Netherlands Journal of Zoology
51 (2): 217-242 (2001)

PERIPHERAL VOCAL MECHANISMS IN BIRDS: ARE SONGBIRDS SPECIAL?

by

RODERICK A. SUTHERS

(*Medical Sciences and Department of Biology, Indiana University, Bloomington, Indiana 47405, U.S.A.*)

ABSTRACT

This paper reviews recent advances regarding the peripheral mechanisms for song production by oscine songbirds and compares the vocal mechanisms of songbirds with those of certain non-oscines. The tracheobronchial syrinx of songbirds has several pairs of intrinsic muscles specialized for controlling particular aspects of sound production. The syringeal and vocal tract anatomy of non-oscines is much more diverse than that of songbirds and has fewer or no intrinsic syringeal muscles. Often the same extrinsic tracheal muscles control both the temporal and spectral properties of vocalizations. Although the vocalizations and vocal anatomy of these two groups are quite different, a number of motor patterns important in oscine song are also used by non-oscines. These include special respiratory techniques, such as minibreaths and pulsatile expiration, for sustained rapid vocalization, as well as the ability to simultaneously produce two acoustically unrelated 'voices'. However, the complex syringeal musculature of songbirds with laterally independent motor control of each side of the syrinx provides a more versatile vocal system in which the left and right sound sources can be coordinated in different ways, by specialized song control nuclei capable of vocal learning, to achieve diverse vocal effects.

KEY WORDS: syrinx, song, phonation, respiration, neural lateralization, vocal tract, bird, motor control, electromyogram.

INTRODUCTION

Oscine songbirds are noted for their vocal ability, their elaborate system of central song control nuclei and their capacity for vocal learning. The effector organs for this behavior, the avian vocal organ or syrinx, together with the vocal tract and respiratory system, is also complex. But understanding how it functions is important both in interpreting its neural control and in appreciating potential motor constraints on vocal communication. One goal of this paper is to review several of the recent advances in understanding peripheral mechanisms of song production.

E-mail: suthers@indiana.edu

Vocal communication is also important to non-oscines. Two families of this under-studied group, the hummingbirds and parrots, share with oscines a system of vocal control nuclei and are vocal learners, (*e.g.*, JARVIS *et al.*, 2000). Unlike songbirds, which are monophyletic, the non-oscines are a hetergenous group. In some, the syrinx is of the tracheobronchial type as in songbirds, in others it is entirely tracheal and in still others it is shared between the two primary bronchi (KING, 1989). The non-oscine syrinx has fewer muscles than that of oscines and in many cases intrinsic muscles are entirely absent. A second goal of this paper is, therefore, to compare mechanisms of sound production in a few selected non-oscines with that of oscines. Both of these groups must solve many of the same basic problems to generate vocalizations, but they do so with very different vocal equipment. To what extent have they evolved different motor solutions to similar needs for respiratory-vocal coordination, control of acoustic signals, etc, and to what degree do they share common motor mechanisms? It is hoped that even the very limited and selective comparative approach used here will help put avian vocal mechanisms in a broader perspective and encourage further comparative studies.

THE NATURE OF THE SOUND SOURCE

Two fundamentally different mechanisms have been put forth to explain the physical nature of the sound source in birds. The first of these hypotheses assumes sound is generated by Bernoulli forces created by air flowing across partially adducted syringeal membranes, initially thought to be the medial tympaniform membranes (MTM), causing them to vibrate (fig. 1a) (MISKIMEN, 1951; GREENEWALT, 1968; DÜRRWANG, 1974; FLETCHER, 1988). Subsequently a second mechanism based on the principle of an aerodynamic whistle was proposed, first by NOTTEBOHM (1976) in orange-winged Amazon parrots (*Amazona amazonica*) and then further developed in doves (GAUNT *et al.*, 1982) and songbirds (CASEY & GAUNT, 1985) to account for tonal sounds when it became apparent that a circular, edge-clamped membrane like the MTM should not be able to vibrate in a mode that produces the tonal or harmonic sounds present in their vocalizations.

Direct endoscopic observation of syringeal movements during experimentally induced phonation in pigeons (*Columba livia*) (GOLLER & LARSEN, 1997a), cockatiels (*Nymphicus hollandicus*; LARSEN & GOLLER, 1999), and several songbirds, have required a significant revision of the vibrating membrane hypothesis. These experiments indicate that vocalizations are generated by adduction of either the lateral tympaniform membranes (LTM; pigeons and parrots) (LARSEN & GOLLER, 1999) or lateral labia (LL) and medial labia (ML; oscine songbirds) (GOLLER & LARSEN, 1997b) to form a V-shaped slot in the middle of the syringeal lumen. The LTM folds into the lumen and vibrates in a plane normal to the direction of airflow. Laser measurements of this vibration in pigeons, cockatiels and the hill myna (*Gracula religiosa*) show that its frequency, envelope and temporal pattern matches that of the vocalization (LARSEN & GOLLER, 1999). Immobilizing the MTM in pigeons by painting it with tissue adhesive or surgically removing it in cardinals (*Cardinalis cardinalis*) and zebra finches (*Taeniopygia guttata*) reduced vocal intensity and increased harmonic emphasis but did not prevent phonation, indicating that these membranes are not required for vocalization (GOLLER & LARSEN, 1997a, b).

At present, the Goller-Larsen model seems to adequately explain sound generation without resorting to a whistle mechanism. Other experiments using light gas (heliox; NOWICKI, 1987; BRITTAN-POWELL *et al.*, 1997; BALLINTIJN & TEN CATE, 1998) or tracheal air straighteners (SUTHERS & ZUO, 1991) have also failed to support a whistle mechanism.

TIMING SOUND PRODUCTION

Configuring the syrinx to initiate or terminate phonation is one of the most basic motor actions involved in vocalization. This is accomplished in different ways in different avian groups depending on their syringeal anatomy and the properties of their vocalizations. During silent respiration the syringeal aperture is kept open to provide a low resistance pathway for respiratory airflow. Sound production is initiated by increased activity in expiratory muscles that raises the air sac or subsyringeal pressure about an order of magnitude and activation of tracheal or syringeal muscles that adduct the sound generators into the syringeal airflow. Vocalization can be terminated either by withdrawing the membranes out of the airflow or by further adducting them into the lumen until they block airflow by closing the aperture. Abduction is commonly used in tracheal syringes since full adduction would block respiration. Adduction is typical of tracheobronchial syringes since it avoids creating a low resistance path that shunts air from the contralateral side, interfering with contralateral phonation and wasting the expiratory reserve (see below).

Gating phonation without intrinsic syringeal muscles

When the syrinx has no intrinsic muscles, phonation must be gated by antagonistic actions of extrinsic muscles. One of the simplest and clearest examples of this is found in the Australian swiftlets (*Aerodramus terraereginae*; formerly the grey swiftlet, *Collocalia spodiopygia*). Swiftlets nest in often totally dark caves through which they navigate by echolocation using very brief click-like sounds. The double clicks are produced as the labia at the cranial end of each bronchus pass through their phonatory position first during adduction and again during abduction (fig. 1). Both sides of the tracheobronchial syrinx contribute to both members of each click. The sternotrachealis muscle (ST) and tracheolateralis muscles (TL) contract sequentially and have opposite actions (SUTHERS & HECTOR, 1982). The click is initiated by contraction of ST which stretches the trachea, reducing tension on the bronchi and causing the first bronchial semi-ring and adjacent LL to rotate into the bronchial lumen (fig. 1d and e). The first member of the double click is produced as these structures are adducted into the expiratory air stream before sound is terminated by continued adduction that momentarily closes the bronchus. The second part of the double click is generated when the TL contracts as ST relaxes, stretching the syrinx and abducting the labia (fig. 1b and c) (SUTHERS & HECTOR, 1982).

Similar antagonistic actions of ST and TL have been described in other birds such as chickens (*Gallus gallus*; YOUNGREN *et al.*, 1974; GAUNT & GAUNT, 1977). In chickens they are simultaneously active during most vocalizations, perhaps to regulate syringeal tension, and the degree of adduction depends on the balance between their opposing forces. In ring doves phonation is likewise accompanied by essentially simultaneous contraction of TL and ST (GAUNT *et al.*, 1982). In both ring doves and collared doves (*Streptopelia decaocto*) ST attaches to the trachea craniad from the LTM and stretches the trachea in a caudal direction, compressing LTM, and folding it into the tracheal lumen. In collared doves, the caudal end of TL attaches to the LTM (BALLINTIJN *et al.*, 1995). The same is true in ring doves except some tendinous slips may extend to the first tracheal ring on the caudal side of LTM (GAUNT *et al.*, 1982). The details of TL's attachment are important since if it pulls mainly on the first tracheal ring it may act synergistically with ST to reduce tension across the LTM, but if it pulls instead on LTM it may abduct or stretch this membrane in a manner that is antagonistic to the action of ST.

