Chapter 9

How birds sing and why it matters

RODERICK A. SUTHERS

INTRODUCTION

Songbirds have both an aesthetic and a scientific impact on our lives. Birdsong adds beauty and vitality to our environment. The possibility of its absence due to increasing levels of environmental toxins, so eloquently described by Rachel Carson (1962) in her groundbreaking book, Silent Spring, was a potent factor in mobilizing public opinion to become better stewards of our environment. Scientifically, the highly developed vocal communication of this group, sharing as it does a number of parallels with speech, has made songbirds especially suited for the study of complex, learned vocal communication at every level, from its molecular biology to its evolution.

This chapter is about how birdsong is produced. How do birds generate such a variety of sounds and what vocal gymnastics are required to produce them? The vocal system is the interface between the bird's brain and its song. Knowing how it functions, and coming to appreciate its limitations as well as its capabilities, is important in understanding vocal communication. Birdsong is the product of the carefully coordinated activity of many different muscles. Some of these are associated with the vocal organ but many belong to other muscle groups such as the respiratory system and the vocal tract. Together they convert nerve impulses from the brain into song.

Less is known about the vocal mechanisms of non-songbirds, and they will be mentioned only briefly to indicate the variety of avian vocal systems, and to provide a perspective from which to focus on the oscine songbirds. Readers interested in additional information on songbirds should consult reviews of this subject (Nowicki & Marler 1988; Suthers 1997, 1999a, b; Gaunt & Nowicki 1998; Doupe & Kuhl 1999; Suthers et al. 1999; Goller & Larsen 2002).

AN ORGAN FOR SINGING

The avian vocal organ, the syrinx, is located deep in the chest in an air sac that is connected to other air sacs and the lungs. It is present in all birds except vultures, but its exact location and structure varies considerably (King 1989). In some species, including doves, pigeons and parrots, the syrinx consists of modified rings of cartilage near the lower end of the trachea (Fig. 9.1).

In other species, such as penguins, many owls, nightjars, oilbirds and some cuckoos, the syrinx exists as two semisyringes located in the primary bronchi (Fig. 9.1). In many birds, however, including but by no means limited to the oscine songbirds, the syrinx is at the junction where the two primary bronchi join to form the trachea. This tracheobronchial syrinx includes modified cartilages from both the upper end of each bronchus and the lower end of the trachea (Fig. 9.1).

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Figure 9.1 Examples of variation in syringeal anatomy. The tracheal parrot syrinx has two syringeal muscles and a pair of lateral tympaniform membranes. The bronchial syrinx of the oilbird has one pair of syringeal muscles and a pair of medial and lateral tympaniform membranes in each bronchus. Songbirds have a pair of syringeal muscles in their tracheobronchial syrinx. Tr, trachea; St, sterno-tracheal muscle; Sy, supralaryngeal syringeal muscle; Sy PROF, deep syringeal muscle; Sy VAL, pneumatic valve; LDM, lateral tympaniform membrane; BCI, first bronchial cartilage; Sy, syringeal muscle; ML, medial labium; LL, lateral labium; SYR, muscles of syrinx. (Oilbird modified after Suthers & Hector 1985; parrot and canary modified after King 1989).

The Timings of Vocalization and the Tempo of Song

The timing of vocalization and the tempo of songs begins with the respiratory cycle (Vicario 1991). Expiratory muscles compress the bellows-like air sacs in the thorax and abdomen, increasing respiratory pressure so air flows out through the syrinx and trachea (Hartley 1990). During song, a small inspiration called a 'mini-breath' (Calder 1970) is usually taken after each syllable, except at very high syllable repetition rates (Hartley & Suthers 1989). Inspiratory muscles expand the thorax and abdomen, reducing pressure in the air sacs and reversing the direction of airflow through the syrinx (Wild et al. 1998). Vocalization occurs during expiratory airflow, aside from rare exceptions when it occurs during inspiration, as in the 'walt' sounds of doves (Gaunt et al. 1982), and certain syllables in the songs of some zebra finches (Goller & Daley 2001). Most birds sing with their beaks open, but doves and pigeons coo with their beaks and nares closed. Sound is produced during expiratory airflow in an expiratory direction through the syrinx and into the esophagus. After each coo there is a short expiration followed by a brief inspiration (Gaunt et al. 1982).

The Source of Sound

It is now generally agreed that vocalizations are generated by airflow-induced oscillation of elements in the wall of the syrinx that convert some of the air's kinetic energy into acoustic energy. These oscillations are presumably sustained by interaction between Bernoulli forces and the inertia of air in the vocal tract, in much the same way as are oscillations of human vocal folds (Titze 1994; Gardner et al. 2001). An alternative mechanism for sound production based on the principle of an aerodynamic whistle was put forth (Gaunt et al. 1982) to explain pure tone vocalizations in birds such as doves. However, this aerodynamic whistle hypothesis is not supported by the observation of...
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In other species, such as penguins, many owls, nightjars, oilbird, and some cuckoos, the syrinx exists as two semisyrinxes located in the primary bronchi (Fig. 9.1). In many birds, however, including but by no means limited to the oscine songbirds, the syrinx is at the junction where the two primary bronchi join to form the trachea. This tracheobronchial syrinx includes modified cartilages from both the upper end of each bronchus and the lower end of the trachea (Fig. 9.1).

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tymaniform membrane vibration in pigeons (Goller & Larsen 1997a), or by experiments with collared doves vocalizing in light gas mixture (Ballintijn & ten Cate 1998). In both collared doves and ringdoves, there is evidence that the sound generated in their syrinx contains prominent harmonics, which must be filtered out by the vocal tract to produce the tonal properties of the coo (Beckers et al. 2003b).

The anatomical structures in the syrinx that produce the sound differ with the syringeal anatomy. Goller and Larsen used a fiberoptic endoscope to make direct observations of syringeal motion during vocalizations elicited by stimulating vocal control regions in the brain of anesthetized birds (Box 37, p. 277). In the tracheal syrinx of pigeons they showed that the lateral tymaniform membranes (LTMs), on each side of the trachea bulge toward each other into the syringeal lumen during vocalization where they form a slit-like aperture and vibrate during respiratory airflow (Goller & Larsen, 1997a, b; Larsen & Goller 1999). The LTMs (Fig. 9.1) also can be seen to fold into the tracheal lumen and vibrate during vocalization in the tracheal syrinx of the cockpitel (Larsen & Goller 1999, 2002).

In songbirds, the relatively well-developed medial tymaniform membrane (MTM) at the cranial end of each bronchus was long assumed to be the source of sound (~iskimen 1951; Greenewalt 1968; Fletcher 1988; Gaunt 1988; Figs. 9.1 & 9.2). However, endoscopic observations of the songbird syrinx during vocalization reveal that it is the connective tissue forming the internal and external labia at the anterior end of each bronchus that is adducted into the syringeal lumen and vibrates during vocalization (Larsen & Goller 1999). Surgical removal of both MTMs has only a minor effect on the vocalization, demonstrating that whatever their function, they are not essential for song production.

Syringeal Muscles Have Separate Functions

The muscular apparatus capable of acting on the syrinx to control vocalization receives input from the brain by the hypoglossal nerve. In some species, such as swiftlets, there are no intrinsic syringeal muscles, meaning muscles having both their origin and insertion on the syrinx (Box 36, p. 275). In these birds, syringeal function during vocalization is controlled by muscles that have at least one of their attachments outside the syrinx. Other birds, such as parrots, have one or more pairs of specialized syringeal muscles.

Doves have two pairs of extrinsic syringeal muscles (see Fig. 10.5, p. 310). One, the sternotraechalis, reduces the tension across the syrinx and allows the lateral tymaniform membranes to fold into the tracheal lumen where airflow causes them to vibrate. Contraction of the other muscle, the tracheolateralis, abducts the tymaniform membranes out of the lumen and terminates phonation (Goller & Larsen 1997a). The role of these muscles, if any, in frequency modulation of coos is uncertain. Gaunt (1988) reported that during a coo both muscles are simultaneously active in ring doves, and Beckers et al. (2003) demonstrated that gradual modulation in the coo, but not abrupt frequency jumps, closely parallels pressure changes in the interclavicular air sac, suggesting expiratory muscles may be important regulators of sound frequency. Amplitude modulation of coos is associated with interruptions of tracheal airflow presumably due to tracheal closing and opening of a valve, perhaps formed by the adducted tymaniform membranes or the glottis (Beckers et al. 2003).

