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1

Vocal Mechanisms for Avian Communication

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1.1 Introduction

Vocal signals are an important means of avian communication. The variety and complexity of the vocal repertoire varies greatly between species, as does the morphology of the vocal organ, but the correlation between vocal anatomy and acoustic output is not always apparent. Recent years have seen important advances in understanding how birds sing, including new insights into sound generation, production constraints, and vocal tract filtering, as well as a growing interest in the nonlinear components of vocalizations. Here we attempt to provide an overview of the peripheral mechanisms by which both songbirds and non-songbirds control the acoustic properties of their vocalizations, in the hope that it will help strengthen the bridge between mechanistic and behavioral approaches to avian acoustic communication.

1.2 Avian vocal systems

1.2.1 The syrinx

The avian vocal organ is located in the interclavicular air sac, where it is formed by modified bronchial and/or tracheal cartilages, and contains structures that vibrate in airflow to generate sound. Syringeal anatomy varies significantly across different groups. At one extreme are the vultures, which have no syrinx. At the other extreme are various songbirds whose well-developed syrinx includes multiple pairs of muscles with specialized functions in sound production (Fig. 1.1). In between these extremes are a variety of non-oscine syrinxes controlled by an intermediate number of tracheal and/or syringeal muscles.

Syrinxes are often categorized anatomically as being tracheal, bronchial, or tracheobronchial, but the location of the sound-generating oscillators is of

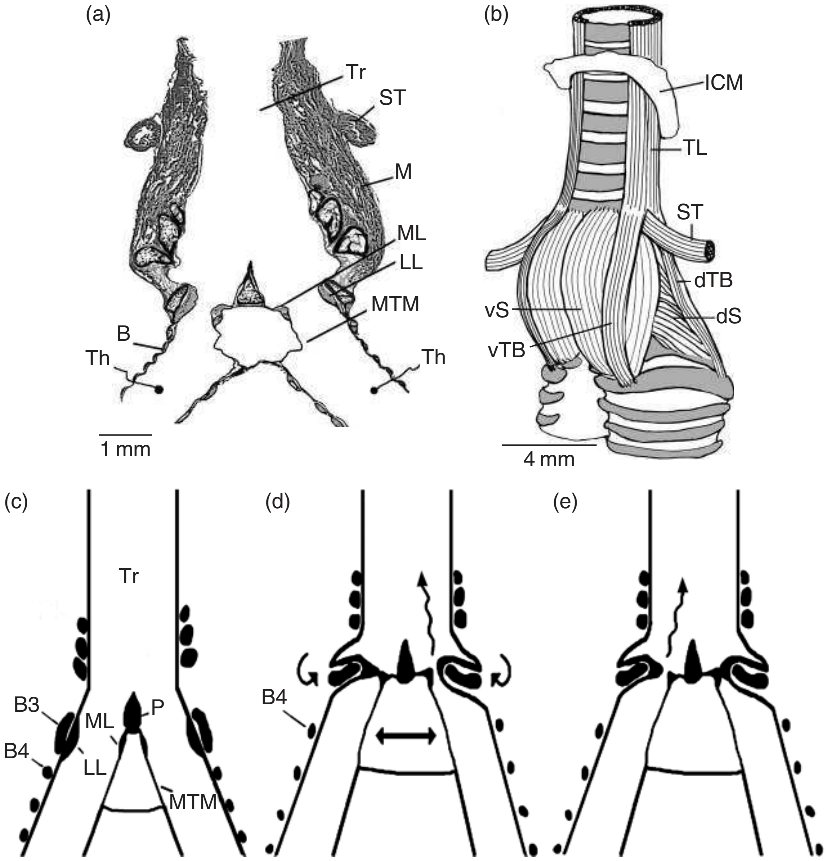

Figure 1.1. The songbird syrinx is a bipartite structure located at tracheobronchial junction. (a) Frontal section through the syrinx of a brown thrasher, showing the dual nature of the vocal organ and placement of microbead thermistors (Th) for recording airflow. (b) Ventrolateral external view of syrinx illustrating syringeal musculature. (c) Schematic ventral views of songbird syrinx during quiet respiration (d) phonation on the left side with labial valve closed on right side and (e) phonation of right side with left side closed. In preparation for phonation the syrinx moves rostrad. Contraction of the ipsilateral dorsal syringeal muscles (dS and dTB) rotates the bronchial cartilages (curved arrows) into the syringeal lumen, moving the labia into the airstream, where they are set into vibration, producing sound (wavy arrows). Phonation may be bilateral (not shown) or unilateral (shown). Tr: trachea; M: syringeal muscle; ML: medial labium; LL: lateral labium; 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; B3 and B4: third and fourth bronchial cartilages; P: pessulus (b: modified from Goller and Suthers, 1996a; c–e: modified from Suthers and Goller, 1997).

