Motor Dynamics of Song Production by Mimic Thrushes

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SUMMARY

In brown thrashers (*Toxostoma rufum*) and grey catbirds (*Dumetella carolinensis*) neither side of the syrinx has a consistently dominant role in song production. During song, the two sides operate independently, but in close cooperation with each other and with the respiratory muscles which are capable of adjusting expiratory effort to maintain a constant rate of syringeal airflow despite sudden changes in syringeal resistance. Phonation is frequently switched from one side of the syrinx to the other, both between syllables and within a syllable. When both sides of the syrinx produce sound simultaneously, their respective contributions are seldom harmonically related. The resulting "two-voice" syllables sometimes contain difference tones with prominent sinusoidal amplitude modulation (AM). Rarely, both sides simultaneously produce the same sound. In general, however, the frequency range of sound contributed by the right syrinx is higher than that of the left syrinx. The right syrinx is also primarily responsible for producing a rapid cyclical amplitude modulation which is a characteristic feature of some syllables. This kind of AM is generated by either repetitive brief bursts of sound from the right side that modulate the amplitude of a continuous sound arising on the left side or cyclically opening the right syrinx, allowing unmodulated expiratory air to bypass the phonating left side. © 1994 John Wiley & Sons, Inc.

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INTRODUCTION

The syrinx of songbirds is formed by the modified cranial ends of the two primary bronchi and the caudal end of the trachea (Fig. 1). Each bronchus contains its own set of membranes believed to generate sound and act as a valve controlling respiratory airflow. Syringeal motor action is controlled by several bilaterally paired syringeal muscles. The muscles on each side of the syrinx are separately innervated by a tracheosyringeal branch of the ipsi-

lateral hypoglossal nerve. The left and right sides of the syrinx are thus each potentially capable of producing sound.

Several kinds of evidence indicate that the two sides of the syrinx can function independently of each other. Some birds are capable of simultaneously singing two independent, nonharmonically related notes which Greenewalt (1968) and Stein (1968) postulated most likely arise from separate sound generators in opposite sides of the syrinx. Subsequent experiments on several species of songbirds in which one side of the syrinx was experimentally disabled indicate a lateralization of song production in which most of the song is generated on one side of the syrinx, nearly always the left. Section of the tracheosyringeal branch of the left hypoglossal nerve abolishes the majority of notes in the song repertoire of the chaffinch (*Fringilla coelebs*), canary (*Serinus canaria*), white-throated and white-crowned sparrows (*Zonotrichia albicol-*

lis and *Z. leucophrys*), and java sparrow (*Padda oryzivora*) (Nottebohm, 1970, 1971; Nottebohm and Nottebohm, 1976; Lemon, 1973; Seller, 1979). In addition, in all of these species, unilateral section of the right nerve was followed by relatively small song deficits. Thus, these birds exhibit a left hypoglossal dominance. As yet, right hypoglossal dominance has been demonstrated in only two species, the zebra finch (*Poephila guttata*) (Williams et al., 1992) and the brown-headed cowbird (*Molothrus ater*) (Allan and Suthers, 1994). In neither of these birds is dominance as pronounced as in the canary.

The extent of left hypoglossal dominance in canaries was questioned by McCasland (1987) who found smaller differences between song from the left versus right side of the syrinx when one side was disabled by plugging its bronchus. He suggested that lateralized song production might be a peripheral rather than a central phenomenon, but Hartley and Suthers (1990) were unable to duplicate his results.

Direct evidence for independent motor control of each side of the syrinx was obtained by using microbead thermistors to monitor syringeal airflow in singing catbirds and brown thrashers (Suthers, 1990). These birds sang some syllables or parts of syllables with one side of their syrinx and some with the other side. Often both sides produced different sounds at the same time. Thus, unlike canaries and most other passerines that have been studied, the song of mimic thrushes is not lateralized to a dominant side.

Respiratory, as well as syringeal, muscles play a vital role in controlling vocalization. Their action is essential in setting the temporal pattern of a song (Simpson and Vicario, 1990; Vicario, 1991a,b). The amplitude of electromyograms (EMGs) from abdominal expiratory muscles of singing canaries follows the temporal pattern of the song, including even the rapid modulations within syllables produced at high repetition rates (Hartley, 1990). However, data presented below on catbirds and thrashers suggest respiratory motor patterns also contribute to song production in ways that go well beyond determining its temporal pattern.

In this article, we further examine the syringeal mechanisms controlling vocalization in grey catbirds and brown thrashers (family Mimidae; mimic thrushes). Experiments reported here address in more detail the peripheral control of phonation, the properties of sounds generated on each side of the syrinx, and the interaction of respiratory and syringeal motor patterns.

METHODS

Collection and Rearing of Birds

Young catbirds and brown thrashers were collected as nestlings when they were about 1 week old. In most cases nestlings were immediately sexed by laparotomy (Risser, 1971; Fiala, 1979), and females were returned to the nest. The young males were hand raised in the laboratory, housed in groups, and tutored with adult catbird and brown thrasher songs. Most were also exposed to adult song of northern cardinals (*Cardinalis cardinalis*), rufous-sided towhees (*Pipilo erythrophthalmus*), and canaries. When they were fully independent—usually at about 6 weeks of age—they were placed in individual cages in the aviary and maintained on a photoperiod that simulated the seasonally changing local daylength.

Preparation for Syringeal Recordings

Adult birds were monitored in the aviary for song during the spring and summer of their first and subsequent years. Vigorously singing birds were moved from the aviary to a cage in the laboratory. A 3-week timed-release pellet of testosterone propionate (10 mg, catbird; 15 mg, thrasher; Innovative Research of America) was implanted subcutaneously along the neck under halothane or isoflurane anesthesia. An elastic belt was placed around the thorax with a small self-gripping fastener (Velcro) exposed on the back to which a miniature connector with leads to recording instruments was subsequently attached.

Preoperative song was recorded from each bird on a cassette recorder (Marantz, model PMD 221) using a dynamic microphone (Panasonic, model WM-2298) mounted outside the cage. The cassette recorder was controlled by an acoustic switch (Uher, Akustomat F413) and the sound signal was delayed about 1 s by a digital delay circuit (Digitech, model RDS 1900 or 2001) to allow the tape to reach its proper speed. The frequency response of this system was ±3 dB from 500 Hz to 4.5 kHz (±6 dB to 11 kHz), being limited by the microphone. Although we observed no obvious differences between the song of our hand-reared and that of wild birds, we cannot rule out the possibility that some differences may exist.

Measurement of Air Sac Pressure

After preoperative song was recorded, a Silastic cannula was implanted in the cranial thoracic air sac for the measurement of subsyringeal pressure. The bird was anesthetized with isoflurane delivered in breathing air through a mask over the bill and regulated with a vaporizer (Fluotec, Mark 2). A small hole into the caudal end of the air sac was made through the abdominal wall just posterior to the last rib and a few millimeters lateral to the ventral midline. A flexible cannula (Dow Corning, Silastic tub-

ing 602-205) was inserted into the air sac through this opening and sutured to the adjacent posterior edge of the rib cage. A small amount of n-butyl cyanoacrylate tissue adhesive (Tri-Point Medical L.P., Nexaband) was applied to the skin around the cannula to hold it in place and seal the incision. The distal end of the cannula was temporarily sealed with a plug and routed caudally to the base of the tail where it turned dorsally and cranially, crossing the rump to an attachment at the Velcro tab on the back. This air sac cannula was usually inserted one or a few days before thermistors were placed in the bronchi.

Air sac pressure was monitored with a miniature temperature-compensated piezoresistive pressure transducer (Endevco model 8507-5 or 8507B-5 or Fujikura model FPM-02PG) mounted on the back pack and connected to the distal end of the air sac cannula. Wires carrying the excitation voltage (current) and output signal extended from the back pack through the top of the cage to appropriate signal-conditioning circuits before being recorded on magnetic tape.

Measurement of Bronchial Airflow and Sound

Bronchial airflow and sound were measured by a microbead thermistor inserted in each bronchus. A preanesthetic dose of atropine sulfate (Butler, 0.5 mg/cc: catbird, 6 μl; thrasher, 9 μl) was delivered sc. Anesthesia was achieved by injection of chloropent (recipe available from Fort Dodge Laboratory) into the pectoral muscles at a dosage of 4–5 μl/g body weight. Supplemental injections were administered at intervals as necessary. Surgery was performed under an operating microscope with coaxial illumination. A midline incision was made in the skin between the clavicles, and the membrane of the interclavicular air sac was exposed. After making an incision in this membrane, it was possible to view the syrinx and primary bronchi. Access to each bronchus was improved by gently moving the syrinx slightly to the contralateral side. A small hole was made in the ventral side of the primary bronchus between two cartilaginous rings about midway between the syrinx and the lung. A microbead thermistor was inserted through this hole and positioned near the middle of the bronchial lumen. The thermistor was held in place by a small amount of tissue adhesive applied to the thermistor leads where they entered the bronchus. Care was taken to avoid getting tissue adhesive on the cranial end of the bronchus or on the syrinx. Another thermistor was inserted into the contralateral bronchus using the same procedure. The incision in the interclavicular membrane was closed around the leads from each thermistor with sutures and tissue adhesive. The leads were adjusted with slack in the interclavicular air sac so they did not pull on the bronchi. Additional slack was provided in the space between the interclavicular membrane and the skin. From this space the thermistor leads were routed subcutaneously to the self-gripping fastener in the middle of the back where they

exited through the skin. The incision in the skin ventral to the interclavicular membrane was then closed with sutures.

Each bronchial flow probe was constructed of a 5-mil (0.13-mm) microbead thermistor (Thermometrics, BB05JA202 or Victory Engineering, 32A402A). Electrically conductive silver epoxy was used to connect each thermistor lead to a short length of flexible, insulated 2-mil (0.05 mm) diameter copper-nickel alloy wire which extended from the thermistor to the subcutaneous space ventral to the interclavicular air sac where it was connected to a stronger stranded copper wire that traveled under the skin to the back pack. Thermistor leads and connections between wires were insulated with nonconductive epoxy or silicone adhesive. Wires from the back pack exited through the top of the cage and were connected to a feedback circuit which heated the thermistors and maintained them at a constant temperature (Hector Engineering). The thermistor was therefore cooled by convective heat loss during both inspiration and expiration. The effects of temperature and humidity in the bronchi were empirically corrected by manually zeroing the circuit after the thermistor was in place. The voltage required to provide enough current to maintain the thermistor's temperature was recorded as a measure of the rate of airflow.

We assume that the acoustic response of the thermistor to sound in the bronchus was due to air movement in the near field of the acoustic signal generated by the putative vibratory membrane, the Mtm, which was only a few millimeters craniad. The thermistor did not respond to changes in pressure per se. The response time of a clean thermistor was 90% of full scale in about 6 ms. The actual diameter of individual thermistor beads varies around its nominal value, and their frequency response gradually deteriorates as contaminants, such as micro-drops of mucus or saliva, in the air stream are baked onto their surface. It is thus not feasible to provide an accurate calibration of the *in situ* response during an experiment.