Songbirds have the most complex syringeal musculature of all. They have 5 pairs of muscles that attach to the syrinx and a sixth pair that acts on it indirectly via its insertion on the trachea (King 1989). In general, more muscles provide greater degrees of freedom in configuring the syrinx to produce different sounds (Gaunt 1983). The complexity of song is roughly correlated with the number of syringeal muscles, but this relationship is not a simple one. Parrots, for example, succeed in producing complex vocalizations with only two pairs of syringeal muscles (Fig. 9.1A) and the ~Lstraliaiawbred,

**AVIAN SONAR: CLICKING IN THE DARK**

Two groups of birds, some Aerodramus Asian swiftlets (Medway 1967; Griffin & Suthers 1970; Griffin & Thompson 1982; Coles et al. 1987) and the neotropical oilbird (Griffin 1953; Konishi & Knudsen 1979) make clicking sounds with their syrinx that enable them to navigate by echolocation. Although swiftlets and oilbirds have quite different lifestyles, their syrinx allows them to nest in the relative safety of dark caves. Swiftlets are diurnal insectivores and spend the day on wing catching insects which they locate visually. Oilbirds are nocturnal frugivores with excellent night-time vision. They spend the daytime resting on ledges in their nesting cave and use vision, supplemented by echolocation on dark nights, to feed on the fruits of tropical trees.

Clicks make good sonar signals because they contain energy over a wide range of frequencies and have a short duration, making it easier to hear faint echoes reflected by surrounding objects (CD2 #64). Furthermore, clicks can be produced by an anatomically simple syrinx. Although details of click production differ between oilbirds (Suthers & Hector 1985) and swiftlets (Suthers & Hector 1982), in both it involves rapid, synchronous opening and closing of both sides of the syrinx. Each cycle typically produces a pair of clicks (A). The first click occurs when the syringeal valve, located at the labia and tymaniform membranes, briefly vibrates as it narrows the syringeal lumen just before closing it completely. After a short, silent interval while the valves are closed, a second click occurs as the valve begins to open, again allowing airflow to vibrate the membranes until they are withdrawn from the syringeal air stream.

Swiftlets have no intrinsic syringeal muscles so they operate their syringeal valves by using extrinsic muscles in sequence to first close the valve by pulling the tracheobronchial syringe towards the bronchi (accomplished by the sternotraechalis muscles) and then opening it by stretching the bronchial cartilage (through contraction of the tracheolateralis muscles). The mechanism is similar in oilbirds with two important differences. Oilbirds have a bronchial syrinx (Muller 1841; Garrod 1873; see p. 273, Fig. 9.1), in which each syringeal valve (i.e. semisyringe) is in the primary bronchus and the valve is opened by a syringeal muscle that lies along the surface of each bronchus and attaches to a bronchial cartilage bordering the lateral tymaniform membrane (Suthers & Hector 1985). One of the beauties of this simple mechanism for producing sonar clicks is that the sonar pulses are generated during each cycle of muscle contraction, thus doubling the number of echoes produced.

Why do some birds have a bronchial syrinx? Oilbirds may provide a clue. A puzzling feature of their syrinx is that the two semisyringes are placed at different positions along the bronchus, with this distance fixed between the trachea varying on the right and left sides, and between individuals. By inserting a plug in either the left or right bronchus to seal it off from the trachea, we showed that each bronchus had a quarter wave resonance, like that of a stopped tube, allowing frequencies with a wavelength 4 times the length of the bronchial tube to pass while filtering out other frequencies (Suthers 1994, 6). The distribution of sound energy as a function of frequency thus depends on the length of the segment of rigid bronchus between the trachea and semisyringe. Because this length differs between the left and right bronchus and varies between individuals, the vocalizations of each oilbird contain a pair of frequency bands of high intensity sound, or formants that are unique to that individual. Detectable in some echolocating swiftlets (Suthers & Hector 1982), these formants are prominent in many of the bird's long duration 'broadcast' social vocalizations, and might provide a way for individuals to recognize each other in the dark (CD2 #65). Interestingly, most bronchial semisyringes occur in nocturnal species (Suthers 1994).
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Roderick A. Suthers
known for its vocal versatility and now generally considered to be a songbird (Higgins et al. 2001), has but 3 pairs. The remainder of this chapter focuses on the oscine songbirds.

The function of syringeal muscles in songbirds has been studied by recording their electrical activity in the form of electromyograms (EMGs), while measuring the rate of airflow through each side of the syrinx, and monitoring respiratory pressure as the bird moves about in its cage and sings spontaneously in front of a microphone (Suthers 1990, 1997; Suthers et al. 1994, 1996, 1999; Goller & Suthers 1996a; Box 37, p. 277). Additional insights into syngelig function have been obtained by using an endoscope to make direct observations on the morphology of syringeal structures in response to electrical stimulation of individual muscles in anesthetized birds (Larsen & Goller 2002). Although different muscles may have more than one role in sound production and interact in complex ways that are still poorly understood, two of the most basic aspects of song, its timing and its frequency, are primarily controlled by the dorsal and ventral syringeal muscles, respectively, acting in conjunction with the muscles that mechanically ventilate the respiratory system during breathing.

The dorsal muscles, the syringaeals dorsalis and the tracheobronchialelis dorsalis, play a key role in operating a pneumatic valve at the upper end of each bronchus that controls the timing of phonation on each side of the syrinx (Goller & Suthers 1995b, 1996). Each valve is formed by the medial and lateral labia that are also the structures generating sound (Fig. 9.2). When these dorsal muscles are relaxed during quiet respiration, and during micro-breaths between syllables, the labia are abducted out of the air stream. In this position they do not oscillate and the syringeal lumen is open, presenting minimal resistance to airflow. Contraction of the dorsal muscles initiates sound production by adducting the labia into the lumen where they form a slit and oscillate, as air flows across them (Goller & Suthers 1995b; Goller & Larsen 1997b; Larsen & Goller 1999).

Syringeal muscles, the syringlea ventralis, appear to be involved in regulating sound frequency (Fig. 9.2). The amplitude of their EMG is correlated in a positive way with the fundamental frequency of the vocalization (Goller & Suthers 1995b, 1996a). They presumably control fundamental frequency by varying the tension or elasticity of the oscillating labia. Upward-sweeping frequency modulation (FM) is accompanied by a corresponding increase in ventral muscle activity, which is also high during high-pitched notes with a high fundamental frequency but little FM.

There is great variety in the frequency structure, or "syngelig morphology" of birdsongs. Producing such a variety of sounds would seem to require very complicated patterns of syringeal muscle activity to generate a different vocal gesture for each syllable type, although some theoretical models of song production suggest the vocal gestures required may be much simpler than previously assumed (Gardner et al. 2001; Laje et al. 2002; Suthers & Margoliash 2002).

Syringeal Function: Fine-tuning the Song Motor Program

To achieve or maintain the optimum respiratory pressure and the appropriate configuration of the syrinx during song, the bird needs to monitor these variables as it sings. Using sensory feedback to achieve this, it could then adjust the ongoing motor program being sent from the brain to the muscles to correct any deviations from the intended vocal gesture. Such deviations might occur as a result of changes in posture or ongoing physical activity. We know that auditory feedback is essential during song learning (Konishi 1965a), and continues to play a role in the long-term maintenance of adult crystallized song (Nordeen & Suthers 1997b; Larsen & Goller 1999).

Stronger contraction of these muscles, perhaps assisted by other muscles (Larsen & Goller 2002), terminates or prevents phonation on the same side of the syrinx by moving the labia still closer together and closing the slit, stopping airflow and arresting labial oscillation.

The large ventral syringeal muscles, the syringea ventralis, appear to be involved in regulating sound frequency (Fig. 9.2). The amplitude of their EMG is correlated in a positive way with the fundamental frequency of the vocalization (Goller & Suthers 1995b, 1996a). They presumably control fundamental frequency by varying the tension or elasticity of the oscillating labia. Upward-sweeping frequency modulation (FM) is accompanied by a corresponding increase in ventral muscle activity, which is also high during high-pitched notes with a high fundamental frequency but little FM.

Much can be learned about song production by monitoring respiratory dynamics and the activity of syringeal and respiratory muscles during song. The bird is anesthetized and a tiny thermistor bead is placed in the lumen of each primary bronchus, just below the syrinx (Suthers 1990; Suthers et al. 1994). The thermistors are connected to a circuit that maintains them at a constant temperature of about 60°C. Air flowing through the bronchus during either inspiration or expiration will conduct heat away from the thermistor and the additional current required to maintain its temperature provides a measure of the rate of airflow through each side of the syrinx.

The respiratory pressure driving airflow through the syrinx is measured with a miniature piezoresistive pressure transducer mounted on the bird's back and attached to a small tube inserted into one of the air sacs. The bird's respiratory system is different from that of mammals. Birds have several air sacs that act like bellows pumping air through the lungs. Air sacs are connected to the lungs and to each other by complex passages and openings. A midline interclavicular air sac connects the two sides of the respiratory system and contains the syrinx, so respiratory pressure should be the same in both bronchi. By measuring the respiratory pressure, inspirations and expirations can be distinguished. The movement and position of the labia on each side of the syrinx can be monitored by measuring bronchial airflow and respiratory pressure to calculate changes in syringeal resistance. A positive air sac pressure with no airflow indicates the labial valve on that side of the syrinx is closed, whereas a high flow rate with low pressure indicates the labia are drawn back out of the air stream.

