Performance Constraints And Vocal Complexity In Birdsong: Evidence From A Vocal Mimic

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Learn Some New Songs

(painting by michael sieban)
Accepted by the Graduate Faculty, Indiana University, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Abstract

The diverse vocal performances of oscine songbirds are produced by coordinated patterns of activity in muscles controlling separate sound generators on the right and left sides of their duplex vocal organ, the syrinx. But how do songbirds use these two sound sources to produce their acoustically and temporally complex vocal communication signals? I used northern mockingbirds (Mimus polyglottos) as a model species to investigate peripheral sources of vocal complexity, and to test hypotheses about putative constraints on vocal production. In these experiments, I show that when a vocal mimic accurately copies the song of another species it must also use the same vocal motor pattern employed by the model species. Vocal motor “mistakes” or deviations from the stereotyped motor patterns associated with the most acoustically similar mimicries of each sound type, resulted in predictable deviations from accurate copies of tutor sounds. I present physiological evidence supporting previous hypotheses for mechanical and acoustic coupling between the two sides of the syrinx. Mockingbird mimicries of synthesized tutor sounds designed to test the ability of the two sides of the syrinx to simultaneously generate different sounds, reveal that although the two sides of the syrinx are theoretically independent, there are significant constraints on how different the contribution from the two sides can be. Finally, I found that nonlinear dynamics within the syrinx can give rise to phenomena such as subharmonics, frequency jumps, biphonation and chaos that further increase the acoustic complexity of mockingbird song. By identifying the features of song most difficult for mockingbirds to produce, we can gain insights into the physical and physiological limitations on song production and further the understanding of the types of selective forces that may drive the evolution of vocal communication signals.
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INTRODUCTION

Like human speech, birdsong is a learned, complex vocal signal. In songbirds (suborder Passeri of Passeriformes) song is thought to function primarily in mate attraction and territory defense (reviewed in Nowicki and Searcy, 2004). Song learning and vocal performance have been hypothesized to function as honest indicators of the health, success, genotypic and/or phenotypic fitness of the singer (Howard, 1974; Kroodsma, 1976; Searcy, 1992; Eens et al., 1993; Beecher et al., 1994; Mountjoy and Lemon, 1996; Jarvis et al., 1998; Nowicki et al., 1998; Nowicki and Searcy, 2005; Leitner et al., 2006). Because of the relative rarity of vocal learning within the animal kingdom, songbirds are one of the few viable animal models for human vocal learning, development and production constraints. Northern mockingbirds (Mimus polyglottos) in addition to being vocal learners, are renowned heterospecific vocal mimics who, like humans, continue to learn new sounds throughout their lives (Burnett, 1978; Merritt, 1985; Derrickson and Breitwisch, 1992). Their propensity for vocal imitation and developmental plasticity make them a unique and exceptionally useful model system for studying the process of vocal learning and the limits of the vocal production system.

How do birds produce their species-typical songs?

The subject of study, admiration, wonder and inspiration to artists, writers and composers throughout human history, birdsong is one of the most conspicuous examples of vocal diversity and virtuosity in the animal kingdom. But how do songbirds produce their complex and varied sounds? The songbird vocal organ, the syrinx, is located at the bifurcation of the trachea into the two primary bronchi. Each bronchus contains a set of vibratory tissues, the medial and lateral labium and the medial tympaniform membrane, the activity of which are independently controlled by the ipsilateral sides of the brain and tracheosyringeal branches of the twelfth hypoglossal nucleus. The anatomic complexity of
this dual sound source gives songbirds the potential for song with much greater acoustic and temporal complexity than a single sound source (such as the mammalian larynx) could. And, indeed, the “two-voice” phenomenon in songbirds has been described long before the mechanisms for sound generation in the syrinx were even understood (Setterwall, 1901; Borror and Reese, 1956; Thorpe, 1958; Thorpe, 1961; Greenewalt, 1968). However, the details of sound production (Goller and Larsen, 1997; Larsen and Goller, 2002) and the independent bilateral use of the two sound sources in songbirds have only recently begun to be fully investigated (Suthers, 1990; Allan and Suthers, 1994; Goller and Suthers, 1995; Suthers, 1998; Suthers et al., 2004).

