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The neuromuscular control of birdsong

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Birdsong requires complex learned motor skills involving the coordination of respiratory, vocal organ and craniomandibular muscle groups. Recent studies have added to our understanding of how these vocal subsystems function and interact during song production. The respiratory rhythm determines the temporal pattern of song. Sound is produced during expiration and each syllable is typically followed by a small inspiration, except at the highest syllable repetition rates when a pattern of pulsatile expiration is used. Both expiration and inspiration are active processes. The oscine vocal organ, the syrinx, contains two separate sound sources at the cranial end of each bronchus, each with independent motor control. Dorsal syringeal muscles regulate the timing of phonation by adducting the sound-generating labia into the air stream. Ventral syringeal muscles have an important role in determining the fundamental frequency of the sound. Different species use the two sides of their vocal organ in different ways to achieve the particular acoustic properties of their song. Reversible paralysis of the vocal organ during song learning in young birds reveals that motor practice is particularly important in late plastic song around the time of song crystallization in order for normal adult song to develop. Even in adult crystallized song, expiratory muscles use sensory feedback to make compensatory adjustments to perturbations of respiratory pressure. The stereotyped beak movements that accompany song appear to have a role in suppressing harmonics, particularly at low frequencies.

Keywords: vocalization; respiration; motor control; lateralization; birdsong; syrinx

1. INTRODUCTION: MOTOR SYSTEMS INVOLVED IN SONG PRODUCTION

The songs of oscine birds have a number of features that make them an especially interesting behaviour for the study of motor control. They are one of the very few known examples of complex learned vocal communication aside from human speech. They also encompass a wide range of acoustic and motor complexity, including both simple, rhythmic, stereotyped components as well as others that are complex and variable. The vocal repertoire of an adult songbird can range from only a few 'syllables' or 'notes' up to a few thousand, depending on the species. Each kind of syllable, defined as a note or group of notes occurring in the same pattern each time it is produced (Konishi 1985), is acoustically stereotyped.

Birdsong, like human speech, depends on the ability to accurately coordinate diverse groups of muscles at various levels of the vocal system. The energy for sound production is provided by the respiratory muscles that force air through the vocal organ, the syrinx. The respiratory rhythm during song determines the song's basic temporal pattern. Syringeal muscles provide fine control of the timing of vocalization within expiratory periods and enable the bird to control acoustic properties of song, such as its fundamental frequency, independently of respiratory pressure. The oscine syrinx is especially interesting in that it consists of two separate sound sources under independent motor control, providing additional possibilities for motor and vocal complexity. Finally, the sound that is generated in the syrinx may be modified by the filter properties of the suprasyringeal vocal tract, including not only the trachea but also the mouth and beak. In this paper we review some of the current issues and recent developments related to the way in which these different motor subsystems are controlled and coordinated during singing.

2. RESPIRATORY DYNAMICS DURING SONG PRODUCTION

Sound is produced by expiratory air flowing through the avian vocal organ, the syrinx, which in songbirds is located at the junction of the primary bronchi and the trachea. Respiratory muscles must provide an appropriately timed pattern of subsyringeal air pressure at carefully regulated levels in order to provide the airflow that initiates vibration of the sound-generating structures in the syrinx. Unlike mammals, both inspiration and expiration are active processes in birds. The resting position of the sternum is midway between its positions at the end of inspiration or expiration. In the best-studied species, the domestic fowl (*Gallus domesticus*), respiration involves the coordinated activity of about a dozen muscles innervated by various spinal nerves. Several additional accessory respiratory muscles contribute to laboured breathing. Avian respiratory muscles alternately compress and expand a series of interconnected air sacs in a bellows-like action that ventilates the lungs and moves air through the syrinx and the

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trachea. Abdominal muscles function in expiration whereas most thoracic respiratory muscles are inspiratory (Fedde 1987; McLelland 1989). As yet, the activity of only two inspiratory and one major expiratory muscle has been studied in a singing songbird (Hartley 1990; Goller & Suthers 1995*a*; Wild *et al*. 1998). The possible role of accessory respiratory muscles in song production is unknown.

Song is accompanied by major changes in the pattern of respiratory ventilation, compared with that of a quietly resting silent bird. During song, there is a pronounced increase in the amplitude of contraction in the abdominal expiratory muscles, as measured by changes in the amplitude of their electromyograms (EMGs) and air sac pressure increases about tenfold to 50-fold. For example, the expiratory pressure in the cranial thoracic air sac of the brown thrasher (*Toxostoma rufum*) increases from *ca*. 1 cm H_2O during silent respiration to an average peak value of 16 cm H_2O during song. Maximum peak pressures as high as *ca*. 50 cm H_2O can occasionally occur during phonation (Goller & Suthers 1995*a*; Suthers & Goller 1997). The temporal pattern of expiration corresponds to the song's tempo. In most cases respiratory rate increases, the inspiratory phase is shortened (Wild *et al*. 1998) and expiration may be accompanied by relatively complex, stereotyped patterns of pressure and airflow (Suthers *et al*. 1994, 1996*b*; Suthers & Goller 1997).

The first measure of expiratory muscle activity during spontaneous singing was obtained in waterslager canaries (*Serinus canaria*) by Hartley (1990) who recorded EMGs from abdominal expiratory muscles together with respiratory pressure in the air sacs during song. Each song syllable was accompanied by a burst of electrical activity in these muscles. The expiratory muscle EMG preceded the reversal from inspiration to expiration for phonation by a few milliseconds and terminated several milliseconds before the reversal point between expiration and inspiration. Syllables which had a complex phonetic structure were accompanied by correspondingly complex patterns of EMG amplitude and air sac pressure. Similar changes occur in the abdominal expiratory muscle EMGs of singing brown thrashers (Goller & Suthers 1995*a*), zebra finches (*Taeniopygia guttata*) and brown-headed cowbirds (*Molothrus ater*) (Wild *et al*. 1998). In brown thrashers the amplitude of the expiratory EMG is positively correlated with air sac pressure and with sound intensity, as judged by the amplitude of the envelope of the acoustic waveform.

Most songbirds insert a brief inspiration between syllables or phrases of their song. Recordings of the inspiratory muscles, mm. levatores costarum and m. scaleneus, in zebra finches and brown-headed cowbirds (Wild *et al*. 1998), show that inspiration is accompanied by a substantial increase in the activity of these muscles and that there is no overlap between expiratory and inspiratory EMGs (figure 1). Inspiratory pressure tends to be more negative during intersyllable or interphrase inspirations compared to inspirations that are not associated with singing.

These brief inspiratory breaths between syllables prevent the bird from running out of air for phonation (figure 2). Depending on their volume, they may also contribute to respiratory gas exchange (Hartley & Suthers 1989; Suthers & Goller 1997). This respiratory pattern was initially described by Calder (1970) who showed that singing canaries expand their thorax between syllables. He called these putative inspirations 'minibreaths'. Calder's interpretation of his data was subsequently confirmed by direct measurements of tracheal airflow and respiratory pressure during canary song, demonstrating inspiratory airflow between syllables (Hartley & Suthers 1989). Similar intersyllable inspirations have also been observed in northern cardinals (*Cardinalis cardinalis*) (Suthers 1997; Suthers & Goller 1997), grey catbirds (*Dumetella carolinensis*), brown thrashers (Suthers 1990; Suthers *et al*. 1994) and zebra finches (Wild *et al*. 1998). In the brown-headed cowbird, minibreaths occur between clusters of notes instead of between syllables (Allan & Suthers 1994). The entire song of the brown-headed cowbird lasts only about 1 s and is divided into three or four expirations separated by minibreaths. A cluster of notes is produced during the first two or three expirations and the last expiration produces a loud, high-frequency whistle.