Gating phonation with one intrinsic syringeal muscle

Oilbirds (*Steatornis caripensis*), like swiftlets, breed in caves and echolocate by producing double clicks. Their bronchial syrinx is very different from that of swiftlets and consists of two hemisyringes, each located along a primary bronchus (fig. 2a). The ST functions as a syringeal adductor and generates the first member of the double click, as it does in

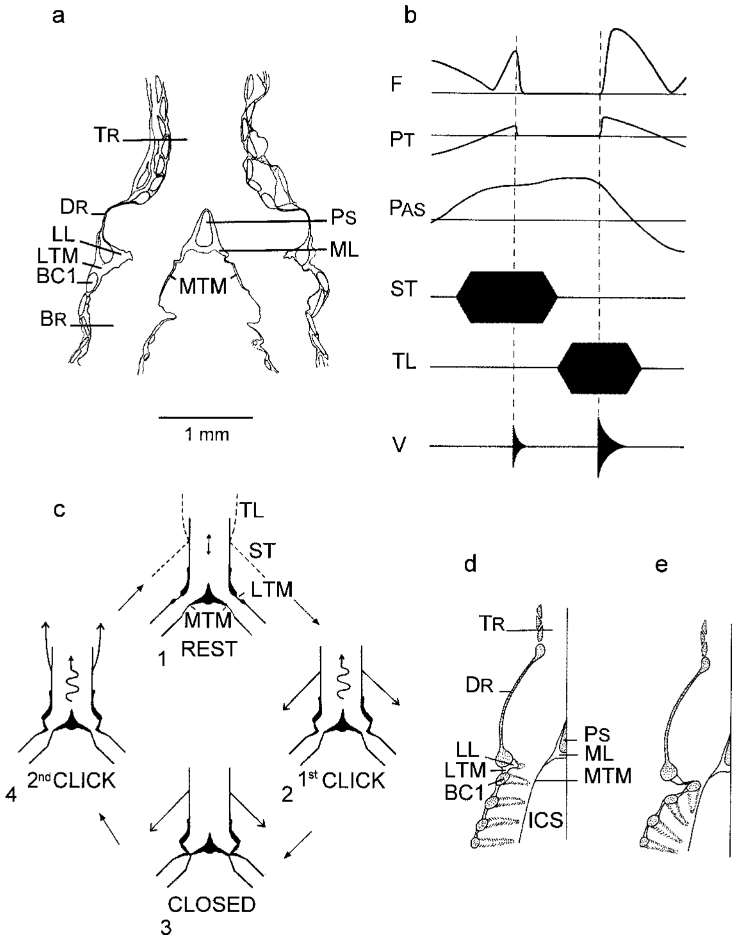

Fig. 1. a. Ventral view of swiftlet syrinx. b. Schematic summary of relationship between events during a double click. c. Diagram of syrinx and tracheal muscles showing cycle of events responsible for click production. Arrows indicate action of tracheal muscles; arrows in trachea indicate airflow/sound. d and e. Ventral view of longitudinal section through right half of syrinx. d. Resting position with bronchus open during silent respiration. e. Inward rotation of first bronchial cartilage when tension across syrinx is relaxed by contraction of ST during click. Tr, trachea; Dr, drum of syrinx, LL, lateral labium; LTM, lateral tympaniform membrane; BC1, first bronchial cartilage; Br, bronchial lumen; MTM, medial tympaniform membrane; Ps, pessulus; ML, medial labium; TL, tracheolateralis muscle; ST, sternotrachealis muscle; F, rate of tracheal airflow (horizontal line = zero flow); Pt, tracheal air pressure (horizontal line = zero, *i.e.*, ambient pressure; Pas, cranial thoracic air sac pressure (horizontal line = zero pressure); V, vocalization. (Modified after SUTHERS, 1982).

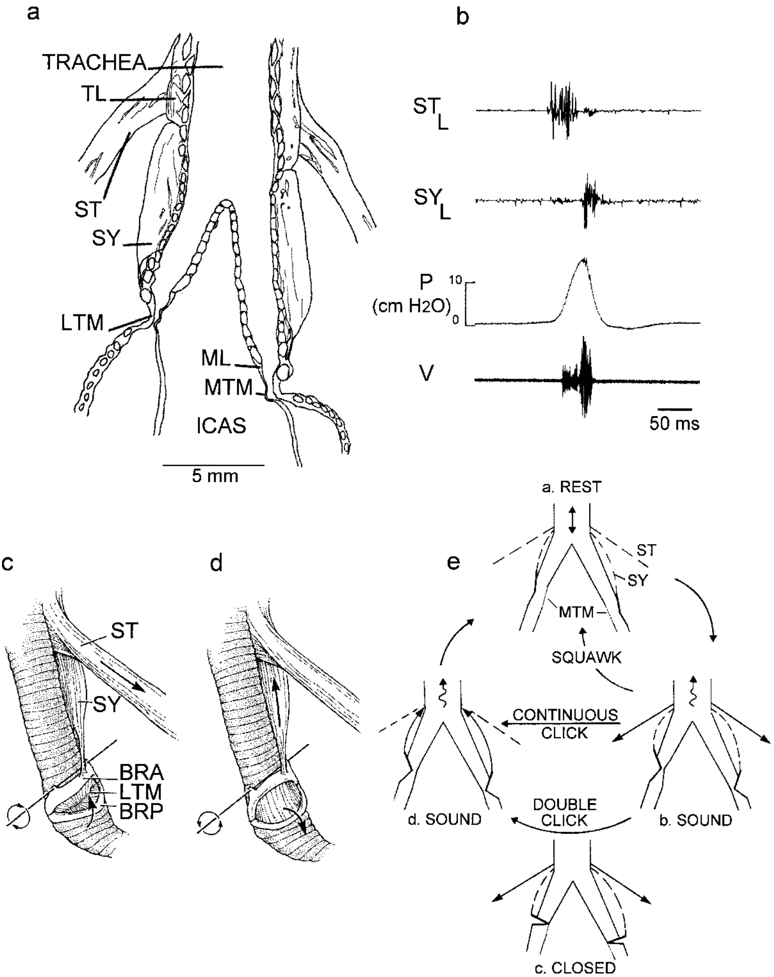

Fig. 2. a. Ventral view of oilbird vocal tract showing asymmetrical bronchial syrinx. b. EMG of left sternotrachealis muscle ($\mathrm{ST_L}$) and left syringealis muscle ($\mathrm{SY_L}$) recorded simultaneously with air sac pressure (P) during a click (V). c and d. Ventral view of semi-syrinx showing how position of lateral tympaniform membrane is controlled. c. Contraction of sternotrachealis pushes bronchus posteriad causing bronchial semi-rings supporting LTM to rotate and fold membrane into lumen. d. Subsequent contraction of syringealis muscle rotates bronchial semi-rings in opposite direction, stretching LTM and removing it from bronchial lumen. e. Schematic representation of sequence of events controlling syrinx during an agonistic squawk, continuous click and double click. SY, syringealis muscle; ICAS, interclavicular air sac; BRA & BRP, bronchial semi-rings supporting anterior and posterior edges, respectively, of LTM. See legend of fig. 1 for other abbreviations. (Modified after SUTHERS, 1985).

swiftlets (fig. 2b, c and e). The bronchi between the hemisyrinx and trachea is composed of complete cartilaginous rings and is not compressible along its longitudinal axis. ST thus transmits a compressive force to each hemisyrinx causing the bronchial semi-ring on the cranial border of the LTM to rotate inward, folding the LTM into the bronchial lumen (fig. 2b). Sometimes ST does not adduct the hemisyrinx past the phonatory position to close the lumen and a 'continuous click' is produced (fig. 2b and e). Unlike swiftlets, TL does not contribute to the timing of phonation. Its role in click production is taken over by the syringealis muscle (SY; called broncholateralis by SUTHERS & HECTOR (1985) and renamed syringealis by KING (1989)). This well developed intrinsic muscle extends along the lateral surface of each bronchus from the trachea to the bronchial semi-ring at the cranial margin of the LTM. SY is specialized for, and used only during, the production of echolocative clicks. Unlike ST or TL it is composed almost entirely of twitch type muscle fibers that allow it to quickly abduct LTM. This action produces the second member of the double click and quickly terminates phonation (fig. 2b and d; SUTHERS & HECTOR, 1985). The active termination of sonar clicks may have evolved through a selective pressure favoring short duration, abruptly terminated sonar signals that are better suited to convey temporal information on target range.

Long duration agonistic 'squawks' are accompanied by a sustained contraction of ST that keeps the hemisyrinx in a partially adducted phonatory configuration. Phonation is terminated when ST relaxes, allowing the forces of passive recoil and the positive subsyringeal pressure to abduct the syrinx without participation of either TL or SY (fig. 2e). Oilbirds thus use different motor patterns for gating sonar clicks and agonistic vocalizations (SUTHERS & HECTOR, 1985). Several other sub-oscines that produce relatively long vocalizations, not used for echolocation, (*e.g.*, ring doves (GAUNT *et al.*, 1982) and adult chickens (YOUNGREN *et al.*, 1974; GAUNT & GAUNT, 1977)) also terminate phonation passively by relaxing syringeal adductors.