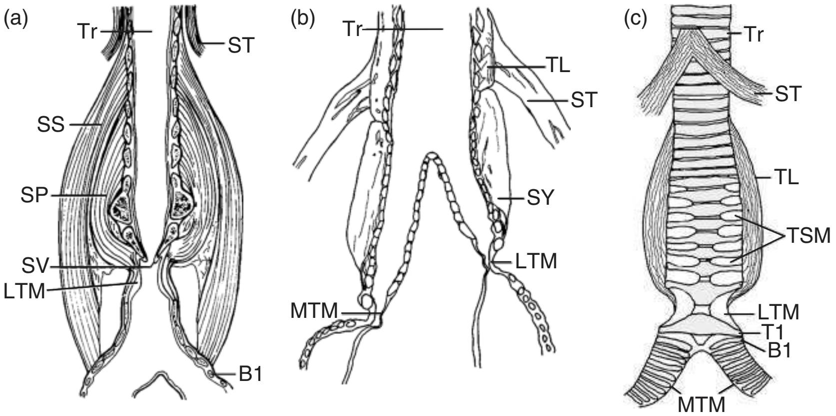

Figure 1.2. (a) Frontal section of monk parakeet syrinx showing tracheal location sound producing LTMs (modified from King, 1989). (b) Asymmetrical bronchial syrinx of the oilbird. Cranial end of each bronchus contributes a formant to the vocalization (Suthers, 1994; Fletcher and Tarnopolsky, 1999). Individual variation in degree of asymmetry endows different individuals in colony with unique formant frequencies (modified from Suthers and Hector, 1985). (c) Syrinx of collared dove. Sound is produced by LTM at base of trachea. Functional significance of the TSM is unknown (modified after Ballintijn and ten Cate, 1997). B1: first bronchial cartilage; T1: first tracheal ring; Tr: trachea; SS: superficial syringeal muscle; SP: deep syringeal muscle; ST: sternotrachealis muscle; SV: syringeal valve; TL: tracheolateralis muscle; TSM: tracheosyringeal membrane; SY: syringeal muscle; LTM: lateral tympaniform membrane; MTM: medial tympaniform membrane.

particular functional relevance. In storks, ibises, ducks, geese, some parrots (Fig. 1.2a), and several families of the suboscines, for example, these oscillators are located in the trachea where they share the same airstream during phonation and are likely to function together as a single sound source (though there may be exceptions). In most birds, including songbirds (order Passeriformes, suborder Oscine), sound is generated by separate bronchial airstreams across oscillating structures at the cranial end of each bronchus (Fig. 1.1). In a few taxa including penguins, nightjars, oilbirds (Fig. 1.2b), and some cuckoos the vocal organ is separated into two semi-syrinxes situated part way along the length of each bronchus.

1.2.2 The labia

Songbirds produce sound at the cranial end of each bronchus by vibration of two small masses of connective tissue, the medial and lateral labia that lie on opposite sides of the syringeal lumen (Fig. 1.1a). Phonation is initiated when syringeal adductor muscles move the labia into the expiratory airstream. Here they are caused to oscillate, presumably by Bernoulli forces acting in combination

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with the physical properties of the labial tissue in much the same way as occurs in the human vocal folds (Titze, 1994).

The motion of the labia has been observed with an endoscope during sounds elicited by brain stimulation of anesthetized northern cardinals (*Cardinalis cardinalis*) and brown thrashers (*Toxostoma rufum*), and during spontaneous vocalizations by an awake crow (*Corvus brachyrhynchus*) (Goller and Larsen, 1997b). In each case sound production was preceded by labial adduction to form a slit and accompanied by labial vibration. In other experiments, the dominant frequency of labial vibration in the hill myna (*Gracula religiosa*), measured with an optical vibration sensor, was found to agree with that in the vocalization (Larsen and Goller, 1999). Prior to these experiments by Goller and Larsen sound was assumed to be generated by vibration of the medial tympaniform membranes (MTMs) (Miskimen, 1951) that border the caudal edge of the medial labium. Destruction of the MTM has only a small effect on cardinal and zebra finch (*Taeniopygia guttata*) song, and its role in phonation needs further study (Goller and Larsen, 1997b).