Quantitative studies of respiratory volumes in singing canaries reveal that the volume of each inspiratory minibreath is closely matched to the volume of air exhaled to produce the adjacent song syllables (Hartley & Suthers 1989). An adult male waterslager canary may have a repertoire of two or three dozen different syllable types that differ from each other in their acoustic structure and their duration. The volume of air that must be exhaled to produce a syllable is correlated with its duration. Hartley & Suthers (1989) found, for example, that the volumes of air required to produce the longest (119 ms) and shortest (11 ms) syllables in a song were 0.25 and 0.04 ml, respectively. In each case the volume of the minibreath between syllables corresponds to the volume of air exhaled to produce the sound. Each syllable type is accompanied by a stereotyped respiratory motor pattern in which the minibreath volume is matched to that of the vocalization so that there is no net loss of respiratory volume during the course of a song. Song duration in canaries does not appear to be limited by the respiratory air supply. However, it is possible that inadequate respiratory gas exchange may limit some songs, especially those containing long phrases at high syllable repetition rates when the volume of minibreaths is small or those that include phrases using pulsatile expiration.

Pulsatile respiration is a different kind of respiratory motor program that is employed at very high syllable repetition rates, greater than *ca*. 30 s^{-1} in canaries or 16 s^{-1} in cardinals (Hartley & Suthers 1989; Hartley 1990; Suthers & Goller 1996, 1997; Suthers 1997). These rapidly trilled phrases are produced by substituting pulsatile expiration for minibreaths. During such a trill, expiratory muscles maintain a continuous positive subsyringeal air pressure and sound is produced by repetitively opening one side of the syrinx to allow successive puffs of air, each producing a syllable as it passes through the syrinx (figure 2). Such phrases are accompanied by a net loss of respiratory volume that is not replaced until the end of the phrase. It is intriguing to speculate that the syntax of canary song, i.e. the sequential arrangement of phrases containing different syllable repetition rates, may to some extent be dictated by the requirements for pulmonary gas exchange.

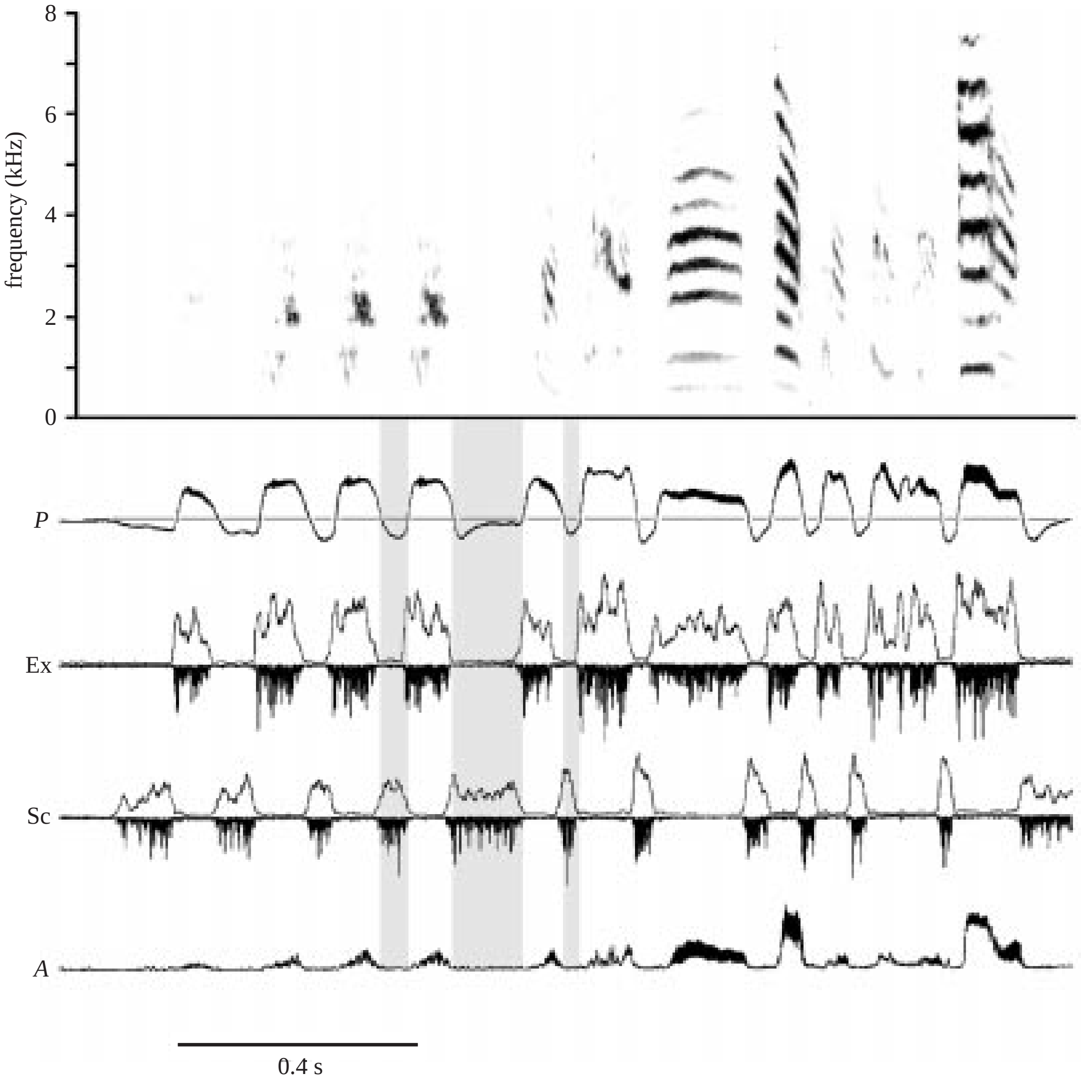

Figure 1. A zebra finch song showing pattern of inspiratory and expiratory muscle EMGs. Positive air sac pressure (*P*) is accompanied by an EMG burst in the abdominal expiratory muscles (Ex). Inspirations between syllables are indicated by a negative air sac pressure accompanied by a burst of activity in the scalenus (inspiratory) muscle (Sc). Inspiratory and expiratory EMG activity does not overlap. EMG traces show integrated EMG (time constant 1 ms) as upward deflections and rectified EMG as downward deflections. The horizontal line through the air sac pressure trace indicates the ambient pressure (zero pressure gradient). Vertical shaded bars indicate three inspirations of varying duration. *A*, sound amplitude represented as the rectified and integrated (time constant 2 ms) acoustic waveform. From Wild *et al.* (1998). © John Wiley & Sons Inc., reproduced by permission.

Respiratory and syringeal motor patterns must be closely coordinated through a series of delicate interactions that determine the vocal output and generate an appropriate song. Respiratory muscles must produce the correct temporal patterns and amplitudes of air sac pressure while syringeal muscles adjust the ipsilateral side of the syrinx to either produce a particular sound, remain silent while the contralateral side produces sound, or facilitate a minibreath by labial abduction. Although communication between the neural circuits controlling respiration and those in the song control system that regulate the syrinx is of vital importance to song production, the exact nature of this interaction has yet to be discovered. A likely pathway for vocal–respiratory coordination consists of a descending projection from the song control nucleus, nucleus robustus (RA), to medullary nuclei involved in respiration. One of these, nucleus retroambigualis (RAm), appears to contain premotor neurons of the abdominal expiratory muscles and may also project to the hypoglossal nucleus (nXII) containing the syringeal motor neurons (Vicario 1993; Wild 1993*a*,*b*, 1994, 1997).