Gating phonation with multiple intrinsic syringeal muscles: songbirds

In oscine songbirds the timing of sound production is controlled primarily by intrinsic syringeal muscles (*e.g.*, CHAMBERLAIN *et al.*, 1968; GAUNT, 1983). The brown thrasher (*Toxostoma rufum*), for example, has 4 pairs of intrinsic syringeal muscles in addition to the tracheal muscles TL and ST (fig. 3). Each side of the tracheobronchial syrinx is under independent motor control via the ipsilateral hypoglossal nerve. The dorsal syringeal (dS) and dorsal tracheobronchial (dTB) muscles increase syringeal resistance by adducting the labia into the syringeal lumen. It is the activity of these muscles that is positively correlated with resistance to ipsilateral

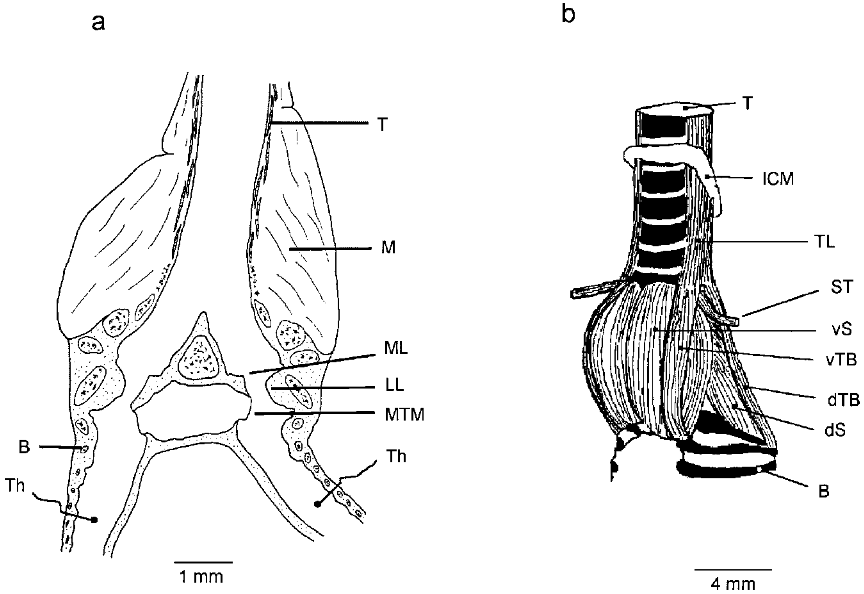

Fig. 3. The oscine syrinx is a bipartite structure containing two sound sources. a. Frontal section through a brown thrasher syrinx, showing the position of the microbead thermistor, Th, used to measure rate of airflow through each side of syrinx. b. Ventrolateral external view of a thrasher syrinx depicting syringeal muscles. Black dots indicate, for one side, the approximate location where bipolar wire electrodes were placed. 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. (Modified from Goller & Suthers, 1996a. Reproduced with permission).

airflow (Goller & Suthers, 1995b). Strong activation of these dorsal muscles closes the ipsilateral lumen, preventing sound production on that side. During song, air flows through the phonating side(s) of the syrinx. During the silent periods between ipsilaterally generated notes, the side is closed by full adduction of the syringeal valve (Suthers, 1990; Suthers *et al.*, 1994, 1999; Suthers & Goller, 1997). Phonation thus typically begins when the dorsal adductor muscles relax enough to allow the subsyringeal pressure to push the labia apart. The ST, which controls syringeal adduction in the simpler syringes described above, has been largely relieved of this function in thrashers and appears instead to facilitate the mechanical action of other muscles by stabilizing the cartilaginous syringeal framework during switches from expiration to inspiration (Goller & Suthers, 1995b, 1996b). During phonation, the subsyringeal respiratory pressure provides most of the abductive force against which the dorsal syringeal muscles work. The abdominal expiratory muscles are in this sense antagonists of the dorsal syringeal muscles. Sound production is usually terminated by shifting the dynamic equilibrium between these opposing forces in favor of closing the syrinx. Direct active abduction by the syrinx depends mainly on increased activity of the ventral tracheobronchialis (vTB) and TL muscles that also help to modulate syringeal resistance during phonation and are active during inspirations between syllables.

Recordings of dS in northern cardinals (GOLLER & SUTHERS, 1997) and canaries (*Serinus canaria*; Goller and Suthers, personal observation) are consistent with that found in thrashers, suggesting the mechanism outlined above may be widespread among oscines. An exception may be zebra finches where further experiments are needed to assess a possible role of the ventral syringeal muscle (vS) in gating the vocalizations (VICARIO, 1991a; GOLLER & SUTHERS, 1996a, b).

RESPIRATORY MOTOR PROGRAMS FOR SINGING

Respiratory-syringeal coordination in songbirds

The respiratory muscles affect the acoustic properties of vocalizations by adjusting the pattern, frequency and amplitude of ventilation (BRACKENBURY, 1987; GAUNT, 1987; HARTLEY, 1990; VICARIO, 1991b; GOLLER & SUTHERS, 1995a, 1999). The amplitude of the abdominal expiratory muscle electromyogram (EMG) is positively correlated with the air sac expiratory pressure and the intensity level of the vocalization. Modulation of expiratory muscle activity is one way of regulating vocal intensity and the temporal pattern of the respiratory cycle determines the rhythm of the song (VICARIO, 1991b; SUTHERS & GOLLER, 1997). Inspirations between sounds are accompanied by a burst of activity in the scalenus thoracic inspiratory muscles (WILD *et al.*, 1998).

During song the respiratory needs for optimal gas exchange must compete with the respiratory requirements for vocalization. Songbirds have evolved motor patterns requiring precise coordination between syringeal and respiratory muscle activity to minimize conflict between these respiratory and phonatory motor programs and limit the motor constraints each imposes on the other. Small birds have a respiratory vital capacity of at most several ml, yet some species can sing continuously for many seconds. A 20 g canary, for example, may sing continuously for more than 30 s. An adult male canary has a repertoire of about 2 or 3 dozen different syllable types. Each song includes a subset of these with each syllable repeated to form a phrase. In order to discover how such a feat is possible without running out of air for sound production, CALDER (1970), using an impedance pneumograph to measure changes in the dorsoventral dimension of the thorax during canary song, showed a cyclical expansion and compression of the thorax in synchrony with each note, suggesting that the expiration to produce each note was immediately followed by a small inspiration, a 'minibreath', before the next note. At the end of a song, the dorsoventral dimension of the chest was similar or even larger than at the beginning indicating no net loss of respiratory volume occurred.

HARTLEY & SUTHERS (1989) expanded on Calder's finding by measuring the actual respiratory airflow with a microbead thermistor in the trachea of singing waterslager canaries (fig. 4). These measurements showed that the volume of each minibreath is approximately equal to the volume of air exhaled to produce the syllable. Since long whistled syllables require more air to produce than do short trilled syllables, minibreath volume varies from phrase to phrase depending on syllable duration, ranging from about 50 μL for syllables 11 ms long sung at a repetition rate of 30 s^{-1} to 260 μL for syllables lasting 119 ms at a repetition rate of 6.5 s^{-1} (fig. 5) (HARTLEY & SUTHERS, 1989).

Minibreaths free the bird from the limitation that otherwise would be imposed by the volume of its expiratory reserve. Although the duration of continuous singing is not limited by the availability of air for phonation, there may be limits imposed by respiratory gas exchange. In canaries, short minibreaths are smaller than the tracheal dead space and may contribute little to oxygenation of the blood, but this may not be true for minibreaths associated with longer syllables sung at lower repetition rates. In theory a canary might even manipulate hypoxia as a factor potentially limiting song length by arranging the syntax of the song so that phrases with long notes (and large minibreaths) occur at appropriate intervals.

The minibreath respiratory pattern requires precisely timed coordination between the respiratory muscles that control the subsyringeal pressure and the syringeal muscles that gate phonation. Each minibreath requires the active participation of inspiratory muscles (WILD *et al.*, 1998). The maximum syllable repetition rate at which minibreaths can be used must also depend on the mass of the walls of the abdominal-thoracic cavity that must oscillate at the respiratory frequency. In canaries these motor constraints limit minibreaths to phrases having a syllable repetition rate of 30 s^{-1} or less. Other songbirds, including brown thrashers, grey catbirds (*Dumetella carolinensis*), northern cardinals, brown-headed cowbirds (*Molothrus ater*) and zebra finches have also been shown to use minibreaths. In cardinals, which have a body mass more than twice that of the canary, minibreaths are only present for syllable repetition rates below about 16 s^{-1}.