The function of various syringeal and respiratory muscles can be deduced by inserting a pair of very fine hair-like stainless steel wires into them and recording the relationship of their electromyograms (EMG) while monitoring syringeal airflow, respiratory pressure and the acoustic properties of the song at a microphone in front of the bird (Goller & Suthers 1996b). All of these physiological signals are carried by fine wires to a velcro tab on the bird's back where they connect to other wires that travel up through the top of the cage to recording instruments. Birds instrumented in this way are free to move around in their cages and sing spontaneously. At the end of an experiment, which may last a week or more, the bird is again anesthetized, the apparatus is removed and it is returned to the aviary.

Observing syringeal motion directly, Goller and Larsen did some elegant experiments using an angioscopescope to view the mechanical action of the syrinx in response to electrical stimulation of the song control system in the brain of anesthetized birds (Goller & Suthers 1997b; Larsen & Goller 2002). A 1.4 mm diameter optical fiber was inserted, either down the trachea to view labial movements, or into the air sac containing the syrinx to see the muscles on its external surface. In some experiments they electrically stimulated individual muscles, and in others (Larsen & Goller 1999) they used a laser optical system to detect the vibration of sound-producing structures. Although the vocalizations produced by this method are not normal song, they provide valuable information about how sound is produced.
Alth~ugh~different muscles may have more than stream. In this position they do not oscillate syllables, the labia are abducted out of the air system during breathing.

The function of syringeal muscles in songbirds has been studied by recording their electrical activity in the form of electromyograms (EMGs), while measuring the rate of airflow through each side of the syrinx, and monitoring respiratory pressure as the bird moves about freely in its cage and sings spontaneously in front of a microphone (Suthers 1990, 1997; Suthers et al. 1994, 1996, 1999; Goller & Suthers 1996a; Box 37, p. 277). Additional insights into syringed function have been obtained by using an endoscope to make direct observations on the motion of syringeal structures in response to electrical stimulation of individual muscles in anesthetized birds (Larsen & Goller 2002). Alth-ugh-difference~muscles may have more than one role in sound production and interact in complex ways that are still poorly understood, two of the most basic aspects of song, its timing and its frequency, are primarily controlled by the dorsal and ventral syringeal muscles, respectively, acting in conjunction with the muscles that mechanically ventilate the respiratory system during breathing.

The dorsal muscles, the syringeals dorsalis and the tracheobronchialis dorsalis, play a key role in operating a pneumatic valve at the upper end of each bronchus that controls the timing of phonation on each side of the syrinx (Goller & Suthers 1995b, 1996b). Each valve is formed by the medial and lateral labia that are also the structures generating sound (Fig. 9.2). When these dorsal muscles are relaxed during quiet respiration, and during mini-breaths between syllables, the labia are ab ducted out of the air stream. In this position they do not oscillate and the syringeal lumen is open, presenting minimal resistance to airflow. Contraction of the dorsal muscles initiates sound production by adding the labia into the lumen where they form a slit and oscillate, as air flows across them (Goller & Suthers 1995b; Goller & Larsen 1997b; Larsen & Goller 1999). Stronger contraction of these muscles, perhaps assisted by other muscles (Larsen & Goller 2002), terminates or prevents phonation on the same side of the syrinx by moving the labia still closer together and closing the slit, stopping airflow and arresting labial oscillation.

The large ventral syringeal muscles, the syringeals ventra lis, appear to be involved in regulating sound frequency (Fig. 9.2). The amplitude of their EMG is correlated in a positive way with the fundamental frequency of the vocalization (Goller & Suthers 1995b, 1996a). They presumably control fundamental frequency by varying the tension or elasticity of the oscillating labia. Upward-sweeping frequency modulation (FM) is accompanied by a corresponding increase in ventral muscle activity, which is also high during high-pitched notes with a high fundamental frequency but little FM.

There is great variety in the frequency structure, or 'syllable morphology' of birdsongs. Producing such a variety of sounds would seem to require very complicated patterns of syringeal muscle activity to generate a different vocal gesture for each syllable type, although some theoretical models of song production suggest the vocal gestures required may be much simpler than previously assumed (Gardner et al. 2001; Laje et al. 2002; Suthers & Margoliash 2002).

Sensory Feedback: Fine-tuning the Song Motor Program

To achieve or maintain the optimum respiratory pressure and the appropriate configuration of the syrinx during song, the bird needs to monitor these variables as it sings. Using sensory feedback to achieve this, it could then adjust the ongoing motor program being sent from the brain to the muscles to correct any deviations from the intended vocal gesture. Such deviations might occur as a result of changes in posture or ongoing physical activity. We know that auditory feedback is essential during song learning (Konishi 1965a), and continues to play a role in the long-term maintenance of adult crystallized song (Nordeen...
thermistors used to sense airflow through each side. The medial and lateral labia form pneumatic valves at the cranial end of each bronchus and oscillate to produce sound. On the right is a ventrolateral view of the same syrinx depicting the syringeal muscles. vS, ventral syringeal muscle; vTB, ventral tracheobronchialis muscle; dS, dorsal syringeal muscle; dTB dorsal tracheobronchialis muscle. For other abbreviations see Figure 9.1. (Modified after Goller & Suthers 1996a).

Similar recordings from syringed muscles indicate that they also adjust their activity to compensate for unexpected perturbations in subsyringeal pressure during phonation (Suthers & Wild 2000). The sensory receptors that provide the feedback underlying these responses have not been identified, but likely include mechanoreceptors or proprioceptors in the muscles, air sacs or walls of the respiratory and vocal systems.

Lateral independence of Motor Control

Each side of the syrinx is capable of acting independently, since it is innervated separately by the tracheosyringeal branch of the hypoglossal nerve on the same side, which in turn receives most of its input from the same side of the brain (Nottebohm & Nottebohm 1976; Nottebohm 1977; Vicario & Nottebohm 1988; Wild et al. & Nordeen 1992; Okanoya & Yamaguchi 1997; Leonardo & Konishi 1999; Box 38, p. 279).

Non-auditory feedback from mechano-receptors or proprioceptors that may sense the tension can provide a rapid response to correct a parameter that is too high or too low. Air pressure or the relative position of structures in the respiratory and vocal system are also important, even in adult crystallized song. For example, if the respiratory pressure is momentarily increased experimentally during a syllable by injecting a small, randomly timed puff of air into the air sac of a singing cardinal, it elicits a compensatory partial relaxation of the abdominal expiratory muscles that returns the pressure to near its original level (Suthers et al. 2002). Since this muscle response does not require extensive processing at higher levels of the brain, it can occur rapidly—often within the same syllable during which the pressure perturbation occurred.

SONG IS DISRUPTED BY DELAYED FEEDBACK AND THEN RECOVERS

Songbirds use auditory feedback to both learn and maintain their songs, and the dynamics of this process may be investigated by manipulating the auditory feedback heard by singing birds. Deafening adult zebra finches results in a complete loss of auditory feedback and, after roughly four weeks, a marked degradation in song structure (Nordeen & Nordeen 1982). However, it is difficult, though not impossible (Wooley & Rubel 2002), to restore auditory feedback to deafened birds. In contrast, by using a computer-controlled system to continuously monitor a bird’s vocalizations, specific types of artificial auditory feedback may be generated in real-time, played back to the bird as he sings, and started and stopped at any moment (Leonardo & Konishi 1999). If the artificial feedback signal is a 100 ms delay of the bird’s song (ABC2D) as he sings it, then when the bird sings syllable B he will hear B+A, with the normal feedback for B superimposed with the delayed feedback for A. Two to four weeks of exposure to delayed auditory feedback caused a dramatic loss of the spectral and temporal stereotypy seen in crystallized song, consisting of stuttering, deletion, and distortion of song syllables and the creation of new ones (CD2 #65). Stuttering sometimes increased the length of a song bout of 2-6 s to more than 60 s. Restoration of normal feedback enabled the recovery of the original songs of each bird. All of the changes in song structure gradually became more infrequent, and were eventually replaced by the temporal and spectral organization characteristic of the original song. A complete recovery took 2-4 months. Thus adult zebra finches appear to retain a great deal of potential song plasticity, even though they do not normally modify their songs after crystallization. Furthermore, despite destabilization of the behavior, a memory of the original song persists, and can be used to correct the vocal output upon restoration of normal auditory feedback. This indicates that the song is maintained by an active control process which requires both a memorized song model and the auditory feedback generated during singing. Elucidating the neural mechanisms underlying this feedback control process remains an area of vigorous research.