A different design of flow probe was used in thrasher 02. A microbead thermistor was mounted on each side of a thin metal septum, 2 mm high and 4.6 mm long. This septal flow probe was inserted through an incision in the trachea several millimeters craniad to the syrinx. The caudad edge of the septum was aligned with the semi-lunar membrane on the pessulus, to which it was sealed with tissue adhesive. Fine wires from the thermistors were brought out through the tracheal incision which was then sutured shut. The septum thus maintained the separation of air flowing through each side of the syrinx, allowing the rate of airflow on each side to be monitored by the thermistors (Fig. 1). The complete separation of airflow on each side was confirmed during autopsy at the end of the experiment. This bird served as a control for possible major mechanical effects of bronchial thermistors, or their leads, on the gating of airflow through the two sides of the syrinx.

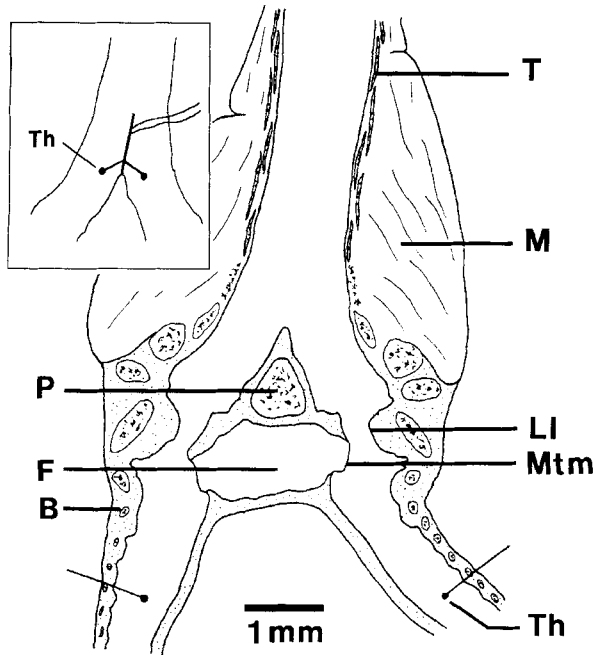It was not feasible to determine the absolute rate of

Figure 1 Frontal section through syrinx of brown thrasher. *Abbreviations:* T = tracheal ring; M = syringeal muscles; L1 = lateral labium; Mtm = medial tympaniform membrane; Th = microbead thermistor; P = pessulus; F = interbronchial foramen; B = bronchial ring. Septal flow probe used in one bird is shown in inset. (Modified after Suthers, 1990.)

airflow in these experiments since the flexible bronchial wall may allow the cross-sectional area of its lumen to vary as the syrinx moves during singing. Thermistor calibration assumes a rigid tube. The septal flow probe was not calibrated. The data in this article are thus based on the nonlinearized thermistor output which only indicates changes in the relative rate of airflow.

Data Recording

After surgery the bird was returned to its cage where it moved about freely and usually resumed singing within a few days. Leads ascending from the back pack through the top of the cage to electronic conditioning and recording instruments were maintained under a slight tension by a counter-balanced arm above the cage that prevented the bird from becoming entangled in them.

In some experiments, data on airflow, pressure, and sound were recorded on two four-channel instrumentation tape recorders (Racal, model 4DS) at a tape speed of 3.75 ips (9.5 cm/s). At least one of these variables was recorded on both tape recorders so that the two tapes could be synchronized during playback and analysis. Pressure and respiratory airflow were recorded in the FM wide band 1 mode having a frequency response of DC to

2.5 kHz. In order to record the small fluctuations in thermistor output resulting from the cyclical fluctuation of rate of airflow due to the vibratory motion of the syringeal sound generator, a parallel output of the thermistors was bandpass filtered at 200 Hz to 8 kHz (Krohn Hite, model 3550 or 3700) or at 200 Hz high pass by a 10-pole Butterworth filter (TTE Inc., Model AHB10) to attenuate the low-frequency respiratory signal and noise. The output of the filter was amplified (Princeton Applied Research, model 113) and recorded in the direct mode with a frequency response from 100 Hz to 18 kHz. The output of the microphone was also amplified and recorded on a direct channel.

In other experiments, data were recorded on a digital eight-channel rotary storage recorder (Metrum Information Storage, model RSR 512). The frequency response was flat from DC to 10 kHz and each channel was sampled at 40 kHz. The wide dynamic range of this recorder (>70 dB) made it unnecessary to separately record a high-pass-filtered output from the bronchial thermistors in order to monitor bronchial sound.

Data reported here are from six brown thrashers (not including one with the septal flow probe) and three grey catbirds.

Data Analysis

An 8-channel thermal array recorder (Graphtec, model WR3600) was used to obtain continuous strip chart records of portions of the recorded data. The frequency structure of vocalizations and bronchial sound was determined from sound spectrograms (Uniscan II, Multigon, Mt. Vernon, NY).

Much of the data analysis was done on a 486 PC using signal processing software (Signal, Engineering Design, Belmont, MA) for data acquisition, analysis, display, and editing. Tapes were played back at half speed (with time and frequency scales appropriately adjusted) and digitized (Data Translation, DT-2821-G) at a sample rate of 20 or 25 kHz/channel (= 40 or 50 kHz real time) using anti-alias filters (TTE Inc, Los Angeles, CA; series J87, stopband attenuation 60 dB/one-third octave) with a high cutoff at 8 kHz for a real-time bandwidth from DC to 16 kHz. Multichannel data were first saved as successive song segments up to several seconds long and containing a number of syllables. These were then edited and data for each syllable—including the concurrent air sac pressure, airflow through each side of the syrinx, and sound in each bronchus—were stored in files for further analysis.

Measurements of sound frequency were made visually from spectrograms generated with Signal. Sound amplitude and duration were measured from the time waveform using Signal. A two-tailed, unpaired Student t test and chi-square test was used to determine the level of significance between various data sets.

RESULTS

Characteristics of Catbird and Thrasher Song

The songs of catbirds and brown thrashers are similar in many ways. Both consist of fairly evenly paced notes or syllables delivered at a repetition rate of about 3/s in singing bouts that range from a few seconds to many minutes (Fig. 2). The phonetic structure of the song is highly variable. Most syllables are infrequently repeated with the exception of couplets, that is, an immediate single repetition of a syllable, which characterize the brown thrasher's song. Occasionally, these birds mimic parts of the songs of other species. The variability and plasticity of thrasher and catbird song makes it impossible to determine a complete repertoire of syllable types for an individual or systematically compare the same syllable type before and after an experimental procedure. Kroodsma and Parker (1977) have estimated that brown thrashers may have a repertoire of about 2000 syllable types. Given this limitation, postoperative song in the following experiments was not detectably different from that recorded before surgery.

Syringeal and Respiratory Dynamics of Song Production

Mimic thrushes, like other oscines, have a bronchotracheal syrinx (King, 1989) (Fig. 1). We have found no qualitative differences in the motor aspects of song production in brown thrashers and catbirds so the following remarks apply to both species. Data obtained with the septal flow probe in thrasher 02 are not included below since neither bronchial sound nor subsyringeal pressure were recorded. Measurements of airflow during song by this bird showed a pattern of switching between unilateral flow involving either side of the syrinx and/or bilateral airflow that was similar to that observed in subsequent experiments using bronchial thermistors.

Gating of Phonation. The gating, or onset and termination, of phonation is usually controlled by syringeal muscles that open or close the lumen on each side of the syrinx and are innervated by ipsilateral tracheosyringeal branches of the hypoglossal nerve. There is no evidence that the avian larynx plays an important role in this process (Suthers, 1990). Vocalization is preceded by a substantial increase in subsyringeal pressure presumably brought about by contraction of the expiratory

muscles and by activity of appropriate syringeal muscles that bring one or both sides of the syrinx into a partially adducted, phonatory configuration. Air sac pressures between approximately 20 and 35 cm H_2O are typical during phonation, being an order of magnitude or more greater than the pressure developed during silent respiration at rest. Bilateral connections of the interclavicular to other air sacs enable air to move from one side of the respiratory system to the other and ensure that the subsyringeal pressure is the same on both sides of the syrinx. During respiration the pressure differences between various air sacs are extremely small (Brackenbury, 1972) so it is reasonable to assume that the pressure recorded in the cranial thoracic air sac is essentially equal to that in each primary bronchus.

Although the precise mechanism of sound production is unknown (Gaunt and Gaunt, 1985) and the possibility exists that voiced and whistled vocalizations may be produced by fundamentally different mechanisms (Fletcher, 1988, 1989), it is likely that voiced and perhaps whistled song originates from vibration of the medial tympaniform membrane (Mtm) when air flows across it through a constriction formed between it and the lateral labium (Ll). We hypothesize that Ll thus acts as a valve controlling the syringeal aperture—opening it for inspiration, partially closing it to a phonatory position for song, or fully closing it to block the flow of air. The rate of airflow sometimes decreases at the onset of sound production despite increasing or constant air sac pressure—confirming that syringeal resistance increases. The fundamental frequency of the sound is assumed to be determined by the physical properties of the tympaniform membranes and to depend on their tension as determined by the syringeal muscles and aerodynamic forces.

Phonation on a given side of the syrinx is normally stopped or prevented by closing that side, but occasionally one side of the syrinx is partially opened during a song syllable without producing sound. Rapid cyclical amplitude modulated (AM) syllables produced by shunting airflow through the side (usually the right) contralateral to that generating sound is an example of this kind of gating [see below, Fig. 10(b)].

