

Sound Production in Birds: Acoustics and Physiology Revisited

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1 Introduction

In a volume concentrating on methods in the analysis of acoustic communication, two roles are served by a chapter on how one group of vocal virtuosos, namely birds, make sound. The first is to inform the reader of those innovations that have led to new insights into avian vocal physiology. There are several advances worth noting in this context, such as the use of miniature thermistors to monitor airflow and record acoustic signals in a bird's vocal organ during song (e.g., Suthers 1990), or the use of quantitative kinematic analysis to analyze motions of the vocal tract (e.g., Westneat et al. 1993).

Such innovations pale, however, by comparison to the technical advances in the analysis of sound that form the bulk of this Volume. A more important role for this chapter, then, is to lay the groundwork for the interface between advances in the analysis of vocal behavior and our understanding of how sounds are produced. Indeed, in his classic work, *Bird song: acoustics and physiology*, Crawford Greenewalt (1968) relied almost entirely on acoustic evidence to produce what still stands as the most comprehensive analysis of song production. His hypotheses were formulated largely by deducing how the available anatomy was likely to work based on detailed analysis of the sounds that were actually produced. Perhaps the best example of Greenewalt's success is his masterful argument that songbirds are capable of producing two sounds simultaneously as a kind of *internal duet*. Although this *two-voice theory* had been suggested earlier (Potter et al. 1947; Borror and Reese 1956), Greenewalt (1968) presented evidence in the form of oscillograms and hand-calculated spectrograms of electronically filtered sounds that convincingly argued for the existence of two independently modulated *voices* in the songs and calls of over two dozen species of birds.

The limitations of an acoustic-deductive approach to understanding vocal mechanisms are obvious, and experimental verification is necessary to elucidate the strengths and weaknesses of any theory. Nonetheless, it is clear that there is also limited value in trying to understand the mechanisms responsible for the production of a behavior such as birdsong without first understanding that behavior in some detail. In the case of vocal behavior, that understanding necessarily entails acoustic analysis.

The reverse is also true. Animal communication is best described as a system that includes the sender, signal, and receiver in all aspects of functional analysis (Shannon and Weaver 1949; Cherry 1966). Thus, a full appreciation of communication must consider the mechanism by which the signal is produced. From the point of view of a func-

tional understanding of communication, the mechanism by which a signal is produced will restrict the problem by defining the possible "acoustic space" that a signal can occupy (e.g., Dabelsteen and Pedersen 1985; Nelson 1989; Nelson and Marler 1990; see also Nowicki et al. 1992). From an analytical point of view, the biomechanics of production will at least help to define the technologies necessary to approach the whole communication system, or more specifically, to analyze the relevant signal space (see, for example, Rubin and Vatikiotis-Bateson, this Volume).

In the following discussion, we first describe our current understanding of the relationship between syringeal structure and function. This section is brief, as the subject has been treated extensively in recent years (Brackenbury 1982, 1989; Gaunt and Gaunt 1985b; Gaunt 1987; Nowicki and Marler 1988; King 1989). We then consider recent modifications of available functional models, some of which have arisen from new data garnered with old techniques, some from new interpretations of older data, and some from the applications of newer techniques. Our goal is not to review this material exhaustively, but instead to highlight particular problems of recent interest and their solutions. We conclude with an overview of central unresolved issues and the technical approaches that might be taken to solve these problems.

1.1

Diversity and Uniformity of Syringeal Structure and Function

Birds are capable of producing a remarkable variety of sounds, especially if one considers the entire class Aves as a group. Even within a single suborder such as the Oscines (true songbirds), an astounding diversity of sounds is produced. Typical avian vocalizations include (but are hardly limited to) pure-tone whistles, tones with clearly defined harmonics, broad-band sounds with formant-like structures, coupled amplitude and frequency modulations, click-like sounds, and noise (Greenewalt 1968; Marler 1969; Gaunt 1987; Nowicki and Marler 1988). The simultaneous presence of two harmonically unrelated, often independently modulated tones is common, suggesting that the membranous portions of some syrinxes that serve as acoustic sources may be independently activated and controlled in some cases (Borror and Reese 1956; Greenewalt 1968). This diversity in the kinds of sounds produced by birds leads readily to the suggestion that avian vocal systems perhaps work (function) in more than one way. In other words, the same anatomical structures may, through differences in how they are activated and operated, produce qualitatively different kinds of sounds.

When comparing various orders of birds, such as chickens (*Galliformes*) and parrots (*Psittaciformes*), some differences in sounds produced are obviously attributable to profound differences in syringeal anatomy (Youngren et al. 1974; Nottebohm 1976; Gaunt et al. 1976 1982; Gaunt and Gaunt 1977). However, even anatomically similar syrinxes, e.g., those of the Oscines, can produce radically different sounds, with resulting diversity that is as great within orders or families as between them. Even a single species may include in its repertoire a vast array of qualitatively different sounds. Given this diversity of output, and the possibility that similar vocal structures might function in different ways in the production of different kinds of sounds, it is a futile exercise in typological thinking to consider "the function" of "the syrinx." Rather, it may be more productive to think in terms of a flexible system in which structure-function relation-

ships may vary not only among taxa but also transiently within a species, or even within an individual.

1.2

Structural Considerations

The organ primarily responsible for generating sound in birds is the syrinx. Like feathers, syrinxes are unique to the class Aves and evolutionary antecedents are not known outside the class (Beddard 1898; King 1989). That is, all birds have some form of syrinx (except New World vultures, who have lost it secondarily), whereas no other animals do. Despite this commonality within the Aves, the shared characteristics of syrinxes among orders of birds are remarkably few. The anatomical complexity and taxonomic diversity of the syrinx has been well illustrated by Beddard (1898) and more recently by King (1989).

Syrinxes, like the larynx in other animals, occur as elaborations of structures in the vocal tract. A syrinx always occur in a more caudal position than the larynx. Most syrinxes lie at or near the point where the primary bronchi join to form the trachea (see Figure 1), and all occur within the interclavicular airsac¹. In some cases where the syrinx occurs high in the trachea (cranially), such as in hummingbirds, the air sac itself extends between the furcula (the fused clavicles of birds) and up into the neck (Beddard 1898).

All syrinxes contain at least one pair of relatively membranous, flexible walls that can be distended into the lumen of the airway. All are also associated with extrinsic tracheal musculature that, by changing the length of the trachea, can tighten or relax membranous portions, thereby allowing them to extend into or out of the airstream (Figure 1). Many, but not all syrinxes also have denser pads of tissue that are flexible and may be moved relative to the airstream. Most complex syrinxes, especially those of oscine birds, have associated musculature that is presumed to be able to change the position and configuration of their flexible membranes and the tissues of the syrinx itself. Such changes in syringeal configuration are presumed, in turn, to facilitate sound production during vocalization, and are further thought to be responsible for actively modulating the acoustic features of the sound being produced. As suggested by the two-voice phenomenon, this musculature can presumably also change the configuration of membranes in different parts of the organ independently.

The extensive variation in syringeal structures observed in different groups of birds, coupled with the suggestion that similar structures may exhibit a diversity of functions, might lead one to despair of uncovering any general principles of syringeal structure and function. Certainly, there is no obvious correlation between syringeal complexity, especially in terms of the extent of intrinsic musculature, and the complexity of sounds that may be produced (Greenewalt 1968; Gaunt 1983; Baptista and Trail 1992). Some

1 This airsac is one of the many membranous outpocketings of the bird's lungs that extend throughout the body cavity and even ramify into the hollow centers of bones. Most airsacs are bilaterally paired, but the intraclavicular airsac is a fused midline cavity that extends from the middle of the thoracic region anteriorly up to the furcula and the neck.

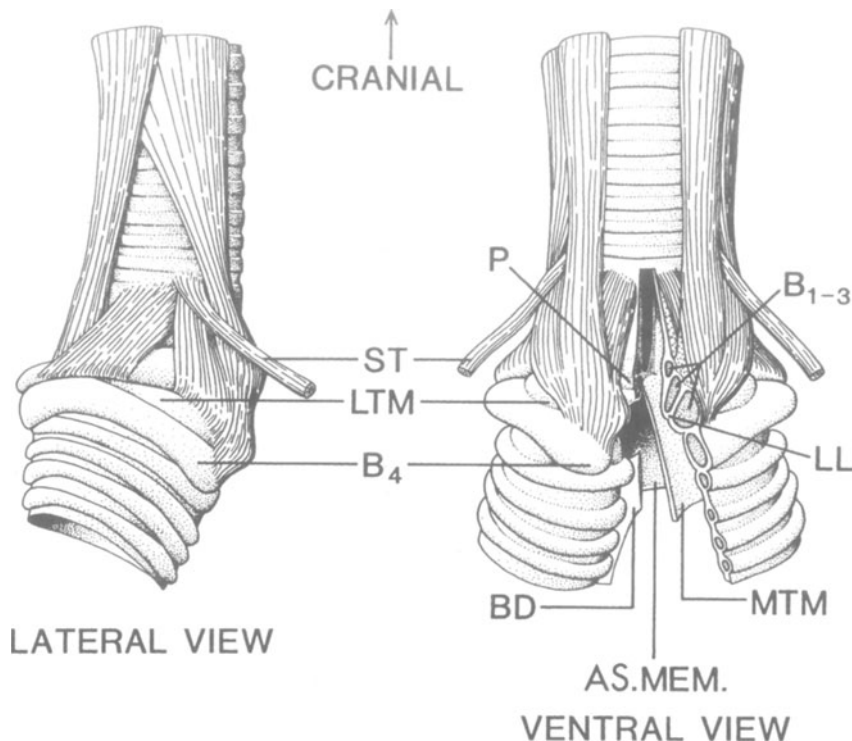


Fig. 1. Lateral and ventral views of a typical oscine syrinx. A portion of the left bronchus has been removed from the ventral view (*right*) to reveal internal structures. The bronchidesmus (*BD*), which has been cut in this view, extends between the medial surfaces of the two bronchi just caudal to the medial tympaniform membranes (*MTM*). The intraclavicular air sac (the dorsal wall of which is labeled *AS.MEM.*) surrounds the entire structure. Other abbreviations: *B₁₋₄* bronchial semi-rings; *LL*, lateral labium; *LTM* lateral tympaniform membrane; *ST* sternotrachealis muscle; *P* pessulus. (Reprinted with permission from Gaunt 1987, CRC Press, Boca Raton, Florida)

generalizations can be made, however. For example, the ability to learn vocal material through imitation is generally confined to species that possess intrinsic musculature (Gaunt 1983), even though the correlation between overall syringeal complexity and vocal learning is not strong (Baptista and Trail 1992). Another example is a general correlation between body size and emphasized frequencies in song, which likely results from allometry of syringeal morphology (Ryan and Brenowitz 1985). Unfortunately, such generalizations provide relatively little guidance in addressing more specific questions about the relationship between syringeal structure and vocal production.

