



Vocal mechanisms in birds and bats: a comparative view

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ABSTRACT

Vocal signals play a very important role in the life of both birds and echolocating bats, but these two unrelated groups of flying vertebrates have very different vocal systems. They nevertheless must solve many of the same problems in producing sound. This brief review examines avian and microchiropteran motor mechanisms for: 1) coordinating the timing of phonation with the vocal motor pattern that controls its acoustic properties, and 2) achieving respiratory strategies that provide adequate ventilation for pulmonary gas exchange, while also facilitating longer duration songs or trains of sonar pulses.

Key words: birdsong, echolocation, minibreaths, respiration, vocalization.

AVIAN AND MICROCHIROPTERAN VOCAL ORGANS

The motor control of phonation has been studied during spontaneous song in birds with an intact vocal system by implanting microbead thermistors in each bronchus to measure airflow while monitoring subsyringeal pressure through an air sac cannula attached to a miniature piezoresistive pressure transducer (Suthers 1990, Suthers et al. 1999). Similar experiments in restrained bats (Suthers and Fattu 1973, Durrant 1988, Suthers 1988) have monitored tracheal airflow and pressure during the emission of sonar pulses. In combination with measurements of electrical activity (electromyograms or EMG's) in vocal organ and respiratory muscles, these data add to our understanding of how vocalizations are produced.

THE AVIAN SYRINX

The vocal organ of birds is the syrinx, which is located at the caudal end of the trachea in the thorax, close to the heart. Syringeal anatomy varies

considerably among taxa (King 1989), but in songbirds (suborder Oscines or Passeres) and many other birds, it includes modified cartilages at the cranial end of the two primary bronchi and caudal end of the trachea (Fig. 1a). This tracheobronchial syrinx contains a separate sound source in each bronchus. Vocalization normally occurs during expiration by the adduction of medial and lateral labia at the cranial end of the bronchus. The labia are pads of loose connective tissue that, when adducted into the air stream, are caused to vibrate in response to aerodynamic forces and thus generate sound (Goller and Larsen 1997). In most songbirds vocalization is controlled by 4 pairs of syringeal muscles and 2 pairs of extrinsic muscles that attach to the trachea. Each side of the syrinx is separately innervated by the tracheosyringeal branch of the hypoglossal nerve that conveys motor commands from a system of song control nuclei in the ipsilateral side of the brain (Brenowitz et al. 1997).

Experiments show that songbirds control sound production separately on each side of the syrinx (Suthers 1990, 1997, 1999). Sound is produced as

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air flows through a slit between the adducted labia. A further increase in the activity of the adductor muscles can close this slit and prevent phonation by stopping airflow (Suthers 1990, Larsen and Goller 1999, Goller and Larsen 2002). Songbirds switch song production from one side of the syrinx to the other, or simultaneously produce different harmonically unrelated sounds using both sides. Song diversity is increased by the fact that the two sides of the syrinx tend to have different sound frequency ranges and may be specialized for different acoustic effects (Suthers 1999).

THE MICROCHIROPTERAN LARYNX

Echolocating bats (Microchiroptera), like other mammals, produce vocalizations with their larynx, located at the cranial end of the trachea. The bat larynx is specialized to produce ultrasonic vocalizations with wavelengths short enough to be reflected from very small objects, such as insect prey. The greatly hypertrophied cricothyroid muscles (Fig. 1b, D) envelop the larynx, the cricoid and thyroid cartilages are unusually large and there are thin vocal membranes on the vocal folds (Fig. 1b, A). Ultrasound is produced by vibration of the vocal membranes in the expiratory air stream (Griffin 1958, Durrant 1988). Similar membranes are present in various primates and a number of other mammals that produce high frequency sounds (Mergell et al. 1999). The bat larynx is innervated by two branches of the vagus nerve. The superior laryngeal branch innervates the cricothyroid muscles and a smaller recurrent branch innervates all other laryngeal muscles.

TIMING PHONATION

During vocalization, the muscles that determine the fundamental frequency and spectral properties of the sound by controlling the tension of the oscillating labia or vocal folds and membranes must be precisely coordinated with those that control the timing of airflow through the vocal organ to generate sound. The more rapidly sounds are produced,

the more critical is this coordination.