Anthony Leonardo
Figure 9.2 A songbird syrinx showing its bipartite structure with 2 sound generators and multiple pairs of muscles. On the left is a frontal section through a brown thrasher syrinx showing the location of microbead thermistors used to sense airflow through each side. The medial and lateral labia form pneumatic valves at the cranial end of each bronchus and oscillate to produce sound. On the right is a ventrolateral view of the same syrinx depicting the syringeal muscles. vS, ventral syringeal muscle; vTB, ventral tracheobronchialis muscle; dS, dorsal syringeal muscle; dTB dorsal tracheobronchialis muscle. For other abbreviations see Figure 9.1. (Modified after Goller & Suthers 1996a).

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How birds sing and why it matters

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Anthony Leonardo
The Stereotopy of Adult Song

Most adult songbirds sing a stereotyped repertoire in which reiterations of the same syllable type vary little in their acoustic properties. This acoustic stereotopy, together with the fact that there is, at least sometimes, no immediate change in the vocalization if auditory feedback is removed by deafening, is part of the evidence suggesting that the pattern of syringeal and respiratory muscle activity required to produce a particular syllable is stored in the brain as a ‘motor program’ (Konishi 1985; Vu et al. 1994). According to this hypothesis, the syllables of crystallized song might be produced by activating the appropriate network of neurons in the brain; these are presumably wired together in such a way that they automatically generate the basic pattern of coordinated muscle contractions, the vocal gesture, needed to produce that syllable. Auditory or somatosensory feedback may not be required, at least in the short term, to produce the basic vocal gesture, but it could adjust or modify it to correct for errors that might otherwise occur if, for example, conditions vary in the peripheral vocal or respiratory system. Although central pattern-generating circuits for different syllable types have not yet been identified in songbirds, they have an important role in controlling many rhythmic behaviors in other animals (Getting 1989; Pearson 1993).

CARDINAL SONG: A CASE STUDY

Even relatively simple songs like that of the northern cardinal require skillful coordination of syringeal and respiratory muscles. An adult male cardinal assembles its songs from a repertoire of between 8 and 21 different syllables (Harkin & Linville 1999). A song, a few seconds long, consists of from one to several of these syllables, each repeated several times to form a series of phrases (CDI #67). There are distinctive patterns of airflow and pressure associated with each syllable type. These patterns reflect the fact that each is produced by a stereotyped motor pattern coordinating the respiratory and syringeal muscles to produce the particular vocal gesture for that syllable (Fig. 9.3). Many syllables include extended upward or downward frequency sweeps that sometimes exceed 2 octaves. Cardinals are unusual in that females also sing, though their song is less stereotyped and harmonics are more prominent compared to the songs of males (Lemon & Scott 1966; Dittus & Lemon 1969; Yamaguchi 1998).

Except during a rapid trill, each syllable is followed by a mini-breath that replenishes respiratory air. Since both inspiration and expiration are active processes, each syllable-mini-breath cycle is accompanied in sequence by contraction first of the abdominal respiratory muscles (Hartley 1990), followed immediately by the thoracic respiratory muscles (Wild et al. 1998). During trills with high syllable repetition rates there is not enough time for a mini-breath between syllables. Instead, respiratory muscles continue to contract and maintain a positive pressure below the syrinx during the entire trill. One side of the syrinx is kept closed and the other side produces the trill by repetitively opening and closing so that each puff of air generates a syllable (Fig. 9.3).

To our ears, the long FM sweeps of a cardinal sound smooth and continuous. It was therefore surprising when closer examination revealed that each side of the syrinx contributes to a different part of the same syllable. Fundamental frequencies below about 3.5 kHz are consistently sung on the left side, and those above this frequency are sung on the right side (Suthers & Goller 1996, 1997; Suthers 1997, 1999a; Suthers et al. 1999; Fig. 9.3). The two sides of the cardinal syrinx are thus specialized to operate over different frequency ranges, facilitating the production of extended FM sweeps that cross the boundary between sides. Each syllable thus contains sequential contributions from each side. A syllable that sweeps from 2 to 7 kHz, for example, begins in the left syrinx and is switched to the right syrinx midway in the upward sweep. This sequence of lateralized production is reversed in syllables that begin from high to low frequencies. Most impressively, the song generally contains no hint of this switch from one set of oscillating labia to the other. To the human ear, and when viewed as time-frequency sonograms, there is usually no obvious interruption or discontinuity in the frequency sweep at the moment of change from one side to the other.

This is an extraordinary feat of virtuosity. Consider the sequence of actions that a cardinal must execute with precision to produce even an acoustically simple note lasting less than half a second. A single broadband FM sweep from high to low begins with: (i) closure of the left syrinx; (ii) expiratory muscle contraction; (iii) opening the right syrinx and configuring it to produce the first portion of the sweep; (iv) closing the right syrinx while (v) opening the left syrinx and configuring it to continue the sweep; (vi) closing the left syrinx to terminate phonation; (vii) relaxing inspiratory muscles, and (viii) contracting inspiratory muscles: (ix) opening both sides of the syrinx for an inspiratory mini-breath to replace the air used to produce the syllable. Depending on the repetition rate of the syllable, this entire sequence of events may take place in scores of milliseconds and be repeated with precision up to 16 times per second to produce a phrase in the song!

LEARNING TO SING

Juvenile songbirds must meet many developmental challenges on their way to adulthood. Not the least of these is learning to sing their species’ song. Males must become expert vocalists before they are a year old if they are to have a chance of reproducing during their second year. How does a young cardinal, of either sex, go about learning to execute this ‘checklist’ of actions that are necessary to produce even a simple wideband frequency sweep (see Chapter 3)?

Vocal Learning

Cardinals are age-limited, closed-ended learners and their adult song repertoire is learned during their first year (Lemon & Scott 1966; Dittus & Lemon 1969; Harkin & Linville 1999). Shortly
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Figure 9.3  Phrases from songs of an adult northern cardinal. (A) Two long, downward sweeping FM syllables followed by faster upward FM syllables. In each syllable, frequencies below about 3.5 or 4.0 kHz are sung on the left side (L) as indicated by airflow through the left syrinx; higher frequencies are produced on the right side (R). Absence of flow through either side during a positive respiratory pressure indicates that the labial valve is closed, preventing both airflow and sound production on that side. Note the mini-breaths between each syllable and the stereotypical patterns of airflow and pressure that are characteristic of each syllable type. (B) Another syllable with a low frequency fundamental produced entirely on the left side (L). This is followed by a trill using pulsatile expiration instead of mini-breaths. Expiratory pressure remains positive during the entire phrase. $F_L$ and $F_R$ show the rate of airflow through the left and right syrinx, respectively. $P$ is the pressure in the cranial thoracic air sac. Horizontal lines indicate zero airflow and ambient air pressure. Shaded portions of the airflow are inspiratory mini-breaths.

After fledging, juveniles begin to produce sequences of low intensity, highly variable notes having little resemblance to adult song. Gradually during the autumn, and then again early in the following spring, these vocal ramblings become louder and some notes begin to recur in a recognizable form. This early stage of vocal development, ‘subsong,’ (Fig. 9.4) is slowly transformed into the next stage, ‘plastic song,’ as a recognizable, though initially poorly controlled, syllable morphology develops (CD1 #067). Eventually, when the bird is about 20 months old plastic song becomes indistinguishable from adult song. Instead of being plastic or malleable, the song becomes fixed or ‘crystallized.’ Subsong and plastic song are thought to involve trial and error motor learning during which the juvenile relies on auditory feedback of his own vocalizations (Konishi 1965a), and presumably somatosensory feedback (Suthers et al. 2002); he learns the muscle actions underlying the motor patterns that are required to produce adult song based on an auditory ‘template’ in the brain, which may be either innate or shaped by experience early in life (Marler 1997). Experiments on zebra finches, in which this process of sensorimotor integration was temporarily disrupted at different stages of song development by using botulinum toxin to reversibly block transmission of nerve impulses to the syringeal muscles, suggest that in addition to the sensitive period for song memorization, there is another one for sensorimotor integration during the latter part of song development (Pytte & Suthers 2000).

Milestones in Vocal Motor Control

Little is known about how the respiratory or vocal motor skills of adult song develop. At what stage in their development are young birds able to coordinate respiratory and syringeal muscles.

Figure 9.4  Subsong from a 92-day-old juvenile cardinal. Arrows indicate periods of expiration without sound production. Abbreviations as in Figure 9.3. In those marked B, both sides contribute.
after fledging, juveniles begin to produce sequences of low intensity, highly variable notes having little resemblance to adult song. Gradually during the autumn, and then again early in the following spring, these vocal ramblings become louder and some notes begin to recur in a recognizable similar form. This early stage of vocal development, 'subsong,' (Fig. 9.4) is slowly transformed into the next stage, 'plastic song,' as a recognizable, though initially poorly controlled, syllable morphology develops (CD1 #067). Eventually, when the bird is about 20 months old plastic song becomes indistinguishable from adult song. Instead of being plastic or malleable, the song becomes fixed or 'crystallized.' Subsong and plastic song are thought to involve trial and error motor learning during which the juvenile relies on auditory feedback of his own vocalizations (Konishi 1965a), and presumably somatosensory feedback (Suthers et al. 2002); he learns the muscle actions underlying the motor patterns that are required to produce adult song based on an auditory 'template' in the brain, which may be either innate or shaped by experience early in life (Marler 1997). Experiments on zebra finches, in which this process of sensorimotor integration was temporarily disrupted at different stages of song development by using botulinum toxin to reversibly block transmission of nerve impulses to the syringeal muscles, suggest that in addition to the sensitive period for song memorization, there is another one for sensorimotor integration during the latter part of song development (Pytte & Suthers 2000).