1.3

Functional Considerations

It is generally agreed that sound is produced by the syrinx through the interaction of syringeal membranes with expiratory air flow. A variety of mechanisms for the induc-

tion and control of vibration in these membranes have been suggested (Greenewalt 1968; Stein 1968; Casey and Gaunt 1985; Gaunt and Gaunt 1985b; Fletcher 1988, 1989, 1992), but direct evidence is still lacking. Most models propose that air flowing past syringeal membranes induce the membranes to vibrate (see Sect. 3.1). One alternative model, dubbed the *whistle hypothesis*, suggests that syringeal membranes need not vibrate at all during sound production. Instead, the configuration of membranes and other tissues in the syrinx may enable the production of an aerodynamic *hole-tone whistle* (Chaunaud 1970) in which a stable pattern of vortices is produced (the vortices being the acoustic source) by the passage of air through two consecutive constrictions. This mechanism is found in human lip whistling and is also the way most tea kettles whistle. Available evidence (see below) shows that a true whistle is not likely to be involved in sound production in oscine birds. It might operate in doves (*Streptopelia*) and parrots, the two groups for which the mechanism was originally proposed (Nottebohm 1976; Gaunt et al. 1982), although recent work with the collared dove (*Streptopelia decaocto*) suggests that this species does not produce a true whistle (M. R. Ballintijn and C. ten Cate, pers. comm.).

The location of most types of syrinxes within the thoracic cavity and the high fundamental frequencies of vibration (often several thousand Hertz) make it difficult to measure the activity of syringeal membranes directly². Indeed, the precise nature of vibration and its induction in the syrinx remains one of the least understood features of the system. Each of the current models does, however, incorporate the assumption that changes in the configuration of the syringeal membranes, mediated by the activity of the musculature associated with the syrinx, are responsible for actively modulating the acoustic characteristics (that is, time-varying frequency and amplitude variations) of the sounds produced. The most widely accepted model of syringeal function, developed independently by Greenewalt (1968) and Stein (1968), proposes that such modulations are affected by adjustments in the position and tension of the vibrating membranes. The anatomy of the syringeal musculature (e.g., Ames 1971), as well as electromyographic analyses (EMG; see for example Gaunt and Gaunt 1977, 1985; Gaunt 1987a; Vicario 1991), both support this general view.

A related supposition of the Greenewalt-Stein model is that *all* modulations are source-generated. In contrast, the *source-filter* model of human speech production (Fant 1960; see also Rubin and Vatikiotis-Bateson and Owren and Bernacki, this Volume) proposes that the supralaryngeal vocal tract makes a major contribution to producing the time-varying changes in acoustic structure that are characteristic of speech. The idea that the source alone must be responsible for all acoustic modulations in bird song arose, in part, from the two-voice phenomenon. How could a single resonating system independently modulate two simultaneous tones? Imagine two larynges pro-

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- 2 In contrast, the relatively low fundamental frequency of vocal fold vibration (about 120 Hz in males) and the relatively accessible position of the larynx at the anterior end of the trachea in humans has allowed the development of many simple and precise techniques for measuring vocal fold activity.

ducing speech signals that passed through and were modified simultaneously by the same vocal tract. It is difficult, if not impossible, to conceive of how such a vocal system could independently modulate both source signals! In spite of this argument, recent empirical work (see Sect. 3.3) has demonstrated that the suprasyringeal vocal tract does play a critical role in sound production, at least in songbirds (Nowicki and Marler 1988). Although the acoustic effects of the avian vocal tract on the emitted signal are different from those observed in speech, some of the same physical and physiological principles appear to be at work in both systems.

Certainly, one of the most fascinating features of avian vocal production is the possibility of an internal duet being produced by birds that have syrinxes with two membranes that are capable of vibrating independently, such as oscines. This possibility was initially suggested as an afterthought in a book describing the use of the sound spectrogram in speech analysis (Potter et al. 1947). Twenty years later, Greenewalt (1968) used essentially the same acoustic techniques to marshal an impressive array of examples that seemed to require the production of two separate voices for their explanation (see Figure 2). Although few doubted the two-voice theory following Greenewalt's treatment, it was more than another twenty years before Suthers (1990) developed a technique that experimentally demonstrated the action of two separate sound sources in song production and provided a means for exploring the mechanisms underlying this phenomenon in more detail (see also Sect. 2.2).

In summary, birds have vocal systems of considerable capabilities. The mechanics of sound production almost certainly differ among different taxa, and may differ even during the production of various kinds of sounds within the same species. Moreover, the syrinx has proven to be difficult to observe directly, making it difficult to reach



Fig. 2. Spectrogram of terminal trill of wood thrush song, illustrating the simultaneous presence of two voices that are independently modulated and harmonically unrelated (Kay Digital Sona-Graph model 7800, 16-kHz analysis range, 300-Hz frequency resolution) (from Nowicki and Marler 1988, Regents of the University of California, used with permission)

unequivocal and broadly applicable conclusions based on empirical data. Comparisons of data gathered with different techniques or from different species, not to mention different orders, must be made with extreme caution and be confined to those issues directly tested.

2

New and Old Insights from New and Old Techniques

2.1

Air Flow and Phonation

One topic of long-standing interest has been the mechanism by which birds are capable of producing loud, prolonged songs without apparently pausing for breath. With the possible exception of nightjars (Hunter 1980), few birds seem to vocalize on inhalation. Yet many birds, including some notably small species, emit continuous vocalizations for seemingly improbable durations (e.g., 41 s for a winter wren, *Troglodytes troglodytes*, Clark 1949; at least 60 s and possibly up to 117 s for a grasshopper warbler, *Locustella naevia*, Brackenbury 1978a; Schild 1986). Estimates of tidal volume suggest that birds should run out of breath long before the end of such sustained vocalizations (Brackenbury 1978a).

Calder (1970) proposed that songbirds might partially replenish their air supply during song by using *minibreaths*, which he defined as shallow inhalations between successive notes. He made this proposal based on data obtained from singing canaries (whose prolonged songs can continue for up to 45 s) by using an *impedance pneumograph*. This device uses skin electrodes attached to the front and back of the bird. The impedance between these two electrodes covaries with the size of the thoracic cavity, which presumably correlates with patterns of inhalation and exhalation. Calder (1970) discovered that there was not a sustained expiratory motion during production of rapidly trilled notes. Instead, the birds he tested appeared to inhale slightly before each note, even when the bird was singing a rapid trill.

Gaunt et al. (1976) objected to Calder's interpretation, suggesting that impedance measurements could not be used to distinguish among several competing hypotheses for the production of prolonged vocalizations. Specifically, there was no evidence that airflow was being reversed during song, as would occur during a small inhalation. Gaunt et al. (1976) proposed four models: (1) oscillating valves in the airstream, (2) pulsatile output of airflow, (3) reciprocal oscillating air chambers, and (4) true minibreaths, all of which might explain Calder's data equally well. Only the last two of these hypotheses would effectively extend the duration of vocalization beyond that predicted by the characteristic tidal volume for a given species.

Various studies using implanted devices for measuring flow or pressure, sometimes combined with EMG, have demonstrated the presence of pulsatile output in evening grosbeaks, *Coccothraustes vespertinus* (Berger and Hart 1968), starlings, *Sturnus vulgaris* (Gaunt et al. 1973), chickens (Gaunt and Gaunt 1977; Brackenbury 1978b) and doves (Gaunt et al. 1982). Similar data from parrots support the existence of an oscillating valve in this group (Gaunt and Gaunt 1985a). In each of these cases, however, the dura-

tion of vocalization is not so extreme as to require a mechanism that extends the tidal volume of the bird.

Calder's (1970) hypothesis was again addressed by Hartley and Suthers (1989), who used miniaturized flow transducers to directly monitor air flow in the trachea of singing canaries. Interestingly, Calder's main reason for using an indirect measure of respiratory activity, as stated in his paper, was the infeasibility at that time of obtaining direct flow measurements in a small bird. Hartley and Suthers (1989) overcame this difficulty by improving on a method used earlier by Suthers and Hector (1982, grey swiftlets, *Collocalia spodiopygia*; 1985, oilbirds, *Steatornis carpiensis*) in which the cooling of a microbead thermistor is calibrated to provide a very accurate measure of air flow. Suthers and his coworkers also implanted small pressure transducers in the subjects' air sacs. Pressure data from these instruments indicate the direction of the flow detected by the thermistors, and thus help to provide a complete picture of respiratory mechanics.

Hartley and Suthers' (1989) data unequivocally demonstrated reversal of flow between song notes at repetition rates of up to about 30 Hz. As the note repetition rate exceeded 30 Hz, the canaries switched to a pulsatile output. Thus, canaries do use minibreaths as Calder (1970) originally proposed. At the same time, short repeated syllables are produced by canaries in two different ways, by minibreaths or pulsatile output, depending on the repetition rate of these notes. Evidently there is some upper rate beyond which the use of mini-breaths is constrained by the functional morphology of respiration.

The resolution of the minibreath controversy is tied directly to a specific technological improvement — the miniaturization of flow transducers that can be implanted in a bird's vocal tract. The unequivocal evidence obtained this way that canaries *do* use minibreaths to extend the duration of their phonations shows that three of the four mechanisms proposed by Gaunt et al. (1976) have now been demonstrated. The fourth, reciprocally oscillating chambers, has been described only in anurans (Martin and Gans 1972). In birds, both among species and within a single species, we see evidence for multiple physiological mechanisms leading to similar acoustic results.

2.2

Two-Voicing and Peripheral Lateralization of Function

The two-voice theory suggests that birds possessing a tracheobronchial syrinx with separate syringeal membranes in both bronchi should be capable of simultaneously producing two independent sounds. This theory was finally verified by Suthers (1990), although it had been generally accepted for over two decades in spite of the lack of direct experimental evidence. Recently, it also has become apparent that the two sides of a syrinx, in addition to being able to operate in isolation, might interact in the production of sound in a variety of ways. The possible interactions between the two sides of a syrinx, as well as the implications of two potential sound sources for control of song production, has been the subject of considerable work and discussion. Much of this discussion involves the relationship between neural control and the action of the two sound sources in songbirds.