1.2.3 Syringeal membranes

According to King (1989), the medial labium has not been reported in non-passerines. A lateral labium is present in some species, but whether it generates sound or acts only as a pneumatic valve is not known. Direct observation of oscillating syringeal structures during vocalization are available for only two non-passerines, neither of which has a lateral labium. In both of these species sound is produced by vibration of syringeal membranes. Endoscopic observations of the cockatiel syrinx indicate that in parrots sound is generated by oscillation of the lateral tympaniform membranes (LTMs) (Fig. 1.2a) as they are adducted into the syringeal lumen (Larsen and Goller, 1999). The syrinx of doves contains a thin MTM on each bronchus and thicker LTMs between the first and second tracheal rings where they extend around the dorsal side of the trachea (Fig. 1.2c) (Gaunt *et al.*, 1982). A third membrane, the tracheosyringeal membrane is also present in some species between narrow portions of tracheal rings along the dorsal side of the trachea (Ballintijn *et al.*, 1995). Sound was long assumed to be generated either by vibration of the MTMs (Warner, 1972; Ballintijn *et al.*, 1995) or possibly by an aerodynamic whistle mechanism (Gaunt *et al.*, 1982). The whistle mechanism is not supported by recent experiments (e.g. Ballintijn and ten Cate, 1998). Goller and Larsen (1997a) observed that when they induced phonation by blowing air through the trachea of a pigeon, the LTMs bulged into the syringeal lumen and vibrated. Stiffening the MTMs with tissue adhesive caused the coos to become "soft" and changed the spectral distribution of their energy, but the temporal and frequency patterns remained, indicating that the LTM is the primary sound source. A similar production mechanism presumably occurs in the closely related ring dove (*Streptopelia risoria*; a domesticated form of the African collared dove, *Streptopelia roseogrisea*, with which it is now thought to be conspecific) and the Eurasian collared dove (*Streptopelia decaocto*). Measures of the membrane vibration frequency in cockatiels and pigeons (Larsen and Goller, 1999) showed a dominant frequency similar to that of the fundamental in the vocalization (but see Beckers *et al.*, 2003b).

The LTM is absent in about half of the non-passerines (King, 1989) leaving other syringeal membranes, notably the MTM, as the presumptive sound source.

1.2.4 Integration with respiration

Since air flowing through the syrinx provides the energy for sound production, the control of respiratory ventilation is a critical component of vocalization. The temporal pattern of ventilation changes during song and sets the song's basic temporal pattern (Vicario, 1991). The avian respiratory system consists of a series of air sacs distributed in various parts of the body. Air sacs do not participate in gas exchange but act as bellows, moving air through the lungs and vocal tract as they are alternately expanded and compressed by inspiratory and expiratory respiratory muscles, respectively. The unpaired median interclavicular (= clavicular) air sac, which contains the syrinx (McLelland, 1989), also provides a pathway between the two sides and minimizes any pressure differences between the left and right bronchi (Wild *et al.*, 1998).

With only a few known exceptions, birds vocalize during expiratory airflow. Some zebra finches include inspiratory syllables in their song and these syllables which have a distinctively high fundamental frequency, are copied by juveniles (Goller and Daley, 2001). In all songbirds studied, singing is accompanied by a large increase in the amplitude of electromyograms (EMGs) in both the external oblique abdominal expiratory muscle (Hartley, 1990; Goller and Suthers, 1999) and thoracic inspiratory muscles (Wild *et al.*, 1998), which are alternately active during expiration and inspiration, respectively. Song requires precision coordination between syringeal and respiratory motor patterns. The robust nucleus of the arcopallium (RA) in the forebrain is likely to have a key role in this coordination, since it projects to premotor inputs of spinal respiratory motor neurons (Wild, 1997), as well as to syringeal motor neurons.

Different species vary greatly in the tempo of their songs and in the demand this makes on respiratory ventilation, which must continue to meet the needs for pulmonary gas exchange while supplying air to the syrinx at the appropriate pressure for phonation. This is usually accomplished by taking a small inspiration or minibreath (Calder, 1970) between syllables (Fig. 1.3a). In canaries,