3. THE VOCAL ORGAN

(a) *Structure and innervation*

The oscine vocal organ is a duplex structure consisting of modified cartilage at the cranial end of each primary bronchus and the base of the trachea. Each bronchus contains a pair of sound-generating medial and lateral labia. These can be adducted into the bronchial lumen and function as valves to regulate syringeal airflow by restricting or closing the lumen of the ipsilateral side of the syrinx (Goller & Larsen 1997). The syringeal aperture and other aspects of syringeal configuration are controlled by half a dozen pairs of muscles (four intrinsic

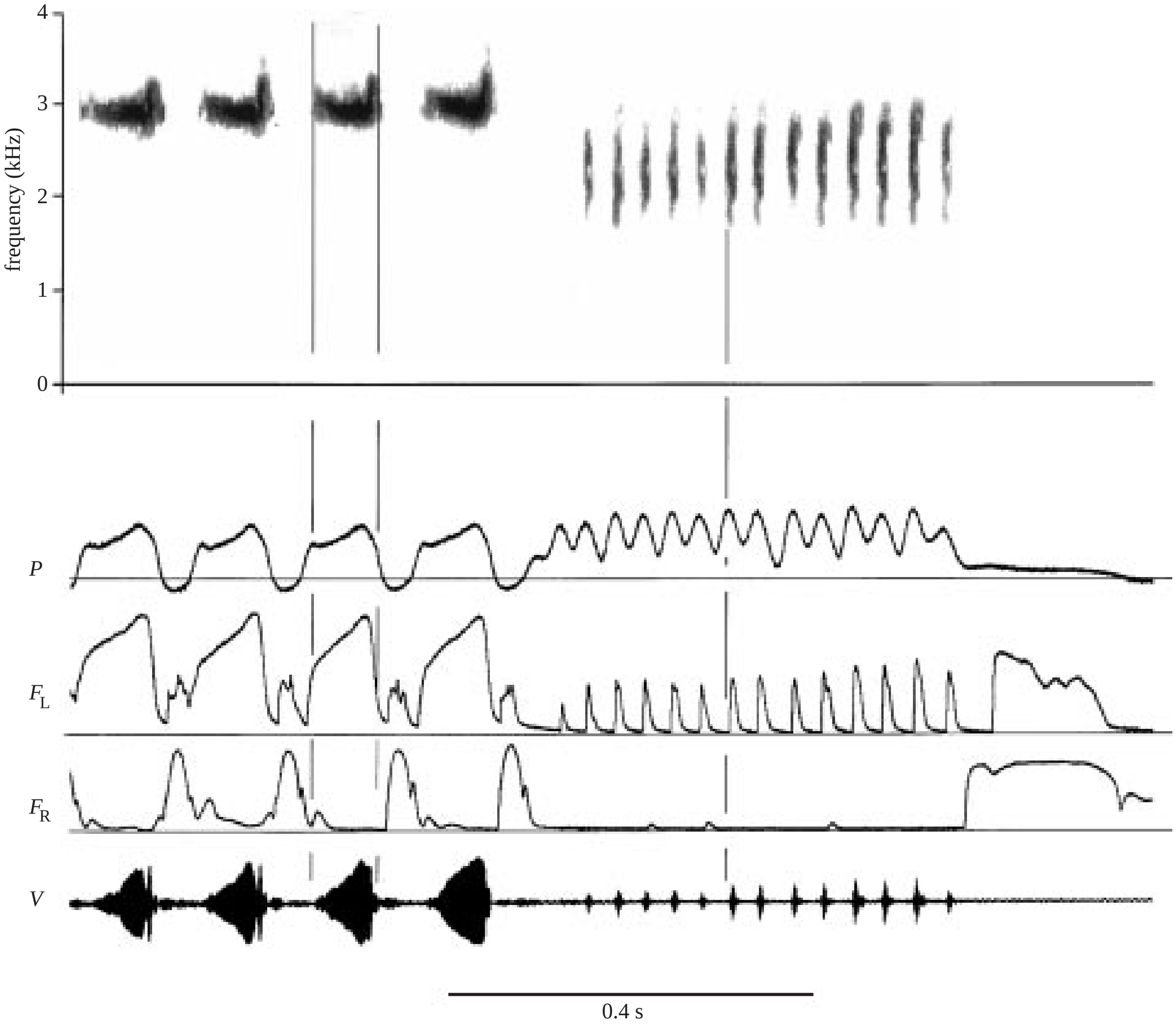

Figure 2. Segment of a waterslager canary song. First four syllables are sung by left syrinx and each is followed by a minibreath. During phonation a positive air sac pressure drives expiratory air through the left, but not through the right, side of the syrinx, indicating that it is closed. During minibreaths air sac pressure is negative and, in this example, 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 trilled phrase, despite transient drops during each expiration. Both sides of the syrinx open at the end of the trill to exhale remaining air before inspiration. *P*, cranial thoracic air sac pressure. F_L and F_R, rate of airflow through left and right side of syrinx, respectively. Horizontal lines equal zero flow. Inspiratory and expiratory flow are distinguished by the sign of the air sac pressure. V, oscillographic representation of vocalizations shown in top panel as spectrograms. Vertical lines align events during sound production.

and two extrinsic) that envelop the syrinx (King 1989) (figure 3). The muscles on each side of the syrinx are separately innervated by the ipsilateral tracheosyringeal branch of the hypoglossal nerve (NXIIts). The oscine vocal organ is thus effectively two separate vocal organs, each with its own airway and with potentially independent motor control of each sound source. Although this dual vocal organ permits greater song complexity and diversity (Suthers 1997; Suthers & Goller 1997), it also introduces significant additional challenges for vocal motor control. A separate motor pattern must be generated for each side of the syrinx. These motor patterns must be coordinated with each other as well as with those controlling respiratory and other vocal tract muscles.

Songbirds devote a significant portion of their brain to a prominent network of song control nuclei that have key roles in song learning and production. The classic motor pathway to the syrinx begins in the telencephalic song control nucleus, the high vocal centre (HVC). Neurons in the HVC project to RA. Cells in RA in turn project to the tracheosyringeal portion of the hypoglossal nucleus (nXIIts), which contains the motor neurons of the ipsilateral syringeal muscles. This descending motor pathway projects almost entirely to the ipsilateral syringeal muscles. For a more complete description of the central motor pathway to the syrinx and for information on other parts of the song control system, see recent reviews by Wild (1997) and by Brenowitz & Kroodsma (1996).