Following Greenewalt's (1968) acoustic analysis in support of the two-voice theory, Nottebohm (1971) asked whether both sides of a songbird's syrinx contribute equally to song production. He did so by selectively denervating the left or right syringeal musculature of chaffinches (*Fringilla coelebs*) and observing the resulting deficits in song production. This technique involved severing the roots of the XIIth cranial nerve (the hypoglossus nerve) proximal to the point where this nerve forms an anastomosis with the Xth cranial nerve (the vagus); later work showed that severing the descending branch of the hypoglossus (the tracheosyringealis) achieves very similar results (Nottebohm and Nottebohm 1976). Nottebohm (1971) found that denervation of the right side of a chaffinch's syrinx resulted in only minimal degradation in song production, whereas denervation of the left side almost totally disrupted a bird's ability to sing. This apparent left side dominance was also demonstrated in several other species, most notably the canary (Nottebohm and Nottebohm 1976; see Nottebohm 1980, for a review).

The suggestion that one side of a bird's syrinx appears to play a dominant role in song production suggested an intriguing parallel to the well-known phenomenon of cerebral lateralization in speech (Marler 1970; Nottebohm 1971, 1980). Nottebohm (1977) pursued this idea by performing unilateral lesions of regions in the central nervous system known to be involved in the motor control of song production (HVC and RA; Nottebohm et al. 1982) and comparing differences in the effects of left versus right lesions. Lesions of the left HVC and RA had profoundly disruptive effects on song production in canaries (similar to those observed following unilateral lesion of the motor nerve leading to the syrinx), whereas those on the right side had a minimal effect. Thus, Nottebohm's work both supported the idea that the two sides of a bird's syrinx work independently and further demonstrated, for at least some species, that one side plays a dominant role in song production (although see below). The latter finding, along with the attendant description of a discrete set of brain regions involved in song control, contributed to an explosion of interest in the neurobiological underpinnings of song production, perception, and development. An overview of work on the *song system*, as it is commonly called, is beyond the scope of this chapter, but reviews may be found in Nottebohm (1980, 1991), and Konishi (1989).

The two sides of a bird's syrinx *are capable of* independently producing two distinct sounds, but do they *always* do so during production? Using Nottebohm's denervation technique, Nowicki and Capranica (1986a,b) demonstrated a counterexample in which both halves of the syrinx work together when the black-capped chickadee (*Parus atricapillus*) produces its complex *dee* syllable. This note (which occurs at the end of the familiar *chick-a-dee* scold call of this species) is highly modulated, resembling a harmonic series in which the fundamental frequency and the next one or two harmonics are missing (shown in Figure 3). Based on Nottebohm's earlier work, one might expect that this complex sound is produced entirely by one side of the syrinx, or perhaps that some of its frequency components are produced by one side of the syrinx while others are produced simultaneously by the other. In either case, one would expect the contributions from the two syringeal halves to add in a linear fashion. Contrary to this expectation, unilateral denervation of the left and right halves of the syrinx resulted in comparable postoperative deficits (Figure 4). Furthermore, a simple summation of the frequency components that remained following unilateral left denervation with those that remained intact following unilateral right denervation did not approximate the normal

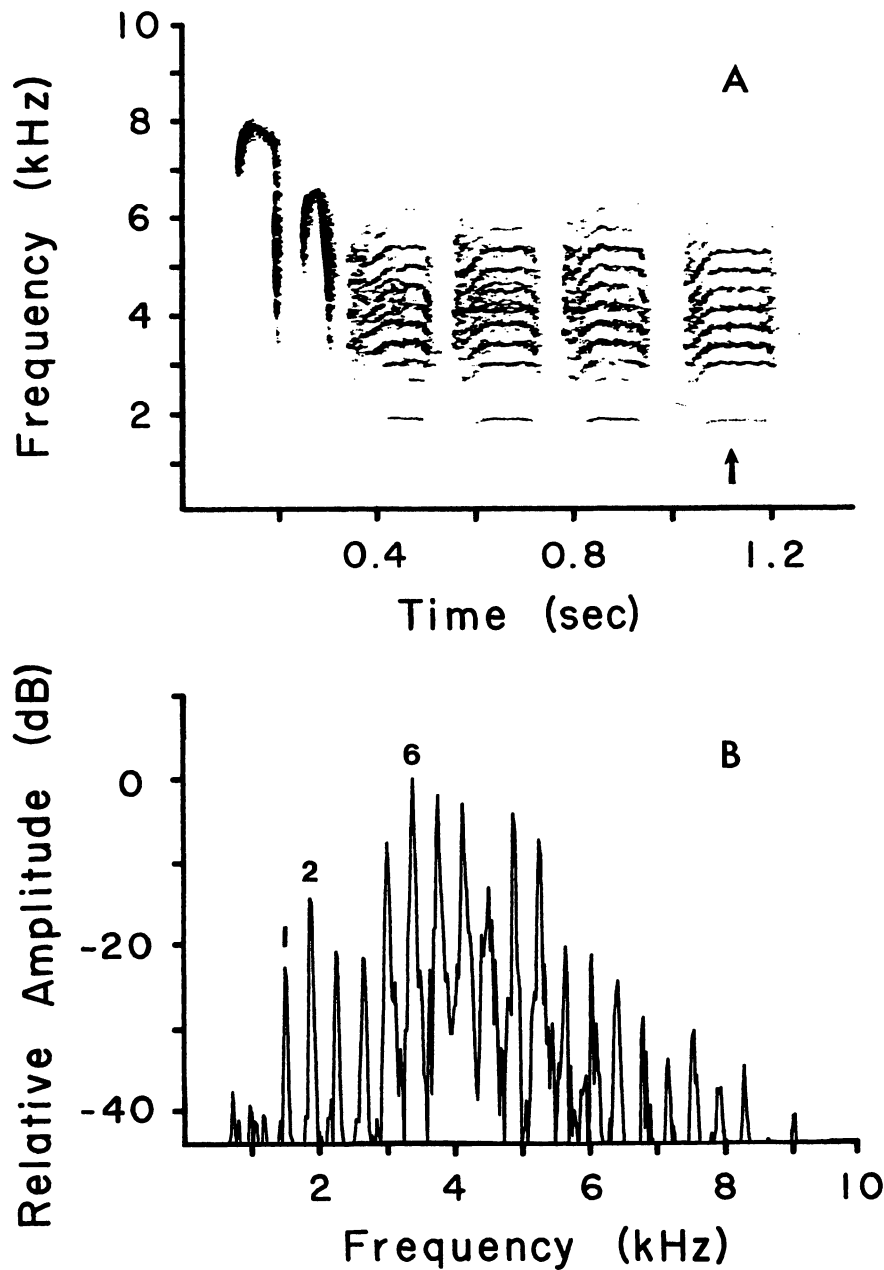


Fig. 3. a Spectrogram of a normal chick-a-dee call of the black-capped chickadee showing two introductory pure-tone notes and four dee notes (Kay Digital Sona-Graph model 7800, 8-kHz analysis range, 45-Hz frequency resolution). b Amplitude spectrum of a dee note, calculated from a 40 msec section of the last note as marked by an arrow in A (Nicolet Mini-Ubiquitous FFT analyzer, 25-Hz frequency resolution) (Reprinted with permission from Nowicki and Capranica 1986b, American Association for the Advancement of Science)

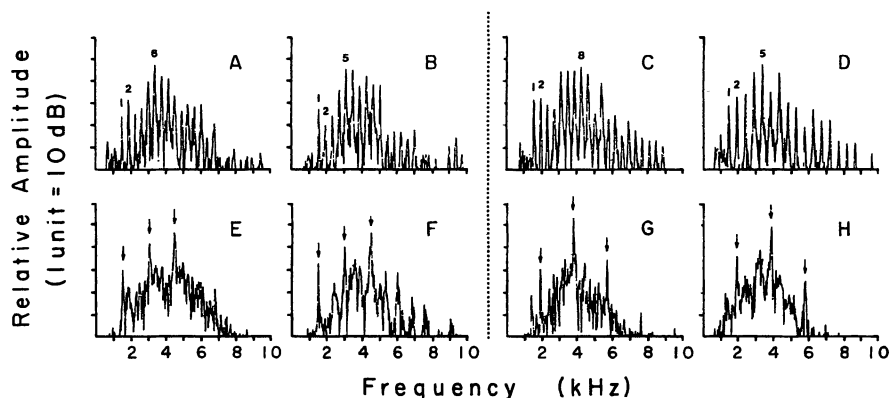


Fig. 4. Comparison of pre- and postoperative amplitude spectra of dee notes produced by four different chickadees. A-D Preoperative spectra of dee syllables. The first two frequency components with significant energy and the component of maximum amplitude are numbered. E,F Postoperative spectra of dee notes produced by the same birds as in A and B, respectively, following section of the right tracheosyringalis (TS) nerve. (G,H) Postoperative spectra of dee notes produced by the same birds as in C and D, respectively, following left TS nerve section. Arrows indicate postoperative harmonic components. Note the relationship between preoperative component 1 and the postoperative fundamental frequency in the case of a right nerve section, and between preoperative component 2 and the postoperative fundamental in the case of a left nerve section (Reprinted with permission from Nowicki and Capranica 1986b, American Association for the Advancement of Science)

sound. This result indicates that both sides are indeed independently innervated and are capable of operating independently, but that adding the signals produced by the two sides when working alone does not recreate the normal, intact signal.

Nowicki and Capranica (1986b) solved this apparent puzzle by mathematically modeling possible nonlinear interactions between the signals presumed to be generated by the two syringeal sources, as inferred from signals produced following unilateral denervation. They found that multiplying the two source signals, equivalent to an amplitude modulation of one by the other, produced a pattern of modulation *sidebands* (summation and difference frequencies) that closely matched the pattern observed in normal production. Thus, they argued that the *dee* syllable is normally produced by a coupling of the two syringeal sources, i.e., that the two sources do not act independently. Interestingly, other syllables produced by the chickadee in the same call (*chick-a*) have a simple, pure-tone structure and they are affected by unilateral nerve section in a fashion that is more similar to that observed by Nottebohm in the chaffinch or canary. This outcome suggests that the nonlinear interaction between the two syringeal sound sources can be “turned on and off,” even in the context of a single call produced by the same bird.