**Milestones in Vocal Motor Control**

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or achieve independent control of their two syringeal sound sources? Are there bottlenecks in the process underlying motor development and coordination that limit song acquisition? Does the progression through successive stages of juvenile song contribute to the mastery of specific hurrles in vocal production? To better understand the motor development of song, we studied its production in juvenile male cardinals at various stages of vocal learning (Suthers & Goller 1998a, b).

Even young nestlings may produce different sounds simultaneously on each side of the syrinx. Two-voice elements in the begging calls of young chaffinches indicate that separate sounds are being generated on each side of the syrinx in nestlings only a few days old (Nottebohm 1971b; Wilkinson 1980). It is not clear, however, if these two-voice vocalizations are simply a passive byproduct of poorly controlled airflow through both sides of the syrinx, or if they are under active control of the syringeal muscles.

In cardinals, the ability to control which side of the syrinx produces sound is present in fledglings singing subsong when they are less than 6 weeks old. Juveniles at this age are already capable of unilateral sound production by closing one or the other side of their syrinx, as do adults. Sometimes both sides of the syrinx produce sound at the same time, but often a note is generated on only the left or the right side, the silent side being closed to airflow (Fig. 9.4). Unlike adult song, each note is quite variable and the frequency structure of successive left and right notes is not coordinated or linked (Suthers & Goller 1998a).

When adult cardinals sing, the timing of expiratory airflow is carefully coordinated with vocalization. Each syllable typically begins as soon as the syringeal valve opens and ends when the valve closes (Fig. 9.3). As a result, nearly all of the exhaled air contributes to phonation and very little is 'wasted' between syllables, even during the fast pulsatile trills. The respiratory--syringeal coordination necessary for this efficient use of air during song is not present at the beginning of juvenile song, and emerges only gradually during the early stages of song development. During early subsong and even into plastic song, expiration sometimes continues into or through the silent intervals between notes (Fig. 9.4, arrows). As subsong progresses, there is a tendency to alternate sides and to produce at least a pair of notes, one from each side, during a single expiration. This foreshadows the adult motor pattern of using the two sides in sequence to make a single continuous frequency sweep. But in early juvenile song the pair of notes within a single expiration are not joined, nor is there any clear, consistent coordinated sequence in their frequency patterns. The linking of a high frequency sound from the right with a lower frequency contribution from the left side of the syrinx to form a coordinated, seamless frequency sweep occurs in the latter part of song development.

**PUSHING THE ACOUSTIC ENVELOPE**

In adult song, the respiratory and syringeal muscles act together like experienced partners in a dance choreographed by the brain, but the dance steps differ between species. The possession of two parallel sound sources, each with its own pneumatic valve and neural control, gives oscine songbirds an additional degree of freedom absent in species that have a tracheal syrinx or that lack independent control of the two sides of the bronchotracheal or bronchial syrinx. Studies of how different species use the two sides of their syrinx during song suggest that the distinctive styles of singing among various songbird taxa are achieved by using their duplex vocal organ in different ways. These may optimize particular acoustic effects at the cost of sacrificing virtuosity in other aspects of sound production (Suthers 1997, 1999a, b; Suthers & Goller 1997).

**Longer Song Bouts Versus Faster Temporal Increasing Song Duration**

Respiratory air is an essential, but potentially limited, resource for vocalization. Sustained song or even the duration of individual notes might be limited by the volume of air that can be exhaled to produce them. This possible limitation is particularly acute in small birds that sing big songs. Canaries are small birds that can sing in a seemingly continuous fashion for up to about a minute. During a single song they may produce scores or hundreds of syllables, yet their resting respiratory tidal volume is only a fraction of a milliliter! Calder (1970) showed that the depth of the thorax increases slightly between most notes in a canary song. From this he hypothesized that the bird takes a mini-breath between syllables, to replenish its air supply. Measurements of respiratory pressure and tracheal airflow during song showed that each mini-breath replaces about the same volume of air that is exhaled to produce the syllables (Hartley & Suthers 1989). As a result, there is probably little or no net change in respiratory volume during mini-breath song.

The mini-breath respiratory pattern is not unique to songbirds. It appears to be used by many species, including non-songbirds as diverse as parrots and ebbirds (Suthers 2001). In our own species, shortened inspirations, analogous to mini-breaths, are also present during conversational speech (Hixon 1972). In all these cases brief inspirations permit a continuity of vocal communication that is free from periodic interruptions by long inspirations.

**Increasing Syllable Repetition Rate**

Although mini-breaths allow a bird to sing longer songs, they limit the song's tempo to rates of syllable repetition having silent intervals long enough to accommodate an inspiration. Some birds get around this constraint by switching to a different respiratory technique involving pulsatile expiration described above for cardinals, which does not require the reversal of airflow between syllables. Pulsatile expiration can almost double the maximum syllable repetition rate that is possible with mini-breaths. This increase in syllable repetition rate is achieved at the cost of depleting the volume of respiratory air available for sound production. This limits the length of phrases based on pulsatile expiration, but it is unclear how often this limit is actually reached, though this may sometimes occur (see Chapter 11).

The syllable repetition rate that requires a bird to switch from mini-breaths to pulsatile expiration is probably determined by the physical properties of respiratory structures—particularly the mass and elasticity of the thorax and abdomen—that must oscillate at the syllable repetition rate to drive ventilation. Small birds can sustain a mini-breath respiratory pattern at higher syllable repetition rates than can large birds. The "cut off" repetition rate for mini-breaths for an 18 g canary is about 30 syllables per second compared to about 16 syllables per second for a 35–40 g cardinal. Pulsatile expiration is not subject to this limit since it requires little movement of the body wall, and the labia, whose valve-like action gates airflow, have little mass.

Some zebra finches attempt to get the best of both worlds by vocalizing during some mini-breaths between normal expiratory syllables (Goller & Daley 2001). These inspiratory syllables have a distinctive high fundamental frequency and are copied by young zebra finches exposed to them in tutor songs. It is not known if inspiratory syllables have special perceptual significance in communication or why more birds don't use them. It is possible that they may be energetically expensive to produce since the labia must remain in the air stream during inspiration, resulting in a higher resistance to airflow and presumably requiring more effort from the inspiratory muscles.

**Increasing Spectral Diversity**

Songbirds use the frequency of their syrinx in different ways to extend the bandwidth of their song or to produce syllables that vary widely in their tonal quality. The range of frequencies a song encompasses, its bandwidth, is increased by having each side of the syrinx specialized to cover a different frequency band. In all species studied, the fundamental bandwidth of the right side is shifted upward compared to that of the
or achieve independent control of their two syringeal sound sources? Are there bottlenecks in the process underlying motor development and coordination that limit sound acquisition? Does the progression through successive stages of juvenile song correspond to the mastery of specific hurdles in vocal production? To better understand the motor development of song, we studied its production in juvenile male cardinals at various stages of vocal learning (Suthers & Goller 1998a, b).

Young nestlings may produce different sounds simultaneously on each side of the syrinx. Two-voice elements in the begging calls of young chaffinches indicate that separate sounds are being generated on each side of the syrinx in nestlings only a few days old (Nottebohm 1971b; Wilkinson 1980). It is not clear, however, if these two-voice vocalizations are simply a passive byproduct of poorly controlled airflow through both sides of the syrinx, or if they are under active control of the syringeal muscles. In cardinals, the ability to control which side of the syrinx produces sound is present in fledglings singing subsong when they are less than 6 weeks old. Juveniles at this age are already capable of unilateral sound production by closing one or the other side of their syrinx, as do adults. Sometimes both sides of the syrinx produce sound at the same time, but often a note is generated only on the left or the right side, the silent side being closed to airflow (Fig. 9.4). Unlike adult song, each note is quite variable and the frequency structure of successive left and right notes is not coordinated or linked (Suthers & Goller 1998a).