Although specific patterns of respiratory and syringeal motor dynamics have only been studied in a handful of species so far, highly specialized motor strategies for production of their species-typical songs have been found in each. The existing hypotheses about the diversity of these syringeal and respiratory specializations are that these different motor patterns enable songbirds to exploit the dual nature of their syrinx in different ways to increase the spectral and temporal complexity of their song, and that these different motor programs represented ways for birds to circumvent respiratory or motor constraints within their vocal production system (Suthers, 1990; Allan and Suthers, 1994; Goller and Suthers, 1995; Suthers, 1998; Suthers et al., 2004). However, since most songbirds have innate filters to selectively learn the songs of their own species, testing hypotheses on why different species sing their songs the way they do was challenging. In Chapter 1 of this volume, I use northern mockingbirds tutored with the songs of heterospecific songbirds to test hypotheses about motor production constraints in the songbird vocal production system.

Sources of vocal complexity

Besides the presence of two sound sources, there are many other possible sources for the acoustic complexity observed in birdsong. Vocal learning itself is a powerful
tool for increasing the complexity of acoustic signals (Logan, 1983; Baptista and Trail, 1992; Nelson et al., 1995), and vocal imitation may allow a bird the plasticity to respond to dynamic social and environmental situations (Baylis, 1982; Aoki, 1989; Brown and Farabaugh, 1997). One widely accepted hypotheses explaining the expansive radiation of the songbirds into one of the largest and most diverse orders of vertebrates (ca. 5600 species) is that the evolution of vocal learning in this group allowed for rapid behavioral speciation (Baptista and Trail, 1992; Slabbekoorn and Smith, 2002).

Additionally, the songbird syrinx has been demonstrated to be a nonlinear system of coupled oscillators (Fee et al., 1998; Fee, 2002). Four acoustic phenomena are predicted by nonlinear systems, biphonation (the production of two harmonically unrelated frequencies by a single pair of oscillators) subharmonics, frequency jumps and deterministic chaos (Herzel et al., 1994; Fee et al., 1998; Wilden et al., 1998). In general, nonlinear dynamics explain how simple systems can generate complex behavior. In vocal systems, this can explain the production of complex sounds, which are simply the result of passive, biomechanical bifurcations in the regular periodic behavior of the oscillating tissues. But as in any physiological system, the complexity of behavior possible has bounds. And so while increased complexity can arise from central, peripheral and mechanical sources, constraints on that complexity should be predicted to exist at many levels as well. While the syrinx ex vivo has been demonstrated to exhibit nonlinear behavior, the dual nature of the songbird syrinx has precluded identification of most nonlinear phenomena in the songs of intact songbirds. In Chapter 2 of this volume, I measured air flow through the right and left sides of the syrinx to monitor the acoustic contribution from each side of the syrinx toward production of calls and song. I present data to show that nonlinear dynamics within each side of the syrinx greatly increases the spectral complexity of the sounds that can be produced unilaterally. The results presented in Chapter 2 are the first evidence of syringeal lateralization of nonlinear dynamics during certain types of bilaterally-produced chaotic calls, and support previous hypotheses for
mechanical and acoustic coupling between the two sides of the syrinx.

Sources of vocal constraints

Identifying potential constraints on the vocal production system is key to understanding the evolution of vocal communication systems in general, and potential selective pressures on both song learning and the peripheral vocal production system. For instance, limitations on the kinds of sounds that songbirds produce could be physiological, behavioral, environmental or morphological in origin.

Physiological constraints on song can be predicted that would limit the behavior of both the respiratory system and syrinx. Respiratory parameters such as absolute lung/air sac capacity or respiration rate, will limit the duration or repetition rate of syllables in song (Goller and Suthers, 1998; Suthers and Goller, 1998; Franz and Goller, 2003; Suthers et al., 2004; Zollinger and Suthers, 2004), however the metabolic costs of singing are probably minimal (Oberweger and Goller, 2001) compared with other behaviors (such as flight) that a bird may engage in. At the level of the syrinx, mechanical constraints surely limit the frequencies at which each pair of labia can oscillate, and while a more comprehensive understanding of right/left syringeal morphology is wanting, there are some data showing slight size differences between the right and left side in some species (Luine et al., 1980).