Contributions from the Left and Right Syrinx. The adductive action regulating expiratory airflow through the syrinx is controlled independently for each side of the syrinx by the ipsilateral syringeal muscles (Suthers, 1990). Sound may be
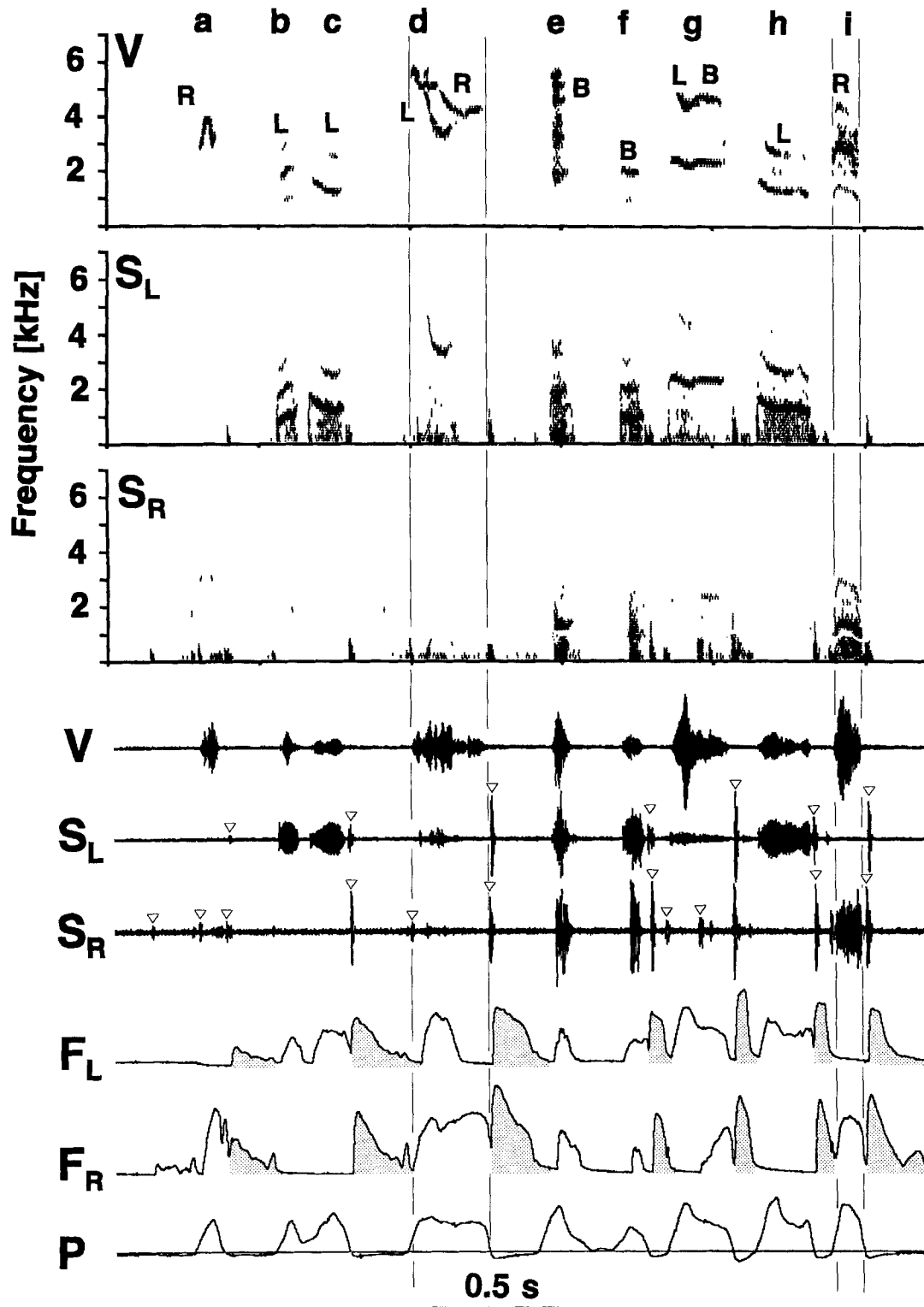
Figure 2 A segment of song from catbird 02 showing contributions from each side of the syrinx. Vocalizations (V), recorded with microphone in front of bird, are represented both spectrographically (top) and oscillographically (bottom) to show frequency structure and amplitude, respectively. a through i are successive song syllables. Syllables are produced on the right side (R), left side (L) or both sides (B) of the syrinx. Vertical lines align events at the onset or end of some syllables. Spectrograms (S_L and S_R) of high-pass filtered and amplified

produced by both sides of the syrinx simultaneously [Fig. 2 (syllables e and f)] or by only one side at a time [Fig. 2 (a, b, c, h, i)]. Often song syllables contain sequential contributions from both sides [Fig. 2 (syllables d and g)].

Many syllables contain frequency components that are produced simultaneously but that are not harmonically related. The separate components of these "two-voice" syllables are generated on opposite sides of the syrinx (Suthers, 1990).

Four two-voice catbird syllables are shown in Figure 3. In syllable a the two sides of the syrinx simultaneously produce elements with frequency modulation in opposite directions. In syllables b and c, the output from one side is frequency modulated (FM) while that from the contralateral side is more nearly a constant frequency (CF). The temporal overlap of the two elements can range from complete (syllable a) to partial (syllables b, c) reflecting the bilaterally independent motor control of gating as well as of frequency.

Two-voice syllables are also common in brown thrasher song. The examples in Figure 4 contain various combinations of FM and nearly CF components alternating with a steeply rising FM note that is produced only on the right side.

Occasionally both sides of the syrinx simultaneously produce the same sound as judged by the output of the bronchial thermistors. This occurs in only a small fraction of the syllables (Table 1). In these cases, the entire syllable is usually generated only by one side—the contralateral side producing sound during only a part of the syllable (Fig. 5).

Interactions between the Left and Right Syrinx.

Crosstalk. Bilateral interactions, which we loosely interpret here as *crosstalk*, are present in up to about 15% of song syllables. Sometimes when both sides of the syrinx are open, a sound generated at a high intensity on one side appears at a reduced intensity on the contralateral side. In such cases it is difficult to determine if the contralateral side is also actively producing the sound or if the thermistor is responding to air movement associated with passive vibrations that are driven by the ipsilateral side of the syrinx.

Sometimes, however, a sound produced on one side of the syrinx is also present at reduced intensity in the bronchus of the closed contralateral side [Fig. 6 (syllable a)]. This most often happens with high intensity sounds and we assume that acoustic energy in the interclavicular air sac or interbronchial lumen between the Mtm is transmitting vibration to the membranes of the contralateral bronchus, either causing air trapped in the closed bronchus to oscillate around its thermistor or the thermistor itself to vibrate. Alternatively, sound energy might be conducted through the tissues of the syrinx.

Crosstalk is usually minimal in two-voice syllables and is not consistently present, even during very intense vocalizations. An example is seen in the case of syllable b in Figure 6 which is produced immediately after syllable a with an intensity at least as great and at a somewhat lower frequency. Both syllables are produced on the same side of the syrinx while the contralateral side is closed. We do not know why crosstalk was detected in the silent bronchus during syllable a, but not during syllable b.

Linear Acoustic Interaction. The production of different frequency elements on each side of the syrinx sometimes gives rise to a beat note or difference tone which appears in the emitted vocalization as a sinusoidal amplitude modulation at a fre-