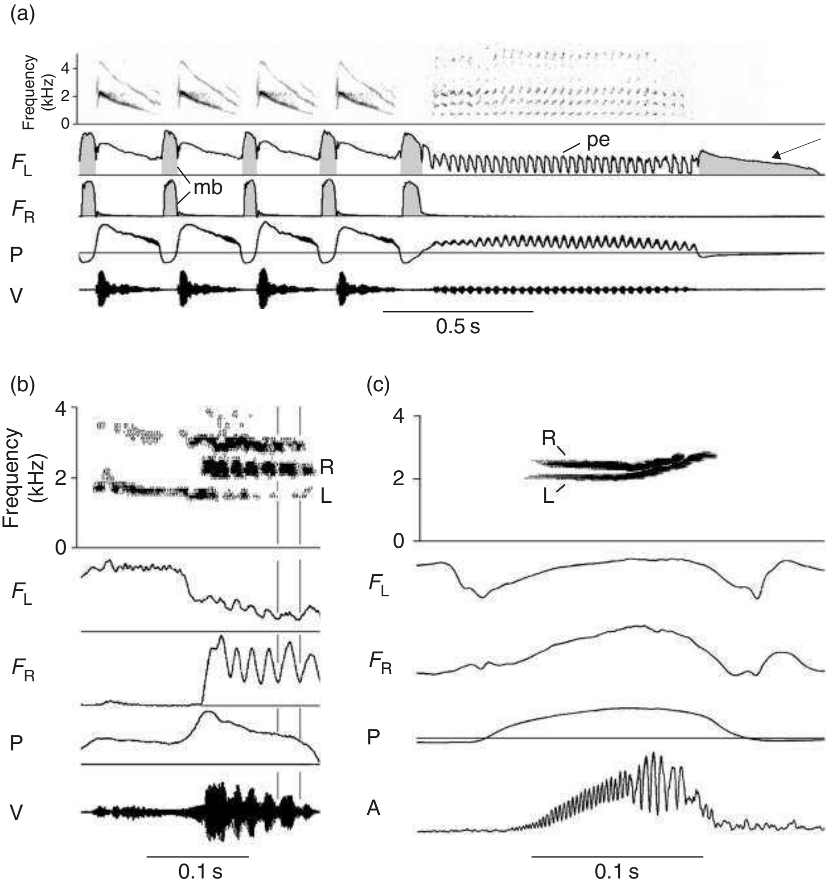

Figure 1.3. (a) Songbirds use different respiratory motor patterns during song, depending on syllable repetition rate. This segment of cardinal song includes the last 4 syllables of a phrase sung at about 2 syllables per second using a minibreath (mb) after each syllable. Note that both sides open for each mb during negative air sac pressure. These low-frequency syllables are sung entirely on the left side with the right side closed. This is followed by a trill at 30 syllables per second produced by pulsatile expiration in which the left side of the syrinx is repetitively opened while the right side remains closed and air sac pressure is positive during the entire phrase. Cardinals switch from a mb to a pulsatile pattern at about 16 syllables per second. Note the longer inspiration (arrow) immediately following the pulsatile portion of the trill. (b) A syllable from a catbird song. First half consists of fundamental and 2nd harmonic generated on left side of syrinx. Syllable becomes two-voice during last half when cyclically varying airflow controlled by syringeal muscles on right side produce a rapid AM. (c) Rapid amplitude modulation (A) generated by sustained simultaneous sounds in a brown thrasher two-voice syllable. F_L and F_R, rate of airflow through left and right sides of syrinx, airflow associated with positive pressure is expiratory; shaded flow is inspiratory (corresponds with

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and probably many other birds, the volume of the minibreath is adjusted to match the volume of air exhaled to produce the syllable (Hartley and Suthers, 1989). This ensures that the bird does not run out of available air during long songs. There is, however, a physical limit on how quickly the respiratory movements necessary to produce a minibreath can occur. At some point, as syllable repetition rate increases, the interval between syllables becomes too short for a minibreath. Birds which exceed this repetition rate are forced to change to a different respiratory motor pattern of pulsatile expiration in which expiratory muscles maintain a positive subsyringeal pressure for the duration of a fast trilled phrase (Fig. 1.3a). The timing of each syllable within the phrase is controlled by the syringeal muscles that repetitively open and close the syrinx, and generate a syllable with each puff of escaping air.