The suprasyringeal vocal tract (the trachea, oropharyngeal-esophageal cavity (OEC) and beak) also impose constraints on the range of frequencies that can be produced effectively by a bird (Nowicki, 1987; Beckers et al., 2003; Daley and Goller, 2004; Fletcher et al., 2004; Nelson et al., 2005; Riede et al., 2006). While both beak gape and the volume of the OEC are dynamically modified during song to selectively attenuate or support the sounds produced at the syrinx (Goller et al., 2004; Riede et al., 2006), this tuning is limiting both in the range of resonant frequencies possible as well as the mere fact that the sounds from both of the two sources must pass through the same vocal tract filter, so
that two very different frequencies produced simultaneously would likely not both pass effectively through the filter (Riede, 2007, personal communication).

Further constraints on the simultaneous independent behavior of the two sides of the syrinx have been hypothesized (Nowicki and Capranica, 1986; Laje and Mindlin, 2005), but the extent to which interactions between the two sides of the syrinx might limit vocal production is not clear. Chapter 3 of this volume presents results from an experiment designed to test the independence of the two sides of the syrinx during two-voice syllables (simultaneous bilateral phonation). I tutored mockingbirds with a variety of computer-generated sounds consisting of two different non-harmonically related frequency components designed to test how different the fundamental frequencies and rates or complexity of frequency modulation on the right and left sides of the syrinx can be when phonating simultaneously.

Why study vocal production?

The three studies in this volume were designed to test assumptions about peripheral vocal constraints, to identify novel sources of peripheral vocal complexity and to evaluate the limitations of the bilateral use of the songbird syrinx. The results presented herein contribute several important new ideas to the current understanding of the avian vocal production system, as well as give new insights for understanding why birds make the decisions they do about how to produce a certain sound, and perhaps just as critically, illustrates the acoustic consequences of making “bad” production decisions. Vocal speech disorders in humans often are the result an inability (either physiologically or cognitively) to produce the correct vocal motor patterns necessary for production of normal speech sounds (Zocchi et al., 1990; Herzel et al., 1994; Holstege, 1996; Duffy, 2005). However, in many developmental vocal disorders, the deficit is not always easily pinpointed. While central motor control is often a factor, genetic, behavioral or peripheral constraints are often involved as well (Feuk et al., 2006; Mostofsky et al., 2006). Studies of
vocal limitations in songbirds are a first step toward understanding the role that similar constraints play in human speech production. And on a broader scale, by identifying the aspects of song most difficult for the mockingbird to produce and the sources of complexity and chaos in bird vocalizations, we gain insights into the physical and physiological limitations on vocal communication and the selective forces that drive the evolution of vocal signals.
Chapter 1

Motor mechanisms of a vocal mimic: Implications for birdsong production
Abstract

The diverse vocal performances of oscine songbirds are produced by the independent but coordinated patterns of activity in muscles controlling separate sound generators on the left and right sides of their duplex vocal organ, the syrinx (Suthers, 1999). Species with different song styles use the two sides of their syrinx in different ways to produce their species-typical songs. Understanding how a vocal mimic copies another species’ song may provide an insight into whether there are alternative motor mechanisms for generating the model’s song and what parts of his song are most difficult to produce. We show here that when a vocal mimic, the northern mockingbird, accurately copies the song of another species it also uses the vocal motor pattern employed by the model species. Deviations from the model’s production mechanism result in predictable differences in the mockingbird’s song. Species-specific acoustic features of the model seem most difficult to copy, suggesting they have been exposed to the strongest selective pressure to maximize their performance.
INTRODUCTION

Acoustic communication in oscine songbirds has been facilitated by vocal learning and a highly versatile vocal organ, the syrinx, which contains two independently controlled sound sources located in the cranial end of each primary bronchus (Nottebohm, 1971; Suthers, 1990). Different species of songbirds use the two sides of their syrinx in different stereotyped ways to generate the species-specific spectral and temporal features of their songs (Nottebohm, 1971; Nottebohm and Nottebohm, 1976; Hartley and Suthers, 1990; Suthers, 1990; Allan and Suthers, 1994; Suthers, 1999).

The songs of brown-headed cowbirds (*Molothrus ater*), for example, are notable for their broad range of fundamental frequency and the abrupt, step-like shifts in frequency that often occur between successive notes. Cowbird songs consist of 2 or 3 introductory note clusters followed by a final whistle. The notes in these clusters are produced on alternate sides of the syrinx and increase in a staggered fashion in frequency and intensity (Fig 1a). The final whistle is always produced on the right side and includes very high frequencies (Allan and Suthers, 1994).