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signal from thermistors showing sound, up to about 4 kHz on the left and 3.5 kHz on the right, present in the left and right bronchus, respectively. Open triangles on oscillograms indicate transients in airway that are associated with the opening or closing of the syringeal valve. Rate of airflow through the left (F_L) and right (F_R) syrinx as measured by a heated thermistor in each primary bronchus. Both inspiration (stippled) and expiration cause an upward deflection of trace from baseline which indicates zero flow. Due to the time constant of the thermistor, airflow trace does not always return to zero during rapid reversals in flow direction. Respiratory phase is determined by the sign (positive or negative) of the accompanying air sac pressure. Respiratory pressure (P) recorded in cranial thoracic air sac is applied equally to both sides of the syrinx. Ambient pressure (zero pressure gradient) is indicated by horizontal line. The production of song syllables is switched from one side of the syrinx to the other by closing the silent side as indicated by a positive subsyringeal pressure without ipsilateral bronchial airflow. Sometimes both sides contribute to the same syllable. Although the thermistor in the right bronchus did not pick up the higher frequency element of syllable d (presumably because its time constant was longer than that of the left thermistor), respiratory flow confirms that this element was produced on the right side. Inspiration occurs through both sides of the syrinx between each syllable.
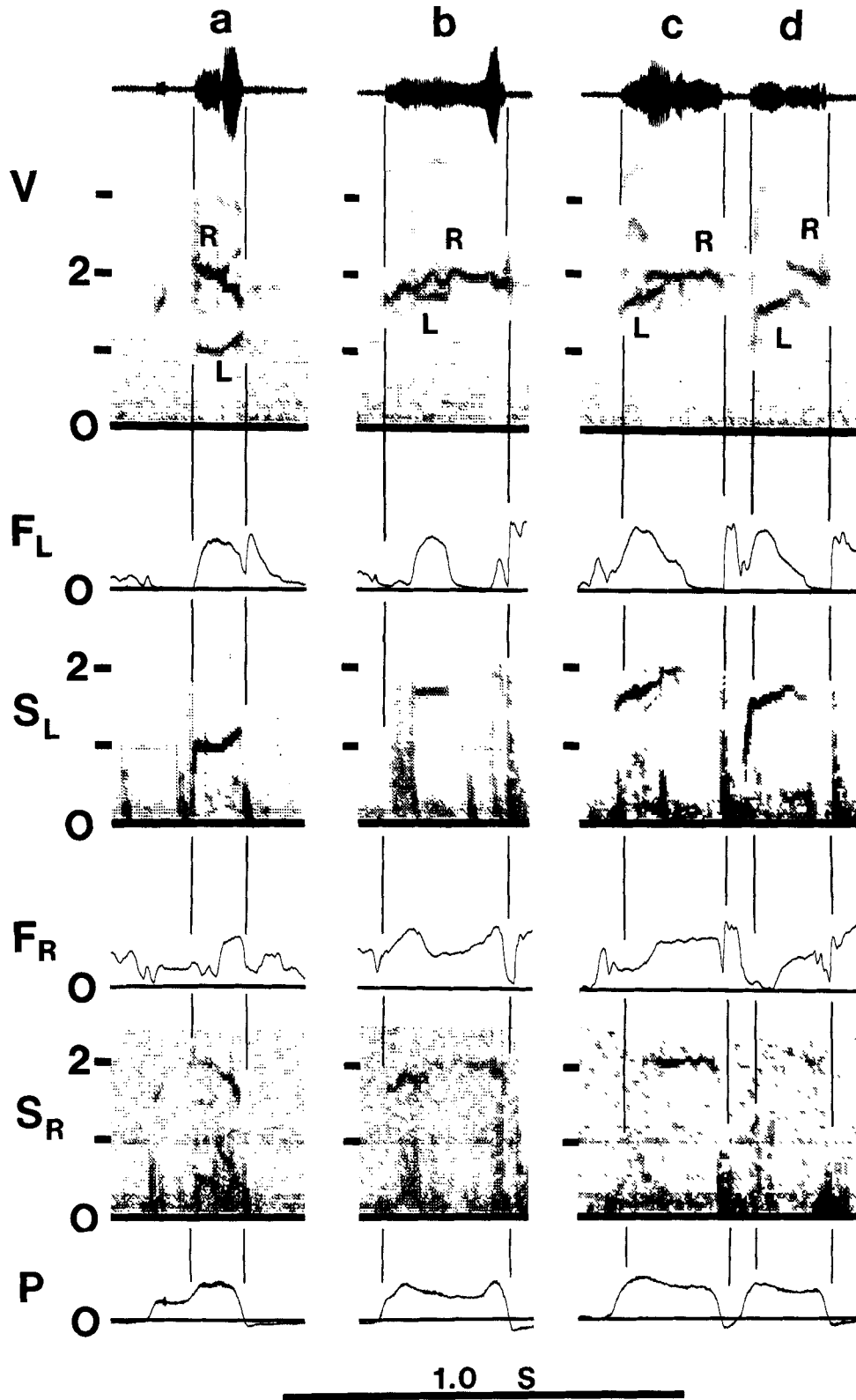
Figure 3   Examples of two-voice syllables sung by catbird 05. The contribution made by each side of the syrinx can be determined from the bronchial sound and often by the sequential gating of airflow through each side. The component from the right side is always at a higher frequency than that generated on the left. Two voices may be present during all or only part of a syllable. Sound frequency is in kHz. See legend of Figure 2 for symbol identification.
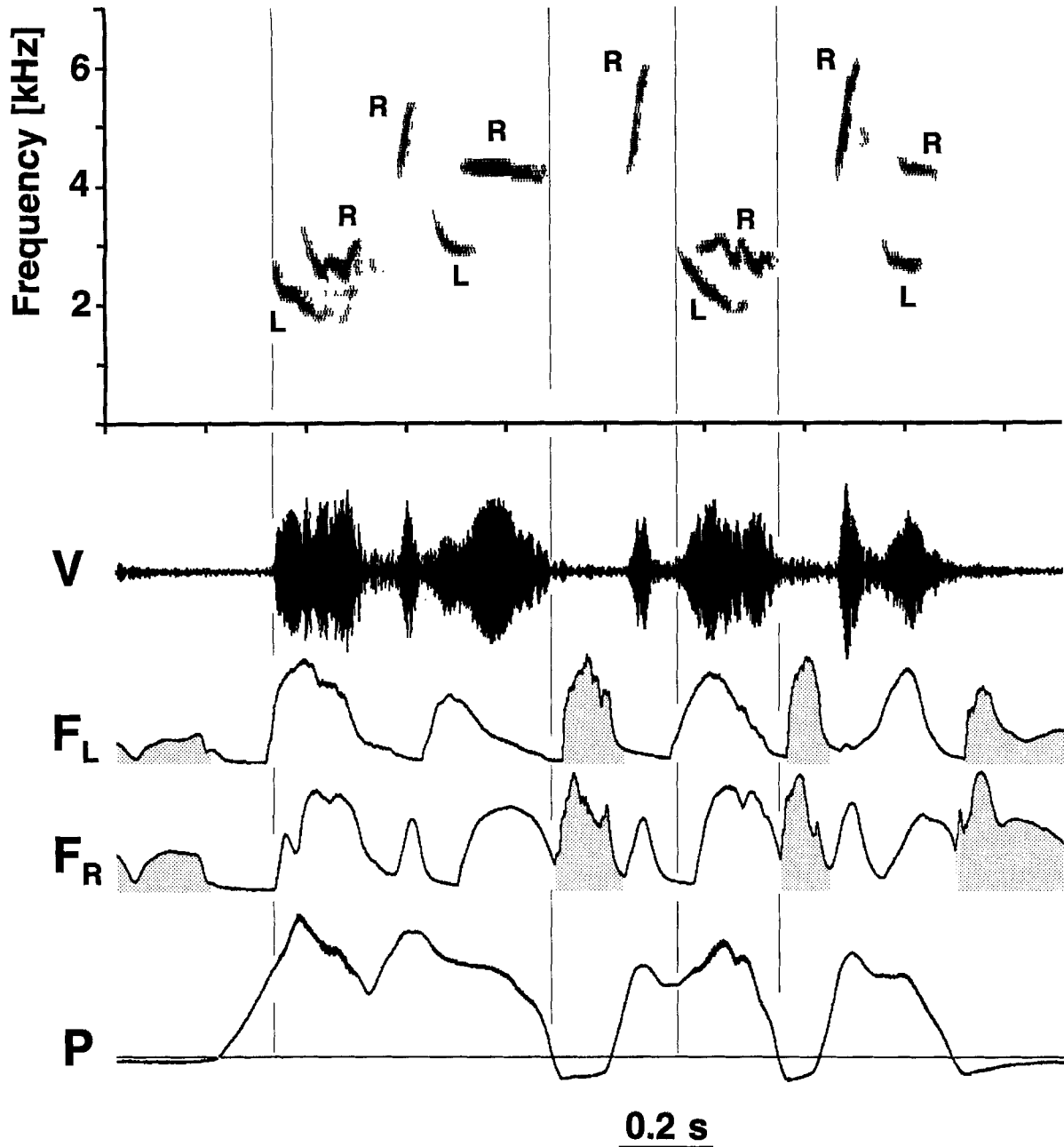
Figure 4 A short segment of song by thrasher 41 containing syllables with two-voice and single-voice components. See legend of Figure 2 for explanation of symbols.

quency equal to the difference in frequency between the two sides. This is clearly evident during the overlap of the rising FM from the left side with the CF element from the right side of the two-voice catbird syllable in Figure 7(a). The frequency of the resulting amplitude modulation is equal to the difference between these two frequency components [Fig. 7(b)] and presumably arises when the sounds from the two bronchi sum in the trachea.

This same vocalization also appears as syllable c in Figure 3 where it can be seen that there is no oscillation in syringeal airflow or pressure that could provide an alternate explanation for the rapid AM during the second quarter of the syllable.

Integration of Respiratory and Syringeal Muscle Activity. Syringeal muscles act in close coordination with respiratory muscles that provide the driv-

ing pressure for syringeal airflow. During some syllables, air sac pressure and the rate of syringeal airflow parallel each other, indicating that syringeal aperture is being held more or less constant; other syllables suggest that the respiratory muscles controlling expiratory pressure can rapidly adjust their activity to maintain a constant driving pressure despite rapid changes in total syringeal resistance caused by the opening and/or closing of one side of the syrinx. The syllable in Figure 8(a) is produced mainly by the left syrinx which generates a whistle at a frequency that varies with the rate of airflow. The right syrinx opens during the first half of the syllable and contributes a component having a frequency seemingly unrelated to the rate of airflow. When the right side closes half way through the syllable, syringeal resistance is suddenly increased but subsyringeal pressure does not rise abruptly. This stabilization of the driving pressure must be accomplished by reducing expiratory effort just enough to maintain a gradually increasing pressure and flow through the left syrinx.

A more complex example of syringeal–respiratory motor integration is shown in Figure 8(b). In this syllable the resistance to expiratory airflow abruptly decreases when the left syrinx opens to produce sound during the middle third of the syllable. If the expiratory effort remained unchanged, then this decrease in total syringeal resistance should be accompanied by a drop in air sac pressure and in the rate of airflow through the right syrinx. Since neither pressure nor right airflow change, the expiratory muscles must have increased their activity to maintain a constant pressure and thus a constant rate of airflow through the right side. These motor adjustments must have been reversed when the left side closed.

Inspiration between Syllables. Catbirds and thrashers normally insert a short inspiration between song syllables. Rare exceptions occur when
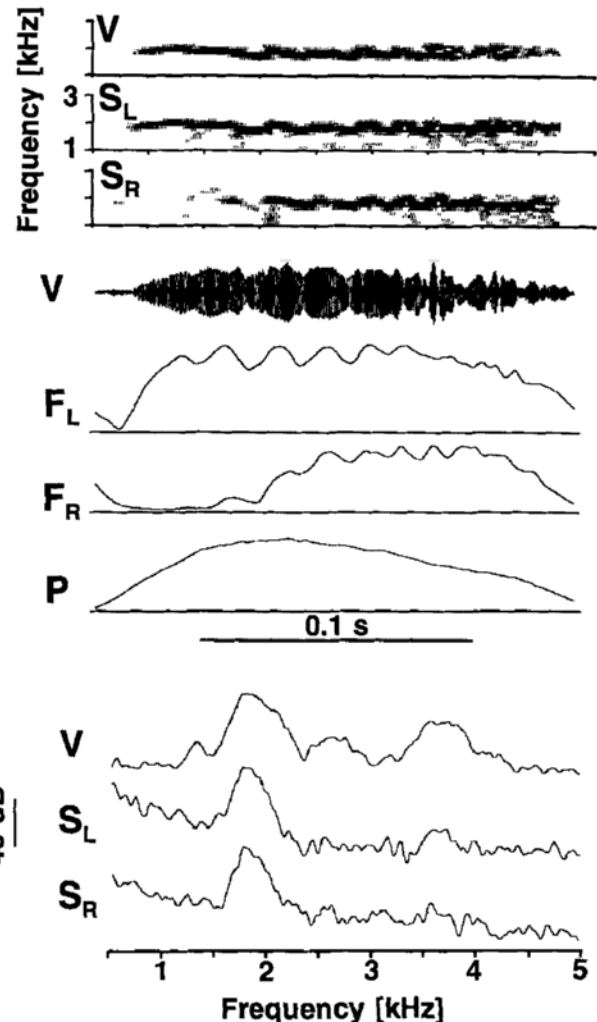

Figure 5 A syllable from the song of thrasher 10 in which both sides of the syrinx are producing the same sound for most of the vocalization. Note that frequency and amplitude oscillation is correlated with fluctuations in the rate of airflow. No oscillation appears in the subsyringeal pressure, suggesting flow is controlled by changes in syringeal resistance. Lower panel shows FFT-derived amplitude spectra of sound generated on each side of the syrinx and the emitted vocalization. Note similar fundamental frequency on each side of syrinx. See legend of Figure 2 for explanation of symbols.