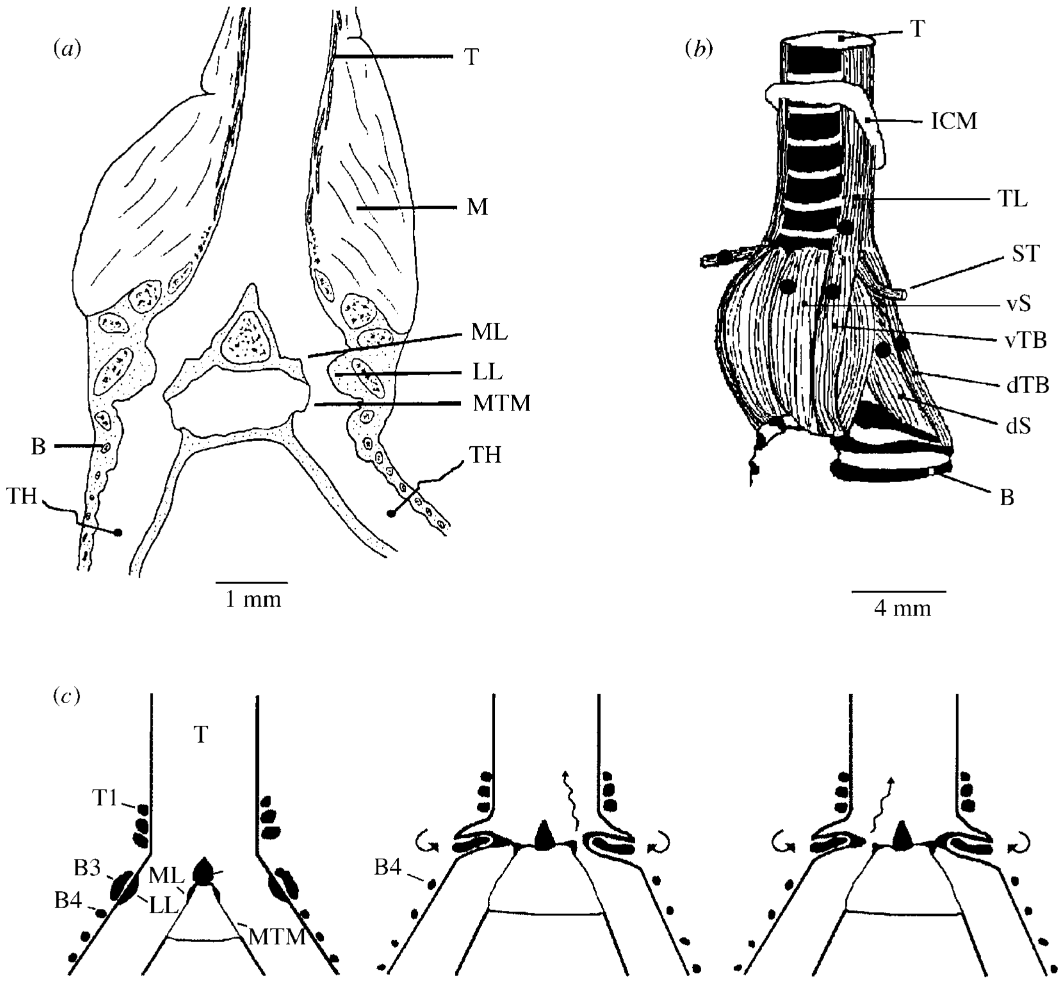

Figure 3. The songbird syrinx is a complex bipartite structure at the tracheobronchial junction. (*a*) Frontal section through the syrinx of a brown thrasher, illustrating the two sound sources and the placement of microbead thermistors (TH) for airflow recordings (for detailed methods and surgical procedures see Suthers (1990)). Unilateral phonation can be achieved by fully adducting the labia on one side of the syrinx, thus blocking airflow and silencing that side. (*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. (*c*) Schematic ventral view of the songbird syrinx in quiet respiratory (left panel) and phonatory (centre and right panels) configurations. During vocalization, the medial and lateral labia are set into vibration when they are adducted into the expiratory air stream. In preparation for phonation, the syrinx moves rostrad. Contraction of the ipsilateral dorsal syringeal muscles (dS and dTB) rotates the bronchial cartilages (curved arrows) into the syringeal lumen, moving the lateral and medial labia into the expiratory air stream where they are set into vibration to produce sound. Phonation may be bilateral (not shown) or unilateral. Unilateral phonation is achieved by closing one side of the syrinx through full adduction of the labia, so that sound (wavy arrows) is only generated on the partially open contralateral right (centre panel) or left (right panel) side. Abbreviations: 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. T1, first tracheal cartilage; B3 and B4, third and fourth bronchial cartilages; P, pessulus. ((*a*) and (*b*) modified from Goller & Suthers (1996*a*); © American Physiological Society. (*c*) modified from Suthers & Goller (1997)).

The relatively stereotyped nature of most adult birdsong and the ability of many adult birds to continue singing apparently normal song after being deafened in adulthood, suggest that song is produced by a central motor programme (Konishi 1965, 1985; but see Nordeen & Nordeen 1992). The manner in which song is perturbed by electrical stimulation of various song control nuclei led Vu *et al.* (1994) to believe that the motor programmes are located in the telencephalon. Recordings of single and multiunit responses from the HVC and RA in singing zebra finches suggest that song motor control is hierarchically organized. The patterns of activity in the HVC are unique to specific syllable types, whereas activity patterns in the RA are associated with different sub-syllabic notes (Yu *et al.* 1996; Margoliash 1997). Furthermore, studies with retrograde tracers injected into syringeal muscles reveal that motor neurons for each muscle are grouped together in different regions or 'control zones' of nXIIts in zebra finches (Vicario & Nottebohm 1988), and brown-headed cowbirds (Ruan & Suthers 1996). This muscular organization is apparent in the song motor pathway as early as the RA where cells are organized according to the particular control zone in nXIIts to which they project. Tracers injected into specific control zones of nXIIts or into restricted portions of the RA indicate that the different syringeal muscles are represented in different horizontal layers of the RA (Vicario 1991).

(b) *Controlling syringeal aperture*

Many details of the biomechanical and functional effects of the syringeal muscles are still unexplored. Nevertheless, electromyographic recordings of various muscles in combination with measurements of syringeal airflow, subsyringeal air sac pressure and direct muscle stimulation provide a consistent interpretation of the basic function of the intrinsic muscles and their role during sound production. Activity patterns of the smaller extrinsic muscles are more difficult to interpret and will not be discussed in detail.

The syringeal valve consists of the medial and lateral labia that can be moved into and out of the bronchial lumen through rotation of cartilaginous components of the syrinx (figure 3). The precise rotational movement of the third bronchial semi-ring, which is involved in controlling the position of the lateral labium is still not sufficiently understood (e.g. Chamberlain *et al.* 1968; Goller & Larsen 1997), and the biomechanical mechanisms responsible for moving the medial labium have not been described. The muscles involved in this process of controlling the syringeal aperture have, however, been identified. The dorsal muscles (m. tracheobronchialis dorsalis and m. syringealis dorsalis) act to close the syringeal valve, i.e. they are the primary adductors. During song in brown thrashers the EMG activity of these muscles is increased just prior to and during episodes of full closure of the syrinx (as determined by zero airflow despite a high air sac pressure). If one side of the syrinx contributes to song production, EMG activity of the ipsilateral dorsal muscles generally increases as airflow is reduced for given air sac pressure values, indicating a positive correlation between muscle activity and syringeal resistance to airflow (Goller & Suthers 1996*b*) (figure 4). In two other investigated species, the northern cardinal (Goller & Suthers 1997) and the canary (F. Goller and R. A. Suthers, personal observations) full adduction during phonation is also accompanied by strong EMG activity of dorsal muscles. EMG activity in the dorsal muscles of brown-headed cowbirds is high during full ipsilateral adduction during the introductory note clusters (in which left- and right-side notes alternate), but is low in the left dorsal muscles during the right-side-generated final whistle. This low activity level suggests that an unknown alternative adductive mechanism is operating during the final whistle (Allan & Goller 1995).

When electrically stimulated in the *in situ* syrinx, contraction of the dorsal tracheobronchial muscle moves the ipsilateral lateral labium into the syringeal lumen. Stimulation of the medial portion of the dorsal syringeal muscle results in adduction of the medial labium, but the maximal excursion of the medial labium is distinctly smaller than that of the lateral labium (O. N. Larsen and F. Goller, unpublished data).

The antagonist to the adductors is the thin ventral tracheobronchial muscle. Direct stimulation of this muscle causes withdrawal of the lateral and medial labia from the lumen. This evidence is consistent with EMG data for this muscle. Strong bursts are associated with inspiratory activity during song as the syringeal valve opens for maximal airflow during minibreaths. EMG activity during song can be quite variable, however, suggesting that syringeal adductor muscles are more actively engaged in syringeal closure than the abductor muscles are in opening the syrinx. Due to the relatively high subsyringeal pressure during song, a decrease in adductive force will passively reduce syringeal resistance so that active abductive control may only be needed for precise fine regulation of syringeal configuration to achieve specific acoustic effects (Goller & Suthers 1996*b*). The activity of the largest syringeal muscle, m. syringealis ventralis, does not have any noticeable effect on the aperture of the syrinx. Direct stimulation does not result in a displacement of either labium into or out of the bronchial lumen.