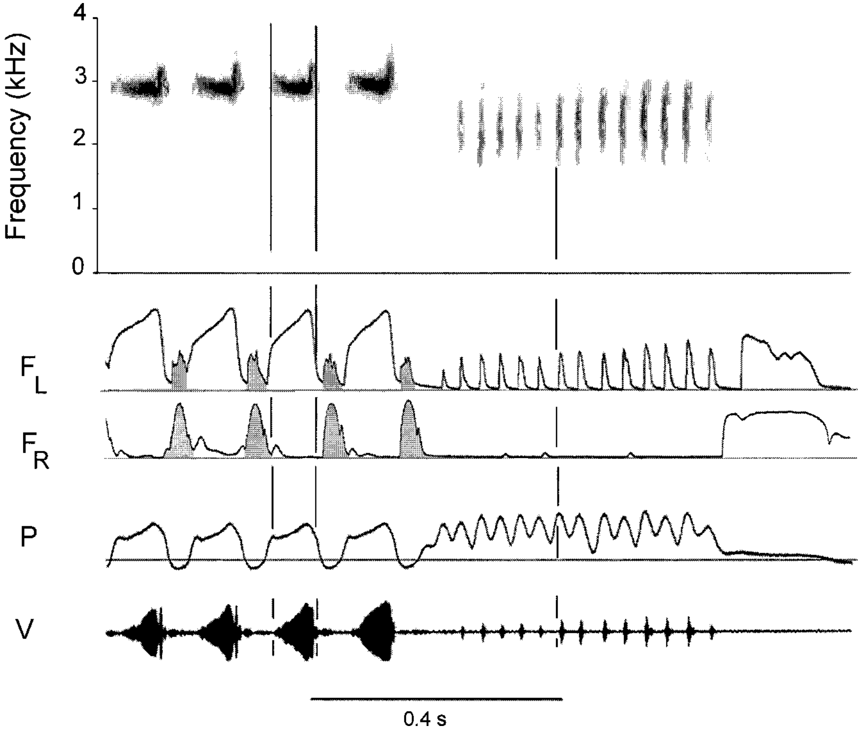

Fig. 4. Segment of a Waterslager canary song. First four syllables are sung by left syrinx and each is followed by a minibreath (shaded). During phonation a positive air sac pressure drives expiratory air through left syrinx but not through the right which is therefore closed. During minibreaths air sac pressure it 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 trilled phrase, despite transient drops during each expiration. Both sides of 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 side of syrinx, respectively. Horizontal lines equal zero flow. Inspiratory and expiratory flow are distinguished by sign of the pressure. V, oscillographic representation of vocalizations show in top panel as spectrograms. Vertical lines align events during sound production. (Modified after SUTHERS, 1999).

When canaries sing phrases at note repetition rates greater than about 30 s^{-1} (HARTLEY & SUTHERS, 1989), or cardinals sing a rates greater than 16 s^{-1} (SUTHERS & GOLLER, 1996), the intervals between notes are too short to include a minibreath and the bird uses a different respiratory pattern that we have called ‘pulsatile expiration’ (fig. 4). Subsyringeal pressure remains high during the entire phrase. The syringeal

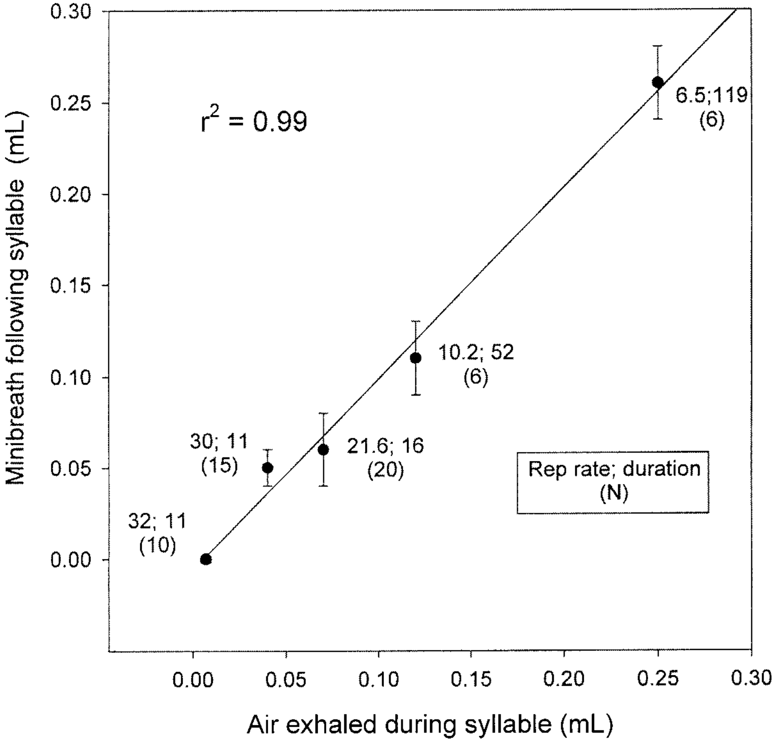

Fig. 5. Relationship between volume of air required to produce a syllable and volume of associated minibreath for Waterslager canary syllables of different durations and repetition rates. Numbers indicate syllable repetition rate; syllable duration and sample size. (Based on data from HARTLEY & SUTHERS, 1989).

valve opens briefly to release a puff of air that produces each note but remains closed during the internote intervals. The pulsatile expiration motor program permits songbirds to achieve higher note repetition rates because it reduces the mass of the structures that must oscillate at the note repetition rate by eliminating the need for the respiratory muscles and thoracoabdominal body wall to oscillate. During a pulsatile song phrase, a positive respiratory pressure is maintained by a sustained contraction of expiratory muscles (HARTLEY, 1990). This high note repetition rate comes at the price of expending the air available for phonation. The expiratory reserve volume may limit the duration of pulsatile phrases.

Respiratory patterns during vocalization by non-oscines

Minibreaths and pulsatile expiration require the coordinated, rapid action of both respiratory and syringeal muscles. To what extent are these respiratory requisites for long songs and very fast tempos dependent on the relatively complex intrinsic muscles of the oscine syrinx? Can non-oscine species having few or no intrinsic syringeal muscles accomplish similar motor patterns during vocalization?

The scanty data on the respiratory patterns in vocalizing non-oscines contain convincing evidence for minibreaths in at least two species: oilbirds and budgerigars. Oilbirds flying in the dark produce clicks at repetition rates up to about 12 s^{-1}. At such times a 50 to 80 ms minibreath with bilateral airflow is often inserted between each double click (fig. 6a). Budgerigars have a tracheal syrinx with two pairs of intrinsic muscles (KING, 1989). Inspirations during warble song vary greatly in duration but some are as short as 30 ms, about one-tenth their duration in a silent resting bird (R.E. Davis, pers. comm.). During a particularly interesting vocalization consisting of a train of notes at a repetition rate of about 14 s^{-1} (fig. 6b), a minibreath lasting about 30 ms is repeated after every 4th or 5th note. Air sac pressure remains positive during the intervening notes, which are produced by pulsatile expiration using the air inhaled in the preceding minibreath (Davis, Banta Lavenex & Suthers, in prep.). Interestingly, the internote interval during the minibreath is similar to or only slightly longer than those between pulsatile notes, suggesting that the bird adjusts the duration of its minibreath to avoid a substantial change in the note repetition rate.

Pulsatile expiration, perhaps even more than minibreaths, requires extremely accurate control of the balance between the adductive force and abductive forces on the syringeal valve. It is an interesting question whether this degree of control or rapidity of action can be achieved by birds that lack intrinsic syringeal muscles. The bipartite oscine syrinx with its intrinsic musculature may facilitate faster syringeal gating of airflow to generate faster trills and shorter notes, but it is clear that neither minibreaths nor pulsatile expiration are respiratory patterns unique to oscine songbirds.

CONTROLLING SPECTRAL PROPERTIES OF VOCALIZATIONS

Some factors affecting sound at the syringeal source

Controlling fundamental frequency. Much remains to be learned about how birds control the spectral content of their vocalizations. We are only