Whereas cowbirds use the two sides of their syrinx to achieve abrupt frequency changes between successive notes, northern cardinals (*Cardinalis cardinalis*) emphasize bilateral coordination and spectral continuity. The songs of cardinals are characterized by extended broadband frequency modulated (FM) sweeps in which frequencies above about 3.5 kHz are sung on the right side and lower frequencies are sung on the left with a coordinated, seamless mid-syllable switch from one side to the other (Suthers, 1999).

Song motor programs have evolved to operate within the limitations of respiratory, as well as syringeal, motor performance. Female preference for longer songs (Eens et al., 1993; Neubauer, 1999) or faster syllable repetition rates (Vallet et al., 1998; Draganoiu et al., 2002) place special demands on respiratory ventilation during long songs having a high syllable repetition rate. Canaries (*Serinus canaria*), for example, can sing songs that
last up to almost a minute. The air necessary to sustain such songs is acquired by taking a minibreath after each syllable that replaces the air exhaled to produce the sound (Hartley and Suthers, 1989).

The diversity between species in how they use the syrinx to produce their songs affirms the vocal flexibility of having two sound sources. It is not clear to what extent performance level of various acoustic properties or features of song are limited by physical or physiological constraints (i.e., production constraints) on how syringeal motor patterns produce sound or even if there may be alternative motor mechanisms for producing a similar song. Although there is evidence that birds vary the filter properties of the vocal tract during song to suppress harmonics (Nowicki, 1987; Westneat et al., 1993; Moriyama and Okanoya, 1996; Suthers, 1997; Hoese et al., 2000; Beckers et al., 2003), little is known about production constraints at the sound source, the syrinx. Based on inconsistent effects of partial syringeal denervation in sparrows, Nowicki (1992) postulated that the syrinx exerted minimal constraints on song, but the mechanism of song production by the intact syrinx was not known and potential individual differences in the ability to compensate for partial paralysis make interpretation difficult. Podos (1996) hypothesized that the inability of young sparrows to accurately imitate songs with an artificially increased syllable repetition rate was most likely due to mechanical constraints on respiration, the syrinx or the vocal tract. However, in subsequent experiments showing an inverse correlation between syllable repetition rate and bandwidth (Podos, 1997), and of both these variables with beak size (Podos, 2001), Podos proposed physical limitations on beak or vocal tract movements during song as the most likely motor constraint. None of these studies directly monitored respiratory or syringeal motor patterns.

In this paper we examine how a vocal mimic, the northern mockingbird (*Mimus polyglottos*), copies heterospecific song. Vocal mimics, like other songbirds, presumably learn new songs by a process of trial and error motor learning, guided by auditory feedback, but the motor aspects of vocal mimicry have not been studied. If there are
alternative ways of producing the same song, or acoustic element, a mimic by trial and error might use a different motor pattern than its tutor. If, on the other hand, physical or physiological limitations restrict a particular sound or song to a single production mechanism, the mimic must use the same motor mechanism as the model to reproduce his song. The accuracy with which a mimic copies various acoustic features of another species’ song might also provide an indication of which features are most difficult for the mockingbird to produce, suggesting that selection pressure on these song components in the tutor has given rise to specialized motor skills for their production.

The vocal repertoires of northern mockingbirds are large (Burnett, 1978; Derrickson, 1987) and consist mostly of heterospecific imitations (Derrickson and Breitwisch, 1992). Taking advantage of this propensity for vocal copying, we tutored hand-reared mockingbirds with songs of cowbirds, cardinals and canaries, as well as with several computer-synthesized sounds. We selected these species because we know the motor patterns they use to produce their distinctively different songs (Hartley and Suthers, 1990; Allan and Suthers, 1994; Suthers, 1999). We measured phonation on the right and left side of the syrinx by recording the pattern of airflow through each side in spontaneously singing northern mockingbirds. In most cases mockingbirds copied not only the sound, but also used the tutor’s species-specific motor pattern of syringeal lateralization. When the mockingbird’s motor pattern deviated from the one used by the tutor, the resulting vocalization also differed from that of the tutor.