When adult cardinals sing, the timing of expiratory airflow is carefully coordinated with vocalization. Each syllable typically begins as soon as the syringeal valve opens and ends when the valve closes (Fig. 9.3). As a result, nearly all of the exhaled air contributes to phonation and very little is 'wasted' between syllables, even during the fast pulsatile trills. The respiratory–syringeal coordination necessary for this efficient use of air during song is not present at the beginning of juvenile song, and emerges only gradually during the early stages of song development. During early subsong and even into plastic song, expiration sometimes continues into or through the silent intervals between notes (Fig. 9.4, arrows). As subsong progresses, there is a tendency to alternate sides and to produce a pair of notes, one from each side, during a single expiration. This foreshadows the adult motor pattern of using the two sides in sequence to make a single continuous frequency sweep. But in early juvenile song the pair of notes within a single expiration are not joined, nor is there any clear, consistent coordinated sequence in their frequency patterns. The linking of a high frequency sound from the right with a lower frequency contribution from the left side of the syrinx to form a coordinated, seamless frequency sweep occurs in the latter part of song development.

**PUSHING THE ACOUSTIC ENVELOPE**

In adult song, the respiratory and syringeal muscles act together like experienced partners in a dance choreographed by the brain, but the dance steps differ between species. The possession of two parallel sound sources, each with its own pneumatic valve and neural control, gives oscine songbirds an additional degree of freedom absent in species that have a tracheal syrinx or that lack independent control of the two sides of the bronchotracheal or bronchial syrinx. Studies of how different species use the two sides of their syrinx during song suggest that the distinctive styles of singing among various songbird taxa are achieved by using their duplex vocal organ in different ways. These may optimize particular acoustic effects at the cost of sacrificing virtuosity in other aspects of sound production (Suthers 1997, 1999a, b; Suthers & Goller 1997).

**Longer Song Routes Versus Faster Tempus**

*Increasing Song Duration*

Respiratory air is an essential, but potentially limited, resource for vocalization. Sustained song or even the duration of individual notes might be limited by the volume of air that can be exhaled to produce them. This possible limitation is particularly acute in small birds that sing big songs. Canaries are small birds that can sing in a seemingly continuous fashion for up to about a minute. During a single song they may produce scores or hundreds of syllables, yet their resting respiratory tidal volume is only a fraction of a milliliter! Calder (1970) showed that the depth of the thorax increases slightly between most notes in a canary song. From this he hypothesized that the bird takes a mini-breath between syllables, to replenish its air supply. Measurements of respiratory pressure and tracheal airflow during song showed that each mini-breath replaces about the same volume of air that is exhaled to produce the syllable (Hartley & Suthers 1989). As a result, there is probably little or no net change in respiratory volume during mini-breath song.

The mini-breath respiratory pattern is not unique to songbirds. It appears to be used by many species, including non-songbirds as diverse as parrots and ebbirds (Suthers 2001). In our own species, shortened inspirations, analogous to mini-breaths, are also present during conversational speech (Hixon 1972). In all these cases brief inspirations permit a continuity of vocal communication that is free from periodic interruptions by long inspirations.

*Increasing Syllable Repetition Rate*

Although mini-breaths allow a bird to sing longer songs, they limit the song's tempo to rates of syllable repetition having silent intervals long enough to accommodate an inspiration. Some birds get around this constraint by switching to a different respiratory technique involving pulsatile expiration described above for cardinals, which does not require the reversal of airflow between syllables. Pulsatile expiration can almost double the maximum syllable repetition rate that is possible with mini-breaths. This increase in syllable repetition rate is achieved at the cost of depleting the volume of respiratory air available for sound production. This limits the length of phrases based on pulsatile expiration, but it is unclear how often this limit is actually reached, though this may sometimes occur (see Chapter 11).

The syllable repetition rate that requires a bird to switch from mini-breaths to pulsatile expiration is probably determined by the physical properties of respiratory structures—particularly the mass and elasticity of the thorax and abdomen—that must oscillate at the syllable repetition rate to drive ventilation. Small birds can sustain a mini-breath respiratory pattern at higher syllable repetition rates than can large birds. The "cut off" repetition rate for mini-breaths for an 18 g canary is about 30 syllables per second compared to about 16 syllables per second for a 35–40 g cardinal. Pulsatile expiration is not subject to this limit since it requires little movement of the body wall, and the labia, whose valve-like action gates airflow, have little mass.

Some zebra finches attempt to get the best of both worlds by vocalizing during some mini-breaths between 'normal' expiratory syllables (Goller & Daley 2001). These inspiratory syllables have a distinctive high fundamental frequency and are copied by young zebra finches exposed to them in tutor songs. It is not known if inspiratory syllables have special perceptual significance in communication or why more birds don't use them. It is possible that they may be energetically expensive to produce since the labia must remain in the air stream during inspiration, resulting in a higher resistance to airflow and presumably requiring more effort from the inspiratory muscles.

**Increasing Spectral Diversity**

*Bandwidth: Left and Right Vocal Registers*

Songbirds use their syrinx in different ways to extend the bandwidth of their song or to produce syllables that vary widely in their tonal quality. The range of frequencies a song encompasses, its bandwidth, is increased by having each side of the syrinx specialized to cover a different frequency band. In all species studied, the fundamental bandwidth of the right side is shifted upward compared to that of the
left (Suthers 1999a), but there is often substantial overlap in the frequencies produced by each side. Cardinals are unique, among the small sample of species studied, for their limited overlap between frequencies produced on each side and their habit of combining sound from the two sides to produce a single FM note. The anatomical or physiological basis for these separate left–right vocal registers is not known. In many songbirds there are anatomical asymmetries between the two primary bronchi that might include subtle differences in the labia or muscles on each side, as yet unidentified. Whatever its mechanism, the increased overall bandwidth available for vocalization increases the possibilities for spectral diversity in songs.

The influence on song of lateralized specialization for particular frequency ranges is evident in different strains of canaries. One of these is the Waterschlager canary, which was inbred for its distinctive low-pitched song. Another strain is the outbred domestic canary. Nottebohm and Nottebohm (1976) conducted a series of experiments on Waterschlagers in which either the left or right side of the syrinx had been denervated by cutting the tracheosyringeal nerve on one side. They demonstrated that this strain produces about 90% of its syllable repertoire in its left syrinx. As a result of the strong lateral dominance of the left side, most of this bird’s song is below 3 kHz, except for an occasional right side syllable that has a median frequency range between 2.5 and 4.2 kHz (Nottebohm & Nottebohm 1976). This left dominance is in contrast to song of the outbred domestic strain in which each side of the syrinx contributes about an equal proportion of the repertoire, and some syllables include notes from both sides (Suthers et al. 2001). In these domestic birds, syllables frequently have fundamental frequencies as high as 5 or 6 kHz, and a single bilaterally generated syllable may have a bandwidth of 6 or 7 kHz compared to 3 or 4 kHz in the case of unilaterally produced syllables.

Several experiments show that Waterschlager canaries have an inherited auditory defect that decreases their sensitivity to sounds above 2 kHz by as much as 40 dB (Okanoya & Doubling 1985; Gleich et al. 1994a, b; Gleich & Klump 1994). Their strong left syringeal dominance may well be the result of being partially deaf to most of the sounds from the right syrinx.

In the family Fringillidae, which includes sparrows, cardinals and Darwin’s finches, there is an inverse relationship between syllable bandwidth and repetition rate – rapidly trills have narrower bandwidths (Podos 1996; see Chapter 11). It is suggested that syllable bandwidth might be constrained at high repetition rates by the time required to change the shape and tuning of the mouth and throat to track the rapidly changing fundamental frequency (Nowicki et al. 1992; Podos 1997, 2001). In many cases, beak opening is correlated with sound frequency and appears to be a factor in tuning resonances of the vocal tract by altering its effective length and suppressing harmonics. Podos argues that beak size and syllable repetition rate have evolved together in Darwin’s finches. He suggests that the relatively low syllable repetition rate of finches with large beaks is due to the difficulty of moving larger mandibles rapidly to quickly change the tuning of the vocal tract filter (Podos 2001).

The role of vocal tract resonance and beak movements in birdsong is covered in Chapter 11 (Nowicki 1987; Westneat et al. 1993; Moriya & Okanoya 1996; Suthers & Goller 1997; Suthers 1999a; Suthers et al. 1999; Hoeke et al. 2000; Williams 2001).

Inharmonic Sounds

The songbird syrinx is well suited to achieve dissonant sounds by singing two overlapping notes that are different in pitch but not harmonically related to each other. The widespread occurrence of these ‘two-voice’ notes and their likely origin from separate sides of the syrinx was pointed out by Greenewalt (1968) and Stein (1968). Two-voice syllables require airflow through both sides of the syrinx, while different motor programs to the muscles on each side generate unrelated sounds that can be independently modulated in frequency and amplitude. Two voice syllables are especially prominent in songs of some mimic thrushes such as grey catbirds and brown thrashers (Suthers 1992; Suthers et al. 1994, 1996; Goller & Suthers 1995a, b; 1996a, b, 1999). The separate, simultaneous ‘voices’ that form the distinctive inharmonic elements in these songs (Fig. 9.5; CD1 #68) tend to differ less from each other in their fundamental frequency than when each side sings alone, suggesting that simultaneous two-voice phonation comes with constraints on the degree of frequency separation between the two sides that is possible when they operate simultaneously. This limitation might be due to biomechanical interactions between the two halves of the syrinx or to a need to keep both fundamentals within the frequency pass band of the vocal tract, with which both sides connect.

