) reported that when the left syrinx was silenced by a unilateral bronchial plug, the song syllables were noisy and distorted, but could still be matched with their preoperative counterparts. Right bronchial plug was followed by essentially normal

song but at a reduced intensity. The significance of this finding is unclear, however, since a subsequent attempt to repeat these experiments with unilateral bronchial plugs (Hartley and Suthers, 1990) resulted in song deficits similar to those observed after unilateral hypoglossectomy.

Left hypoglossal dominance can be reversed in canaries and chaffinches if the left nXIIts is cut prior to the period of motor plasticity during which vocal learning occurs (Nottebohm, 1971b; Nottebohm and Nottebohm, 1978; Nottebohm et al., 1979).

White-throated sparrows (Lemon, 1973), white-crowned sparrows (*Zonotrichia leucophrys*) (Nottebohm et al., 1976), and the Java sparrow (*Lonchura oryzivora*) (Seller, 1979) also show greater song deficits after left-side compared to right-side tracheosyringeal nerve section, but the difference is less dramatic than in the canary. Left hypoglossal neurotomy did not silence white-throated or Java sparrows, but resulted in a lowering of the fundamental frequency, usually with the addition of harmonic overtones. The white-throats lost their ability to maintain a constant frequency within their whistled notes, and Java sparrows lost the ability to produce the rapid large-frequency modulation characteristic of some of their notes. In zebra finches, right tracheosyringeal neurotomy has a greater effect on song than does left neurotomy (Price, 1977; Williams et al., 1992). This has been interpreted as right dominance, but again, the differences between left and right nerve section are mostly qualitative (changes in syllable phonology and frequency) rather than quantitative (loss of syllables), and left neurotomy also produces consistent changes in the song (Floody and Arnold, 1997).

Caution is needed when assessing the laterality of normal song production based on the effects of unilateral nerve cuts. Paralysis of half the syrinx might significantly alter the sound produced by the intact side. The uncontrolled loss of air through the denervated side of the syrinx might result in abnormal air flow or pressure on the intact side and change the sound it produces. Sound produced on the intact side may also be affected by the absence of contralateral muscle tone to stabilize the cartilaginous framework of the syrinx against which the innervated muscles operate. Lateral asymmetries in syringeal morphology—in its muscle mass or in the size of the syringeal aperture or bronchial lumen, for example—could produce different song deficits, depending on which side is denervated. This problem is minimized in waterslager canaries by the fact that after left neurotomy, the left side remains closed during song production in the intact right side (Suthers, unpublished observation). This ability,

which has not been observed in other species, is presumably due to mechanical crosstalk from the intact side and accounts for the absence of distorted syllables or prominent noise after unilateral neurotomy.

The prominent left dominance of waterslager canaries makes them the most strongly lateralized songbird investigated to date. Their unilateral production of syllables, however, is well suited to sustained high syllable repetition rates, characteristic of trilled phrases, and relatively long songs uninterrupted by long pauses for inspiration. Since only one side of the syrinx is open during phonation, respiratory air is conserved by unilateral phonation, and minibreaths between syllables replace the volume expelled during each syllable (Fig. 2).

Unilateral dominance may also permit these birds to reduce the conflict between syringeal motor programs that require labial adduction during phonation and those producing abduction for inspiration between syllables, by assigning each to opposite sides of the syrinx. Thus, the right syrinx, which is closed during left phonation, opens widely for inspiration between each syllable. The left side may stay partially or even fully adducted during these minibreaths and be better able to quickly resume its phonatory configuration at the end of the minibreath or achieve complex phonetic structure at high syllable repetition rates (Fig. 2).