METHODS

Rearing and tutoring of birds

Mockingbirds 2 to 5 days old were collected from nests in North Carolina and Indiana and hand-reared in the laboratory. Birds were housed in groups of individual cages in sound attenuating chambers and tutored with heterospecific songs of northern cardinal, brown-headed cowbird, Wasserslager canary, and eastern towhee (Pipilo
erythrophalmus) or with computer-synthesized sounds similar to these songs. We do not include towhee song in this article because its production mechanism is not yet known. Three groups of 10 birds were tutored with different sets of tutor sounds as follows: Group 1: natural cardinal, cowbird, canary and towhee songs. Group 2: synthetic sounds. Group 3: both natural and synthesized sounds, including most of the stimuli presented to Groups 1 and 2, plus some additional synthesized sounds. The digitally recorded or synthesized tutor sounds were copied onto compact discs for playback from a compact disc player (TEAC model CD-P1120 and speakers (Yamaha model MS101II). The tutor sounds were presented for approximately 2 hours a day between the age of 10 d and 6 mo and then every other day until 12 months old. Each tutor file was approximately 50 seconds in duration and consisted of several repetitions (6 – 11, depending on duration of syllables) of a syllable or song phrase with silent pauses between. Daily tutor presentations typically consisted of 5-8 repetitions of each tutor file presented in a random order each day. Birds may have also been exposed to occasional song from northern cardinals, eastern towhees and zebra finches that were sometimes housed in adjacent rooms in the laboratory, but at the time of the physiological recordings only the tutor songs of these species were recognizable in the birds’ repertoires.

**Surgery and Recording of Vocal Mechanisms**

Preoperative song was recorded for 1-2 weeks from adult birds (>250 days) (Avisoft-Recorder v. 1.7). Birds were anaesthetized by injection of chloropent (recipe available from Fort Dodge Laboratory) into the pectoral muscle at a dosage of 4.1 ul /g body weight, and a silastic cannula (Dow Corning Corp., ID 1.02 mm, OD 2.16 mm) was inserted into the cranial thoracic air sac for measurement of subsyringeal pressure. The cannula was attached to a miniature piezoresistive pressure transducer (Fujikura FPM-02PG) mounted on a backpack attached to an elastic belt around the bird's thorax. An incision was made between the clavicles and the syrinx was exposed through an opening
in the interclavicular membrane. A microbead thermistor (Thermometrics, BB05JA202) was inserted into each bronchus just caudal to the syrinx. The interclavicular membrane was sealed around the thermistor leads that were routed under the skin to the backpack. For more detailed surgical methods see (Suthers et al., 1994). Pressure and airflow signals were transmitted from the backpack on leads that exited through the top of the cage to signal conditioning instruments and a digital data recorder (Metrum DataTape, model RS512). During an experiment the bird could move freely about the cage. Pre and post-operative song was recorded with a microphone (Audio-Technica, AT835b) positioned 30 to 50 cm in front of the cage. All procedures were approved by the Institutional Animal Care and Use Committee of Indiana University, Bloomington.

Surgeries were conducted on 14 males. Bilateral bronchial airflow and respiratory pressure were recorded from 5 male birds during song, including 1 bird in Group 1, 2 in Group 2 and 3 in Group 3. Unilateral airflow and pressure were recorded from an additional 4 birds, consisting of 1 bird in Group 1, 2 in Group 2 and 1 in Group 3. The fine wires routed under the skin from both thermistors to the backpack broke before the remaining 7 birds sang. Pre and post-operative songs from each bird were compared by visual inspection of spectrograms and no differences were observed.

Signals were analyzed with Signal 3.1 (Engineering Design) and in Igor Pro v. 4 (WaveMetrics Inc.) using scripts written by Brian S. Nelson for use in Igor Pro. Statistical analysis was conducted using Two-tailed t tests or One Way ANOVA and Tukey test with Igor Pro v.4 and SigmaStat v. 2.03 (SPSS Inc.) software. Data are given as M±SD unless otherwise noted. Spectra for bandwidth measurements were generated in Igor Pro using 512 point FFT and a sampling rate of 40 kHz. Power spectra of 25 ms segments of FM sweeps were generated and bandwidth was measured at –10 dB below the peak frequency. Bandwidth measurements of complete syllables were done in a similar manner, by generating a power spectrum of the whole syllable, and measuring the frequency bandwidth at –20 dB.
RESULTS