1.3 Vocal learning

The vocal mechanisms of songbirds have received particular attention because they are one of the few groups capable of vocal learning, a capacity known to be shared only by humans, a few groups of birds, marine mammals, and perhaps some bats. Vocal learning in oscine songbirds involves a distinct system of interconnected song control nuclei in the brain (Nottebohm *et al.*, 1976; Nottebohm, 1991), which are absent in other passerines and non-passerines that lack vocal learning (Kroodsma and Konishi, 1991; Gahr *et al.*, 1993; Gahr, 2000). This song control system is usually best developed in males (Nottebohm and Arnold, 1976) and undergoes seasonal, hormonally controlled changes in size, being largest during the reproductive season (Brenowitz and Kroodsma, 1996). A detailed discussion of the song system is beyond the scope of this chapter. It receives input from the auditory system and includes two major circuits. One of these is the anterior forebrain pathway which is particularly important for song learning. The other circuit includes the motor pathway to syringeal muscles and a connection to respiratory premotor neurons. The brain stem, below the mesencephalon, motor pathway to the syrinx is generally similar for both vocal learners and non-learners (Wild, 1994), but songbirds have a major projection from the forebrain premotor nucleus, RA, to various

Caption for fig. 1.3. (cont.)
negative pressure). P: pressure in cranial thoracic air sac; V: oscillograph of vocalizations; A: amplitude envelope of rectified vocalization; R and L: sound generated on right or left side of syrinx, respectively; mb: minibreath; pe: pulsatile expiration. Horizontal lines indicate zero airflow and ambient pressure ((a) modified from Suthers and Zollinger, 2004; (b) modified after Suthers *et al.*, 1994; and (c) modified after Suthers and Goller, 1997).

song control brain stem nuclei and directly to syringeal motor neurons in the tracheosyringeal portion of the hypoglossal nucleus (nXIIts).

Vocal learning has also evolved in two other avian orders that are not closely related to songbirds: parrots (Psittaciformes) (Gramza, 1970; Todt, 1975; Pepperberg, 1981; Farabaugh *et al.*, 1992; Farabaugh *et al.*, 1994) and some hummingbirds (Trochiliformes) (Snow, 1968; Wiley, 1971; Snow, 1977; Baptista and Schuchmann, 1990).

Although vocal learning takes place in the brain, central plasticity in vocal motor programs is only useful if the peripheral vocal system can translate these motor patterns into sound. It has been suggested (Gaunt, 1983) that a peripheral prerequisite for vocal learning may be the possession of multiple pairs of syringeal muscles that increase the versatility of the oscine syrinx, and presumably increases the range of sounds that can be accurately reproduced during imitative learning. However, parrots also learn vocalizations, though they have only two pairs of syringeal muscles and a seemingly simple tracheal sound source. The details of psittacine vocal control are still poorly understood. Active modulation of the syringeal sound by the suprasyringeal vocal tract, for example by moving the fleshy tongue, may provide important added vocal versatility (Warren *et al.*, 1996; Beckers *et al.*, 2004). Central plasticity and peripheral vocal flexibility have apparently co-evolved in different ways as separate groups acquired vocal learning.

1.4 Controlled and intrinsic modulation of the vocal source

Bird vocalizations assume their complexity by modulating the amplitude and frequency of phonation. This is achieved through coordinated neuromuscular control of the respiratory, syringeal, and craniomandibular systems, but complex modulation can also arise spontaneously from intrinsic properties of the vocal production system. Songbirds have an additional way of achieving vocal complexity through independent motor control of the two separate sound sources in their duplex syrinx.

Neuromuscular systems are likely to be constrained due to limitations in how rapidly muscles are able to expand and contract. Thus, while most research has focused on how birds perceive relatively slow modulations, it is of interest that recent investigations have begun to suggest that avian auditory systems may also be well suited to perceiving the rapid fluctuations in both frequency and amplitude that may not always be under direct neuromuscular control (e.g. Langemann and Klump, 1992; Dooling *et al.*, 2002).

Such fluctuations can be produced when relatively low-frequency spectral components in a harmonic signal do not radiate well or are filtered by the vocal tract (e.g. Dooling *et al.*, 2002), but can also be generated independently using mechanisms that remain unclear (e.g. Nowicki and Capranica, 1986a; Banta-Lavenex, 1999; Beckers and ten Cate, in press). For example, it is rather easy for humans to imitate the relatively slow frequency and amplitude modulation (FM and AM, respectively) patterns that exist in the eastern towhee's (*Pipilo erythrophthalmus*) onomatopoeic call (Nelson, 2004). Indeed, the relatively slow (<10 Hz) modulations that occur in this call are highly sinusoidal and are therefore easily whistled by humans. Unlike a human whistle, however, towhee calls are also modulated rapidly in frequency and amplitude (>450 Hz), and these rapid modulations give towhee calls a "rough" or "buzzing" acoustic quality that is not easily imitated when whistling. FM and AM span a wide range of periods (<2 ms to >1 s) in numerous vocalizations, and it is therefore interesting to consider how avian species are, in general, able to generate both relatively slow and surprisingly rapid modulations in their vocalizations.