(c) *Initiation of phonation*

The reconfiguration of the syrinx for phonation is an active process, involving partial adduction mediated by the dorsal muscles. Two lines of evidence indicate an active adductive process. (i) The initiation of phonation is always accompanied by increased EMG activity in the adductor muscles in comparison with quiet breathing, suggesting that the activity of these muscles generates partial closure of the syringeal valve (Goller & Suthers 1996*a*,*b*). (ii) In anaesthetized songbirds low intensity HVC stimulation often results in partial adduction of the syrinx but no simultaneous increase in subsyringeal air sac pressure. In these cases the syringeal valve must be actively controlled because expiratory muscles do not generate elevated air sac pressure that could passively lead to a partial adduction (O. N. Larsen and F. Goller, unpublished observations).

(d) *Frequency control*

Active control of the sound frequency is an important aspect of vocal control. Indirect factors such as changes in labial tension resulting from varying pressure and/or airflow conditions may play a small role in determining the fundamental frequency. However, the activity of the ventral syringeal muscles appears to be the main mechanism for controlling the tension of the labia (Goller & Suthers 1995*b*, 1996*a*). Direct stimulation of m. syringealis ventralis generates a visible change in tension in the medial labium along the rostro-caudal axis (O. N. Larsen and F. Goller, unpublished data), suggesting that this muscle is involved in adjusting the tension of the sound-generating structures. EMG data confirm this interpretation. EMG activity in the ventral syringeal muscle increases exponentially with increasing fundamental frequency of ipsilaterally generated sounds. The high correlation between these parameters is further illustrated by the fact that modulation in EMG activity accurately parallels frequency modulation of the sound (Goller & Suthers 1996*a*) (figure 5). Because contraction of the medial portion of the dorsal syringeal muscle affects the position of the medial labium, it is probable that it also has an effect on the tension of this labium. However, no EMG recordings from the medial part of the dorsal muscles are available to test this interpretation.

The high correlation between EMG activity and fundamental frequency in all investigated species (brown

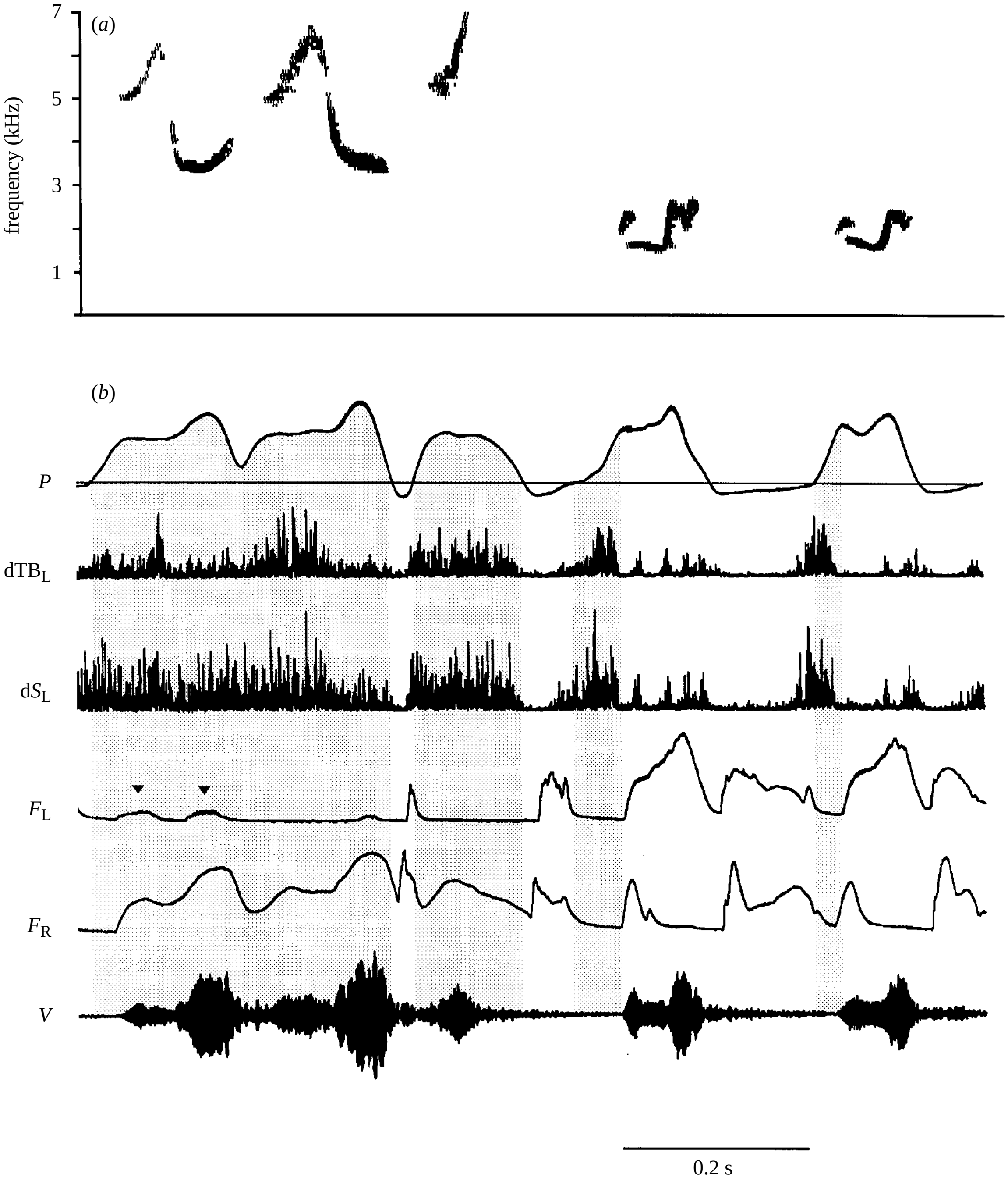

Figure 4. Activity in the dorsal syringeal muscles is correlated with adduction of the labia to reduce the syringeal aperture. Segment of a brown thrasher song showing the rectified EMG activity of the left dorsal muscles during full adduction (shaded columns) as indicated by a positive air sac pressure (*P*) but no airflow through the left side of the syrinx. Zero pressure and airflow are indicated by horizontal lines. Arrows indicate periods with a small amount of airflow through the left syrinx that is preceded by weaker EMG activity. F_L and F_R, rate of airflow through the left and right sides of the syrinx, respectively; V, oscillographic representation of vocalizations which are also represented spectrographically in top panel; muscle abbreviations as in figure 3. From Goller & Suthers (1996*b*). © American Physiological Society, reproduced with permission.

thrasher, northern cardinal, brown-headed cowbird, canary) indicates that this mechanism of frequency control may be common to all songbirds. Two observations indicate that generation of high-frequency sound involves substantial effort by the ventral syringeal muscle. It is the largest syringeal muscle and its EMG activity increases exponentially with increasing frequency. Although we do not have any information about the characteristics of muscle shortening, the exponentially increasing EMG activity suggests that substantially increased force is needed for the production of high frequencies.