Cowbird-like abrupt, stepped frequency shifts

Mockingbirds in this study attempted to sing the cowbird tutor sounds, however, they did not reproduce the exceptionally wide frequency range of the cowbird's song. When copying a tutor song that included notes outside their frequency range (lower than ~750 Hz or higher than ~7 kHz), mockingbirds either omitted these notes or substituted a note at a frequency within their vocal range (Fig 1b), indicating that their frequency limitation is due to a production, as opposed to auditory, constraint. As in other songbirds (Suthers, 1999), mockingbirds sing their lowest frequencies with the left syrinx and the highest frequencies with the right. Within its vocal frequency range, the side of the syrinx on which a mockingbird produced a note depended on its frequency, syntax and the acoustic effect to be achieved. For frequencies between 1.6±0.35 to 2.9±1.28 kHz (n = 5 males), notes can be produced on either side of the syrinx. Frequencies below or above this range were always produced on the left or right side of the syrinx, respectively. Since the first two left-side notes of the cowbird's note clusters (Fig 1a) are below the frequency range of mockingbird 123, he omits them and begins his copy of each note cluster (Fig 1b) with 2 notes on the right side of the syrinx. The 2 mockingbirds that sang cowbird songs (N = 45) always sang each of these notes on the same side as the cowbird tutor (Fig 1b), even though they were within the frequency range of both sides of the syrinx. When notes were omitted, the lengths of the remaining notes were increased to approximately maintain the duration and tempo of the song (Fig 1b).

We examined 140 mimicries by 3 mockingbirds of computer-synthesized pairs or sequences of constant frequency tones, presented in immediate succession with no silent interval between members of the series. Tone duration was 100 to 200 ms and both members of each pair of tones (or individual pairs within a longer series of tones) were identical except that the second tone was at a higher or lower frequency than the first.
Figure 1. (a) Tutor song of brown-headed cowbird. Spectrogram (top panel) shows 2 note clusters (NC 1 & 2) in which notes were sung on alternate sides of the syrinx beginning with the first (lowest) note on the left (L) followed by a note on the right (R). Final whistle (FW) produced on right side. The side on which sound is produced is controlled by dorsal syringeal muscles that can silence one side by closing it to airflow, despite a positive pressure. Ventral syringeal muscles control fundamental frequency (Suthers 1997). Shaded bands across spectrogram indicate frequencies outside vocal range of mockingbird 123. Note that the lowest frequency notes in NC1 and 2 as well FW were outside this mockingbird's range. (b) A mockingbird copy of (a). Omission of notes in NC1 and 2 that were outside the mockingbird's vocal range (italicized letters denote notes in the tutor song omitted by the mockingbird) resulted in silent intervals (arrows) between the remaining notes which were sung on same side of syrinx as cowbird. The mockingbirds increased the duration of the remaining notes, thus maintaining the duration of the tutor note clusters. Duration of tutor NC 1 and 2 was 109 ms, and 151 ms, respectively, before note deletion. The portions of NC 1 and 2 copied by mockingbird were sung in 81 ms and 109 ms by cowbird but expanded to 92 ± 11 ms (M ± SD) and 147 ± 16 ms, respectively, by mockingbird. FL and FR, rate of airflow through left and right sides of syrinx, airflow associated with positive pressure is expiratory; shaded flow (corresponds with negative pressure) is inspiratory. P, pressure in cranial thoracic air sac. V, oscillograph of vocalizations. Horizontal lines indicate zero airflow and ambient pressure.
Mockingbirds sang successive tones with opposite sides of their syrinx, like the notes in a cowbird’s note cluster, in 35% (49 syllables) of these mimicries (Fig 2a). In each of these cases they reproduced the abrupt, step-change in frequency between tones. We defined an “abrupt frequency step” in the mimicked songs as a discontinuous, step-wise change between two frequencies with an inter-note interval of 10 ms or less. All 3 mockingbirds who copied synthesized tone pairs achieved abrupt frequency steps between tone pairs only when they alternated sides.