1.4.1 Amplitude modulation

The amplitude of bird vocalization is modulated over different timescales and by different mechanisms. At the largest scale, syllables and notes or elements separated by silent intervals are produced through respiratory dynamics and syringeal motor action in both songbirds and non-songbirds (Brackenbury, 1978b, 1980; Hartley and Suthers, 1989; Beckers *et al.*, 2003a). In birdsong, notes are defined as the smallest units of continuous sound and repeated patterns of notes define a syllable. In the case of single-note syllables these terms are synonymous (Konishi, 1985).

Notes and syllables are produced by the coordinated action of respiratory and syringeal muscles (Brackenbury, 1978a; Gaunt, 1988; Suthers, 1997). Expiratory muscles provide the force to produce airflow through the syrinx (Hartley, 1990; Goller and Suthers, 1999) and the syringeal or tracheal muscles move the sound-generating membranes or labia into the stream of air flowing through the syringeal lumen (Suthers, 1990; Suthers *et al.*, 1999; Goller and Larsen, 2002). When a bird repeats a syllable the pressure pattern is also similar (Allan and Suthers, 1994; Suthers *et al.*, 1996) and different zebra finches use similar pressure patterns to produce similar syllables (Franz and Goller, 2002).

Non-oscines use a variety of mechanisms and syringeal structures to segment their vocalizations into notes or syllables. In swiftlets (*Aerodramus*) (Suthers and Hector, 1982) that lack intrinsic syringeal muscles and in oilbirds (*Steatornis carapensis*) that have but one intrinsic muscle (Suthers and Hector, 1985), this is accomplished by contraction of the sternotrachealis muscles, which stretch the trachea in a caudal direction and, by reducing tension on the syrinx, allow the external tympaniform membranes to fold into the lumen. Among sandpipers, the dunlin (*Calidris alpina*), has a prominent lateral labium, which Gaunt (1988) suggested might function as a syringeal valve and explain the pulsatile nature of the dunlin's call compared to the more continuous FM calls of most other members of the subfamily Calidrinae. In parrots, the syrinx of the monk parakeet (*Myopsitta monachus*) has a pair of flaps extending into the syringeal lumen just cranial to the LTM (Fig. 1.2a) that have been postulated to act as valves controlling airflow for phonation (Gaunt, 1988), but whose function is unknown. These flaps are absent in cockatiels where the antagonistic actions of a pair of syringeal muscles regulates the movement of the LTM into the syringeal lumen (Larsen and Goller, 2002).

In songbirds the labia are adducted into the syringeal lumen by contraction of the two dorsal syringeal muscles (Goller and Suthers, 1995, 1996b; Goller and Larsen, 2002). In addition to producing sound, the labia act as pneumatic valves that when strongly adducted close the ipsilateral bronchus and prevent phonation by stopping airflow (Fig. 1.1) (Suthers, 1990). At moderate or low syllable repetition rates adductor muscle tension is adjusted to let the high expiratory subsyringeal pressure push the labia slightly apart and force air through the slit between them. At the end of each syllable the adductors typically relax and the labia are withdrawn, opening the airway for a brief inspiration or minibreath (Hartley and Suthers, 1989; Goller and Suthers, 1996b).

Not all notes are produced this way, however. Separate notes can also be produced by active opening and closure of the syrinx against a relatively high and stable subsyringeal respiratory pressure, using the pattern of pulsatile expiration described above (Hartley and Suthers, 1989; Suthers, 1997; Suthers and Goller, 1997; Beckers *et al.*, 2003a). Such AM has been termed gating. By increasing the contraction of the adductor muscles (Goller and Suthers, 1996b) to completely close the syringeal lumen and stop airflow, phonation is interrupted to produce silent intervals between notes within a syllable or the short intervals between syllables sung at a high repetition rate. In gating, closure does not have to be complete, or happens only momentarily, which leads to a sound waveform that is not separated by silent intervals, but is continuous with a time-varying amplitude envelope. AM patterns attributable to syringeal regulation of airflow can reach 125 Hz in brown thrashers (Fig. 1.3b) (Suthers *et al.*, 1994; Goller and Suthers, 1996a).

In songbirds, such as the brown thrasher, AM is occasionally generated by the linear interaction, or beating, of tonal sounds having a similar amplitude but differing slightly in frequency, which originate from opposite sides of the syrinx (Fig. 1.3c) (Suthers and Goller, 1997).