Nowicki and Capranica’s (1986a,b) demonstration of bilateral syringeal coupling did not rely on a new technique, but instead sprang from the combination of some mathematical intuition with the serendipitous application of an older technique to a different species. Their work did not suggest that the two-voice theory was incorrect, only that it was incomplete. Birds are able to sing an internal duet, with the two vocal sources

operating independently from each other, but they also can produce more complex modulations in some cases when the two sources are coupled. The precise physical nature of this coupling is unclear, which is not surprising given how little is known about vibration even in a single syringeal membrane. Moreover, it is possible that the bilateral interaction discussed by Nowicki and Capranica is only the tip of an iceberg of possible ways in which the two sides of a bipartite syrinx may conspire to produce intricate (and beautiful) sounds.

McCasland (1987), working with canaries, also reexamined the issue of how the left and right sides of a syrinx contribute to song, but he did so using still another technique. McCasland suggested that a more direct way to assess the contribution of one side of the syrinx to song production is to plug physically the bronchus below the contralateral side. Using this bronchus-plug technique, he found much less profound differences between the left and right than Nottebohm and Nottebohm (1976) had, when using unilateral denervation in the same species. Based on these data, McCasland questioned whether the two sides of a canary's syrinx ever act independently. He suggested instead that Nottebohm's earlier findings might be explained if the two syringeal halves normally produce qualitatively similar signals, but with the larger left side normally producing sound at greater amplitudes. McCasland reasoned that when the left side is turned off by depriving it of muscular control, air still flows through, and the weaker activity of the right side is masked. Plugging the left side, in contrast, not only prevents it from producing sound, but also may increase airflow through the contralateral bronchus, causing the right side to produce its signal (which McCasland suggested was the same as that produced on the left) at higher amplitude.

Hartley and Suthers (1990) replicated McCasland's study, also in canaries, but failed to confirm his result. Instead, they found the effects of bronchus plugging in canaries to be very similar to those produced by unilateral denervation, with the left side being clearly dominant in production. Differences in the results of these two studies remain unexplained. The method used to physically plug the bronchi differed in the two studies; McCasland inserted a filled piece of tubing with an outer diameter that matched the inner diameter of the bronchus; Hartley and Suthers filled the bronchus with an injection of elastic impression medium. The plugs in the latter case were probably longer and extended further towards the lungs, but it is not obvious how this difference would contribute to the observed differences in the data.

After obtaining post-operative recordings from birds with a bronchus plug in place, Hartley and Suthers (1990) then denervated the syringeal musculature on the same side to determine what further effect, if any, this procedure had on the bird's ability to sing. They found that, whereas denervation of the right side did not produce additional effects on singing in a bird with a plug on the right, analogous denervation of the left side caused a further loss in the vocal repertoire. This outcome suggests that neuromuscular activity on the left side of the syrinx can influence the behavior of the contralateral side. Given that no peripheral neural "crossovers" have been identified in oscine birds (i.e., the left tracheosyringeal nerve does not appear to innervate the right side, and vice-versa), Hartley and Suthers (1990) argued that the effect may be due either to an anatomical coupling (perhaps similar to that postulated by Nowicki and Capranica to account for bilateral interactions in the *dee* syllable), or to the loss of sensory feedback.

Another result using the bronchus-plugging technique was obtained by Nowicki (1989, unpubl.data). Working with swamp sparrows (*Melospiza georgiana*), Nowicki found that birds with either their left or their right bronchus plugged were capable of singing entirely normal songs. Unlike earlier studies, Nowicki measured acoustic similarities quantitatively, using the spectrogram cross-correlation technique of Clark et al. (1987). This quantitative approach revealed that post-operative birds sometimes produced normal song notes, but might also produce the same notes with measurable deficits. Ipsilateral denervation of a plugged bird always resulted in deficits that were similar to those seen after unilateral denervation alone. Finally, Nowicki added a third manipulation, immobilizing the syringeal membrane on the plugged side by physically anchoring the posteriormost one-third of the membrane with glue. This manipulation also resulted in deficits comparable to those seen after unilateral denervation alone.

The fact that swamp sparrows with bronchus plugs can sometimes produce normal songs seems at first to support McCasland's (1987) original finding, but this interpretation is misleading for several reasons. First, evidence from unilateral denervation alone shows that swamp sparrows do not exhibit lateral dominance (i.e., denervation of the left side does not result in more severe deficits than does denervation of the right, or vice versa). Many individual notes are partially affected by denervation of either side, suggesting that bilateral innervation, at least, is required for their production. Furthermore, McCasland's interpretation implies that denervation of the plugged syringeal half would not have any additional effect on production (although he did not himself perform this second manipulation), but Nowicki found just the opposite. In fact, Nowicki's findings are in this sense more similar to those of Hartley and Suthers (1990), who also found an effect of ipsilateral denervation following plugging on the left side.

Nowicki's (1989) results, then, are compatible with a two-voice model of production, in the context of a species that does not show functional dominance of one side in production overall. The finding that immobilization of the syringeal membrane ipsilateral to a plug has an effect similar to ipsilateral denervation is the most puzzling in that it suggests that vibration in the membrane on the side of the plug contributes to production. One interpretation is that left and right syringeal membranes are excited as a single unit in swamp sparrows, even by unilateral airflow, and that normal syringeal function requires both bilateral innervation *and* unimpeded mechanical activity of both syringeal membranes.

The bronchus-plugging technique seemed at first to offer an important new source of insight into the two-voice theory. However, the contradictory results obtained by McCasland (1987) and Hartley and Suthers (1990) when testing the same species, along with the additional differences seen by Nowicki (1989) in another species, have not clarified issues of peripheral lateralization of syringeal function. Certainly, comparisons between species must be considered with caution. Imperfect understanding of syringeal mechanics hampers interpretation of these data, as does the fact that bronchus plugging, like denervation, is an indirect method of understanding syringeal function.

The most direct technique for assessing the relative contributions of the left and right halves of the syrinx is that developed recently by Suthers (1990), in which miniature microbead thermistors are implanted in both the left and right bronchi just below the syringeal membranes. This technique is the same as that used by Hartley and Suthers (1989) to explore the mini-breath hypothesis (as described in Sect 2.1), except that two

transducers are used. Each transducer is in a separate airway (one in each bronchus) upstream from the syrinx, as opposed to a single transducer in the common airway (the trachea) downstream from the syrinx. Furthermore, the thermistors used by Suthers (1990) were sufficiently sensitive so as to detect the air oscillations corresponding to the near field of the acoustic signal generated by the syringeal membrane up to about 3 kHz. Thus, using this technique, Suthers could simultaneously measure respiratory flow and record the acoustic activity on each side of the syrinx independently in a singing bird.

Recordings made in this way from grey catbirds (*Dumetella carolinensis*) and brown thrashers (*Toxostoma rufum*) yielded several interesting and important findings (Suthers 1990; Suthers et al. 1994). First, of course, was the unequivocal verification of the two-voice theory as it was first proposed over three decades ago. In both species, 10–23 % of all syllables produced (among the six individuals studied) were produced by either the left or the right side of the syrinx acting alone. Syringeal activity sometimes switched from one side to the other for different syllables within a song, as expected from Greenewalt's (1968) model (see Figure 5). In 21–67 % of the syllables recorded from these birds, both sides of the syrinx were simultaneously active, also as predicted by Greenewalt. In some of these cases, both sides appeared to generate identical sounds, a result that is reminiscent of the argument advanced by McCasland (1987). Most importantly, however, in other such cases the two syringeal halves produced separate sounds with independent frequency modulations that were not harmonically related. These observations provide incontrovertible evidence in support of the long-standing two-voice hypothesis.

These data do not provide evidence, however, for lateral dominance in song production. None of the species Suthers has examined show a consistent pattern of favoring one side over the other (Suthers 1990; Suthers et al. 1994). Some individuals do favor one side in the production of syllables involving only that single side, although never as strongly as the effect observed in chaffinches by Nottebohm (1971) or in canaries by Nottebohm and Nottebohm (1976), but individuals vary as to which side is emphasized. This finding is surprising given the number of species in which lateral dominance was reported using Nottebohm's denervation technique (reviewed in Nottebohm 1980). It is unclear whether catbirds and thrashers are exceptional in showing a lack of lateral dominance in production, or whether canaries and chaffinches are more unusual in showing it strongly. Most of the earlier work using unilateral denervation relied on subjective visual analysis of spectrograms to assess post-operative effects. Studies that have quantified effects (e.g., Nowicki and Capranica 1986b; Nowicki 1989) have failed to find evidence for strong lateral dominance in several species, including black-capped chickadees, swamp sparrows, and song sparrows (*Melospiza melodia*). Taken together, this fact, the more direct nature of Suthers' thermistor technique, and the difficulties in interpreting bronchus-plugging results all suggest that the patterns observed by Suthers may be the most typical of how songbirds sing.

Studies using flow meters implanted in the bronchi show that different species of passerines exploit the potentials of a bilateral syrinx in various ways. Some, such as mimids (Suthers et al. 1994), appear to be able to use either side with equal facility. Even among mimids, however, there is a tendency to produce certain note types or certain portions of the frequency range using one side. In species such as cowbirds, *Molothrus*