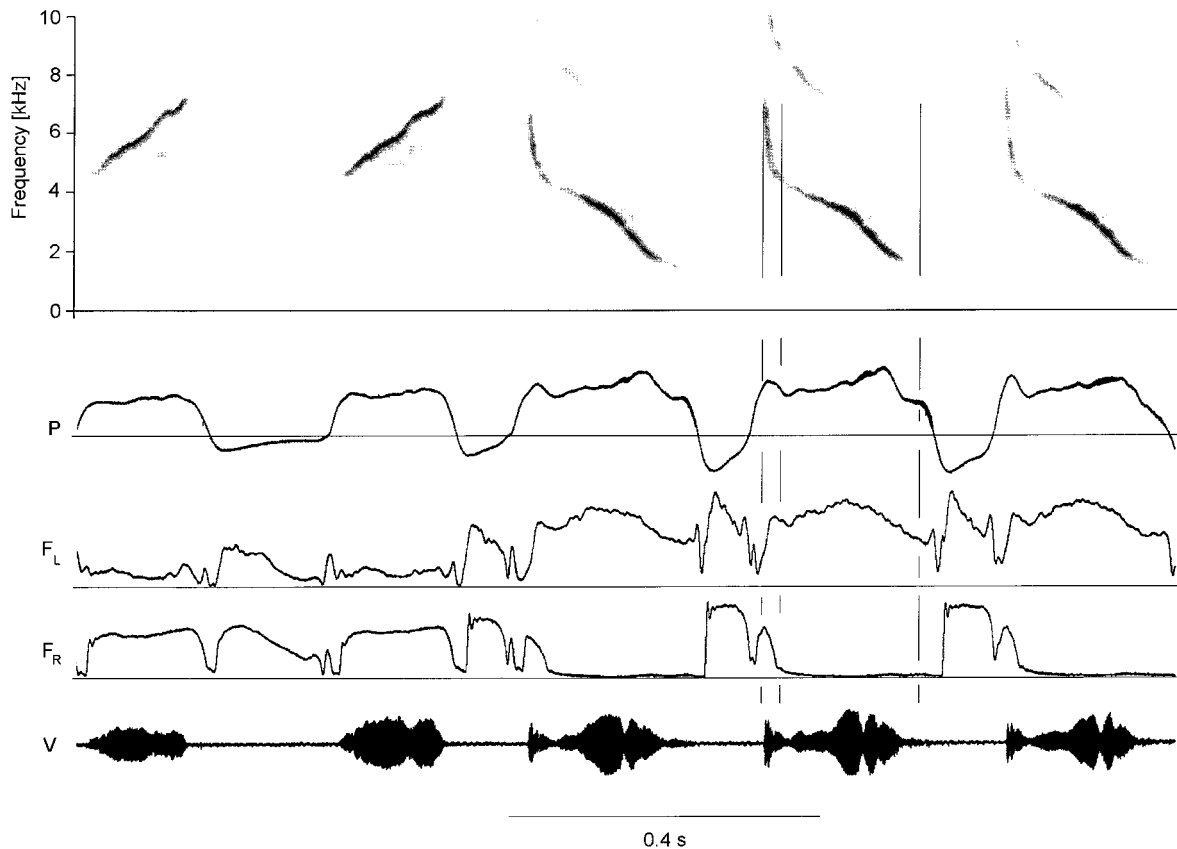
Unilateral song production reduces some kinds of spectral complexity by eliminating two-voice syllables from the song repertoire. Left syringeal dominance limits the frequency range to the lower register covered by the left side so that most waterslager song is below 4 kHz. This is interesting in view of the fact that this strain of canary has a hereditary abnormality of its inner ear which greatly raises its hearing threshold at high frequencies (Gleich et al., 1994a,b; Gleich and Klump, 1994). Aviculturists breed waterslagers for their low-frequency songs, which set them apart from other canaries. It may be that the extreme left dominance of song production in this breed evolved in response to their reduced auditory sensitivity to much of the vocal register normally covered by the right syrinx.

**Independent Bilateral Phonation.** Unlike canaries, catbirds and brown thrashers continually switch phonation from side to side, even within a single syllable (Fig. 5). Many of their syllables include independent simultaneous contributions from both sides of the syrinx (Suthers, 1990; Suthers et al., 1994). This independent bilateral sound production favors maximum spectral diversity and complexity in the form of two-voice syllables, in which simultaneous contributions from each side are indepen-

dently modulated in frequency and amplitude and may interact to produce difference tones. Lateral independence in the timing of sound production increases temporal complexity within syllables. Catbirds and thrashers sing syllables having a relatively long duration, which permits them to take full advantage of this potential complexity. The song repertoires of catbirds and brown thrashers are estimated to contain over a hundred, or thousands, of different syllable types, respectively (Thompson and Jane, 1969; Boughy and Thompson, 1976, 1981; Kroodsma and Parker, 1977), which they sing for many minutes at a time, at a low repetition rate of a few per second.

**Sequential Bilateral Phonation.** The song of northern cardinals is characterized by broadband frequency-modulated sweeps that sometimes span two octaves. One or several different syllable types are repeated in phrases to form a song. Syllable repetition rates are fairly high, and some phrases consist of a very rapidly repeated series of syllables, or trill (Lemon, 1965, 1966; Lemon and Chatfield, 1971). Cardinals have adopted a sequential pattern of syringeal lateralization that takes advantage of the separate left and right vocal registers to achieve a maximum bandwidth of frequency modulation (Fig. 9). There is little overlap in the vocal registers of the two sides of the cardinal syrinx. Fundamental frequencies below about 3.5 kHz are generated on the left; higher frequencies are produced on the right (Suthers and Goller, 1996). A few syllable types contain only frequencies above or below 3.5 kHz and are generated entirely on one side of the syrinx. Most syllables have FM sweeps that cross the boundary between the left and right vocal registers, and these syllables are produced by switching phonation from one side to the other in the middle of the FM sweep. The coordination between the two sides of the syrinx is so precise that the change from one side to the other may not be evident either in the spectrogram or to the human ear. Cardinals thus employ sequential left-right or right-left phonation to extend the frequency range of upward or downward FM sweeps, respectively.