the interval between two syllables is unusually short [e.g., Fig. 2 (syllables b and c)]. The rate of syringeal airflow during inspiration usually exceeds that during phonation even though the inspiratory pressure gradient is much less than the expiratory gradient. During inspiration between syllables the syringeal resistance is presumably reduced by abduction of the Ll or syringeal membranes during inspiration between syllables. The reduction in syringeal resistance between syllables proba-
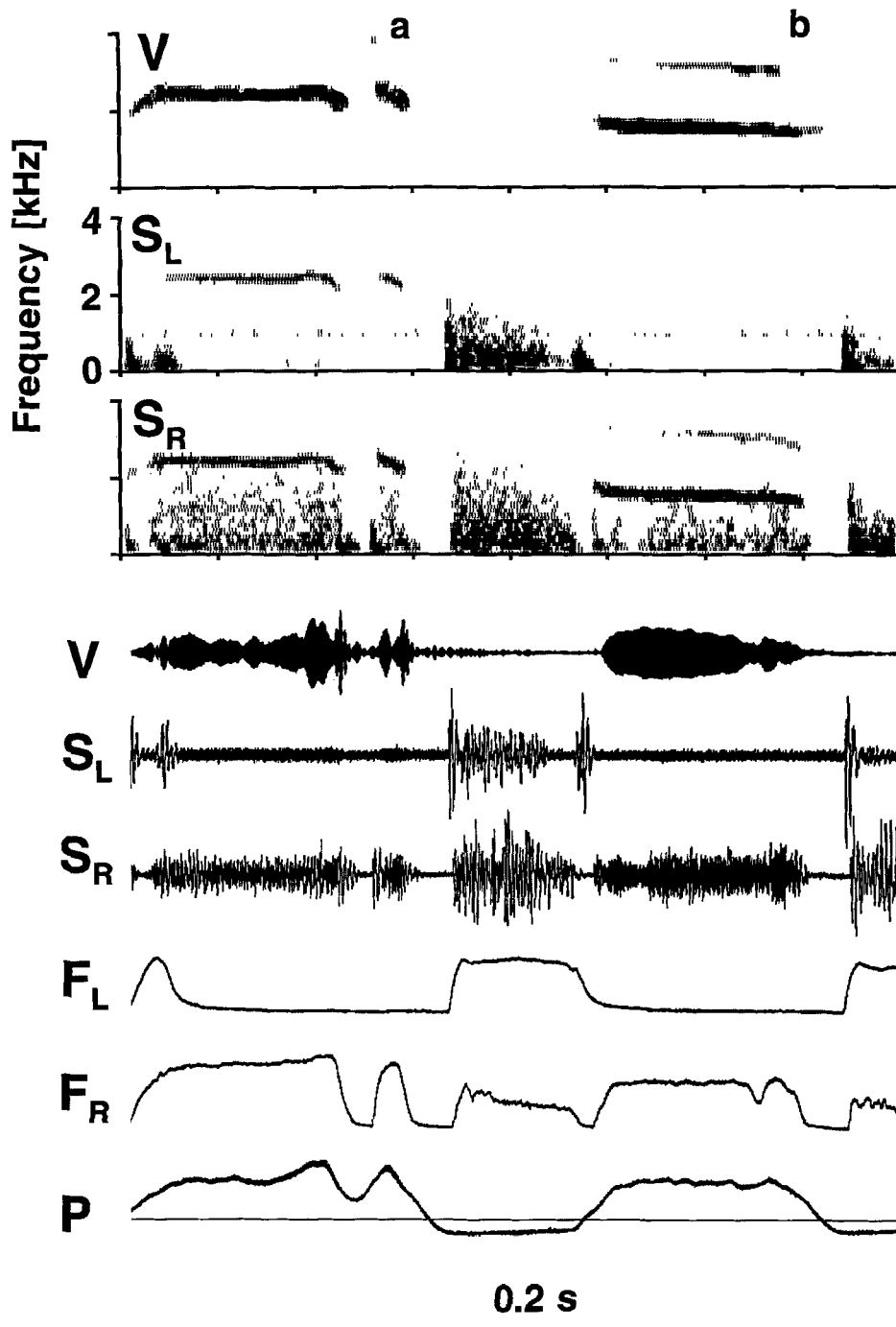
Table 1 Proportion of Syllables in which Both Sides of Syrinx Simultaneously Generate the Same Sound[1]

TH NR	4.3	164
TH 06	0.5	200
TH 10	2.5	119
TH 22	0	102
CT 02	6.9	204

Figure 6 Cross-talk occasionally occurs between the left and right bronchi when one side produces a high-intensity sound. In this example from thrasher 06, both syllables are generated on the right side while the left syrinx is closed. Syllable a is picked up by thermistor in left bronchus. However, since the left side is closed, sound on this side is not present in the vocalization. Syllable b is produced under similar circumstances at an even higher intensity but is not detected in the left bronchus. The basis for selective cross-talk between the two sides is unknown. See legend of Figure 2 for explanation of symbols.
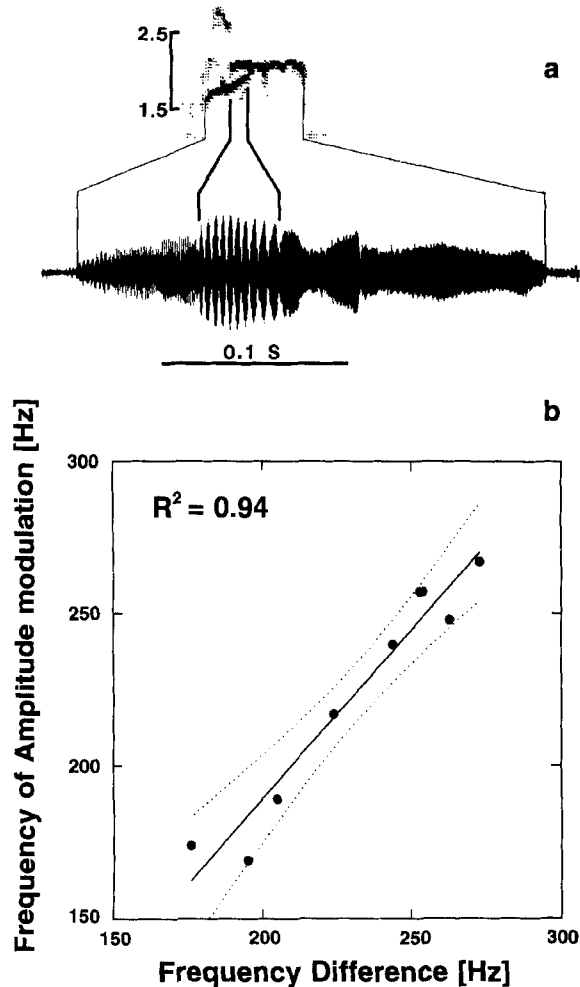
Figure 7   Difference tone or beat note expressed as sinusoidal AM generated during two-voice portion of catbird 05 syllable (syllable c in Fig. 3). (a) Spectrogram and expanded oscillogram of emitted vocalization showing overlap of rising FM from left syrinx with a higher constant frequency element from right syrinx is accompanied by a prominent amplitude modulation. Frequency in kilohertz. (b) Frequency of AM during overlap of left and right sounds corresponds to frequency difference between left and right voices. Dotted lines indicate the 99% confidence interval.

bly allows a short inspiration to replace the volume of air expelled during the previous syllable which is often significantly longer in duration. Both sides of the syrinx normally open between syllables for inspiration (Fig. 2), although a unilateral inspiration occasionally occurs.

The intersyllable inspirations of thrashers last between 50 and 370 ms with a mean duration of about 170 ms. Inspiration in silent, resting thrashers has a duration between approximately 250 and 500 ms with a mean of about 390 ms—

about twice the duration of inspiration during song. The length of inspiration during thrasher or catbird song varies considerably, however, with the duration of the shortest being about one-tenth that of a silent bird.

Properties of Sounds from the Left and Right Syrinx

Frequency. With the exception of thrasher 06, the mean frequency of the fundamental (or lowest frequency component) of syllables produced on the left side of the syrinx was lower than that of those originating in the right syrinx. This was true both for syllables generated entirely on one side of the syrinx and for two-voice syllables. The fundamental of single-voice syllables produced on the left side had mean minimum and maximum frequencies of 1.5 and 1.9 kHz, respectively, compared to corresponding values of 2.8 and 4.2 kHz, respectively, for syllables produced on the right side (Table 2). A similar, though smaller, frequency difference was present in two-voice syllables (Table 3) in which the mean minimum and maximum frequencies of the right voice were 0.63 and 0.93 kHz, respectively, higher than those of the left voice (Fig. 9). Thus in two-voice syllables, the average frequency for all birds from the right side was about 500–1000 Hz above that from the left, except for thrasher 06 in which the converse was true.

Frequency Modulation. The extent of frequency modulation was assessed by determining the proportion of syllables in which the frequency modulation of the fundamental or lowest frequency component of the left or right voice exceeded 1 kHz (Table 4). In song samples from five thrashers and one catbird, between 11% and 60% of the syllables met this arbitrary criterion. There was a tendency, in all birds except thrasher 06, for the right syrinx to contribute more FM syllables than the left, but this difference was statistically significant only in thrasher 18. If the sample size is increased by pooling data for all birds, then the right side contributes significantly more FM than does the left.

Duration of Sound. A comparison of the duration of each side's contribution to song syllables revealed no significant difference between the left (143 ± 79 ms) and right (148 ± 79 ms) syrinx (*n* = 732).

Rapid Cyclical Amplitude Modulation. The right side of the syrinx plays a special role producing

certain kinds of amplitude modulation. Some thrasher and catbird syllables have a rapid cyclical AM produced by rapidly opening and closing the right side of the syrinx (Fig. 10). A total of 78 syllables having bilateral airflow and exhibiting this pattern of AM from 5 thrashers were examined. The amplitude of flow oscillation relative to the peak value of airflow was calculated for each side of the syrinx. The amplitude ratio between change in airflow during oscillation and the peak airflow was greater on the right side of the syrinx in all birds except in thrasher 18 for which the sample included only four syllables [Table 5, (Fig. 11). Similar syllables are produced by catbirds.

Cyclical AM syllables fall into one of two different classes depending on the presumed mechanism responsible for the AM: (a) two-voice cyclical AM and (b) shunt-cyclical AM. In two-voice AM syllables the right side of the syrinx is in a phonatory configuration when it opens so that each pulse of airflow generates a brief sound which, added to the sound emanating from the left side, causes an increase in the overall amplitude of the emitted vocalization [Fig. 10(a)]. During these syllables, amplitude of the vocalization varies in phase with the rate of airflow through the right side of the syrinx.

In the shunt-cyclical AM syllables, the right syrinx is not in a phonatory position and hence generates no sound when air flows through it. Instead, each time the right side opens it provides a shunt for unmodulated air that bypasses the sound generator. AM in these syllables is 180° out of phase with the rate of airflow through the right syrinx [Fig. 10(b, c)].

DISCUSSION

Lateralization of Syringeal Motor Control: Bilateral Independence Versus Unilateral Dominance

Catbirds and thrashers share with other songbirds, such as canaries, the ability to independently activate each side of the syrinx to produce song. In mimic thrushes, unlike canaries, this bilateral independence of motor action is not accompanied by a strong unilateral dominance in which one side of the syrinx produces the great majority of the song. The ability to deliver separate motor patterns to the left and right syrinx facilitates the production of a richly varied vocal repertoire. By utilizing sound generators tuned to different frequency ranges as two independent voices it is possible, for example, to produce syllables containing inharmonic components in which each voice differs in the range or the direction of FM.