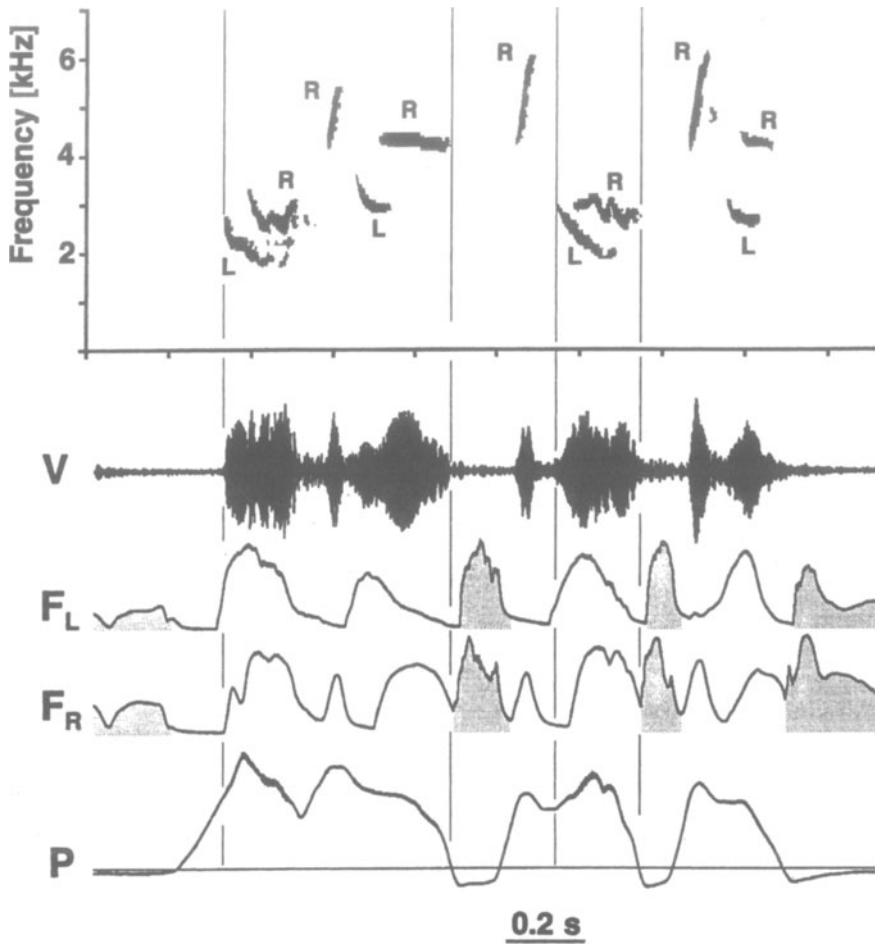


Fig. 5. A segment of brown thrasher song including syllables with two-voice and single voice components. The *top panel* is a spectrogram of the song segment, with contributions from the left side *L* and right side *R* marked. The *lower traces* show the acoustic waveform of the vocalization (*V*), air flow through the left (*FL*) and right (*FR*) sides of the syrinx (measured by a heated thermistor in each primary bronchus), and respiratory pressure (*P*) recorded in the thoracic air sac. *Shaded areas* under the air flow traces indicate inspiration, *unshaded areas* indicate expiration (From Suthers et al. 1994 ©, reprinted by permission of John Wiley and Sons, Inc.)

ater (Allen and Suthers 1994) or northern cardinals, *Cardinalis cardinalis* (R.A. Suthers, pers. comm.), one or more of these tendencies may become fixed, so that the two sides are each dedicated to the production of only a portion of the species' sounds. Extreme dominance, with all or most of the repertoire being produced by one side, appears to be an extension of such specialization.

Suthers' work (Suthers 1990; Allen and Suthers 1994; Suthers et al. 1994) has begun to reveal other, more complex patterns of how the two syringeal halves work together in sound production. He has documented, for example, cases in which the two sides alternate in the production of a sound that otherwise appears continuous. Responsibility for producing the sound appears to be passed back and forth between the two sides, sometimes several times in a single syllable (illustrated in Figure 6). In other cases, one side is active first, with the other side then joining in, again in the context of a single continuous acoustic element. Perhaps most interesting are cases in which both sides are active and the emitted signal is amplitude-modulated at a periodicity that is equal to the difference in frequencies between the two sides. This phenomenon (referred to as *beating*) is a linear interaction between the two syringeal sides that approaches the complexity of the nonlinear cross-modulation proposed by Nowicki and Capranica (1986a,b). We expect that work using microbead thermistors to measure airflow will continue to reveal new and interesting facts about the functioning of the syrinx.

2.3

Tracheal Modulation

Until recently, it was widely assumed that the suprasyringeal vocal tract plays little or no role in sound production in birds (see reviews in Brackenbury 1982, 1989; Gaunt and Gaunt 1985b; Gaunt 1987). One reason for this assumption is that many bird songs include predominantly pure-tone sounds whose simple spectral characteristics do not appear to require any involvement of vocal tract filtering (Marler 1969; Nowicki and Marler 1988). In contrast, such effects are critical to the source-filter theory of speech production (Fant 1960; see also Rubin and Vatikiotis-Bateson and Owren and Bernacki, this Volume). This model suggests that the human supralaryngeal vocal tract acts as a complex acoustic filter that modifies the amplitude spectrum of the laryngeal source signal through its resonances and anti-resonances. Because the larynx produces a broadband harmonic signal, the acoustic consequences of vocal tract filtering are observed as time-varying changes in the relative amplitudes of different frequency components in the signal. In pure-tone birdsongs, whose acoustic energy is concentrated at a single frequency, there appears at first glance to be no functional role for an acoustic filter that selectively attenuates different frequencies.

Sound production in birds can also be compared to characteristic production processes of musical wind instruments, such as trumpets and clarinets. For the latter, the source energy (i.e., buzzing lips in the case of trumpets and other brass instruments, vibrating wooden reeds in the case of clarinets and other woodwinds) is tightly coupled to the acoustic resonances of the body of the instrument. Specifically, due to this coupling effect, the fundamental frequency of vibration (or its overtones) in the source is constrained to match the resonance frequencies determined by the overall length of the instrument's air flow tube, an aspect that the player may continuously change through adopting various fingering positions (Benade 1976). A significant implication of this model, then, is that there is a necessary relationship between the effective length of the tube and the frequency of sound produced. In the case of birds, the relevant tube is most likely to be the trachea. As the tonal nature of many birdsongs is more reminiscent of

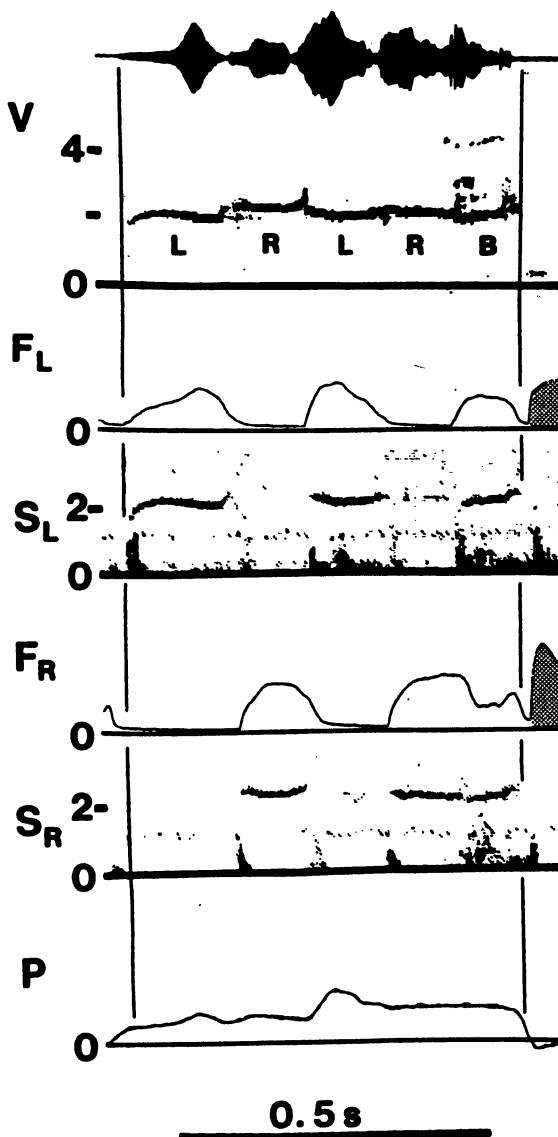


Fig. 6. Syllable from a catbird song showing alternating contributions from the left, right, and both sides of the syrinx. Abbreviations as in Fig. 5. Also shown are spectrograms of the isolated acoustic signals, as recorded directly from the two thermistors in the bronchi, produced by the left (S_L) and right (S_R) sides of the syrinx (From Suthers 1990, used with permission).

the typical sounds of musical instruments than of the broadband sounds of speech (Nowicki and Marler 1988), the analogy seems applicable, at least on the surface.

Greenewalt (1968) addressed this possible similarity by looking for a correlation between tracheal length and dominant song frequencies across many species of birds.

He failed to find such a correlation, however, and therefore argued that tracheal resonances are not important in the production of birdsong. Greenewalt further proposed that the changes in tracheal length that would be necessary to account for the range of acoustic frequencies often observed within a single species' vocal repertoire were too great to provide a plausible mechanism for frequency modulation. Finally, Greenewalt argued that if tracheal resonances influenced the acoustic properties of a bird's song in any way, one should find evidence of resonances and anti-resonances in song notes exhibiting large continuous changes in the fundamental frequency (*glissandi*). These resonances and anti-resonances should be observed as amplitude increases and decreases, respectively, at frequencies predicted by the length of the birds vocal tract. Greenewalt failed to find such evidence in his analysis of the songs of dozens of species.

A related reason why vocal resonances were discounted as an important factor in song production was that the widely accepted Greenewalt-Stein model of song production appeared to adequately account for the modulations typically observed in bird sounds based on the mechanics of the syringeal sound source alone. Changes in the tension of the vibrating membranes and in the position of other tissues (such as the external labia) were held to account for the characteristic patterns of frequency and amplitude modulation that characterize most bird sounds. In other words, the Greenewalt-Stein model did not need to evoke extrasyringeal influences on sound production, either in terms of frequency modulation occurring at the source (the wind instrument analogy) or vocal-tract-based spectral shaping (the speech analogy).

However, these particular analogies represent only the extreme cases in a broad array of ways in which the acoustic properties of a bird's vocal tract might affect sound production. The first question to ask, whether the vocal tract has any influence at all, was readdressed by Nowicki (1987) using a simple technique for manipulating vocal tract acoustic resonances. Acoustic resonance is dependent on the speed of sound, which is in turn dependent on atmospheric density (Rayleigh 1896). If nitrogen, which comprises about 80 % of normal air, is replaced by helium, then the velocity of sound increases from 331 to 578 m/s, which produces a corresponding upward shift of roughly 75 % in the acoustic resonance frequencies of air-filled chambers or tubes. Thus, if the vocal output of a bird is affected by singing in a helium-oxygen atmosphere (i.e., *heliox*), it is safe to conclude that acoustic properties of the vocal tract do play some role in production.