The Big Brown Bat *Eptesicus fuscus*, for example, produces frequency modulated (FM) sonar pulses which start at about 40 kHz and sweep down to about 15 kHz over a period of a few to several milliseconds. When pursuing an insect these sonar cries are produced at repetition rates rising from several per second to nearly 200 s^{-1} as the bat closes in on its prey. The bat larynx has been modeled by Mergell et al. (1999) who suggest that in addition to producing ultrasound, the vocal membranes may also increase vocal efficiency and could facilitate the production of non-linear phenomena such as subharmonics or chaotic vibration. The oscillating vocal membranes have no internal muscles. The frequency at which they vibrate is correlated with the force exerted by the cricothyroid muscles, which presumably control membrane tension. At the beginning of each sonar pulse, muscle force and membrane tension are high and decline during the course of the vocalization to generate a downward frequency sweep (Suthers and Fattu 1973). During a train of sonar pulses this cycle repeats with a period equal to the repetition rate of the pulse train with millisecond precision. If airflow starts too soon, while cricothyroid tension is still increasing, the frequency of the sonar pulse will rise instead of fall; if airflow continues too long, the sonar signal will have a ‘‘U-shaped’’ appearance with a rising frequency at the end.

The Big Brown Bat solves this problem of coordinated timing by having cricothyroid muscles control both the laryngeal aperture and membrane tension. The cricothyroid muscles contract before the sonar pulse. In addition to flexing the cricothyroid joint, they exert a transverse force vector that flexes the thyroid lamina medially and closes the glottis as it also increases tension on the vocal membranes. When the cricothyroids begin to relax, the glottis opens and a downward sweeping sonar pulse is produced as air flows across the relaxing vocal membranes (Durrant 1988).

Songbirds use different pairs of their intrinsic syringeal muscles as the primary controllers of syringeal resistance and labial tension (Goller and

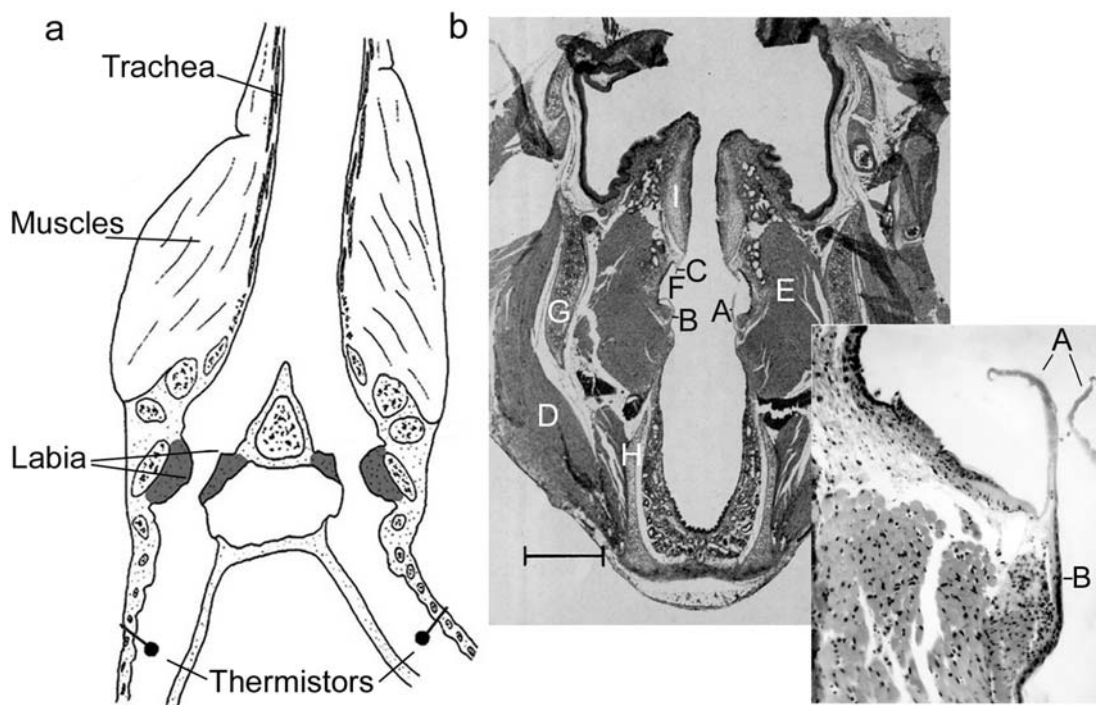


Fig. 1 – **a**: Frontal cross section of songbird syrinx showing its location at the base of the trachea and the presence of two independently controlled oscillators, the labia, which also act as pneumatic valves capable of switching phonation from one side to the other. Individual muscles are not shown. Thermistors implanted in each bronchus provide a measure of the rate of airflow through each side of the syrinx. (After Goller and Suthers 1996a); **b**: Cross section of Big Brown Bat larynx. Expiratory air from trachea flows upward across vocal membranes and into pharynx. Inset (from a different histological section) shows left vocal fold and its vocal membrane and part of the vocal membrane from the right side. Vocal folds form the pneumatic valve; vocal membranes generate the ultrasound. A, vocal membrane; B, vocal fold; C, ventricular membrane; D, cricothyroid muscle; E, thyroid arytenoid muscle; F, ventricle of Morgagni; G, thyroid cartilage. Bar equals 500 microns. (After Suthers and Fattu 1973).