Bilateral independence necessary for two-voice syllables also increases the ways in which AM can be used to achieve a variety of acoustic effects. Data presented above provide the first direct evidence that some kinds of very rapid sinusoidal AM arise from the linear interaction of slightly different frequencies emanating from each side of the syrinx, confirming previous suggestions of Greenewalt (1968), Marler (1969), and Gaunt et al. (1982). In some cases, AM elements are generated on one side of the syrinx and combined with constant amplitude components produced on the opposite side as in the case of two-voice cyclical AM syllables. We have not yet documented instances of nonlinear bilateral syringeal interactions in thrashers or catbirds such as those described by Nowicki and Capranica (1986a,b) in the "dee" syllable of chickadee song. Since these effects probably arise from direct interaction between the sound source in each side of the syrinx, they are likely to be more prominent in small birds.

Canaries and mimic thrushes may occupy opposite ends of a continuum ranging from unilateral dominance to bilateral independence of song production. Vocal virtuosity in the former group includes their ability to execute rapid sequences of complex motor patterns while in the latter group it is achieved to an important extent by their ability to simultaneously produce two different motor patterns. If song complexity provides conspecifics with an indication of fitness, then canaries and mimic thrushes may be expected to emphasize qualitatively different acoustic criteria.

Spectral Differences in Left and Right Sounds

Although the song of mimic thrushes contains about equal contributions from the two sides of the syrinx, there are some differences in the properties of sound generated on each side. The right syrinx operates in a somewhat higher frequency range than does the left. This difference in fundamental frequency may arise from small morphological asymmetries between the two sides of the syrinx or vocal tract. These could include subtle differences in the syringeal muscle mass or in the size or physical properties of the two Mtm which results in the right side having a higher frequency fundamental resonance than the left. Bilateral differences in the size, physical properties, or tension on the Mtm,
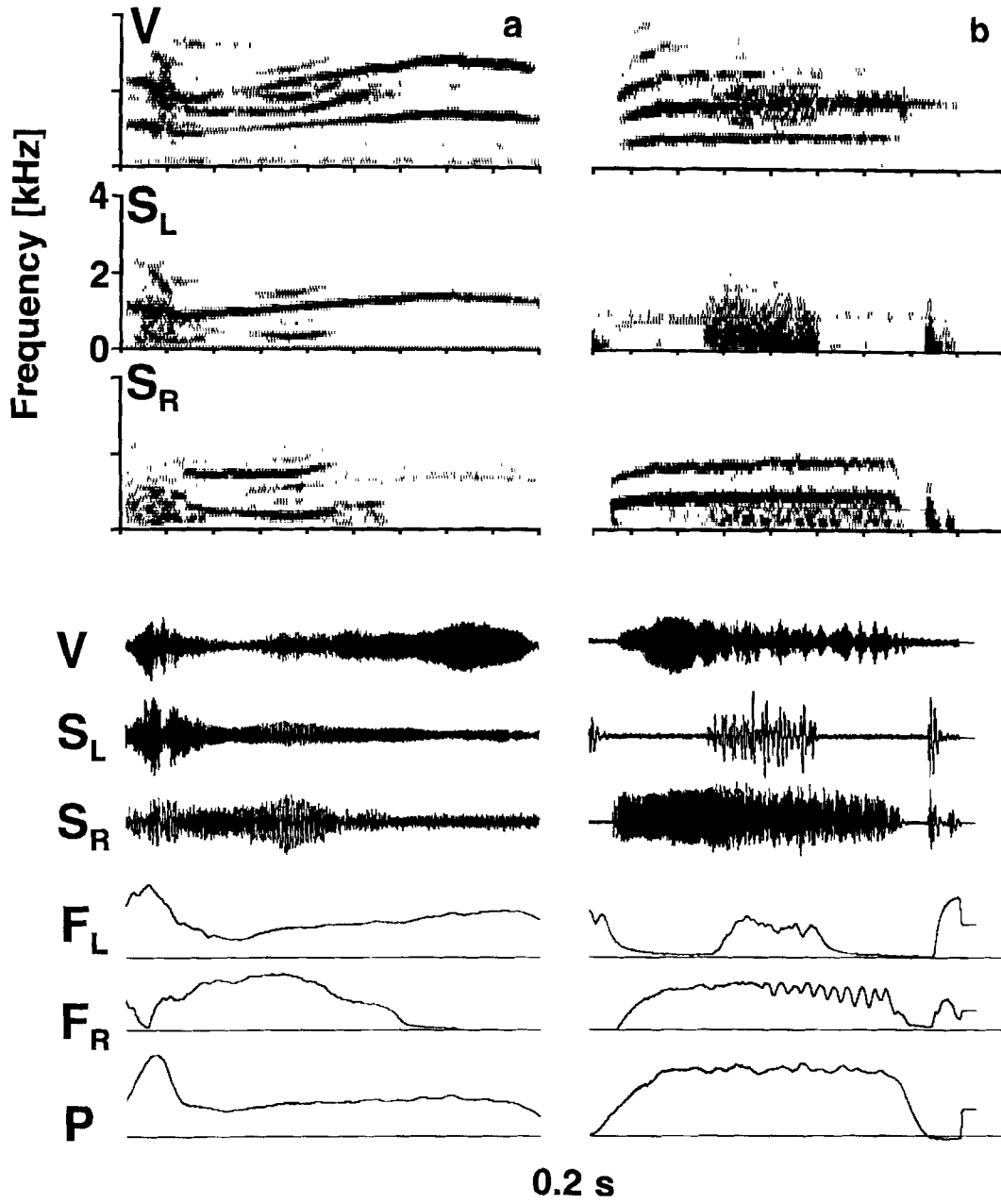
Figure 8   In order to maintain a constant rate of syringeal airflow, respiratory muscles must quickly adjust their activity to compensate for sudden changes in syringeal resistance brought about by action of the syringeal muscles. (a) When total syringeal resistance is increased by closure of the right side, near middle of syllable, there is no abrupt change in either the air sac pressure or the rate of airflow through the left side (thrasher NR). (b) Left syrinx abruptly opens during the middle of a syllable and then closes, decreasing and then increasing, respectively, total syringeal resistance. There is no concomitant change in air sac pressure or right airflow, again indicating precise respiratory motor adjustment for the actions of syringeal muscles (thrasher 06). Explanation of symbols in legend of Figure 2.

for example, should affect the resonant frequency—a smaller, stiffer, or more tightly stretched right Mtm would have a higher fundamental resonance.

Vibrating syringeal membranes may be tightly coupled to the acoustic properties of the vocal tract and influenced by its resonant filter properties. The

Table 2 Frequency Range of Fundamental for Syllables Generated on One Side of Syrinx

Bird	Left Side[1]		Right Side[1]	
	Minimum	Maximum	Minimum	Maximum
TH NR[2]	1.4 ± 0.3 (19)	1.8 ± 0.5 (19)	2.1 ± 0.6 (37)	3.1 ± 0.6 (37)
TH 06[2]	3.6 ± 1.3 (13)	5.1 ± 1.4 (13)	1.6 ± 0.4 (29)	2.2 ± 0.6 (29)
TH 10[2]	1.9 ± 0.4 (11)	2.1 ± 0.6 (11)	4.4 ± 0.9 (10)	5.6 ± 1.1 (10)
TH 18	—	—	2.2 ± 0.6 (23)	4.1 ± 1.1 (23)
TH 22	1.4 ± 0.3 (14)	2.2 ± 0.3 (14)	—	—
CT 01	1.4 ± 0.3 (19)	1.5 ± 0.3 (19)	—	—
CT 02[2]	1.5 ± 0.5 (18)	2.1 ± 0.5 (18)	2.7 ± 0.6 (17)	3.8 ± 1.1 (17)

[1] Minimum and maximum values are recorded in Kilohertz.

[2] In each bird for which there are bilateral data, both the minimum and maximum frequencies on each side are significantly different from the contralateral minimum and maximum frequency, $p < 0.001$. TH 18 sample had no syllables generated only on the left side. TH 22 and CT 01 sample had no syllables generated only on the right side.

right primary bronchus, being slightly smaller in diameter than the left (R. A. Suthers and F. Goller, personal observation), might be tuned to a higher resonant frequency. The right bronchus also lies in a more dorsal and medial position relative to the syrinx but the acoustic significance, if any, of this is unknown.

The reversal of the frequency difference in thrasher 06 compared to the other birds in this study is surprising. This was the only individual tested in which the right syrinx produced fundamentals in a lower frequency range than did the left. The right syrinx was similar to that of other thrashers, however, with regard to its role in the production of rapid AM syllables. It may be that some aspects of functional lateralization are occa-

sionally reversed, either centrally or peripherally, in certain individuals. Unfortunately, we do not have anatomical data from this bird to determine if orientation or relative size of the bronchi were different from the other individuals. Although great care was taken to avoid switching leads from the left and right thermistors, these connections cannot be retroactively verified.

Previous comparisons of the frequency range on each side of the oscine syrinx have involved disabling one side in order to determine which side produces the syllable. After section of the left tracheosyringeal nerve in canaries, the median frequency range of remaining song syllables was 2.57–4.20 kHz, compared to 1.25–2.40 kHz after a right nerve section (Nottebohm and Nottebohm,

Table 3 Frequency Range of Fundamental Generated on Each Side of Syrinx in Two Voice Syllables

Bird	Left Side[1]			Right Side[1]			n
	Minimum	Mean	Maximum	Minimum	Mean	Maximum	
TH NR	1.3 ± 0.4	1.5 ± 0.5	1.7 ± 0.6	1.8 ± 0.6**	2.1 ± 0.6**	2.5 ± 0.8**	65
TH 06	3.2 ± 1.3	3.5 ± 1.3	3.8 ± 1.3	2.3 ± 1.1†	2.6 ± 1.1*	2.8 ± 1.2†	33
TH 10	2.0 ± 0.6	2.4 ± 0.7	2.8 ± 0.8	2.8 ± 0.9**	3.5 ± 1.0**	4.1 ± 1.4**	57
TH 18	1.6 ± 0.6	1.8 ± 0.6	2.0 ± 0.6	2.1 ± 0.6*	2.5 ± 0.7**	3.0 ± 0.9**	32
TH 22	1.4 ± 0.4	1.8 ± 0.4	2.3 ± 0.5	2.1 ± 0.7**	2.6 ± 0.8**	3.2 ± 1.1**	47
CT 01	1.3 ± 0.4	1.6 ± 0.4	1.8 ± 0.5	2.1 ± 0.5**	2.4 ± 0.6**	2.6 ± 0.7**	40
CT 02	2.0 ± 1.0	2.3 ± 1.1	2.7 ± 1.3	2.4 ± 1.0†	2.9 ± 1.3*	3.5 ± 1.7†	49

[1] Minimum, mean, and maximum values are recorded in kilohertz.