**Alternating Bilateral Phonation.** The songs of brown-headed cowbirds are composed of two or three clusters of notes followed by a complex whistle (King and West, 1983; West and King, 1986). Each note cluster and the whistle is produced during a separate, single cycle of positive expiratory pressure (Fig. 10). The right syrinx generates the whistle, but the left and right syrinx alternate in producing notes within each note cluster. The first note of



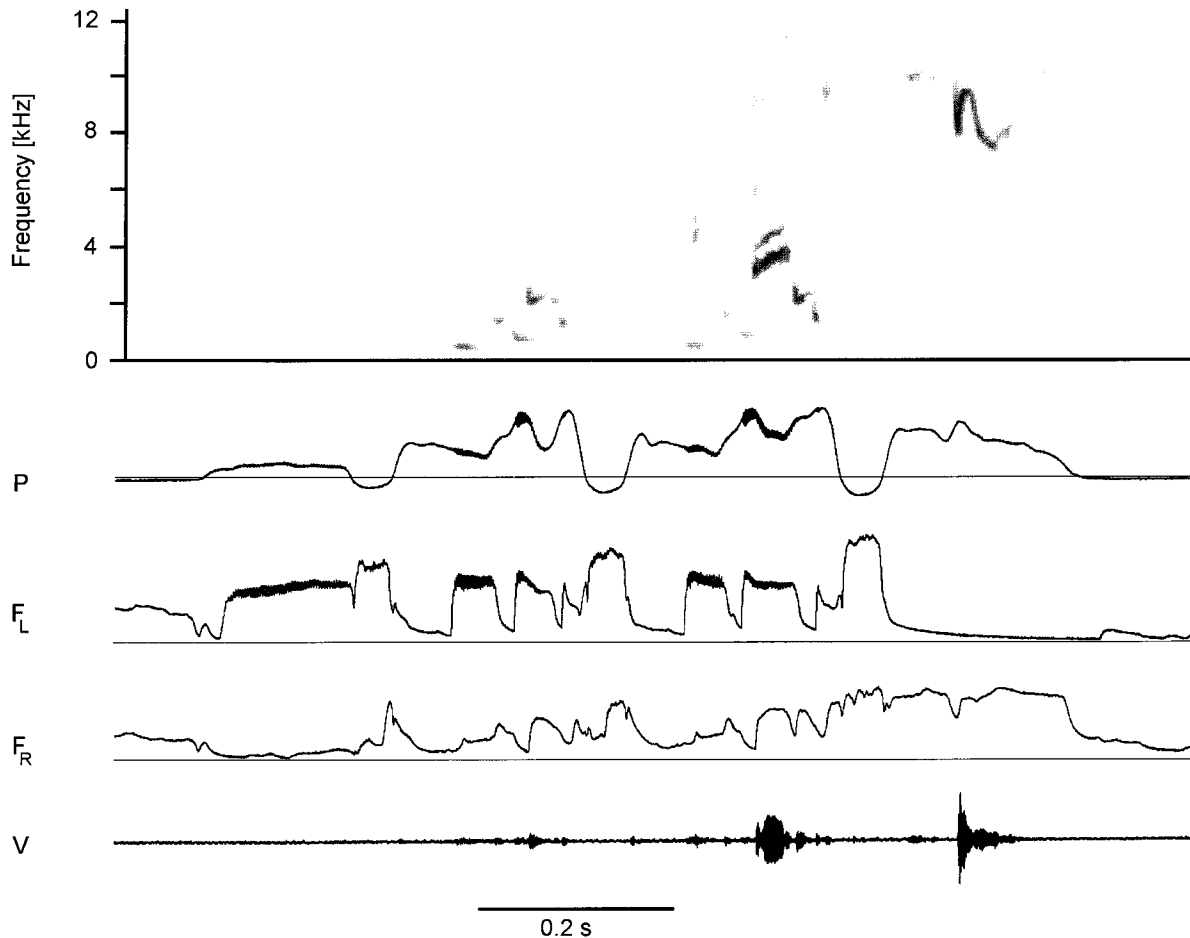
**Figure 9** Portion of a song by a northern cardinal. First two syllables sweep upward from about 4.5 kHz and are generated on the right side with little airflow through the left. The initial high-frequency portion of the last three syllables (first and second vertical lines) is produced by the right syrinx as the left side opens. Remainder of syllable (second and third vertical line) is produced on the left side while the right is closed. Note minibreaths between syllables. See Figure 2 for abbreviations.

each cluster is generated on the left side and is at a low frequency. The next note is generated at a higher frequency on the right, followed by a left note higher than the first left, but lower than the previous right side note. The frequency and intensity of notes generated on each side thus increases in a stepwise fashion to the end of the cluster. Although there is some overlap between the beginning and end of successive notes, most of the note cluster consists of alternating unilateral sound production (Allan and Suthers, 1994). The behavioral significance of this motor strategy is not clear, but its effect is to enhance spectral contrast between successive notes and emphasize the ability to rapidly and precisely switch phonation from side to side.