Whereas two-voice syllables depend on the capacity of the two sides of the syrinx to function independently during sound production, inharmonic vocalizations can also result from the nonlinear interaction between the sounds generated on each side. The ‘dee’ syllable of the black-capped chickadee’s song consists of a series of overlapping frequency components that differ from those produced by either side of the syrinx alone. It is not the sum of the sounds produced on each side after unilateral syringeal denervation. It appears instead to be composed of the sum and difference heterodyne frequencies generated by nonlinear interactions between the sounds produced by each side of the syrinx (Novicki & Capranica 1986a, b). The coupling between left and right sound generators might be mediated by air pressure fluctuations associated with sound or transmitted mechanically through the syringeal
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tissue. Similar nonlinear bilateral coupling has not yet been noted in other species, perhaps because bilateral interaction is less prominent in the larger syrinx of most other birds studied.

Other kinds of nonlinear phenomena may also account for the abrupt transitions from periodic to chaotic sounds, as well as period doubling and other acoustic effects that are present in some songs, such as those of the zebra finch (Fee et al. 1998). The realization that nonlinear vocalizations may have a role in social communication has led to an increased interest in their production (Fitch et al. 2002).

Spectral Contrast

The duplicate sound sources in the oscine syrinx facilitate the introduction into song of abrupt changes in fundamental frequency. The song of the brown-headed cowbird, for example, begins with 2 or 3 expiration each containing a 'cluster' of notes, rapidly produced using pulsatile expiration (Allan & Suthers 1994, Fig. 9.6 CD 1 # 69). Successive notes are produced on opposite sides of the syrinx. In each case, the first note is sung on the left side and is immediately followed, or may partially overlap, the next note, which is sung on the right side at a higher frequency. The frequency of these alternating notes increases in a staggered step-wise sequence until the end of the expiration. Abrupt frequency steps between successive notes that follow each other with little or no silent interval between them are possible if separate generators are involved. While one side of the syrinx is producing a note, the muscles of the other closed, silent side can adjust the tension on its labia so that it starts the next note on pitch without a slurred FM between the end of one note and the beginning of the next, something considered again below.

PERFORMANCE CONSTRAINTS:
INSIGHTS FROM A VOCAL MIMIC

Have these species-specific patterns of song production evolved because they are the best way to generate that species' style of song, perhaps the only way, or are they simply independent modes of singing, each with the potential to generate a wide range of song types? To what extent have the evolutionary forces shaping the acoustic properties of a species' song influenced the evolution of production mechanisms, and vice versa? Here I approach from a different viewpoint, some of the issues considered by ten Cate (see Chapter 10), and by Podos and Nowicki (see Chapter 11).

Vocal mimics, such as mockingbirds, provide an opportunity to investigate these questions. When a mimic copies another species' song does it also use the same mechanism employed by that species to produce the song, or does it invent a different way to produce the song? The northern mockingbird is renowned for its ability to mimic other species (Baylis 1982), but the vocal mechanism it uses to accomplish this is unknown. When a mockingbird imitates a cardinal's song, for example, does it do so by joining sounds produced sequentially on each side of the syrinx to generate extended FM sweeps as the cardinal does, or does it produce an unbroken sweep on one or both sides together?

Zollinger and I (2004) tutored hand-reared juvenile mockingbirds with recorded songs of other species. We found that when a mockingbird sings a cardinal song it usually mimics the vocal mechanism of the cardinal, switching between sides of the syrinx in mid-frequency sweep, but the switch is seldom as seamless or the frequency sweep as smooth as when the cardinal sings it. When the mockingbird's motor pattern differed from that of the cardinal, the mockingbird's vocalization also differed from that of the model. In a similar experiment, juvenile mockingbirds were tutored with recorded cowbird songs. The cowbird's song covers an exceptionally wide range of frequency, from a few hundred Hz for the lowest introductory notes to 10 kHz or more in the final whistle. Although mockingbirds were unable to reproduce the highest or lowest frequencies of this tutor, they mimicked both the sound and the cowbird's vocal production mechanism for other notes in the introductory note clusters, singing alternate notes on opposite sides, beginning with the lowest frequency note on the left.

To test the possibility that the taped tutor songs of cardinals or cowbirds contained some subtle cues such as brief pauses or discontinuities, other than frequency, that might influence when the mockingbird switches from one side of the syrinx to the other, some juvenile mockingbirds were tutored, not with natural songs, but with computer synthesized cardinal-like FM sweeps or cowbird-like note clusters. When as an adult, the mockingbird mimicked the synthesized cardinal-like FM sweeps, it sang the high frequency portion on the right side and the low frequency portion on its left, switching sides at 3 or 4 kHz, during both upward and downward
tissue. Similar nonlinear bilateral coupling has not yet been noted in other species, perhaps because bilateral interaction is less prominent in the larger syrinx of most other birds studied.

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Spectral Constraints
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To test the possibility that the taped tutor songs of cardinals or cowbirds contained some subtle cues such as brief pauses or discontinuities, other than frequency, that might influence when the mockingbird switches from one side of the syrinx to the other, some juvenile mockingbirds were tutored, not with natural songs, but with computer synthesized cardinal-like FM sweeps or cowbird-like note clusters. When as an adult, the mockingbird mimicked the synthesized cardinal-like FM sweeps, it sang the high frequency portion on its right side and the low frequency portion on its left, switching sides at 3 or 4 kHz, during both upward and downward
sweeping sounds (Fig. 9.7; CD1 #70). When copying a sequence of frequency-stepped tones similar to the cowbird's note cluster, the mockingbird likewise switched back and forth between sides of his syrinx producing each tone on the same side as would a cowbird.

Perhaps the mockingbirds determine which side of their syrinx to use simply on the basis of the note's frequency. In mockingbirds, like other songbirds, the frequency range of the right syrinx is shifted upward compared to that of the left. Although the absolute frequency of a note is a factor in determining which side of the syrinx will sing it, the context and other acoustic properties of the song are also important and can override frequency bias. This is shown by an experiment in which mockingbirds were tutored with two pairs of synthesized tones similar to those often present in cowbird's note clusters. In each pair, the second tone was at 2 kHz. In one pair this sound was preceded by a lower frequency tone whereas in the other pair, it was preceded by a higher frequency tone, (Fig. 9.8).

In both cases, the frequency difference between tones was 300 Hz and the second tone started immediately after the first. When the mockingbird mimicked these tone pairs, the side it used to produce the 2 kHz note differed, depending on whether the immediately preceding tone was higher or lower. If the first tone was higher, it was sung on the right and the 2 kHz tone was sung on the left. If, however, the first tone was lower it was sung on the left and the 2 kHz tone was produced on the right (Fig. 9.8).

It is clear from this experiment that a 2 kHz tone can be produced on either side of the syrinx. Why then did the mockingbird change sides between the tones in each pair? Why not sing the second tone on the same side that was used to produce the first? The answer is apparent from the occasional times a mockingbird failed to change sides between tones. When both tones were sung on the same side of the syrinx, the abrupt step-wise frequency change between tones was lost, and the end of the first note became slurred into the frequency of the second note so that the two were connected with an FM sweep.

The ability to achieve abrupt step-wise frequency changes without a significant silent period between notes may depend on exploitation of the two voices of the bipartite syrinx. Perhaps it is only by switching sound production from side to side during the rapidly produced notes in their note clusters that cowbirds are able to achieve the clean frequency steps, or spectral contrast, between notes. This use of the bipartite syrinx circumvents the limited ability of a single sound source to abruptly change the frequency at which it oscillates. To achieve this acoustic effect without slurring, the mimic must exploit the vocal flexibility made possible by two sound sources, as the cowbird does in its song.

Our findings on how mockingbirds copy other species support the view that the songs of different species have been selected to maximize the performance of certain species-specific acoustic features, such as the abrupt frequency steps between cowbird notes, or the smooth extended FM sweeps of cardinals. Most songbirds have become vocal specialists who push the performance limits of singing in certain directions, often at the expense of some other kinds of acoustic skills. To be a successful vocal mimic, the mockingbird must remain to some extent a vocal generalist, a jack-of-all-trades but master of none, who does a fairly good job of mimicking other species, but usually with less expertise than the rightful owner.

VOCAL GYMNAS'TICS: ARE FEMALES IMPRESSED?

Two important functions of song are, a role in competition between males for breeding territories, and in attracting a mate. Exactly what aspects of song are most important in fulfilling these needs is poorly understood, and may differ between species (Catchpole & Slater 1995; Gil & Gahr 2002; see Chapter 2). Most studies of the relationship between singing and mating success have focused on variables such as repertoire size, or the frequency or duration of singing. These are all amenable to measurement.