(e) *Sound intensity and AM generation*

Air sac pressure and the rate of airflow across the syrinx are important variables in determining sound intensity. Together with expiratory muscles, the syringeal muscles involved in controlling the syringeal valve are therefore the main effectors for amplitude control. This role of the adductors and abductors becomes especially

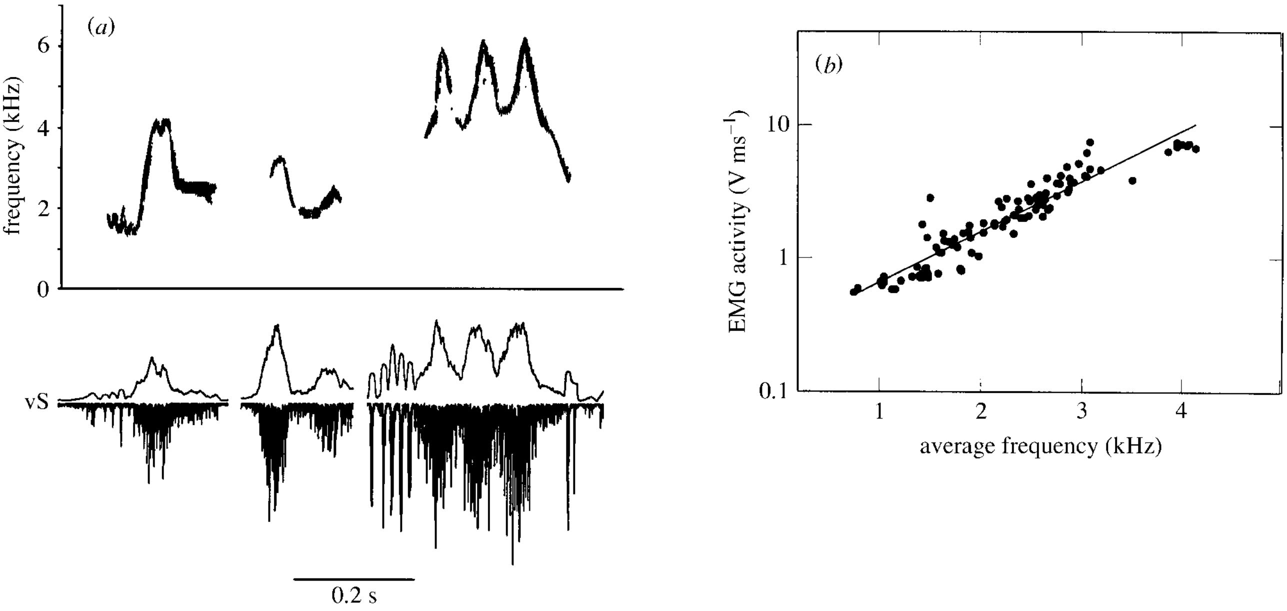

Figure 5. Role of ventral syringeal muscles in the control of sound frequency by brown thrashers. (*a*) Amplitude of EMG activity is positively correlated with frequency modulation of sounds produced on the ipsilateral side. (*b*) Amplitude of EMG activity is exponentially correlated with the fundamental 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 & Suthers 1996*a*). © American Physiological Society, reproduced with permission.

evident during generation of oscillatory amplitude modulation in brown thrashers (Suthers *et al*. 1994). Various patterns of adductor and abductor muscle activity accompany sounds exhibiting different AM patterns. For example, dorsal tracheobronchial muscles can be activated in bursts that correspond to a decrease in syringeal airflow and a decrease in sound amplitude. More complicated AM patterns arise if the ventral tracheobronchial muscles are also active in bursts that vary in their phase relationship with those of the dorsal muscles. AM rates attributable to direct syringeal regulation of airflow can reach 125 Hz in brown thrashers (Goller & Suthers 1996*a*). Higher AM rates can probably not be generated by regulating the syringeal valve directly because of temporal constraints on muscle contraction. Another mechanism for generating AM is the use of both sides of the syrinx to produce slightly different frequencies producing difference tones (Suthers *et al*. 1994; Goller & Suthers 1996*a*).

4. LATERALIZATION OF SONG PRODUCTION

(a) *Lateralized syringeal control*

Songbirds have two independently controlled sound sources that can be used alternately or simultaneously for sound production. Silencing of one side of the vocal organ is achieved by fully closing it (Suthers 1990, 1997). This is manifested as zero airflow through that side despite elevated subsyringeal pressure and by a high level of EMG activity in the adductor muscles. Surprisingly, other syringeal muscles on the closed side that are not involved with adduction are also active. In brown thrashers EMG activity of the ventral syringeal muscle of the closed side is highly correlated with the contralaterally generated sound frequency. Activity patterns of the ventral tracheobronchial muscle are similar to those occurring during ipsilateral sound generation (Goller & Suthers 1995*b*, 1996*b*). These observations suggest that the phonatory motor pattern of the silent side is executed despite the fact that it is closed by the dorsal muscles. It is unknown whether this ongoing activity of phonatory motor patterns enables rapid switching between the sides or may even enhance the contralaterally generated sound by optimizing resonance. Whatever the function of this ongoing activity may be, silencing one side is not a mechanism for simplifying central control of sound production. This is also true for waterslager canaries, a species with high asymmetry of contributions to song by the two sides of the syrinx. EMG activity of the ventral syringeal muscles of the mostly silent right side follows the same pattern of song-like activity, while EMG activity in the dorsal muscles is high, corresponding to full adduction (F. Goller, unpublished observations).

Syringeal lateralization in the form of lateral independence in motor programmes sent to the right and left sides of the syrinx is an important feature of song production. Comparative studies of song production reveal that although laterally independent motor control of the left and right syrinx is widespread and perhaps universal among songbirds, the proportion of song that is contributed by each side of the syrinx varies greatly in different species. Unilateral dominance, in which one side of the syrinx produces most of the song, is most strongly expressed in the waterslager canary. This strain of canary sings *ca*. 90% of its syllable repertoire with the left syrinx, the remainder with the right (Nottebohm & Nottebohm 1976). The muscles of the left syrinx are somewhat larger than those of the right (Luine *et al*. 1980) and the tracheosyringeal portion of the left hypoglossal nucleus is slightly larger than the right (Nottebohm & Arnold 1976;

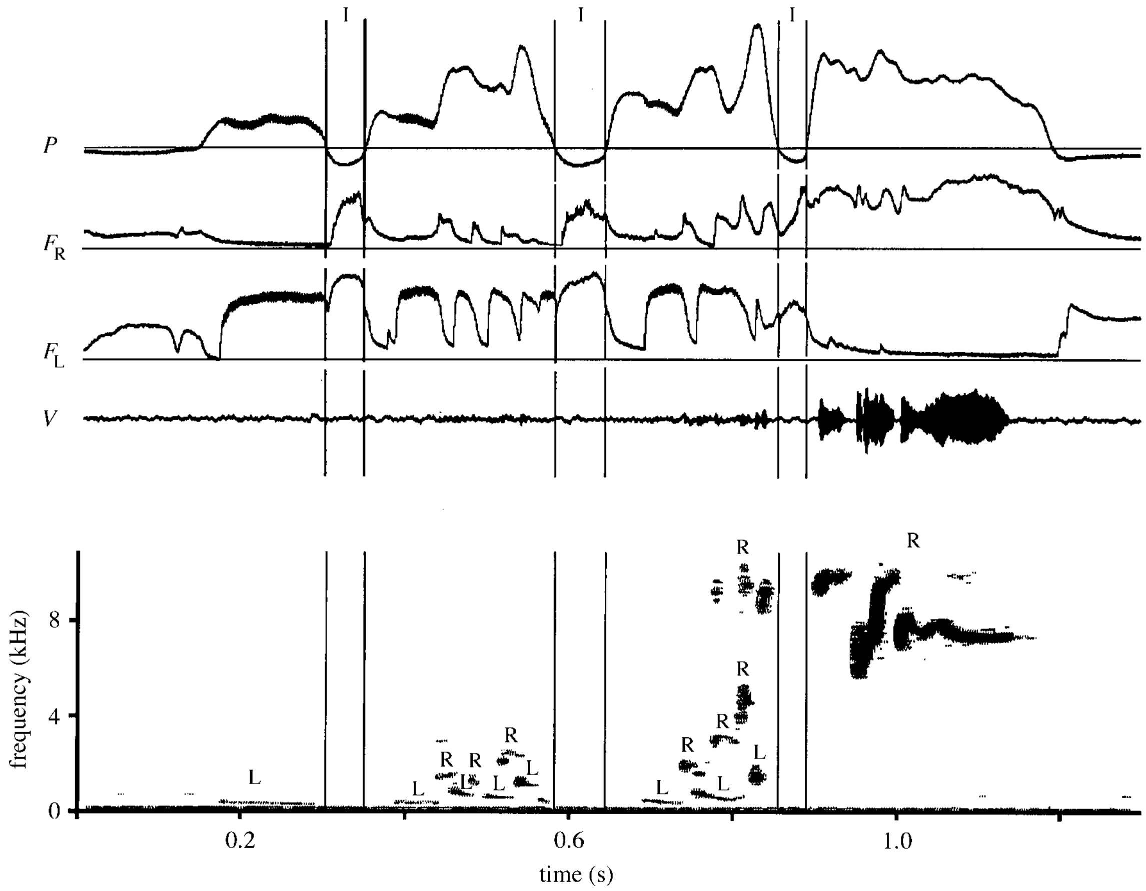

Figure 6. A song of a brown-headed cowbird produced in four expirations that are separated by minibreaths (I). During each of the first three expirations a cluster of notes is produced that gradually increase in frequency and intensity. Each cluster begins with a left-side note (L). Successive notes are produced on alternate sides of the syrinx with their frequency increasing in a staggered manner. Most left-side notes are lower in frequency than those on the right side (R) and lack prominent frequency modulation. Some left- and right-side notes overlap to produce 'two-voice' components. The final whistle during the last expiration is generated entirely on the right side. It is at a much higher intensity than the note clusters, which are barely visible in the oscillographic trace. See legend of figure 2. (From Suthers 1998.) © MIT Press, reproduced with permission.