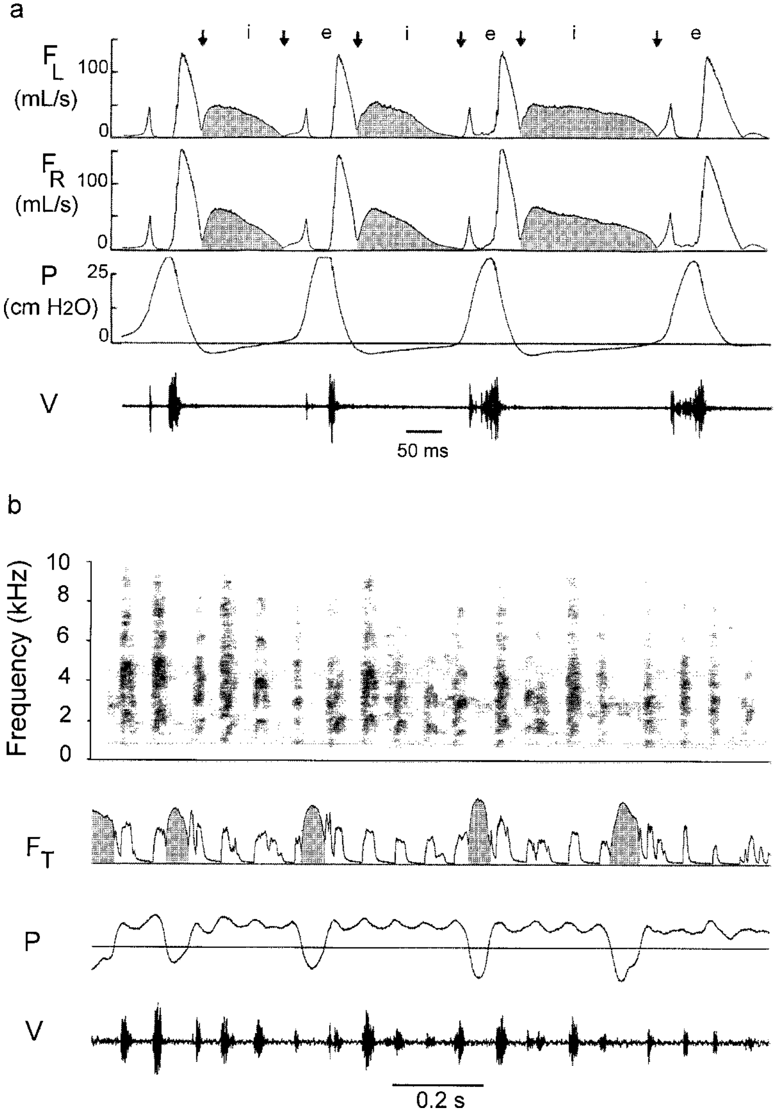

Fig. 6. a. Example of minibreaths (shaded airflow) between echolocation clicks of the oilbird. b. Minibreaths (shaded airflow between notes) and pulsatile expirations (unshaded airflow during notes) during budgerigar vocalization. F_L and F_R, airflow through left and right hemisyrinx, respectively; horizontal line = zero flow; F_T, tracheal airflow; i, inspiration; e, expiration; P, pressure in cranial thoracic air sac, horizontal line = zero (ambient) pressure; V, vocalization. (Oilbird data from Suthers & Hector (1985); budgerigar data from Davis, Banta Lavenex and Suthers, in prep.).

beginning to appreciate the variety and complexity of this process. In songbirds, the activity of the large ventral syringeal muscles has a strong positive correlation with the fundamental frequency of the vocalization. EMG activity in this muscle increases exponentially with fundamental frequency in brown thrashers, northern cardinals, Waterslager canaries and brown-headed cowbirds, suggesting that frequency control may be an important function of this muscle in many oscines (GOLLER & SUTHERS, 1995b, 1996a; SUTHERS *et al.*, 1999). The ventral syringeal muscle probably acts to increase the tension on the medial labium (Larsen and Goller, pers. observation) and the medial portion of the dorsal syringeal muscle might also have a role in frequency regulation. The tension on the labia may also be affected by the subsyringeal pressure. When syringeal muscles of the grey catbird are paralyzed by sectioning their motor nerve, the fundamental frequency of vocalizations parallels changes in air sac pressure (Suthers, pers. observation).

The means by which birds that have no intrinsic syringeal muscles control the fundamental frequency of their vocalizations is poorly understood. Presumably the extrinsic muscles that gate sound production also help regulate the tension of the labia or LTM (*e.g.*, GAUNT & GAUNT, 1977). Subsyringeal respiratory pressure may also affect frequency by stretching the LTM.

Amplitude modulation. Amplitude modulation due to the non-linear interactions between two separate signals influences the spectral content of some bird vocalizations. The amplitude of one signal, the carrier, is modulated by the second signal, creating new frequencies not present in either signal. Sounds produced in this way lack a fundamental frequency or a harmonic structure and contain side-bands around the dominant frequency. So far the only clear example of this kind of vocalization that has been described in songbirds is the “dee” call of the black-capped chickadee (*Parus atricapillus*), which Nowicki and Capranica (NOWICKI & CAPRANICA, 1986a, b) showed is produced by the non-linear coupling of the vibrating structures on the two sides of the bipartite syrinx.

Amplitude modulation is an important feature in many parrot vocalizations, however, where BANTA LAVENEX (1999) has shown it to be present in portions of budgerigar contact calls and English vowel sounds that these birds learned to mimic. It is not known how the carrier and modulating signals are produced.

Other non-linear phenomena. Complex interactions between the biomechanical and aerodynamic properties of the vocal organ can give rise to other kinds of non-linearity’s such as period doubling, biphonation and chaos that increase the spectral complexity of a vocalization. WILDEN *et al.* (1998) have presented a helpful discussion of these phenomena in mammals. FEE *et al.* (1998) used stroboscopic imaging techniques to observe the oscillations of an excised zebra finch syrinx during experimentally controlled airflow. They observed rapid transitions between different oscillatory states, including period doubling, mode-locking and switches from periodic to chaotic motion in the isolated syrinx. They believe that the large amplitude movements of the vibrating membranes relative to the size of the bronchial lumen and the mass of ML results in a highly non-linear relationship between membrane displacement and the Bernoulli forces driving their oscillation. Although their data are based on *in vitro* observations from an isolated syrinx, it is reassuring that frequency transitions occur in zebra finch song. FLETCHER (2000) has also recently reported evidence suggesting the presence of chaotic acoustic waveforms in segments of calls by the sulfur-crested (*Cacatua galerita*) and gang-gang cockatoos (*Callocephalon fimbriatum*). This non-linear and possibly chaotic behavior of the syrinx can increase vocal complexity and, as Fee *et al.* point out, poses interesting questions regarding vocal learning, production and perception.

Vocal tract acoustics

In birds, as in humans, the sound generated by the vocal organ can be modified by the vocal tract. The important role of vocal tract resonance in several species of oscine songbirds has been demonstrated by observing the effect of breathing a light gas mixture of helium and oxygen on the spectral properties of the song. Light gas has minimal effect on the vibration of the syringeal sound generating structures but increases the velocity of sound nearly two fold so that the wavelength of a second harmonic in light gas is almost as long as that of the fundamental in air. If the vocal tract dimensions are tuned to a certain resonant frequency band, then vocalizations in light gas should have their acoustic energy shifted to a higher harmonic than is transmitted in air. Experiments by NOWICKI (1987) on 9 species of songbirds demonstrated that in air the vocal tract is tuned to the fundamental frequency of song syllables and harmonics present at the syrinx are suppressed. In light gas a prominent second harmonic appeared. These experiments further indicated that songbirds are able to vary the tuning or resonant frequency of their vocal tract as they sing. Sometimes the second harmonic of one syllable in helium was the same frequency as the fundamental of an adjacent syllable. Since the second harmonic is normally suppressed in air, Nowicki reasoned that songbirds are able to adjust the tuning of their vocal tract resonance to track the fundamental frequency. The mechanism by which tracking is accomplished is not clear but may involve altering the effective length of the vocal tract and its coupling to the environment by varying the beak opening during song (WESTNEAT *et al.*, 1993; MORIYAMA & OKANOYA, 1996; SUTHERS & GOLLER, 1996, 1997; FLETCHER & TARNOPOLSKY, 1999; HOESE *et al.*, 2000).

Vocal tract resonance also plays a role in the vocalizations of non-oscines. BALLINTIJN & TEN CATE (1998) found that vocal system resonance may be important in the production of frequency-modulated elements in the coo of the collared dove. In birds breathing heliox, the upper frequency limit of these modulated elements increased as the concentration of helium increased, but the base frequency did not change. Interestingly, the upper limit of this helium induced frequency shift was about 1.5 times the frequency in air. Beyond this point a further increase in the concentration of helium was not accompanied by an increase in frequency. Helium had little effect on the frequency of coo elements with minimal frequency modulation, suggesting these two components of the coo involve different vocal mechanisms.

Tracheal elongation has evolved independently in several families where the trachea forms loops or coils in the sternum or thorax. A number of different hypotheses, both physiological and acoustic, have been put forth to explain the significance of this unusual phenomenon but none are completely satisfactory or fit all the comparative data (reviewed by FITCH, 1999). The exception is an hypothesis by FITCH (1999) in which he shows that formant dispersion, *i.e.*, the distance between adjacent formant frequencies, is inversely related to vocal tract length and argues that tracheal elongation has evolved as a means for birds living in dense habitats to acoustically exaggerate their size.

In the oilbird, bronchial resonances produce formants in the vocalizations. The non-echolocative, social vocalizations that are produced at their breeding colonies in darkened caves consist of a stack of harmonics at varying intensities that typically give rise to 3 formants. The length of the bronchus between the hemi-syrinx and the base of the trachea is nearly always longer on the left side than on the right. Furthermore, the absolute length and the difference in length between sides varies among individuals. SUTHERS & HECTOR (1994) found that the frequency of the second and third formants was near the predicted resonant frequency of the left and right bronchus, respectively, and the first formant probably originated in the trachea (fig. 7; see also FLETCHER & TARNOPOLSKY, 1999). The individual variation in distance of each hemisyrinx from the trachea provides each individual with a particular set of formant frequencies that are potential acoustic cues for individual identification.