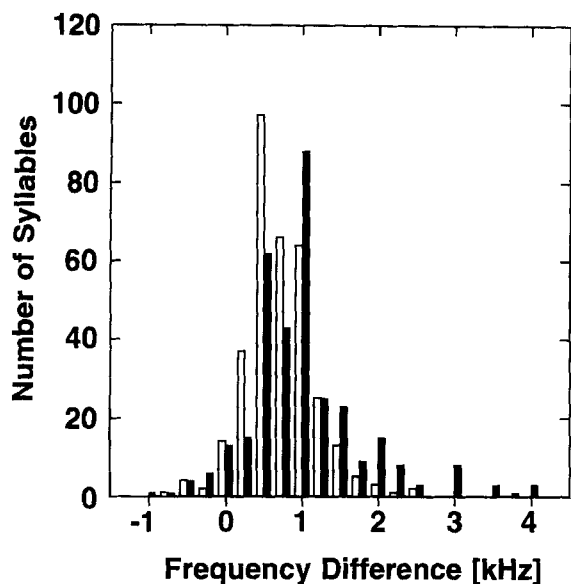** $p < 0.0001$; * $p < 0.01$; † $p < 0.05$ for comparison of left and right minimum, mean and maximum frequencies.

Figure 9 Frequency difference (right voice minus left voice) for the maximum and minimum frequency of fundamentals for 290 two-voice syllables from six birds. Open bars = minimum frequency; solid bars = maximum frequency. Based on data in Table 3 excluding thrasher 06. Bin width = 250 Hz.

1976). In other experiments, three out of four canaries singing with their left bronchus plugged favored high-frequency syllables (Hartley and Suthers, 1990). The pronounced morphological asymmetry of the canary syrinx, in which both the muscle mass and the bronchus are smaller on the right compared to the left, may provide a physical basis for bilateral differences in the frequency of song in this species (Luine et al., 1980). Chaffinches subjected to left hypoglossal neurotomy tend to retain high-frequency notes or syllables, whereas after right neurotomy lower-frequency notes remain (Nottebohm, 1971). Similar results have been obtained from zebra finches (Williams et al., 1992). Nerve cuts in white-crowned sparrows, white-throated sparrows, and java sparrows have not provided evidence for a lateralization of frequency range (Nottebohm and Nottebohm, 1976; Lemon, 1973; Seller, 1979).

Song Requires Integrated Activity in Diverse Muscle Groups

Coordination between respiration and the two sides of the syrinx during song is essential. The respiratory motor pattern used for silent respiration is dramatically altered during song to produce expiratory pressures an order of magnitude higher

than that during rest with a marked increase in frequency and complexity. Respiratory muscles play an important role in setting the temporal pattern of zebra finch song as evidenced by the fact that the pattern of vocalization may be little changed after bilateral syringeal denervation (Simpson and Vicario, 1990; Vicario, 1991a; Williams et al., 1992), although the acoustic structure of the syllables is substantially altered. In zebra finches the thalamic song nucleus, Uva, seems to play a special role in determining the timing and order of song syllables (Williams and Vicario, 1993). Since Uva has bilateral connections to song control nuclei of the forebrain, it is likely to be involved in coordinating motor activity on the two sides of the syrinx.

Our data on the dynamics of syringeal airflow in singing mimic thrushes confirm the vital role of respiratory motor patterns in setting the tempo of the song, but they also strongly suggest that respiratory muscles do much more than simply set the temporal pattern of syllables. The patterns of airflow and pressure we have observed in singing catbirds and thrashers reveal a delicate interplay of activity in syringeal and respiratory muscles during the ongoing syllable. These birds are capable of adjusting expiratory effort almost instantaneously to compensate for changes in syringeal resistance and maintain the frequency of the sound. In other cases, expiratory pressure changes independently from syringeal resistance, often modulating the amplitude of the sound as the syllable progresses. It appears that respiratory motor patterns can be as important as syringeal motor patterns in regulating the frequency structure and amplitude of many syllables. Abdominal expiratory muscles of canaries generate bursts of electrical activity during each syllable (up to about 38 s^{-1}) that reflect its amplitude structure (Hartley, 1990).

Table 4   Lateralization of FM Sounds

Bird	Total Syllables	Left FM Syllables[1]	Right FM Syllables[1]
TH NR	148	8	14
TH 06	144	14	10
TH 10	79	14	22
TH 18	88	0	10**
TH 22	53	15	17
CT 02	134	15	21
Total	646	66	94*

[1] Syllables containing >1 kHz of FM.
* $0.01 < p < 0.05$; chi-square = 5.59.
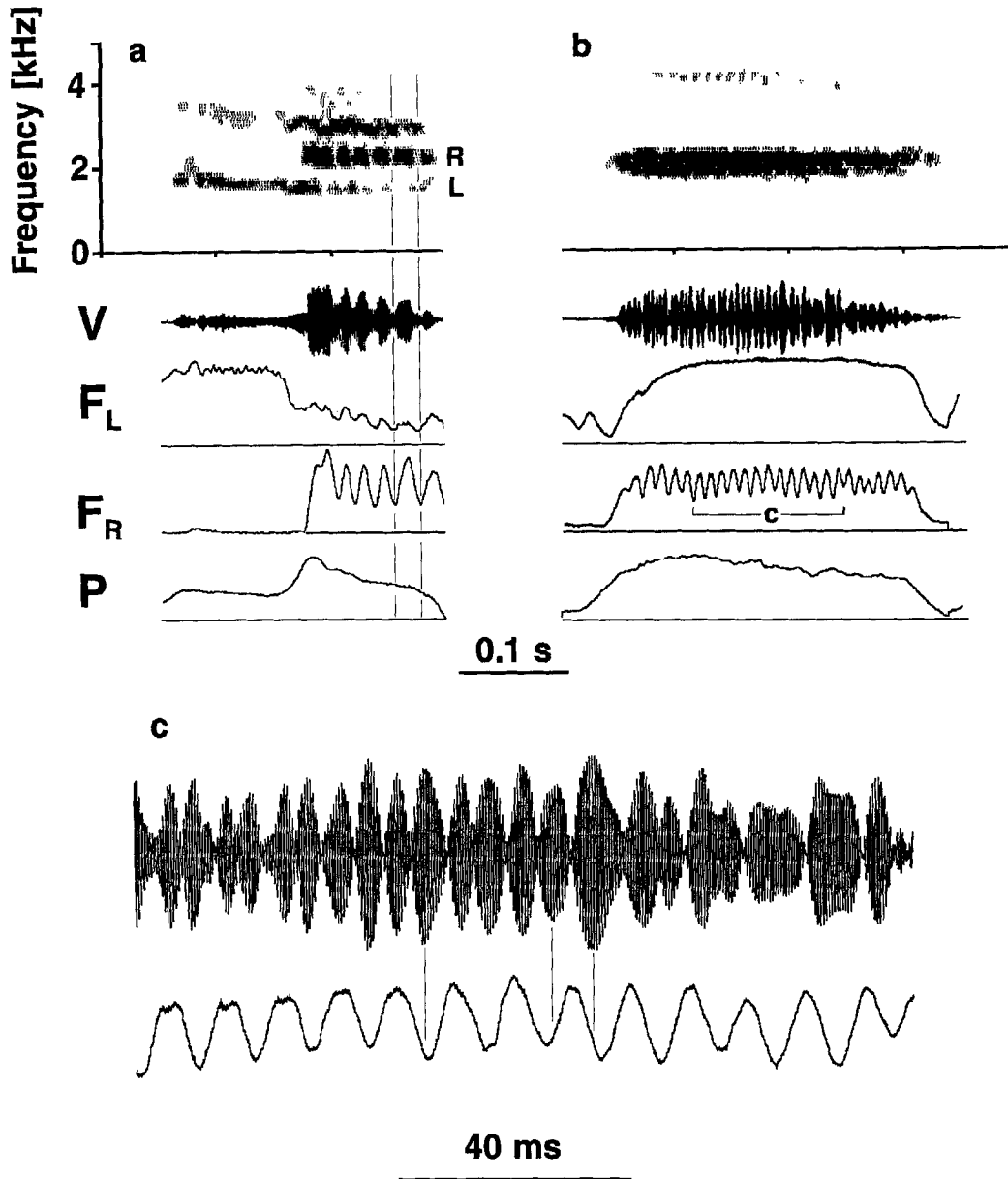** $0.001 < p < 0.01$; chi-square = 10.6.

Figure 10 Rapid, cyclical AM syllables. (a) Two-voice cyclical AM from catbird 01. AM during second half of syllable is produced in phase with sound produced on right side as it is repetitively adducted and abducted. (b) Shunt cyclical AM from thrasher 06. During last half of syllable, AM is out of phase with cyclical fluctuation in rate of airflow through right side of syrinx which is shunting air from phonating left side but is not producing sound. (c) Expanded vocalization (top) and right airflow (bottom) from middle of syllable b. During first portion of this syllable there is a pair of AM cycles per airflow cycle on right side. In this portion of syllable, the amplitude peak accompanying the peak rate of airflow through the right side is generated on the right side and includes a faint second harmonic visible in the sonagram of b. The sound amplitude peak associated with the minimum flow rate on the right side is generated on the left side of the syrinx. Shunt cyclical AM occurs during the last half of the syllable where the right side is silent and the peak sound amplitude on the left corresponds with the airflow minima on the right side.

Table 5   Lateralization of Airflow Modulation in Rapid Cyclical AM Syllables[1]

Bird	Left Side	Right Side	n	p
TH NR	0.27 ± 0.19	0.40 ± 0.22	22	0.0507
TH 06	0.08 ± 0.07	0.53 ± 0.08	14	0.0001
TH 10	0.23 ± 0.11	0.39 ± 0.21	15	0.0142
TH 18	0.17 ± 0.07	0.11 ± 0.07	4	0.271
TH 22	0.15 ± 0.19	0.38 ± 0.25	25	0.0006

[1] Amplitude of airflow oscillation/total flow rate through one bronchus for syllables exhibiting rapid cyclical AM and during which there was airflow through both sides of the syrinx.

Singing canaries also insert brief (10–30 ms) inspirations, referred to as *minibreaths*, between syllables even when they are emitted at repetition rates exceeding $30s^{-1}$ (Calder, 1970; Hartley and Suthers, 1989). A typical canary minibreath is about one-tenth the duration of a normal quiet inspiration. Some intersyllable inspirations of thrashers are as short as one-tenth the duration of a typical inspiration by a resting, silent bird, but the average duration during song is about one-half that when silent. Intersyllable inspiration in thrasher song thus forms a continuum from true minibreaths to essentially normal inspirations, enabling these birds to sing continuously for many minutes.

The intimate relationship between respiratory and syringeal muscles is reflected in the respiratory modulation of excitability in hypoglossal motor neurons, such that excitability is high during expiration and low during inspiration (Manogue and Paton, 1982). Wild (1993) has identified nucleus retroambigualis as an important avian respiratory nucleus which projects to respiratory spinal motor neurons in pigeons and songbirds. Nucleus retroambigualis also receives inputs from the song control nuclei DM and RA. It thus provides a link between motor pathways and the syringeal and respiratory muscles.