Nottebohm *et al.* 1981; DeVoogd 1991). Despite the dominance of the left syrinx in song production, no anatomical asymmetry is evident in song control nuclei above nXII (DeVoogd & Nottebohm 1981; Nottebohm *et al.* 1981; DeVoogd *et al.* 1985).

The functional lateralization of the syrinx is not limited to song production *per se*. During song, the right syrinx is often the main pathway by which air enters the respiratory system during the minibreaths between syllables. In waterslager canaries, for example, the right syrinx, which is closed during phonation on the left, typically opens between syllables to provide a low-resistance pathway for inspiration. During each minibreath, the left side remains in its partially adducted phonatory configuration until the next syllable, or may even close completely in the absence of a positive subsyringeal pressure (Suthers 1992). This lateralization of inspiration during song is especially prominent in waterslager canaries (figure 2), but is also present to some degree in other species. Assigning the phonatory motor program and the syringeal component of the minibreath motor programme to opposite sides of the syrinx may reduce the motor constraints that inspiration places on phonation and facilitate the production of relatively complex syllables at higher repetition rates than would otherwise be possible (Suthers 1992).

Mimic thrushes, such as the brown thrasher and grey catbird, represent the opposite extreme with regard to lateral dominance. In these species both sides of the syrinx make roughly equal contributions to the song. The two sides receive different motor programmes, however, and often give rise to vocalizations containing harmonically unrelated frequency components originating simultaneously on separate sides of the syrinx. At other times phonation is switched from side to side (Suthers 1990; Suthers *et al.* 1994, 1996*b*). Left–right switching of sound production is a prominent feature of the introductory note clusters in songs of the brown-headed cowbird (figure 6) where successive notes are produced on opposite sides of the syrinx (Allan & Suthers 1994). It is also a basic feature of song production by northern cardinals where, within a single FM sweep, the fundamental frequencies above 3.5–4 kHz are generated on the right side and those below this frequency are produced on the left. The often acoustically seamless transition from one side of the syrinx to the other within a single extended frequency sweep is a tour de force of left–right motor coordination (Suthers 1997; Suthers & Goller 1997). The song control nuclei have limited projections to the contralateral side of the brain and it is not known which pathways mediate bilateral motor coordination between the left and right sides of the syrinx (Wild 1997). Songbirds have exploited different patterns of syringeal lateralization in various ways, specializing in various motor skills to achieve particular acoustic effects (Suthers 1997, 1998; Suthers & Goller 1997).

(b) *Respiratory control is not lateralized*

The lateralization of song production does not extend to the respiratory system. Bilateral recordings of abdominal expiratory muscle EMGs in singing brown thrashers (Goller & Suthers 1999) indicate that both the timing and mean amplitude of expiratory muscle activity on each side of the abdomen are similar, regardless of which side of the syrinx is producing sound. The same motor programme is apparently sent to the abdominal expiratory muscles on both sides of the body. Although bilateral activity in other respiratory muscles has not been investigated, we believe that lateralized activity of respiratory muscles during song is unlikely. Since the abdominal muscles play a major role in expiration, one would expect them to be included in any lateralization of respiratory motor control. Furthermore, connections between air sacs on each side of the body make it unlikely that asymmetrical respiratory effort, even if present, could differentially affect air flow or sound production in the two sides of the syrinx.

5. SENSORY FEEDBACK

(a) *The role of sensory feedback during song learning*

Little is known about the ontogeny of song motor programmes or how these motor skills are maintained in adulthood. Sensory feedback must play an important role in coordinating movements within and between the major song motor systems at least during song learning and perhaps also during adulthood. Auditory feedback is known to have an essential role in song learning, but its importance in the maintenance of adult song is less clear (Konishi 1965; Nordeen & Nordeen 1992). Very little is known about the role of feedback through other non-auditory or somatosensory modalities in either juvenile or adult songbirds (Bottjer & Arnold 1982, 1984).

Song learning occurs in two stages: the sensory phase, during which adult conspecific songs are memorized, and the sensorimotor integration phase of motor practice during which vocal output is thought to be compared with, and successively shaped by, the auditory memory of adult songs. Well-defined sensitive periods for the sensory phase of song learning have been identified in numerous species (Konishi 1965; Nottebohm 1968; Marler & Peters 1988). Motor practice during song development is broadly divided into the stages of subsong and plastic song, and is terminated by song crystallization (figure 7). Subsong is characterized by low-amplitude, highly variable sounds bearing little resemblance to the adult song that will eventually be produced. During the onset of plastic song, vocalizations become louder and increasingly stereotyped. By late plastic song, there is selective attrition of song elements, which are dropped from the repertoire, and sounds are stereotyped, reproducible and recognizable as components of adult song. Crystallization is demarcated by a relatively abrupt decrease in immediate dependence upon auditory feedback for executing a stable song motor pattern (Konishi 1965; Nordeen & Nordeen 1992).

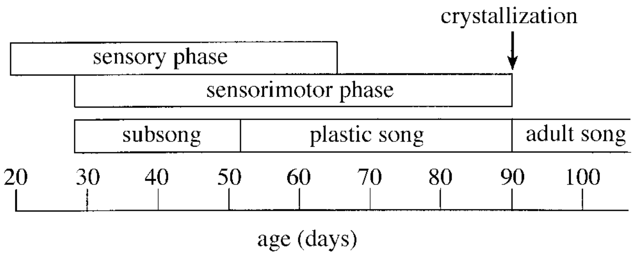

Figure 7. Sequence of song development in the juvenile zebra finch, showing the approximate timing of the sensory and sensorimotor phases.

Reversible paralysis of syringeal muscles at various stages of song learning provides new insights into the importance of motor practice. In the zebra finch, sensory feedback during different stages of motor practice has been found to contribute differentially to song establishment (Pytte & Suthers 1996). Auditory and perhaps proprioceptive sensory feedback was temporarily altered during specific developmental periods by inducing syringeal muscle paralysis with botulinum toxin. Syringeal paralysis causes the spectral structure of vocalizations to be reduced to broadband, noisy sound bursts, thereby interfering with the putative mapping between motor commands and resulting sensory information. This effect persists for 12–24 days, during which time gradual recovery of syringeal function results in a continual mismatch between motor commands and sensory output.

Syringeal paralysis early in development, throughout subsong and early plastic song, does not result in abnormalities in the subsequent expression of adult song. Furthermore, normal songs are learned without extension of the usual developmental period. In contrast, syringeal paralysis late in song development has a marked and irreversible effect on subsequent adult vocal performance. Songs of birds with impoverished syringeal control throughout plastic song, including the process of crystallization, are characterized by aberrations in both temporal patterns and acoustic structure (Pytte & Suthers 1996).