Nowicki (1987) observed striking changes in the acoustic structure of the songs of ten different songbird species recorded in *heliox*. The most obvious effect of *heliox* on song production was the appearance of harmonic overtones for song elements appearing as pure tones in normal atmosphere (see Figure 7). Another effect was an overall reduction of as much as 10 dB in the amplitude of the sounds produced. Unlike the effect that would be predicted for an analogous experiment using a wind instrument, however, there was *not* an appreciable shift in the fundamental frequencies of various song elements. Such an effect would be predicted if coupling between acoustic resonances and the frequency of vibration of the sound source was occurring. A shift of 3 - 5 % was observed, but this outcome was an order of magnitude less than would be expected if coupling were occurring. However, the effects that Nowicki (1987) observed were also not obviously consistent with a source-filter model, such as that proposed for human speech. The dominant effect of *heliox* on speech production is to shift the emphasized

frequencies (formants) in a broadband, harmonic sound to correspondingly higher values. The appearance of harmonics above a previously pure-tone fundamental frequency appears to be quite different. Thus, although the results of the heliox experiment suggested that acoustic resonances do have a role in birdsong production, it is not immediately apparent what this role might be.

In spite of the apparent differences from typical speech production, Nowicki (1987) argued that the effects of heliox on birdsong could be explained by modeling the songbird vocal tract as an acoustic filter. For instance, the appearance of harmonics in heliox might have been due to the upward shift of the filter, allowing acoustic energy that was previously heavily attenuated to pass more readily (see Figure 8). Consistent with this view, broadband bird sounds recorded in this study showed a change in the relative amplitude of overtones at different frequencies. An overall decrease in the amplitude of pure-tone sounds recorded in heliox would result from damping of the fundamental frequency, which would no longer be in the center of a resonance peak. In this view, then, the source-filter model of speech is an appropriate analogy for the role of the vocal tract in birdsong production.

Although the heliox experiment demonstrated that acoustic resonances can influence song production, at least two problems remained in interpreting the results. First, it could be argued that both the magnitude of the upward shift in acoustic resonance frequencies (more than 70 %) and the striking nature of the observed effects (the appearance of strong harmonics in a normally pure-tone sound) were too large to be biologically relevant in normal song production. Furthermore, an important implication of the heliox experiment result is that birds should be capable of dynamically modifying the acoustic properties of their vocal tracts while singing (Nowicki and Marler 1988). It remained unclear if and how birds could accomplish such modification.

Both of these criticisms were addressed by Westneat et al. (1993), who used kinematic analysis to quantify motions of the head, throat, and beak in singing birds. If acoustic properties of the vocal tract are important in production, then changes in resonances should correspond in turn to changes in the physical configuration of the tract. If the vocal tract of a bird is modeled as a tube that is open at one end, there are three simple ways in which its acoustic resonances might be altered (Nowicki and Marler 1988). First, the tube itself could be lengthened or shortened. Second, the open end of the tube could be occluded to varying degrees. Finally, the open end of the tube could be flared to varying degrees.

Greenewalt (1968) argued that it is unlikely that a bird can change the length of its vocal tract to any great degree, even though a bird's trachea may be extensible. He did not, however, address the last two possibilities. The beak is especially well-positioned to modify the acoustic properties of the vocal tract, either by changing the actual length of the tract through the degree to which it is flared (analogous to lip-rounding in human speech production (see Lieberman 1977) or by changing the impedance at the open end and thereby altering the effective length of the tract (a bird might also occlude the open end of its vocal tract, and be able change impedance by varying the opening of the glottis, i.e., the tracheal opening just posterior to the oral cavity). For instance, a more closed beak should correspond to lower-frequency vocal tract resonances, whereas a more open beak should correspond to higher-frequency vocal tract resonances. This is precisely the relationship Westneat et al. (1993) found in the songs of two species, the

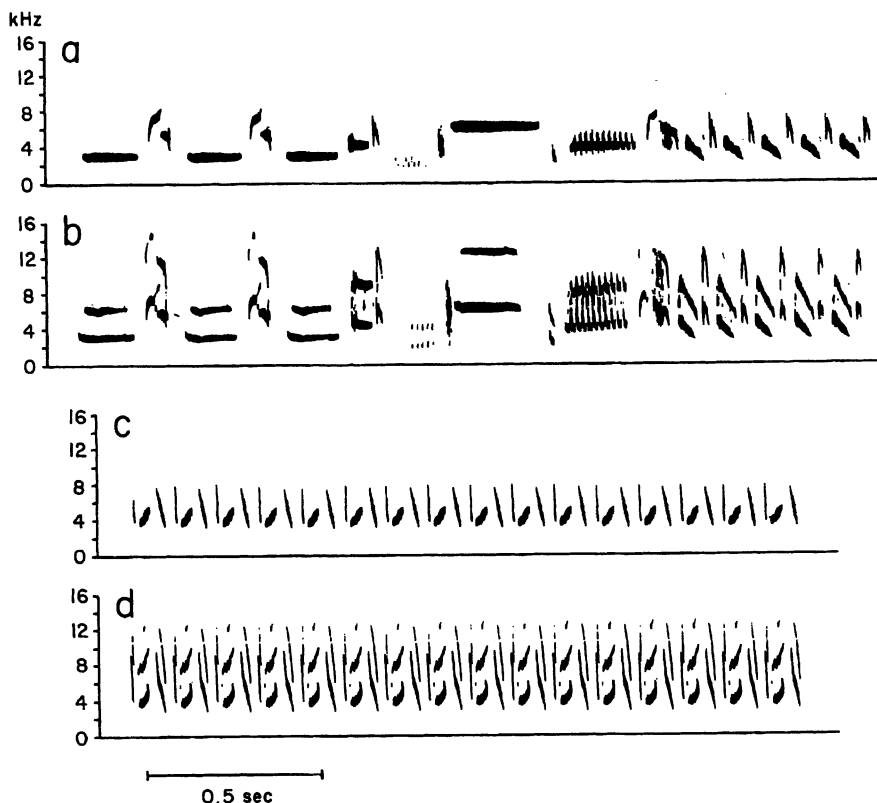


Fig. 7. Spectrograms of sparrow songs recorded in normal air and in heliox. A Song sparrow song in normal air. B The same song-type produced by the same bird as in A, but sung in heliox. C Swamp sparrow song in normal air. D The same song type produced by the same bird as in C, but sung in heliox (from Nowicki and Marler 1988, Regents of the University of California, used with permission)

white-throated sparrow (*Zonotrichia albicollis*) and the swamp sparrow. In white-throated sparrows, species-typical song comprises a series of unmodulated, pure-tone notes, each lasting up to 800 ms, with discrete frequency shifts occurring between adjacent notes. During song production, the beak opening was found to be relatively constant over the course of a given note, but changed abruptly between notes of different frequencies. Data from the swamp sparrow were even more compelling. This species' songs are composed of short, frequency-modulated notes that sweep through several thousand Hertz in as few as 10 to 20 ms. Even at this rapid modulation rate, each bird's beak was observed to open and close in accordance with note frequency (illustrated in Figure 9). In both species, other acoustic properties of the song, such as amplitude, were not correlated with beak opening. Other kinematic variables, such the angle of the head,

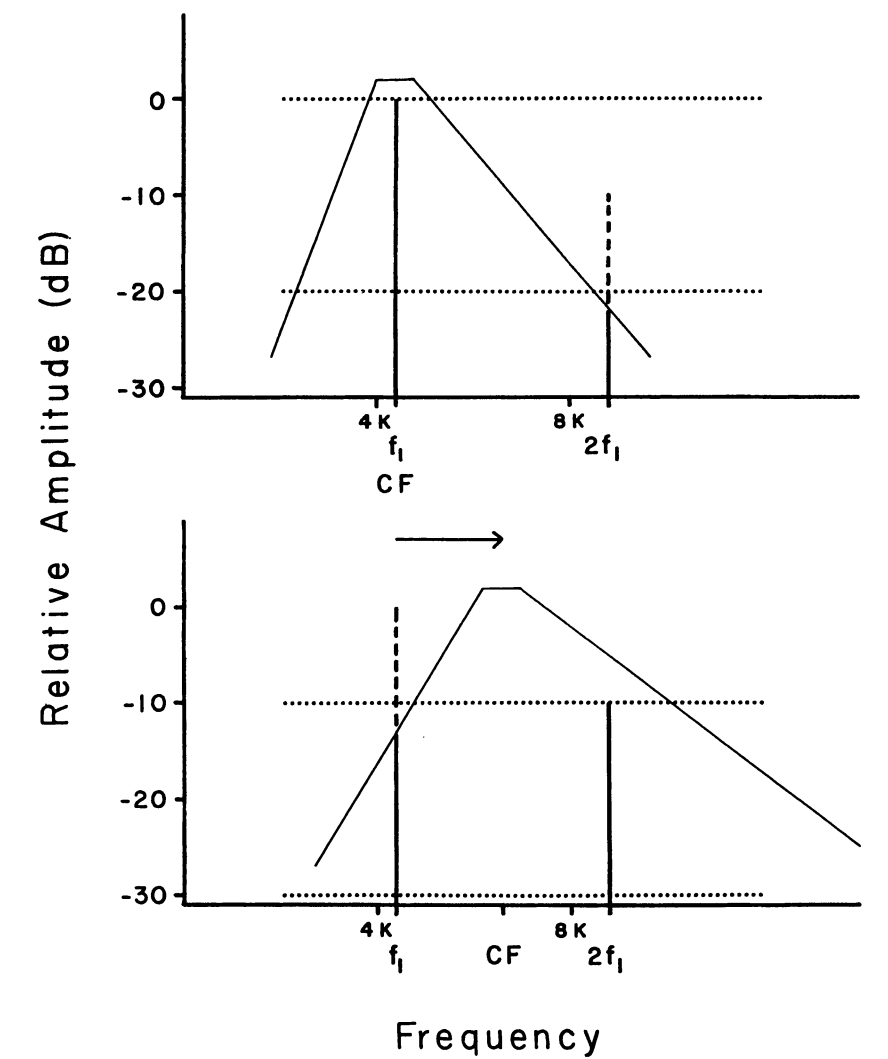


Fig. 8. Schematic illustrating the shifting acoustic filter interpretation of the observed effects of heliox on birdsong production. In normal air (*above*), the filter is centered over the fundamental frequency produced by the syrinxal source, resulting in the attenuation of the second harmonic. In heliox (*below*), the vocal tract filter's center frequency is shifted upward by almost 70 %, attenuating the fundamental and revealing the second harmonic. The hypothetical filter roll-off is 24 dB/octave; the asymmetry is the result of representing the filter function on a linear frequency axis. Horizontal dotted lines represent a 20-dB dynamic range, characteristic of older analog spectrographs (From Nowicki and Marler 1988, Regents of the University of California, used with permission)

were also not related to acoustic properties of the song. Thus, Westneat et al. (1993) concluded that beak opening and closing could provide a mechanism by which a bird dynamically changes the acoustic properties of its vocal tract, consistent with the interpretation that such dynamic changes are involved in normal sound production.