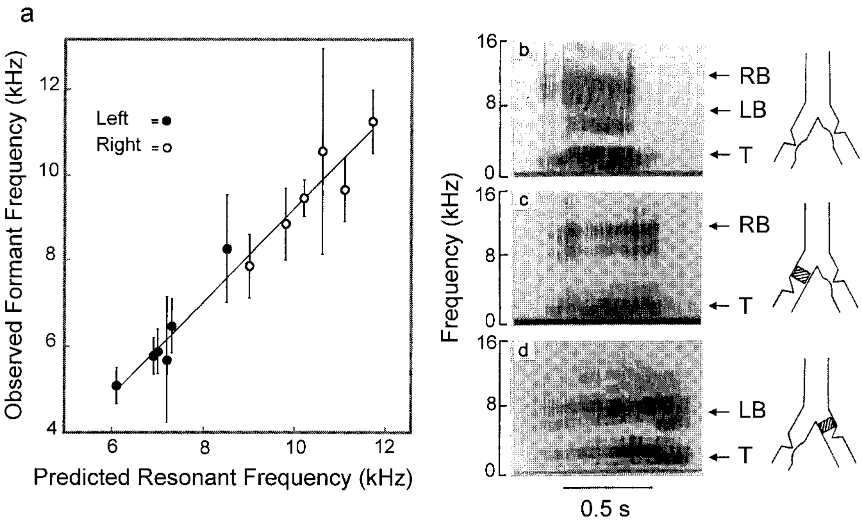

Fig. 7. a. Predicted resonant frequency and observed formant frequency of agonistic 'squawks' in oilbirds for left (solid dot) and right (open dot) portion of bronchus craniad to hemisyrinx. 6 birds, R = 0.98. Social vocalizations in cave often have a similar formant structure. b-d. Effect of unilateral bronchial plug on formant structure of squawks. b. Unplugged control. c. Left bronchus plugged. d. Right bronchus plugged. LB, RB = predicted resonant frequency of left and right bronchus, respectively, assuming is behaves as a stopped tube equal to length of bronchus from hemisyrinx to trachea. T, predicted resonant frequency of trachea assuming it behaves as a tube open at both ends. (Modified after SUTHERS, 1994).

LATERALIZATION OF SONG PRODUCTION

The tracheobronchial syrinx is not unique to songbirds, but the two halves of the oscine syrinx are separately innervated by the ipsilateral tracheosyringeal branch of the hypoglossal nerve. The oscine syrinx thus has a separate set of sound generating membranes in each bronchus, each with potentially its own independent motor control (GREENEWALT, 1968; STEIN, 1968). Since the air sacs on each side of the body are interconnected and the activity of respiratory muscles is not lateralized (GOLLER & SUTHERS, 1999), both sides of the syrinx are presumably subjected to essentially the same subsyringeal pressure (BRACKENBURY, 1987). Among oscines, the capability for vocal learning combined with the possibility of producing two simultaneous or temporally overlapping sounds that are unrelated in frequency and independent in timing, has provided new opportunities for vocal diversity and complexity (SUTHERS, 1990).

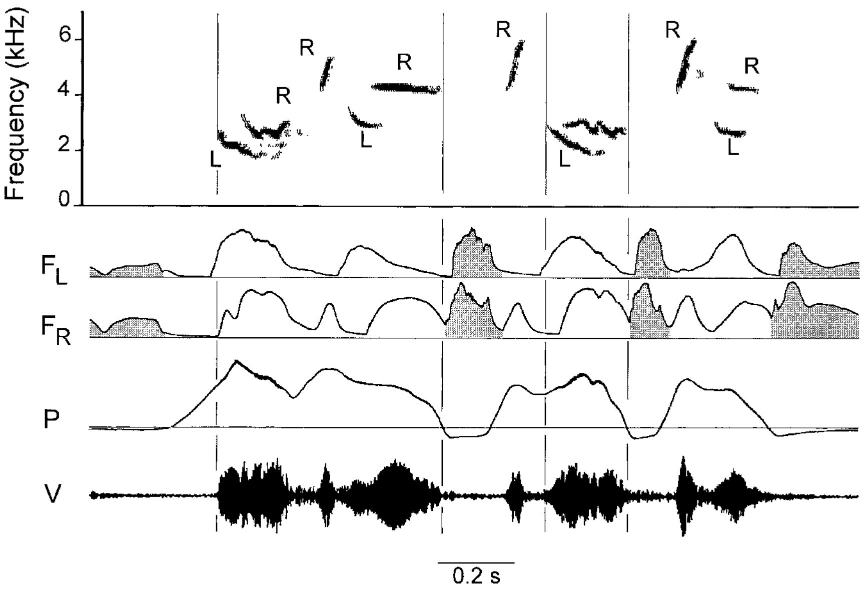

Fig. 8. Segment of brown thrasher song showing four two-voice syllables with independent frequency modulation of the left and right side contributions. These are separated from each other by shorter upward sweeping syllables produced by airflow through the right syrinx while the left side is closed (indicated by positive pressure but no airflow), and therefore silent. Sound production is frequently switched between sides of the syrinx. The vocal register of the right side is higher than that of the left although there is substantial overlap. R and L in spectrogram indicates contributions from right and left side of syrinx; inspiratory airflow (minibreaths) is shaded. Other abbreviations as in fig. 4. (Modified after SUTHERS *et al.*, 1994. Reproduced by permission).

A sense of the way in which the oscine vocal organ contributes to the vocal prowess of this group can be gained by considering the different motor approaches various species have evolved in order to produce their particular kinds of song. Different groups of songbirds utilize the two sides of their vocal organ in different ways to achieve particular acoustic effects (SUTHERS, 1992, 1997, 1999a, b; SUTHERS & GOLLER, 1997; SUTHERS *et al.*, 1999). The song of the brown thrasher provides a good example of this ability as the bird switches sound production back and forth from side to side, even within a single syllable, or uses both sides to produce non-harmonically related sounds (fig. 8) (SUTHERS *et al.*, 1994).

The two-voice components of thrasher song are rarely present in the song of the Waterslager canary. The Nottebohms (NOTTEBOHM & NOTTEBOHM, 1976), demonstrated by denervating one side of the syrinx, that these canaries sing about 90% of their song with their left syrinx. This raises the question of what is the function of the right side. Measurements of airflow and sound in each bronchus during spontaneous song with syringeal innervation intact revealed that the right side of the syrinx is closed during phonation on the contralateral side but opens for the minibreath after each syllable (fig. 4; SUTHERS, 1992, 1999a; SUTHERS & GOLLER, 1997). This arrangement has two likely advantages: 1) Unilateral phonation conserves the expiratory reserve by reducing the volume of air expelled for each syllable. 2) By reserving the right syrinx primarily for inspiration, the conflict between requirements of the respiratory vs the phonatory syringeal motor patterns is reduced. The left side can remain in the adducted phonatory configuration between notes and be prepared to immediately resume the appropriate sound as soon as the next expiration begins. Both of these motor actions should facilitate the bird's ability to sing long phrases that are often composed of relatively complex syllables at a high repetition rate (SUTHERS & GOLLER, 1997; SUTHERS, 1999a).

Songbirds have also taken advantage of their two sound sources to increase the frequency range available to them. The range of fundamental frequencies produced by the right side is typically higher than that on the left. This appears to be the case for a number of species but is a particularly prominent feature of cardinal song (fig. 9). The song of these birds contains many upward or downward frequency sweeps that sometimes cover a range of nearly 2 octaves. Frequencies below about 3.5 or 4 kHz are sung by the left side of the syrinx with the right side closed. Frequencies above this are sung on the right side. During most of the syllable sound production is unilateral, but smoothly switches from one side to the other in the middle of each extended FM sweep (SUTHERS & GOLLER, 1996, 1997; GOLLER & SUTHERS, 1997).

The brown-headed cowbird has evolved yet a different vocal motor strategy for achieving a high tempo and wide frequency range. Cowbirds sing a few stereotyped short songs. Each song begins with 2 or 3 note clusters followed by a loud complex 'whistle' that may extend to 12 kHz (fig. 10; KING & WEST, 1983). Each note cluster is produced during a single expiration and successive notes within it are produced alternately on the left and right side in a very rapid pattern with adjacent notes sometimes overlapping in time. The vocal register of the right side is higher than the left but there is considerable overlap. By alternating sides, each side has a brief silent period in which to configure itself for the next note. The loud, high-pitched whistle at the end is generated entirely on the right side of the syrinx (ALLAN & SUTHERS, 1994; SUTHERS, 1999a).