Suthers 1995, 1996a, b). The timing of airflow and therefore phonation through each side of the syrinx is determined by the dorsal syringeal muscles that adduct the labia into the midline where they oscillate and produce sound or where they act as a pneumatic valve preventing airflow. In the former mode, the frequency of sound is controlled primarily by the ventral syringeal muscles that are believed to tense the labia (Larsen and Goller 1999). This independent control of timing the labial valve and regulating sound frequency gives songbirds more flexibility in the kinds of sounds they can produce at syllable repetition rates below those needed for echolocation.

Echolocating oilbirds (Suthers and Hector

1985) and swiftlets (Suthers and Hector 1982) orient in the dark using broad band clicks, which they produce with a syrinx anatomically simpler than that of songbirds. Swiftlets have no intrinsic syringeal muscles. Vocalizations are controlled by rapid sequential action of two antagonistic extrinsic muscles. First, the sternotrachealis muscle pulls the trachea caudally causing the labia to move into the bronchus. As the airway closes a click is produced. This is followed immediately by contraction of the tracheolateralis muscles that shorten the trachea and abduct the labia by stretching the syrinx. A second click is produced as the airway opens (Suthers and Hector 1982, Suthers 1988). This relatively prim-

itive control mechanism results in an acoustically more variable sonar signal, but one that is adequate for the less demanding requirements of these birds, compared to bats.

RESPIRATORY STRATEGIES FOR EXTENDED SONGS AND TRAINS OF SONAR PULSES

Birds and bats have independently arrived at similar solutions for maintaining an air supply with minimal interruptions in their vocal output. At moderate syllable repetition rates, birds take a brief inspiration after each vocalization (Fig. 2a). In canaries, the volume of this minibreath is equal to the volume of air that was required to produce the syllable (Hartley and Suthers 1989). The horseshoe bat (Fig. 2b) often inserts a minibreath between consecutive sonar pulses. Measurement of respiratory muscle activity in various bats at rest and during flight indicates that the respiratory motor pattern varies with activity and species (Lancaster et al. 1995, Lancaster and Speakman 2001). The volume of minibreaths in bats has not been measured but is likely to also approximately equal the air expelled to generate the sonar pulse. Minibreaths allow the animal to increase the duration of its songs or sonar pulse trains without the necessity of periodic interruptions for a normal inspiration. Small birds like canaries use a minibreath respiratory pattern at syllable repetition rates up to about 30 s^{-1} (Hartley and Suthers 1989). As body size increases, the maximum syllable repetition rate for minibreaths decreases, probably due to physical limitations on the rate at which thoracic structures driving ventilation can oscillate (Zollinger and Suthers 2004). Birds lack a mammalian-type muscular diaphragm between their thoracic and abdominal cavities so respiratory ventilation requires movement of the sternum and rib cage (King and Molony 1971).

At syllable or sonar pulse repetition rates too fast for minibreaths, birds and bats switch to a respiratory pattern of pulsatile expiration in which a short train of very rapid vocalizations is produced by repetitively opening the syrinx or glottis to allow a small puff of air to escape and produce a sound

(Suthers 1988, Hartley and Suthers 1989, Hartley 1990, Suthers 1997). Expiratory muscles continue to contract and maintain a positive respiratory pressure during the whole phrase or pulse train (Fig. 2). Since no minibreath is taken between vocalizations, the duration of these high repetition rate trains or trills is limited by the volume of air available at the beginning of the sequence. Vocal repetition rate is increased at the cost of shortening the length of time the tempo of syllables or sonar pulses can be maintained without interrupting the rhythm for an inspiration.

CONCLUSION

Similar needs for vocal communication in these unrelated vertebrates have led them to similar motor solutions for dealing with the physical and physiological limitations that both bats and birds encounter when vocalizing. Vocal mechanisms that have evolved to improve one aspect of vocal performance do so at the expense of some other vocal ability. Since vocal demands and motor limitations transcend particular vertebrate taxa, the knowledge gained through experiments on one group is likely to have broad applications beyond its taxonomic boundaries.