Whereas these results support the idea of a sensitive period for motor practice occurring in the late stages of song ontogeny, syringeal function during subsong also contributes to song development. Syringeal paralysis during subsong followed by paralysis again in late plastic song results in song abnormalities that differ from those produced by disruption of late plastic song alone. Thus there is a consequence of the period of paralysis during subsong, which is only revealed following the latter period of paralysis. Such findings indicate that differential interference with particular developmental periods results in specific impairments in motor function that vary in type and degree. This probably reflects the emergence and interaction of distinct syringeal and respiratory motor skills for singing during particular developmental times. Perhaps the heuristic model of a single sensitive period is of less value than that of an assemblage of multiple sensitive periods corresponding to the emergence of different attributes of syringeal–respiratory vocal development.

The mechanisms limiting vocal motor plasticity during the process of crystallization are not yet understood. Because birds that are deafened prior to adult song production do not produce stable crystallized songs, it has been proposed that the process of crystallization may require that the bird hears its own vocalizations (Konishi 1965; Nottebohm 1968; Konishi & Nottebohm 1969). Interestingly however, hearing its own stable adult song is not sufficient to bring about an end to the sensitive periods for either acquiring new song models or learning new vocal motor patterns (Morrison & Nottebohm 1993). Moreover, auditory feedback during the process of crystallization need not be consistent, nor an accurate match to vocal motor commands (Pytte & Suthers 1996). While a bird may need to hear his own vocalizations for crystallization to occur, this information need not be appropriate, nor will it alone ensure crystallization.

(b) *The role of sensory feedback in adult song*

Sensory feedback in song production need not be limited to periods of recognized motor plasticity in order to learn coordinated respiratory-syringeal vocal motor patterns. It is also possible that sensory feedback continues to modulate the motor programmes for crystallized song in adulthood. Such feedback might be useful in allowing the singer to adjust to changes in posture and respiration rates, for instance during exercise.

The acoustic and motor stereotypy of most crystallized song and its relative independence from deterioration following the elimination of auditory feedback has led to the assumption that sensory feedback has no significant immediate role in generating the appropriate motor patterns for adult song. Although deafening of adult zebra finches, which are critical period learners, results in a delayed and gradual degradation of the song motor pattern (Nordeen & Nordeen 1992), this result is in contrast to the rapid onset of song degradation that occurs following deafening prior to crystallization. Thus it has been suggested that the central pattern generator for song may require auditory feedback for its long-term maintenance.

However, recent experiments using adult northern cardinals suggest that immediate on-line feedback may also contribute to the execution of song motor commands (Suthers *et al.* 1997). When respiratory pressure was perturbed during song by the randomly timed injection of small puffs of air into an air sac, there was a compensatory decrease in the mean amplitude of the abdominal expiratory muscle EMG. This muscle response did not seem to be related to the extent to which the injected air distorted the vocalization, suggesting that it is probably mediated by some kind of somatosensory, rather than auditory, feedback.

Somatosensory feedback during song could arise from a number of different sites in the vocal system and involve any of several possible modalities. Little is known about the potential receptors in songbirds, but the transverse abdominal expiratory muscles of domestic fowl contain muscle spindle organs (DeWet *et al.* 1967). Various authors have demonstrated the presence of slowly adapting neurons in the vagus nerve that are sensitive to the expansion of air sacs (Gleeson & Moloney 1989). The mechanoreceptive endings of these neurons may be located in the walls of the air sacs. However, other sites within the thoraco-abdominal cavity, but outside the respiratory system cannot be ruled out since, in the absence of a mammalian diaphragm, avian respiratory muscles act to change the volume of this entire cavity. The air sac wall is sparsely innervated, but the saccopleural membrane between the wall of the thoracic air sac and the parietal pleural in chickens is densely innervated (McLelland 1989). It is hoped that future research will clarify the potentially important role of non-auditory feedback in the learning and maintenance of song motor patterns.

6. THE SUPRASYRINGEAL VOCAL TRACT

(a) *Beak movements and harmonic structure of sound*

Configurational changes in structures of the vocal tract, including the glottis, larynx, tongue, and beak, may affect the acoustic structure of vocalizations by altering the shape and acoustic impedance of the vocal tract. Of these components, beak movements are the easiest to measure and are therefore the best studied. Changes in beak gape may modify the resonance properties of the vocal tract by altering its effective length, by changing acoustic interactions affecting acoustic impedance, and by influencing the radiation of sound from the mouth. Furthermore, independent control of the upper and lower mandibles may increase the variations of beak positions and thus influence acoustic parameters (Hoese & Westneat 1996).

Westneat *et al.* (1993) tested the prediction that increasing beak gape, essentially increasing the 'flare' at the end of the vocal tract, effectively shortens its equivalent tube length, thereby increasing the resonance frequency (Nowicki 1987; Fletcher 1988, 1989; Nowicki & Marler 1988). Measurements of beak movements taken from video films of singing swamp sparrows (*Melospiza georgiana*) and white-throated sparrows (*Zonotrichia albicollis*) supported this hypothesis, revealing that beak gape was positively correlated with fundamental frequency in most of the notes that were analysed. Gape was inconsistently correlated with amplitude (Westneat *et al.* 1993). A similar relationship between gape and frequency has also been found in song sparrows (*Melospiza melodia*) after song crystallization (Podos *et al.* 1995) and in Bengalese finches (*Lonchura domestica*) (Moriyama & Okanoya 1996). Among non-songbirds, beak gape of barnacle geese (*Branta leucopsis*) is positively correlated with the amplitude of the vocalization (Hausberger *et al.* 1992) and there is some evidence that beak and tongue movements affect vocal tract resonance in parrots (Warren *et al.* 1996; Brittan-Powell *et al.* 1997).

Continuous measures of changes in beak gape during singing have been obtained in northern cardinals (Suthers *et al.* 1996*a*; Suthers & Goller 1997) using a magnetosensitive electronic chip and magnet attached to the upper and lower mandible, respectively. Each acoustically stereotyped syllable type was produced in conjunction with a unique and stereotyped pattern of beak movements. Thus motor control of beak gape is closely associated with syringeal and respiratory systems in determining vocal gestures. Although a more detailed role of beak movements in influencing acoustic properties has yet to be determined, there is evidence that, in cardinals, gape may contribute to filtering or enhancing particular frequencies. Furthermore, the effects of gape appear to differ between vocalizations produced on the left and right side of the syrinx.

Beak gape is correlated with fundamental frequencies below 3.5 kHz but not with higher frequencies. This range corresponds to sounds that are produced by the left side of the syrinx, while vocalizations with fundamental frequencies above 4.0 kHz are produced predominantly on the right side (Suthers & Goller 1996, 1997; Suthers *et al*. 1996*a*). In addition, when gape is artificially fixed at a large opening the magnitude spectra of the second and third harmonics increases 10–20 dB relative to the fundamental frequencies. However, this occurs only in vocalizations containing fundamental frequencies below *ca*. 3.5 kHz. These results suggest that in adult cardinals beak movements (and/or related movement of internal structures such as the tongue) may function to increase tonal purity by suppressing the harmonics of fundamental frequencies below *ca*. 3.5 kHz. In this respect, the exact pattern of beak opening at high frequencies may be less important than keeping the beak opening small at low frequencies. Studies on song sparrows indicate that tonality is a perceptually important attribute of adult song (Peters & Nowicki 1996; Strote & Nowicki 1996).

It is clear that much remains to be learned about the motor coordination of song production. Research in this area during the last decade has yielded important advances in our understanding of the respiratory, syringeal and craniomandibular contributions to song and underlined the necessity of close coordination between these three motor systems. These experiments have also raised a new set of questions that can only be answered by further research. Fortunately, physiological and anatomical techniques are available to address many of these issues and there is every reason to expect that future studies on the neuromotor control of birdsong will continue to provide significant insights into the neural basis of behaviour.

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