Beak motions are not necessarily the only means by which birds might vary the acoustic properties of the vocal tract. For instance, postural changes involving the opening and closing of the glottis, as well as changes in the length and position of the trachea, might contribute to the acoustic properties of a bird's vocal tract just as the positioning of various articulators in the human vocal tract affect its resonances (Lieberman 1977). However, Westneat et al.'s (1993) kinematic analysis did not conclusively demonstrate that beak motions are necessary for normal production of birdsong. Such a demonstration would require that experimental manipulation of the putative mechanism controlling tract resonances (e.g., the beak) be found to produce a predictable change in vocal output.

Nowicki et al. (unpubl. data) provided just such a demonstration by comparing songs produced under normal conditions with those produced when a subject's beak had been immobilized. They argued that this manipulation would not prevent a bird from being able to produce the full range of frequencies observed in normal song, given that the heliox experiment had demonstrated little or no direct coupling between the activity of a bird's vocal source and suprasyringeal vocal tract resonances (i.e., changes in tract resonances, such as that observed in the heliox atmosphere, did not result in a shift in the fundamental frequency). However, limiting beak motion would restrict a bird's ability to modify vocal tract resonances if such motions do in fact represent a mechanism by which dynamic changes can be effected. In this case, the predicted effect of the manipulation is a frequency-dependent change in the amplitudes of sounds produced, with frequencies that are farther from the experimentally fixed vocal tract resonance being more attenuated than those falling closer to this fixed resonance. Nowicki et al. (unpubl.) recorded three white-throated sparrows and three swamp sparrows before, during, and after their beaks were immobilized. In all cases, the relative amplitudes of sounds at different frequencies were affected as predicted.

This last study conclusively demonstrates that changes in vocal tract acoustic properties, mediated by beak motions (and probably by other postural changes of the vocal tract), are a necessary feature of normal birdsong production. This finding is an important and quite unexpected departure from earlier thinking about this topic. The technical approaches used, however, were not particularly sophisticated or advanced. Instead, a suite of straightforward techniques were combined with simple physical insights to develop the necessary evidence. Not all advances await new technology; sometimes they simply await new ideas.

3

Quo Vadis?

Despite notable progress on several fronts, some of the oldest questions in the field of syringeal function still remain. Many of these questions concern the syringeal membranes and how they produce sound. Questions also remain about the two-voice theory.

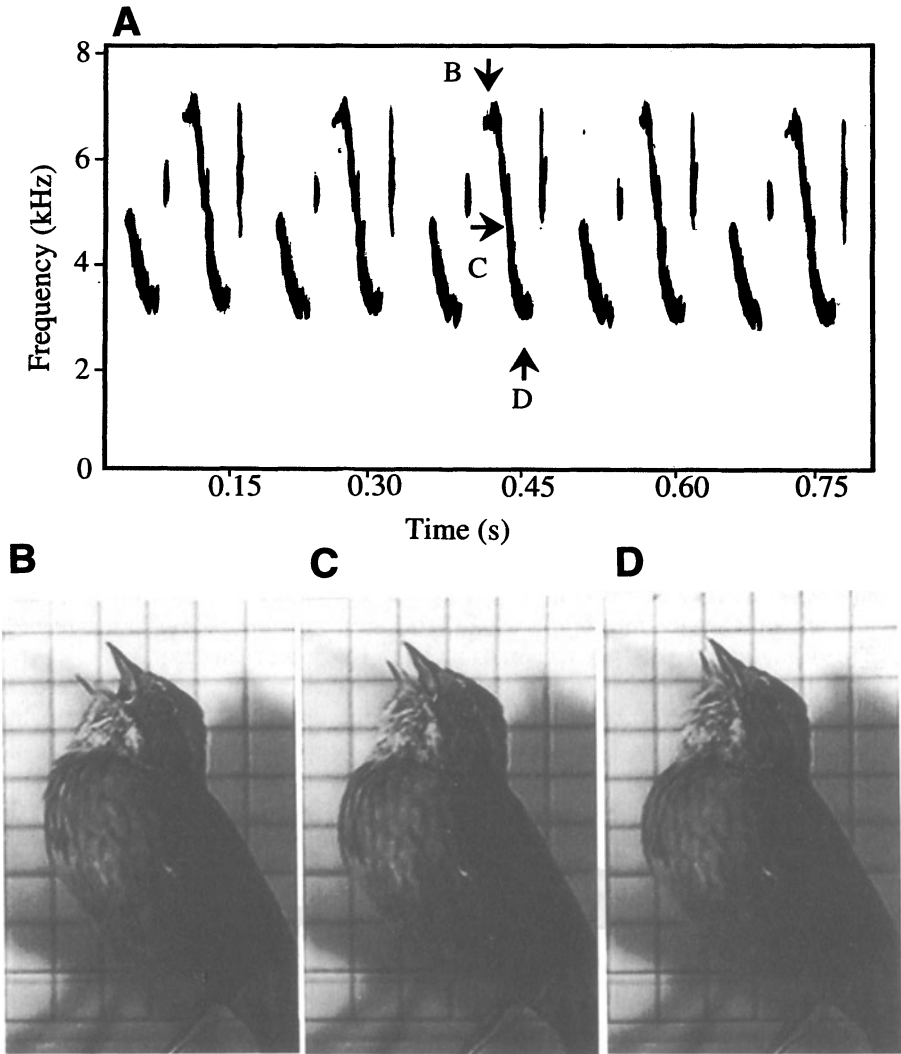


Fig. 9. A Spectrogram and video B-D images of a swamp sparrow song. The three images are adjacent video fields showing the progressive closure of the beak as the bird makes a downward frequency sweep. The *arrows* in A identify the points in time over the duration of the *type-V* note from which the video fields in B, C, and D were taken (From Westneat et al. 1993, used with permission)

Although it has now been demonstrated that birds are capable of singing a true internal duet (Suthers 1990), it also seems clear that multiple acoustic sources may interact in ways that we are only beginning to understand (e.g., Nowicki and Capranica 1986a). Finally, the role of the vocal tract in production remains unclear. Although the importance of the vocal tract in vocal production in songbirds is now firmly established (Westneat et al. 1993), the precise acoustic nature of this action, as well as the possible diverse

modes of action it might take, are still to be explored. The role of vocal tract acoustics in other vocal production in other groups may well be different than in songbirds (e.g., Gaunt et al. 1987) and further study is clearly needed.

3.1

Membrane Physiology and Vibration

The Greenewalt-Stein model suggests that stable vibration in a syringeal membrane arises when airflow from the lungs creates a Bernoulli effect, lessening pressure on the side of the membrane exposed to the flow and thus drawing the membrane further into the lumen of the bronchial tube. As the membrane extends further into the tube, the Bernoulli force and the counteracting forces of the membrane's own elastic tension eventually become equal, and the former decreases through viscous flow losses. The membrane then retracts until the two forces again reach equilibrium and another cycle begins. Thus, the forces responsible for driving oscillation in the syringeal membranes are thought to be similar to those acting on the vocal folds in human speech production (see Rubin and Vatikiotis-Bateson, this Volume). One major problem with this model, however, is the possibility that the Bernoulli effect is not applicable given the particular pressures, flow rates, and membrane diameters characteristic of songbird syrinxes (Fletcher 1989; see also Vogel 1994). Because no one has ever directly observed the vibration of a syringeal membrane, we are left in the uncomfortable position of having an inadequate model of a phenomenon that may or may not even occur!

Granting the likelihood that syringeal membranes are indeed somehow induced to vibrate, there is a further controversy concerning the nature of that vibration and the kinds of sound a syringeal membrane is likely to be able to produce. The question is whether a freely oscillating syringeal membrane will produce pure-tone sounds, harmonic sounds, or sounds with some more complex set of overtones (Goldspink 1983). Casey and Gaunt (1985) raised objections to the possibility that an edge-clamped membrane, vibrating at right angles to the direction of air flow as the Greenewalt-Stein model suggests, could produce either pure tones or even a simple harmonic series. Fletcher (1988, 1992) presented a more sophisticated mathematical model that showed that, in a nonlinear system, the objections of Casey and Gaunt do not hold. Nonetheless, although Fletcher's model worked well for predicting the harmonic tones of a corvid, he also was unable to account for pure tone, or whistled, phonations. The work of Nowicki and his colleagues on vocal tract function in songbirds (Nowicki 1987; Westneat et al. 1993; Nowicki et al., unpubl. data) may obviate this concern, since their results suggest that the primary functional role of the vocal tract is to filter out or otherwise suppress overtones that are present in the source energy. Nonetheless, considerably more work with mathematical models is needed. As Fletcher (1988, p. 457) states: "Only when we can construct a quantitative model with reasonable success can we claim to understand the sound production mechanism".

Interestingly, almost all attempts at modeling (Greenewalt 1968; Gaunt and Wells 1973; Brackenbury 1979, 1982; Casey and Gaunt 1985; Fletcher 1988) have assumed a membrane that enters the lumen as a uniform, semi-hemispherical bulge. Yet some direct observations have suggested that the membrane folds into the lumen rather than

distending, projecting an edge into the airstream rather than a dome-like surface with approximately uniform tension along all axes (Beebe 1925; Paulsen 1967; Suthers and Hector 1982, 1985). In fact, the membranous portions are supported by C-shaped half rings that are either bony and rigid, or cartilaginous and elastic. These rings are positioned so as to maintain tension on the membrane along either a dorso-ventral or medio-lateral axis, depending on its position. If movements of the trachea or syrinx relax the membrane along the antero-posterior axis, tension along the orthogonal axis is maintained. Moreover, most intrinsic syringeal muscles are so arranged that, regardless of whatever else they may do, they will apply an “opening out” vector to the ends of the C-shaped rings. Thus, their activity should tend to increase the uniaxial tension on the membrane.

Clearly, our models will be much improved when we understand the various configurations the membranes may adopt under different conditions. Two kinds of information will be useful. The first will come from more detailed studies of the anatomy and material properties of the syrinx and its membranes. For example, questions about how a membrane distends will be informed by understanding whether the membrane stretches uniformly in all dimensions, which in turn can be predicted from knowledge of the types and orientation of fibers in the membrane (see e.g., Wainwright 1988) and measured *in vitro*. Direct *in vivo* imaging of membrane actions during song production would be more informative still. Such imaging is technologically challenging due to both the inaccessible position of the syrinx in the thoracic cavity in most species and the extremely high vibration rates involved. Although the requisite laser interferometry and small-fiber optic cable might be technology that is available, its application to bird-song physiology requires the use of equipment that can detect a signal under the adverse conditions likely to be associated with the small size of the optic fiber needed to be implanted, as well as development of a surgical procedure for implanting, fixing, and aiming this cable in a bird in a way that still allows singing to occur.