The two-voice phenomenon is also present in a variety of non-oscines (*e.g.*, GREENEWALT, 1968; ROBISSON, 1992). It does not appear to be known if the separate frequencies are due to asymmetries in the physical

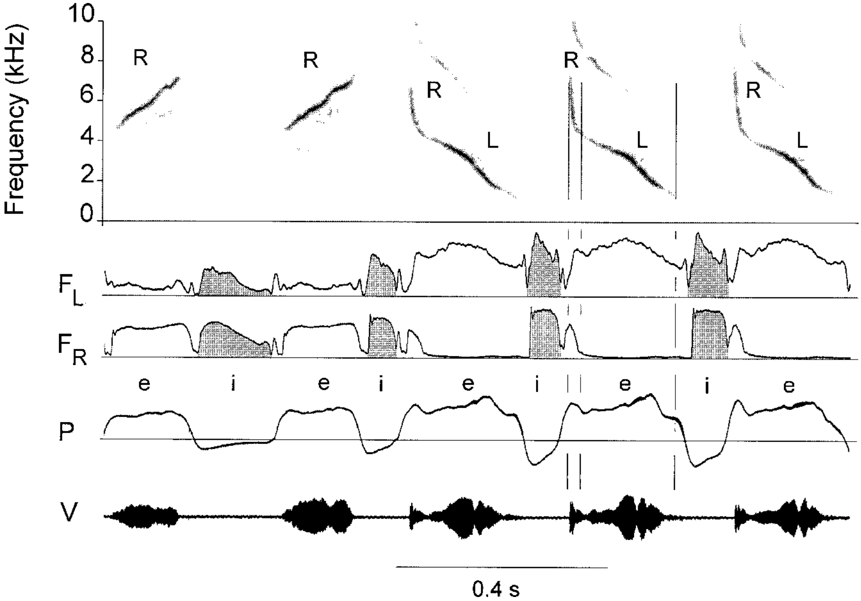

Fig. 9. Portion of a northern cardinal song. The first two syllables sweep upward from about 4.5 kHz and are generated on the right side with little airflow through the left. The initial high frequency portion of the last three syllables (first and second vertical lines) is produced by the right syrinx as the left side opens. Remainder of syllable (second and third vertical lines) is produced on the left side while the right side is closed. Note the shaded minibreaths between syllables. See fig. 8 for abbreviations. (Modified after SUTHERS, 1997).

properties or dimensions of the sound generating structures on each side of the syrinx or if there is active, independent control of each voice. Recent experiments on penguins (AUBIN *et al.*, 2000) provide the first clear behavioral function for two-voices by showing that emperor penguins (*Aptenodytes forsteri*) use a low frequency beat note, generated by the interaction of two-voice components in their display calls, as a cue for individual recognition in the breeding colony.

CONCLUSION

Although only a few species have been studied, it is already clear that oscine songbirds share several important vocal motor mechanisms, such as minibreaths and pulsatile expiration, with at least some of their non-oscine relatives. Some non-oscines also produce two-voice vocalizations. The differences in vocal ability between these two groups may arise from

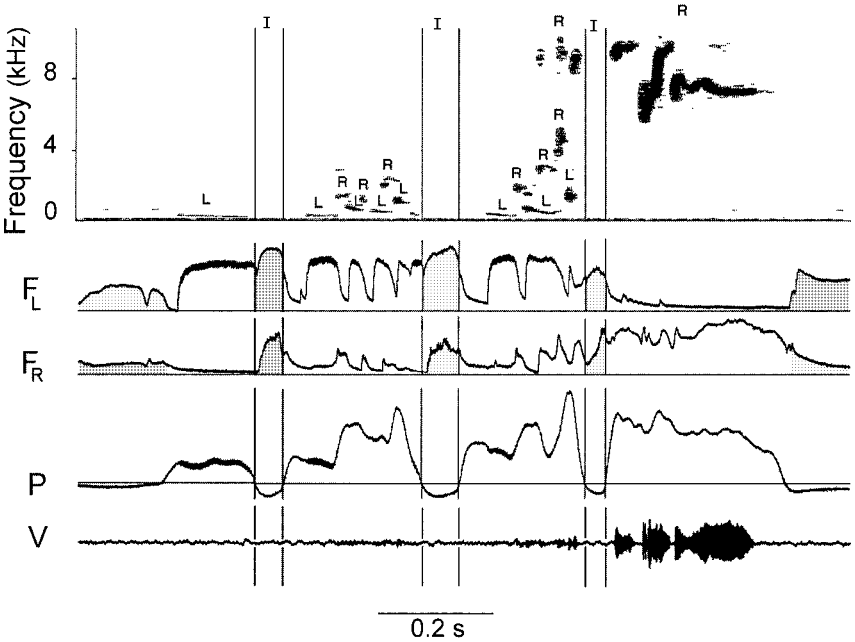

Fig. 10. Songs of the brown-headed cowbird are produced during four expirations separated by minibreaths (I). The first three expirations each produce a cluster of notes that increase gradually in frequency and intensity, beginning with a left side (L) note and alternating sides while the frequency increases in a staggered manner. In contrast to right side notes (R), most left side notes are lower in frequency and lack prominent frequency modulation. Some two-voice components accompany temporal overlap of left and right sounds. The final whistle during the last expiration is produced on the only on the right side. Note clusters are of a much lower intensity than the final whistle and are barely detectable in the oscillographic trace. See legend of fig. 8 for explanation of symbols. (Modified after SUTHERS, 1999a).

the co-evolution of a complex central song control system in the brain connected to a peripheral vocal organ controlled by multiple pairs of intrinsic muscles in songbirds. The brain nuclei provide vocal learning, laterally independent motor control and a potentially rich assortment of vocal motor programs. Analogous nuclei have evolved independently in hummingbirds and parrots, which are also vocal learners with complex vocalizations. The oscines are unique however in the number of intrinsic syringeal muscles available to them, which as GAUNT (1983) pointed out, 'permits isolation and independent control of syringeal components' responsible for modulating sound. Subsequent studies of syringeal function support that view and underline the need for more comparative data on avian sound production.

ACKNOWLEDGEMENTS

I thank Drs Herman Berkhoudt, Jaap Dubbeldam, Franz Goller and Carel ten Cate for their helpful comments on a draft of this manuscript and Sandra Ronan for her assistance in its preparation. The author's research was supported by NIH and NSF.

REFERENCES

ALLAN, S.E. & R.A. SUTHERS, 1994. Lateralization and motor stereotypy of song production in the brown-headed cowbird. J. Neurobiol. **25**: 1154-1166.

AUBIN, T., P. JOUVENTIN & C. HILDEBRAND, 2000. Penguins use the two-voice system to recognize each other. Proc. Roy. Soc. Lond. (Biol.) **267**: 1081-1087.

BALLINTIJN, M.R. & C. TEN CATE, 1998. Sound production in the collared dove: a test of the 'whistle' hypothesis. J. Exp. Biol. **201**: 1637-1649.

BALLINTIJN, M.R., C. TEN CATE, F.W. NUIJENS & H. BERKHOUDT, 1995. The syrinx of the collared dove (*Streptopelia decaocto*): structure, inter-individual variation and development. Neth. J. Zool. **45**: 455-479.

BANTA LAVENEX, P., 1999. Vocal production mechanisms in the budgerigar (*Melopsittacus undulatus*): the presence and implications of amplitude modulation. J. Acoust. Soc. Am. **106**: 491-505.

BRACKENBURY, J.H., 1987. Ventilation of the lung-air sac system. In: T.J. Seller (Eds): *Bird Respiration*: 39-71. CRC, Boca Raton.

BRITTAN-POWELL, E.F., R.J. DOOLING, O.N. LARSEN & J.T. HEATON, 1997. Mechanisms of vocal production in budgerigars (*Melopsittacus undulatus*). J. Acoust. Soc. Am. **101**: 578-589.

CALDER, W.A., 1970. Respiration during song in the canary (*Serinus canaria*). Comp. Biochem. Physiol. **32**: 251-258.

CASEY, R.M. & A.S. GAUNT, 1985. Theoretical models of the avian syrinx. J. Theor. Biol. **116**: 45-64.

CHAMBERLAIN, D.R., W.B. GROSS, G.W. CORNELL & H.S. MOSBY, 1968. Syringeal anatomy in the common crow. Auk **85**: 244-252.

DÜRRWANG, R., 1974. *Funktionelle Biologie, Anatomie und Physiologie der Vogelstimme*. Philosophisch-Naturwissenschaftenlichen Fakultät, Universität Basel, Basel.

FEE, M.S., B. SHRAIMAN, B. PESARAN & P.P. MITRA, 1998. The role of nonlinear dynamics of the syrinx in the vocalizations of a songbird. Nature **395**: 67-71.

FITCH, W.T., 1999. Acoustic exaggeration of size in birds via tracheal elongation: comparative and theoretical analyses. J. Zool. **248**: 31-48.

FLETCHER, N.H., 1988. Bird song — a quantitative acoustic model. J. Theor. Biol. **135**: 455-481.

FLETCHER, N.H., 2000. A class of chaotic bird calls? J. Acoust. Soc. Am. **108**: 821-826.

FLETCHER, N.H. & A. TARNOPOLSKY, 1999. Acoustics of the avian vocal tract. J. Acoust. Soc. Am. **105**: 35-49.

GAUNT, A.S., 1983. An hypothesis concerning the relationship of syringeal structure to vocal abilities. Auk **100**: 853-862.