RESUMO

Os sinais vocais têm um papel muito importante na vida das aves e dos morcegos usando ecolocação, apesar desses dois grupos não relacionados de vertebrados voadores possuírem sistemas vocais muito diferentes. Todavia eles precisam resolver muitos problemas idênticos para produzir sons. Esta breve revisão examina os mecanismos motores, em aves e microquirópteros, para: 1) coordenar a sincronização da fonação com o padrão motor vocal que controla suas propriedades acústicas, e 2) realizar estratégias respiratórias que fornecem uma ventilação adequada para as trocas gasosas nos pulmões, ao mesmo tempo que facilitam maior duração dos cantos ou das séries de pulsos de sonar.

Palavras-chave: canto de aves, ecolocação, “minibreaths”, respiração, vocalização.

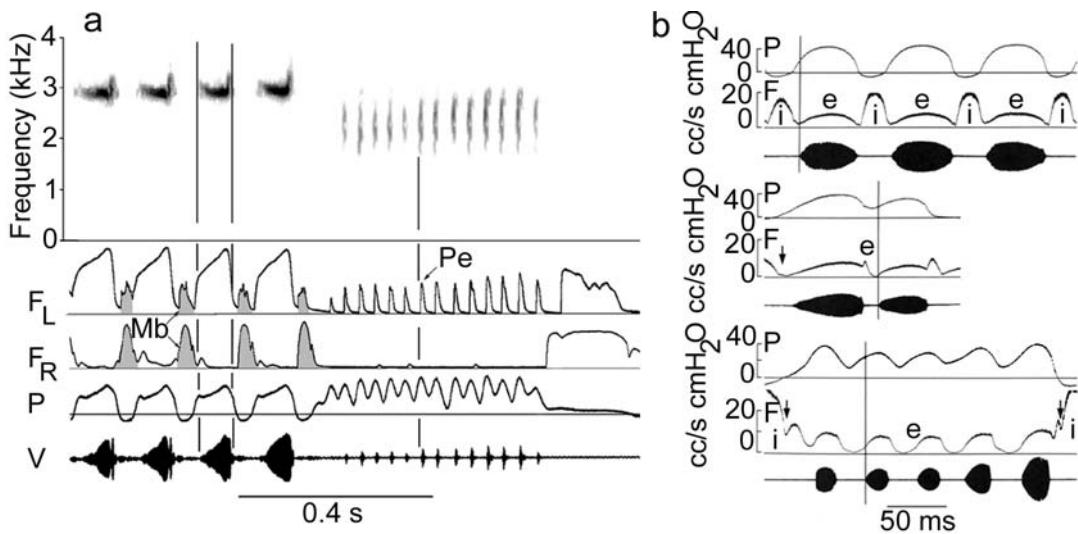


Fig. 2 – a: A segment of a Waterslager Canary *Serinus canaria* song, showing the last 4 syllables at the end of a phrase using a minibreath (Mb) pattern of respiration. This phrase is followed by a high repetition rate trill using pulsatile expiration (Pe). F_L and F_R are rate of airflow through the left and right side of the syrinx. P is subsyringeal (air sac) pressure. V is time waveform showing the amplitude of the vocalizations in spectrogram at top. Horizontal lines represent zero airflow and ambient pressure. Expiratory flow and inspiratory flow (shaded) are both upward deflections of flow signal, but inspiration occurs during negative subsyringeal pressure. (After Suthers 1997). **b**: Use of minibreaths and pulsatile expiration during trains of sonar pulses by two bats that emit predominantly constant frequency sonar pulses. Top: the Horseshoe Bat *Rhinolophus hildebrandti* inserts a brief inspiration (minibreath) between each sonar pulses. Middle: pulsatile expiration by the same species; respiratory pressure remains positive during the interval between sonar pulses so there is no inspiratory airflow. Bottom: Pulsatile expiration by the Moustached Bat *Pteronotus parnellii*, indicated by positive respiratory pressure throughout pulse train. P = subglottal pressure measured in trachea; F = rate of tracheal airflow. Oscillograph of sonar pulses is shown below airflow. Horizontal lines indicate zero (ambient) tracheal pressure and zero tracheal airflow. e = expiration; i = inspiration (minibreath). Vertical arrows indicate reversal points between inspiration and expiration. Rate of airflow changes and reverses direction so quickly during switches between inspiration and expiration that the time-constant of the thermistor prevents the airflow signal from returning to zero at these points. (After Suthers 1988).

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