3.2

Syringeal Physiology and Modulation

It appears likely that the characteristic time-varying changes in the frequency and amplitude of a typical birdsong fundamental (i.e., its *contour*), as well as more rapid frequency and amplitude modulations, are traceable to the syrinx and are controlled by the syringeal musculature (Gaunt and Gaunt 1985b; Vicario 1991). Further, we now have direct evidence that songbirds, at least, can use two sources independently in sound production (Suthers 1990; Suthers et al. 1994). Specifically how modulations are controlled at the source, however, is less clear. There is as yet little direct information about how the syringeal musculature affects the membranes and other aspects of syringeal configuration, let alone the specific acoustic features of a bird's song. The range of possible interactions and combinations of the activity of two sound sources has only just begun to be explored. In some cases, the two sources appear to work in complete independence (Suthers 1990). In other cases, interactions between them produce complex, nonlinear modulations (Nowicki and Capranica 1986a,b). These cases probably represent only two extremes in a continuum of possible interactions.

Studies that combine the use of miniature flow and pressure transducers with EMG have begun to yield important new information on syringeal function. For example, Suthers and Hector (1982, 1985) demonstrated that the gating of sound (passage of air pulses) is mediated by actions of extrinsic syringeal musculature in grey swiftlets and oilbirds. More recently, Goller and Suthers (pers. comm.) have obtained EMG, flow, and pressure data that suggest specific roles for individual intrinsic syringeal muscles. However, these preliminary results are not entirely consistent with earlier models of syringeal function. The intrinsic musculature seems to function as three groups: left-dorsal, right-dorsal, and ventral (Vicario 1991; Goller and Suthers 1995), at least as far as can be determined from present sampling methods. The dorsal muscles appear to be active primarily in gating, possibly by inserting the lateral labium into the syringeal lumen. Gating is independent for the two sides (as would be predicted by the two-voice theory). The ventral muscles appear to moderate the tension on the typaniform membranes. Oddly, both the phonatory and silent sides appear to be active during all song elements. Thus, the oscine syrinx may function in a less complex fashion than its anatomy would suggest. Coupling of flow measurements with precision electromyography will continue to elucidate this problem, but the exceedingly small size of the syrinx, the difficulty of identifying particular muscles and other functionally important elements involved in phonation, and the acoustic complexity of all but the most simple birdsongs will continue to present a challenge to the most adroit experimentalists.

Note added in proof. Progress in the analysis of syringeal function has outstripped the speed of the publishing process. Recent papers, especially from Suthers and his co-workers, have shown that 1) dominance of one side, usually the left, is common; 2) the silent side is closed; 3) the left side is usually responsible for low frequencies; and 4) some birds are capable of a seamless transition from one side to the other during a frequency sweep. Much of this work is reviewed in R.A. Suthers and F. Goller, 1997. Motor correlates of vocal diversity in songbirds. In: *Current Ornithology* (Val Nolan, Jr. and Ellen Ketterson, eds.) Vol. 14. Plenum Press, NY. (In press).

3.3

Vocal Tract Physiology and Tonal Quality

As it has now been demonstrated that the vocal tract is an important element in sound production in birds, a whole new can of worms has been opened for physiologists interested in vocalization. Major questions whose importance was not even recognized previously must now be addressed. One of these concerns how vocal tract properties physically influence sound production. An obvious possibility is that the avian vocal tract acts as an acoustic filter in a manner similar to that proposed for the human vocal tract in speech production (Fant 1960; Lieberman 1977). If so, pure-tone whistles observed in birdsong are in fact likely to be based on harmonically rich source signals, with the vocal tract acting to filter out all but a single frequency (such as the fundamental or second harmonic). Although this model obviates the need to account for production of sinusoidal sounds by the syringeal membranes, it does require a vocal tract filter function with sufficiently sharp roll-off characteristics that all frequency components but one are strongly attenuated.

An alternative model also derives from comparisons to human vocal production, but one that involves soprano singing rather than speech. In the source-filter model of speech, source and filter act more or less independently. In soprano singing, by contrast, recent work suggests that an overlap between the fundamental frequency of vocal fold vibration and the lowest-frequency formant results in nonlinear feedback from the vocal tract to the glottis that effectively suppresses production of harmonics at the source (Rothenberg 1981, 1987a,b). A similar overlap between the fundamental (or second harmonic) of the syringeal source energy and a dominant resonance of the vocal tract is probably very common in birdsong production (Nowicki and Marler 1988). In both the speech-based and *soprano* models, a bird must dynamically coordinate the acoustic properties of its vocal tract with the output of its syrinx during song. In the latter case, however, the effect of this coordination is to suppress the production of overtones at the source, potentially providing a more parsimonious explanation for a bird's ability to produce virtually pure-tone song.

Both models of vocal tract function are compatible with the experimental evidence currently available. For example, one result of the heliox experiment — the appearance of harmonics above sounds that are normally produced as pure tones (Nowicki 1987), could equally well be explained by the shifting of a resonance filter, allowing higher frequency overtones to pass through the filter with less attenuation, or by a decoupling of vocal tract acoustic properties from the source, enabling the production of overtones that are normally suppressed at the source. Two approaches may provide data that would distinguish between these possibilities. The first involves modeling the properties of the avian vocal tract, both physically and mathematically, to determine the passive acoustic properties of the vocal tract and whether these properties can account for the attenuation of overtones occurring in normal song.

The second approach is experimental and involves testing song production in an atmosphere that is *heavier* rather than lighter than normal. In this manipulation, the passive acoustic properties (filtering effects) of the vocal tract are expected to shift to lower frequencies. The fundamental frequency should be attenuated, as in heliox, because it is no longer squarely centered under the passband of a vocal tract resonance. Unlike the case of singing in heliox, however, one might predict, at first, that this attenuation would *not* be accompanied by the appearance of higher-frequency overtones, because the filter function has been shifted to lower frequencies (but see below). If, on the other hand, the vocal tract is normally coupled in some way to the source, then a shift in vocal tract resonances to either higher or lower frequencies should both produce a decoupling effect. Overtones would appear because the source is no longer constrained to produce pure tones, irrespective of the fact that the filter function has been shifted to lower frequencies.

Tetrafluoromethane (TFM) is a gas of sufficiently greater density than nitrogen to produce a strong effect on vocal tract filtering and is also biologically inert. The speed of sound is decreased by about 35 % in an 80:20 mixture of TFM : O₂. Thus, a lowering of resonance frequencies by 35 % would be predicted, as compared to an increase of 70 % in the case of heliox (a total difference of about an octave).

Preliminary work with birds recorded in TFM has shown an effect that is qualitatively similar to that observed in helium, with the appearance of higher-frequency harmonics above the fundamental (Nowicki and Lohr, unpublished data). This result suggests that

the passive filter model is at least insufficient, if not incorrect, but closer examination reveals additional complications. Specifically, the lowering of the first resonance of the vocal tract in TFM : O² would be expected to be accompanied by a proportional decrease in the higher-frequency resonances! Consider a hypothetical case in which the dominant resonance of a bird's vocal tract is 4 kHz. In heliox, this resonance is predicted to shift upward to about 6.8 kHz. In TFM : O², it should shift downward to about 2.6 kHz. But if the vocal tract is modeled as a tube open at one end, an additional resonance is expected to occur at the three times the frequency of the lowest resonance (Benade 1976). This second resonance, normally at 12 kHz and therefore beyond the upper frequency limit of most birdsongs, will also shift downward, to about 7.8 kHz. In other words, in both heliox and TFM : O² we expect a resonance in the upper-frequency range. This unfortunate complication does not rule out the usefulness of the TFM : O² experiment. However, the analysis must include careful quantification of the relative amplitudes of frequency components and more accurate models of vocal tract acoustic properties.

Irrespective of which alternative proves to be the more accurate model of the vocal tract acoustic effects tract on song production, there is also much to learn about the peripheral effectors that control vocal tract acoustic properties and how those effectors are coordinated with the activity of the syrinx. Westneat et al.'s (1993) kinematic analysis of birdsong, which emphasized the role of the beak, merely scratched the surface of the functional morphology that must be considered. In addition, the use of x-ray cinematography to image the motions of internal structures, especially the opening and closing of the glottis, will provide a much broader view of the various effectors that contribute to a bird's ability to dynamically vary the acoustic properties of its vocal tract while singing. Finally, we deem it likely that it will be a futile exercise to consider "the function" of "the vocal tract" in birds. As with syringeal function, there are likely to be multiple modes of operation for the vocal tract and the way in which it interacts with the source signal. One has to consider only the call of the black-capped chickadee, which includes notes that change from extremely tonal frequency sweeps to wideband, harmonically rich sounds within a matter of milliseconds (e.g., Figure 3A; Ficken et al. 1978; Nowicki and Nelson 1990) to gain an appreciation for the possibility of qualitatively distinct modes of operation of a bird's vocal tract filter.

4

Summary

The last several years have seen significant progress in our understanding of some of the mechanisms used by birds to produce sound. Nonetheless, our knowledge in this area is rudimentary and our techniques primitive when compared to the accomplishments and approaches routinely employed by our colleagues who study human speech. We might suggest that birdsong production is more difficult to investigate because the signal is acoustically more variable and involves less accessible anatomical structures, but this argument would be specious. There is, however, one essential difference between birdsong and speech that bears mention. The important outcome of both speech and song is communication. Questions about the physiology underlying production

are restricted, if not informed to some extent, by an understanding of which aspects of the signal being produced are important for communicating information. In studies of speech, a human subject can be asked directly to report their perception or interpretation of a speech feature. We are not so fortunate when analyzing birdsong or other animal communication signals. Instead, clever tests must be devised both for the field and the laboratory that can provide glimpses into the relationship between structure and function in such signals. Recent progress in the use of articulatory synthesis in speech demonstrates the utility of understanding perception and meaning in analyzing the production mechanisms involved. Perhaps the next great advances in our understanding of birdsong physiology await the development, not of more sensitive or precise physiological techniques, but of methods for better understanding the relationship between structure and function in the songs themselves.

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