GAUNT, A.S., 1987. Phonation. In: T.J. Seller (Eds): *Bird Respiration*: 71-94. CRC, Boca Raton.

GAUNT, A.S. & S.L.L. GAUNT, 1977. Mechanics of the syrinx in *Gallus gallus*. II. Electromyographic studies of *ad libitum* vocalizations. J. Morph. **152**: 1-20.

GAUNT, A.S., S.L.L. GAUNT & R.M. CASEY, 1982. Syringeal mechanics reassessed: evidence from *Streptopelia*. Auk **99**: 474-494.

GOLLER, F. & O.N. LARSEN, 1997a. *In situ* biomechanics of the syrinx and sound generation in pigeons. J. Exp. Biol. **200**: 2165-2176.

GOLLER, F. & O.N. LARSEN, 1997b. A new mechanism of sound generation in songbirds. Proceedings of the National Academy of Sciences. U.S.A. **94**: 14787-14791.

GOLLER, F. & R.A. SUTHERS, 1995a. Contributions of expiratory muscles to song production in brown thrashers. In: M. Burrows, T. Matheson, P. Newland & H. Schuppe (Eds): *Nervous Systems and Behaviour. Proceedings of the 4th International Congress of Neuroethology*: 334. Georg Thieme Verlag, Stuttgart.

GOLLER, F. & R.A. SUTHERS, 1995b. Implications for lateralization of bird song from unilateral gating of bilateral motor patterns. Nature **373**: 63-66.

GOLLER, F. & R.A. SUTHERS, 1996a. Role of syringeal muscles in controlling the phonology of bird song. J. Neurophysiol. **76**: 287-300.

GOLLER, F. & R.A. SUTHERS, 1996b. Role of syringeal muscles in gating airflow and sound production in singing brown thrashers. J. Neurophysiol. **75**: 867-876.

GOLLER, F. & R.A. SUTHERS, 1997. Vocal gestures of shared syllable types in cardinals. Soc. Neurosci. Abst. **23**: 243.

GOLLER, F. & R.A. SUTHERS, 1999. Bilaterally symmetrical respiratory activity during lateralized birdsong. J. Neurobiol. **41**: 513-523.

GREENEWALT, C.H., 1968. *Bird Song: Acoustics and Physiology.* Smithsonian Institution Press, Washington, D.C.

HARTLEY, R.S., 1990. Expiratory muscle activity during song production in the canary. Respir. Physiol. **81**: 177-187.

HARTLEY, R.S. & R.A. SUTHERS, 1989. Airflow and pressure during canary song: evidence for mini-breaths. J. Comp. Physiol. A **165**: 15-26.

HOESE, W.J., J. PODOS, N.C. BOETTICHER & S. NOWICKI, 2000. Vocal tract function in birdsong production: experimental manipulation of beak movements. J. Exp. Biol. **203**: 1845-1855.

JARVIS, E.D., S. RIBEIRO, M.L. DA SILVA, D. VENTURA, J. VIELLIARD & C.V. MELLO, 2000. Behaviourally driven gene expression reveals song nuclei in hummingbird brain. Nature **406**: 628-632.

KING, A.P. & M.J. WEST, 1983. Dissecting cowbird song potency: assessing a song's geographic identity and relative appeal. Z. Tierpsychol. **63**: 37-50.

KING, A.S., 1989. Functional anatomy of the syrinx. In: A.S. King & J. McLelland (Eds): *Form and Function in Birds*: 105-192. Academic Press, London.

LARSEN, O.N. & F. GOLLER, 1999. Role of syringeal vibrations in bird vocalizations. Proc. Roy. Soc., Lond. **266**: 1609-1615.

MISKIMEN, M., 1951. Sound production in passerine birds. Auk **68**: 493-504.

MORIYAMA, K. & K. OKANOYA, 1996. Effect of beak movement in singing Bengalese finches. Abstracts. Acoustical Society of America and Acoustical Society of Japan, Third Joint Meeting. Honolulu, 2-6 Dec 1996: 129-130.

NOTTEBOHM, F., 1976. Phonation in the orange-winged Amazon Parrot, *Amazona amazonica*. J. Comp. Physiol. **108**: 157-170.

NOTTEBOHM, F. & M.E. NOTTEBOHM, 1976. Left hypoglossal dominance in the control of canary and white-crowned sparrow song. J. Comp. Physiol. **108**: 171-192.

NOWICKI, S., 1987. Vocal tract resonances in oscine bird sound production: evidence from birdsongs in a helium atmosphere. Nature **325**: 53-55.

NOWICKI, S. & R.R. CAPRANICA, 1986a. Bilateral syringeal coupling during phonation of a songbird. J. Neurosci. **6**: 3595-3610.

NOWICKI, S. & R.R. CAPRANICA, 1986b. Bilateral syringeal interaction in vocal production of an oscine bird sound. Science **231**: 1297-1299.

ROBISSON, P., 1992. Vocalizations in *Aptenodytes* penguins: application of the two-voice theory. Auk **109**: 654-658.

STEIN, R.C., 1968. Modulation in bird sound. Auk **94**: 229-243.

SUTHERS, R.A., 1990. Contributions to birdsong from the left and right sides of the intact syrinx. Nature **347**: 473-477.

SUTHERS, R.A., 1992. Lateralization of sound production and motor action on the left and right sides of the syrinx during bird song. 14th International Congress on Acoustics I: 1-5.

SUTHERS, R.A., 1994. Variable asymmetry and resonance in the avian vocal tract: a structural basis for individually distinct vocalizations. J. Comp. Physiol. A **175**: 457-466.

SUTHERS, R.A., 1997. Peripheral control and lateralization of birdsong. J. Neurobiol. **33**: 632-652.

SUTHERS, R.A., 1999a. The motor basis of vocal performance in songbirds. In: M. Hauser & M. Konishi (Eds): *The Design of Animal Communication*: 37-62. MIT Press, Cambridge, MA.

SUTHERS, R.A., 1999b. Peripheral mechanisms for singing: Motor strategies for vocal diversity. In: N.J. Adams & R.H. Slotow (Eds): *Proceedings of 22nd International Ornithological Congress. Durban*: 491-508. BirdLife South Africa, Johannesburg.

SUTHERS, R.A. & F. GOLLER, 1996. Respiratory and syringeal dynamics of song production in northern cardinals. In: M. Burrows, T. Matheson, P. Newland & H. Schuppe (Eds): *Nervous Systems and Behaviour. Proceedings of the 4th International Congress of Neuroethology*: 333. Georg Thieme Verlag, Stuttgart.

SUTHERS, R.A. & F. GOLLER, 1997. Motor correlates of vocal diversity in songbirds. In: V. Nolan Jr, E. Ketterson & C.F. Thompson (Eds): *Curr. Ornithol.*: 235-288. Plenum Press, New York.

SUTHERS, R.A., F. GOLLER & R.S. HARTLEY, 1994. Motor dynamics of song production by mimic thrushes. J. Neurobiol. **25**: 917-936.

SUTHERS, R.A., F. GOLLER & C. PYTTE, 1999. The neuromuscular control of birdsong. Phil. Trans. Roy. Soc., Lond. B **354**: 927-939.

SUTHERS, R.A. & D.H. HECTOR, 1982. Mechanism for the production of echolocating clicks by the grey swiftlet, *Collocalia spodiopygia*. J. Comp. Physiol. A **148**: 457-470.

SUTHERS, R.A. & D.H. HECTOR, 1985. The physiology of vocalization by the echolocating oilbird, *Steatornis caripensis*. J. Comp. Physiol. A **156**: 243-266.

SUTHERS, R.A. & M.X. ZUO, 1991. A test of the aerodynamic whistle hypothesis for the production of birdsong. Soc. Neurosci. Abst. **17**: 1050.

VICARIO, D.S., 1991a. Contributions of syringeal muscles to respiration and vocalization in the zebra finch. J. Neurobiol. **22**: 63-73.

VICARIO, D.S., 1991b. Neural mechanisms of vocal production in songbirds. Curr. Opinion Neurobiol. **1**: 595-600.

WESTNEAT, M.W., J. LONG, H. JOHN, W. HOESE & S. NOWICKI, 1993. Kinematics of birdsong: functional correlation of cranial movements and acoustic features in sparrows. J. Exp. Biol. **182**: 147-171.

WILD, J.M., F. GOLLER & R.A. SUTHERS, 1998. Inspiratory muscle activity during birdsong. J. Neurobiol. **36**: 441-453.

WILDEN, I., H. HERZEL, G. PETERS & G. TEMBROCK, 1998. Subharmonics, biphonation, and deterministic chaos in mammal vocalization. Bioacoustics **8**: 1-30.

YOUNGREN, O.M., F.W. PEEK & R.E. PHILLIPS, 1974. Repetitive vocalizations evoked by local electrical stimulation of avian brains III. Evoked activity in the tracheal muscles of the chicken (*Gallus gallus*). Brain, Behav. Evol. **9**: 393-421.