### What Is Lateralized?

The dorsal syringeal muscles, which open and close the syringeal lumen to initiate or terminate sound

production, are instrumental in executing these different patterns of song lateralization. It is the motor programs or portions of motor programs that are sent to these muscles that determine which side of the syrinx produces sound and the sequence of sound production between sides. Other syringeal muscles on both sides receive ongoing phonetic motor programs during song, independently of whether they are contributing to the song. Phonetic programs determine the acoustic properties of the sound produced whenever air is flowing out through the syrinx and are usually different on each side (Goller and Suthers, 1995b, 1996a,b). It may be advantageous that these phonetic motor patterns continue on each side of the syrinx without regard to whether the ipsilateral labial valve is open or closed. Ongoing muscle activity on the silent side might stabilize the syringeal framework against which contralateral muscles on the phonating side must act. This could explain the fact that in the canary, denervation of



**Figure 10** Song of the brown-headed cowbird is typically accompanied by four expirations. The first expiration is silent; the second and third expirations are accompanied by note clusters in which the two sides of the syrinx alternate, beginning with a low-frequency note from the left side. Successive notes on a given side increase in frequency, but the frequency of the left side lags behind that of the right to give each note cluster a staggered, stepwise frequency increase. Sound intensity also increases as the song progresses and culminates in a high-intensity, high-frequency final whistle during the fourth expiration.

the more massive left syrinx after it has already been silenced by plugging the lumen results in the elimination of some right side syllables (Hartley and Suthers, 1990). The ongoing phonatory motor program probably also ensures that sound will be initiated almost instantaneously and at the proper frequency when airflow is abruptly switched from side to side.

This peripheral unilateral gating of the expression of ongoing bilateral motor patterns, if it is widespread among songbirds, could explain the absence of hemispheric asymmetry in the morphology (Nottebohm and Arnold, 1976; DeVoogd and Nottebohm, 1981; Nottebohm et al., 1981; DeVoogd et al., 1985) or activity (McCasland, 1987) of the song control nuclei above the hypoglossal nucleus, the tracheosyringeal portion of which in canaries is

about 8% larger on the left than the right (Nottebohm and Arnold, 1976; Nottebohm et al., 1981; DeVoogd, 1991). Central asymmetries are not expected if both hemispheres require circuits to generate both phonetic and gating motor patterns during song.

### Implications for the Evolution of Lateral Dominance

These findings in songbirds reinforce the view that there is no single or simple answer to the question of why some behavior is controlled by one side of the brain. In some cases, lateralization may provide a way to economize on the brain space devoted to a particular task. According to this view, space in the nondominant hemisphere could be freed for

other functions such as additional memory. Neural lateralization may also avoid the generation of conflicting commands by otherwise redundant, coequal control centers on each side of the brain (Nottebohm et al., 1979, 1981; Nottebohm, 1984; Zaidel, 1985).

However, the mechanisms by which song production is lateralized neither economize brain space nor reduce the necessity for bilateral coordination, so one must look for alternative explanations of lateralized song production. The recent comparative studies on song production described above suggest that an ability to use the motor and acoustic potential of the bipartite oscine syrinx in different ways to achieve different acoustical and temporal effects may have been a significant factor in the evolution of syringeal lateralization.

## DIRECTIONS FOR FUTURE RESEARCH

The ability to monitor and manipulate peripheral events in the vocal system of spontaneously singing birds provides many opportunities for research on peripheral mechanisms of singing. These include the role and nature of peripheral feedback in modulating central motor output; the extent of motor plasticity in crystallized song; the ontogenetic development of adult motor patterns, including respiratory-syringeal coordination and syringeal lateralization; and studies on additional species having different types of song, to provide a broader context in which to understand the evolution of vocal mechanisms, respiratory strategies, and the lateralization of song.

In keeping with the position of the vocal system as a link between the brain and vocal behavior, there is also a need to combine techniques for monitoring peripheral motor function with neurophysiologic studies of the central pathways and circuits that generate, coordinate, and control the motor programs sent to syringeal, respiratory, and cranial muscles during song. An understanding of the peripheral consequences of centrally generated motor patterns is an essential part of the study of vocal behavior. Investigations of the peripheral mechanisms of song production can also profitably be combined with studies of vocal communication to assess the role of motor constraints on vocal performance and to search for motor correlates of fitness (Suthers and Goller, 1997).

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