Figure 9.7 (A) A tutor 'song' consisting of a series of computer synthesized downward FM sweeps similar to syllables sung by cardinals. (B) A mockingbird's reproduction of these sweeps (CD1 #70). The timing of airflow through each side of the syrinx shows that the mockingbird begins each sweep on the right side and changes to the left side for the portion of the sweep that is below about 3 kHz. Abbreviations as in Figure 9.3.
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but are not necessarily correlated with the level of motor skill, and are unlikely to reflect the difficulty that is required to execute the vocal performance. A male's quality might be reflected not only in his stamina for sustained singing, but also in his ability to flawlessly and repeatedly sing syllables or phrases that require special motor skills (Suthers & Goller 1997; Nowicki et al. 1998a; ten Cate et al. 2002). Among the species in which the motor mechanisms of song production have been studied, an aspect of singing that seems likely to require special vocal motor skills is coordination between the two halves of the syrinx. Examples are the acoustically seamless switch between right and left sides during-wide band frequency sweeps by cardinals or the concurrent production of independently modulated sounds forming two-voice syllables in brown thrashers. It is not yet known whether females pay attention to these particular aspects of cardinal or thrasher song. However, in brownheaded cowbirds and domestic canaries, there is some evidence suggesting that parts of their songs requiring a high degree of motor coordination may have a special perceptual significance to prospective mates.

Male attraction-singing shows that males have a vocal repertoire that includes several different types of songs. In the eastern subspecies, each song begins with 2 or 3 note clusters followed by a whistle (Fig. 9.6). West, King, and their colleagues showed that some songs are more effective than others in eliciting copulation solicitation displays (CSD) from female cowbirds (King & West 1977, 1983; West et al. 1979, 1981; see Chapter 14). A male's breeding success is correlated with the potency of his songs. Experimental manipulation of songs indicates that the note clusters are more effective than the final whistle in eliciting CSDs. A high-frequency note, designated the 'interphrase unit' at the end of the last note cluster appears to be particularly important. Songs of dominant males were more effective than those of other males. The inclusion of stereotyped note clusters in juvenile plastic song triples the effectiveness of juvenile song in evoking a female copulatory response (Wert & King 1988a). Further experiments with computer-edited songs show that a few notes are needed to identify the specific temporal or acoustic aspects of note clusters that are most important in stimulating a female. But it already seems clear that a male cowbird's mating success is influenced by his bilateral motor skills in singing stereotyped patterns of notes that are rapidly produced, with alternating steps in frequency.

The domestic canary provides another example of a possible relationship between vocal motor dexterity and female choice. Male domestic canaries have a song repertoire of about 20–30 different syllables. Individual songs contain a subset of these syllables, repeated to form a sequence of phrases. Each syllable type is always sung in the same way and at the same repetition rate, but there are large differences in the spectral and temporal properties of a phrase, depending on its syllable type. Some syllables may be almost a pure tone repeated a few times a second, others include upward or downward frequency sweeps of varying complexity sung at various repetition rates which may exceed 30 per second.

Researchers at the University of Paris (Vallet & Kreutzer 1995; Vallet et al. 1998b) found that certain kinds of 'type A' syllables are more effective than others in attracting the interest of a prospective mate (Box 4, p. 58). They played different phrases, each consisting of a single syllable type, to sexually receptive female canaries and recorded their CSD responses. The female invites the male to mate with her by arching her back, raising her tail, and flapping her partially spread wings. Vallet and his colleagues found that wide-band syllables that were more complex than simple frequency modulated sweeps, composed of two or more notes, and sung at a repetition rate of 16 per second or higher evoked significantly more female displays than other syllables. Similar type 'A' syllables recorded from wild canaries also elicit CSDs from domestic canaries when played back to them in the laboratory (Leitner et al. 2001), indicating they are not an artifact of domestication.

Studies of how domestic canaries produce their songs suggest that 'A' syllables may be relatively difficult to sing (Suthers et al. 2001). Domestic canaries sing some syllables in their left syrinx, others in the right, and still other multi-note syllables contain contributions from both sides of the syrinx. The wide-band 'A' syllables of some birds studied, included contributions from both sides of the syrinx (Fig. 9.9; CD1 #71). The syllables that are most effective in eliciting CSDs from a female canary thus require the male to produce stereotyped notes from each side of his syrinx at a note repetition rate at least twice the syllable rate. Furthermore, behavioral playback experiments (Vallet et al. 1998) suggest that the effectiveness of 'A' syllables in stimulating a female is greater if the silent interval between the notes within each syllable is short (between 16 and 23 ms, as opposed to 23–30 ms). This is consistent with the hypothesis that bilateral coordination involving very rapid left–right switching between
in brown thrashers. It is not yet known whether females pay attention to these particular aspects of cardinal or thrasher song. However, in brown-headed cowbirds and domestic canaries, there is some evidence suggesting that parts of their songs requiring a high degree of motor coordination may have a special perceptual significance to prospective mates.

Male attraction-seeking cowbirds have a vocal repertoire that includes several different song types. In the eastern subspecies, each song begins with 2 or 3 note clusters followed by a whistle (Fig. 9.6). West, King, and their colleagues showed that some songs are more effective than others in eliciting copulatory solicitation displays (CSD) from female cowbirds (King & West 1977, 1983; West et al. 1979, 1981; see Chapter 14). A male's breeding success is correlated with the potency of his songs. Experimental manipulation of notes indicates that the note clusters are more effective than the final whistle in eliciting CSDs. A high-frequency note, designated the 'interphrase unit' at the end of the last note cluster appears to be particularly important. Songs of dominant males were more effective than those of other males. The inclusion of stereotyped note clusters in juvenile plastic song triples the effectiveness of juvenile song in evoking a female copulatory response (West & King 1988a).

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'Sexy' Syllables of a Domestic Canary Song

Each syllable is composed of two notes. The first note sweeps upward on the right side for about 20 ms and is followed by an approximately 10 ms downward sweep at a lower frequency on the left side. To be maximally effective in eliciting copulation displays from a receptive female, syllables must be complex and sung at repetition rates greater than 16 per second. Abbreviations as in Figure 9.3.

sides of the syrinx may have special perceptual importance in the vocal communication of birds. The kind of information females get from 'A' syllables remains to be determined. One possibility is that they provide an indication of the male's health or fitness. Of all the syllables in a canary's repertoire, 'A' phrases may demand the greatest precision in bilateral motor coordination within the syrinx, and also between the syrinx and the respiratory muscles and other vocal tract or cranial muscle groups involved in singing. It may be that males who are not in top physical condition have difficulty producing these phrases. If so, the 'A' phrase may be an honest indicator of male fitness (see Chapter 2).

Another possibility is that the presence of 'A' phrases in song may indicate a male's reproductive state— that he is ready to breed. Field studies of wild canaries show that the syllable repetition rate of their repertoire, but not repertoire size, changes seasonally. 'A' syllables sung during the breeding season are replaced during the winter with syllables at lower repetition rates (Leitner et al., 2001). Seasonal changes in steroid levels can affect syringeal muscles and vocal behavior (DeVoogd, 1991; DeVoogd et al., 1991; Beani et al., 1995; Hartley et al., 1997; Tramontin et al., 2000). The presence of 'A' phrases in a male's song might indicate his readiness to mate. Domestic canaries sing longer strings of 'A' phrases in the presence of other male or female canaries than when they are singing alone, even though the number and duration of songs is similar in both situations (Kreutzer et al., 1999).

These two possible functions of 'A' syllables in intersexual communication are not mutually exclusive. Other factors may also play a role in mate selection, and it is not clear if there is a correlation between the presence of 'A' syllables and reproductive success. Whatever the case, a better understanding of how birds sing promises to be a valuable tool in deciphering the communicative functions and evolution of song.

CONCLUSIONS

Twenty years ago, in a review on avian sound production, Brackenbury (1982) lamented that, "many ideas about the functioning of the passerine syrinx are based on guesswork." In the past decade new techniques for recording and observing syringeal function during song have yielded significant progress toward removing some of this guesswork and advancing our understanding how birds sing, though the number of species sampled is still very small. There is every reason to believe the next decade will be equally productive. As we learn more about how the avian vocal system works, and its acoustic possibilities and limitations, we will gain new insights into the neural organization, behavioral significance, and evolution of a behavioral system that is unique in the animal kingdom.

Figure 9.9 A segment of a domestic canary song containing two phrases of type 'A' syllables (CD1 #74). Each syllable is composed of two notes. The first note sweeps upward on the right side for about 20 ms and is followed by an approximately 10 ms downward sweep at a lower frequency on the left side. To be maximally effective in eliciting copulation displays from a receptive female, syllables must be complex and sung at repetition rates greater than 16 per second. Abbreviations as in Figure 9.3.
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'sexy' syllables of a domestic canary song

16s
R

16s
L

0.1
Time (s)

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