Alternative Mechanisms for Gating Vocalization

Phonation presumably requires a restricted syringeal aperture in order for the airflow to develop forces that set the membranes into vibration. Evidence from unilateral syringeal denervation indicates that the syrinx acts as a valve regulating airflow (Suthers, 1990). We postulate that sound production is terminated if the lateral labium moves out of this phonatory position, either by further

adduction which brings it into contact with the Mtm on the opposite side of the lumen and closes the syrinx or by abduction which opens the lumen and eliminates the constricted aperture.

Catbirds and thrashers employ more than one syringeal mechanism to gate phonation on each side of the syrinx and to switch sound production from one side to the other. The most common method is to prevent sound being produced on one side by closing it so no air flows through it. Closing one side in this manner conserves respiratory air and makes vocalization more efficient in converting the subsyringeal fluid energy into acoustic energy than it would otherwise be if unmodulated air was allowed to escape through the silent side of the syrinx.
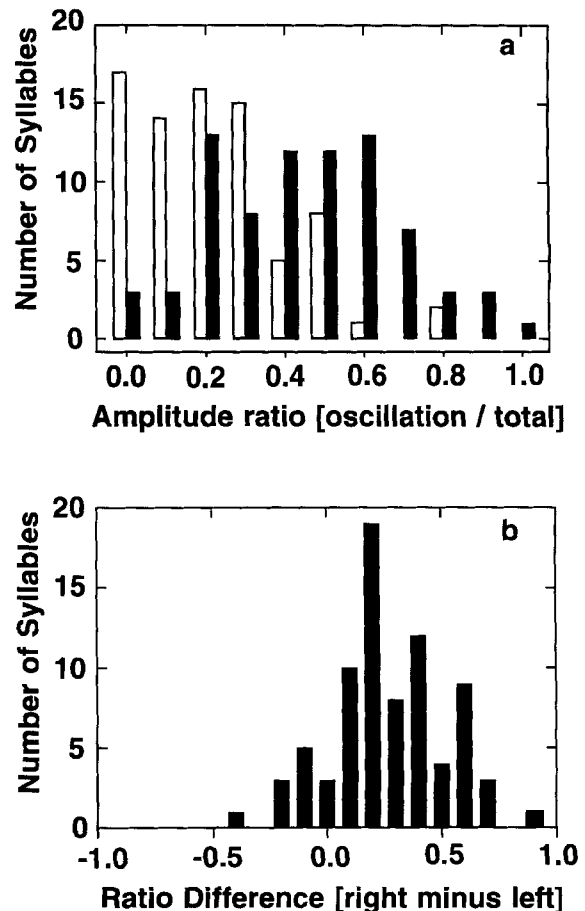

Figure 11   Right syrinx has dominant role in producing syllables with rapid, cyclical AM. (a) Ratio of airflow AM/total rate of airflow in syllables containing rapid, cyclical AM. Data from five thrashers. Left sound = open bars; right sound = solid bars. (b) Difference in ratio of airflow AM/total rate of airflow expressed as right side minus left side ratios.

A second kind of motor action also prevents phonation. Like the first, it involves the use of syringeal adductor and abductor muscles, but instead of turning sound off by closing the syrinx, abductor muscles in this case terminate sound production by fully opening the syrinx and moving the membranes out of the phonatory configuration. This is, of course, an important means of reducing syringeal resistance and preventing sound generation during inspiration. Catbirds and thrashers also occasionally use this method to terminate phonation before the end of the expiratory cycle and open the syrinx for the subsequent inspiration when the air sac pressure becomes negative (e.g., in syllable a, Fig. 2, there is a second narrow peak in expiratory airflow through the right syrinx immediately after the end of the syllable and before inspiration). It provides a way of rapidly exhaling remaining expiratory air that is not needed for phonation.

In some cases no sound is produced even when a closed syrinx is partially opened and expiratory air flows across the Mtm through a constricted syringeal aperture. The fact that phonation can be gated independently of syringeal resistance implies the existence of a third gating mechanism that probably depends on muscles other than those primarily responsible for opening or closing the syrinx. Perhaps these other muscles gate sound production by controlling the tension on the vibratory membranes.

An example of this kind of gating is present in syllables referred to above as "shunt rapid AM." During the rapid AM portion of such a syllable, the left syrinx typically generates a continuous sound upon which the right side superimposes AM by rapidly opening and closing. In "shunt rapid AM," no sound is generated by the cyclic airflow through the right side, even when the right syrinx is in an apparent phonatory configuration. This is not true for "two-voice rapid AM" syllables in which the same cyclic pattern of right airflow generates brief sounds that increase vocal intensity in phase with the airflow.

Although the acoustic output is quite different in the two-voice and shunt-rapid AM episodes, important components of the motor pattern needed to produce them are probably the same. In both of these types of AM, the right syringeal adductor and abductor muscles that regulate syringeal resistance presumably contract in a rhythmic, alternating pattern to produce a sinusoidally varying rate of airflow. These muscles may act primarily on the lateral labium. The difference in the motor pattern

producing two-voice versus shunt AM might only involve muscles that determine if the syrinx is in a phonatory configuration so that each pulse of air causes it to vibrate. In theory, this phonatory or mute "set" could be continuously maintained throughout the rapid AM episode, thus avoiding the necessity for rhythmic repetition in synchrony with the adductor/abductor cycle.

The opening or closing of the syrinx is accompanied by a low-frequency transient signal on the output of the ipsilateral bronchial thermistor (Suthers, 1990). This low-frequency damped oscillation in air flowing over the thermistor may be produced by an oscillatory movement of the Ll or Mtm as they open or close the syringeal lumen. Alternatively, it may be produced by oscillation caused by elastic recoil in the bronchial walls when internal pressure changes with the sudden onset or cessation of airflow. Whatever their origin, these transients are filtered out by the vocal tract and do not appear in the vocalizations.

Little information is available regarding the gating mechanism in most other songbirds. Extrinsic syringeal muscles, m. sternotrachealis and m. tracheolateralis, may have a role in initiating and terminating vocalization in starlings (*Sturnus vulgaris*) (Miskimen, 1951). In crows, (*Corvus brachyrhynchos*), the gating role of these extrinsic muscles may be supplemented or taken over by intrinsic syringeal muscles (Chamberlain et al., 1968). In the nonoscine oilbird, (*Steatornis caripensis*), social vocalizations and echolocating clicks are gated by different muscles (Suthers and Hector, 1985).

Vicario (1991a) obtained the first data on syringeal muscle activity from a singing passerine. He reported that in zebra finches the ventralis muscle fired at the end of each song syllable, suggesting it may terminate sound production by abducting a syringeal semi-ring. The dorsalis muscle, which adducts the semiring, was active during sound production and may shape the ongoing syllable. If Vicario's interpretation of the functional role of these muscles is correct, then zebra finches may differ from other songbirds studied in terminating their syllables by opening, instead of closing their syrinx.

REFERENCES

ALLAN, S. E. and SUTHERS, R. A. (1994). Lateralization and motor stereotypy of song production in the brown-headed cowbird. *J. Neurobiol.* 25 (to appear).

BRACKENBURY, J. H. (1972). Lung-air sac anatomy and respiratory pressures in the birds. *J. Exp. Biol.* 57:543-550.

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

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

FIALA, K. L. (1979). A laparotomy technique for nestling birds. *Bird-Banding* 50:366-367.

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

FLETCHER, N. H. (1989). Acoustics of bird song—some unresolved problems. *Comments Theor. Biol.* 1:237-251.

GAUNT, A. S., and GAUNT, S. L. L. (1985). Syringeal structure and avian phonation. In: *Current Ornithology*, Vol. 2. R. F. Johnston, Ed. Plenum Press, NY, pp. 213-245.

GAUNT, A. S., GAUNT, S. L. L., and CASEY, R. M. (1982). Syringeal mechanics reassessed: Evidence from *Streptopelia*. *Auk* 99:474-494.

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.* 81:177-188.

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

HARTLEY, R. S. and SUTHERS, R. A. (1990). Lateralization of syringeal function during song production in the canary. *J. Neurobiol.* 21:1236-1248.

KING, A. S. (1989). Functional anatomy of the syrinx. In: *Form and Function in Birds*. Vol 4. A. S. King and J. McLelland, Eds. Academic Press, NY, pp. 105-192.

KROODSMA, D. E. and PARKER, L. D. (1977). Vocal virtuosity in the brown thrasher. *Auk* 94:783-784.

LEMON, R. E. (1973). Nervous control of the syrinx in white-throated sparrows (*Zonotrichia albicollis*). *J. Zool., Lond.* 171:131-140.

LUINE, V., NOTTEBOHM, F., HARDING, C., and McEWEN, B. S. (1980). Androgen affects cholinergic enzymes in syringeal motor neurons and muscle. *Brain Res.* 192:89-107.

MANOGUE, K. R. and PATON, J. A. (1982). Respiratory gating of activity in the avian vocal control system. *Brain Res.* 247:383-387.

MARLER, P. (1969). Tonal quality of bird songs. In: *Bird Vocalizations*. R. A. Hinde, Ed. Cambridge University Press, Cambridge, England, pp 5-18.

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

MCCASLAND, J. S. (1987). Neuronal control of bird song production. *J. Neurosci.* 7:23-29.

NOWICKI, S. and CAPRANICA, R. R. (1986a). Bilateral syringeal interaction in the production of an oscine bird sound. *Science* 231:1297-1299.

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

NOTTEBOHM, F. (1970). Ontogeny of bird song. *Science* 167:950-956.

NOTTEBOHM, F. (1971). Neural lateralization of vocal control in a passerine bird. I. Song. *J. Exp. Zool.* 177:229-261.

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

RISSER, A. C. JR. (1971). A technique for performing laparotomy on small birds. *Condor* 73:376-379.

SELLER, T. J. (1979). Unilateral nervous control of the syrinx in Java sparrows (*Padda oryzivora*). *J. Comp. Physiol.* 129:281-288.

SIMPSON, H. B. and VICARIO, D. S. (1990). Brain pathways for learned and unlearned vocalizations differ in zebra finches. *J. Neurosci.* 10:1541-1556.

STEIN, R. C. (1968). Modulation in bird sounds. *Auk* 85:229-243.

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

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

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. *Current Opinion Neurobiol.* 1:595-600.

WILD, J. M. (1993). The avian nucleus retroambigualis: a nucleus for breathing, singing and calling. *Brain Res.* 606:319-324.

WILLIAMS, H., CRANE, L. A., HALE, T. K., ESPOSITO, M. A., and NOTTEBOHM, F. (1992). Right-side dominance for song control in the zebra finch. *J. Neurobiol.* 23:1006-1020.

WILLIAMS, H. and VICARIO, D. S. (1993). Temporal patterning of song production: Participation of nucleus uvaeformis of the thalamus. *J. Neurobiol.* 24:903-912.