Mockingbirds attempted to sing both tones on the same side of their syrinx in 65% (91 syllables) of the mimicries. When using this production mechanism, the tones were either slurred together (28%; Fig 2b) or separated by a silent interval (72%; Fig 2c). Slurring occurred independently of whether the frequency of the second tone was higher or lower than the first. Slurs between tones were never observed in any of the 3 birds when tones were produced on opposite sides of the syrinx. Infrequently (16% of the 49 ‘opposite side’ syllables), mockingbirds inserted gaps greater than 10 ms between tones produced on opposite sides. These silent intervals between notes sung on opposite sides had a mean duration (29 ± 15 ms) significantly shorter than the silent intervals between tones sung on one side only (39 ± 15 ms) (t = 1.67, df = 54, P = 0.05).

The side on which a note was sung depended on its context as well as its frequency. The same bird, for example, sang a 2 kHz note on a different side, depending on the frequency of the preceding note (Fig 2d). Abrupt, transient frequency jumps produced by a single side were observed rarely in mockingbird song (0.1% of 3000 syllables, from 3 birds) and likely due to intrinsic nonlinear behaviour of the syrinx (Fee et al. 1998). This type of frequency jump was never used by birds mimicking a tutor sound.

**Cardinal-like FM sweeps**

The accuracy with which mockingbirds reproduced cardinal sweeps depended on the accuracy with which they reproduced the cardinal’s motor pattern. The cardinal tutor
Figure 2. Mockingbird copies of synthetic cowbird-like note clusters. (a) When mockingbirds sang successive notes in the cluster on alternating sides of the syrinx, like a cowbird, they reproduced the immediate onset, step-wise frequency changes present in the tutor song. When both notes were outside the frequency range of the left syrinx the mockingbird was forced to sing both tones on the right side and deviate from the tutor sound in one of two ways: (b) If he retained the immediate onset of the second tone he introduced a slurred FM between tones due to a motor constraint on how rapidly the syrinx can change the tension of the syringeal labia which vibrate to produce the sound (Goller & Larsen 1997; Larsen & Goller 1999). Alternatively, (c) he sometimes introduced a short silent interval between tones (vertical lines) during which labial tension is adjusted for the second tone. In this case the spectral contrast of the tutor sound is preserved, but the temporal pattern is altered. (d) Within a limited range of frequencies, the decision to sing a tone with the right or left side of the syrinx is context-dependant. In these examples, a mockingbird sings a 2 kHz tone with either the left or right side of the syrinx, depending on the relative frequency of the adjacent tone. R and L denote syllables produced on the right or left side. Other abbreviations see Fig 1.
Table 1: Contribution of left and right syrinx in mockingbirds copying extended FM sweep of cardinal

<table>
<thead>
<tr>
<th>Production pattern</th>
<th>m138</th>
<th>m123</th>
<th>m130</th>
<th>m103</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Good L-R switch*</td>
<td>52%</td>
<td>59%</td>
<td>59%</td>
<td>57%</td>
<td>57%</td>
</tr>
<tr>
<td>L-R overlap†</td>
<td>31%</td>
<td>36%</td>
<td>12%</td>
<td>43%</td>
<td>27%</td>
</tr>
<tr>
<td>Unilateral sweep</td>
<td>17%</td>
<td>5%</td>
<td>29%</td>
<td>0%</td>
<td>11%</td>
</tr>
</tbody>
</table>

N  23  153  17  7

*Overlap <15 ms  
†Overlap ≥ 15 ms
songs we used were characterized by almost seamless switches between sides of the syrinx in mid-syllable. Periods of overlap between sound from the left and right sides in the tutor songs ranged from 0 to 15 ms. All 4 mockingbirds executed a cardinal-like switch from one side of the syrinx to the other, with periods of simultaneous bilateral sound production lasting less than 15 ms, in more than half of their copies of FM sweeps (Fig 3a; Table 1). In 12 to 43% of each mockingbird’s cardinal sweeps, the phonating side of the syrinx did not close when the contralateral side opened, resulting in a mid-sweep temporal overlap of the fundamental from each side (Fig 3c, Table 1). We measured the frequency bandwidth of a 25 ms portion of the sweep centered on the overlapping region or the point where the bird switched sides. Bandwidths of these segments from mockingbird sweeps in which sides overlapped (1472 ± 237 Hz, N = 35) were significantly greater than those of the tutors (557 ± 159 Hz, N = 21, P<0.001, df = 3, one-way ANOVA and Tukey Test) and also from sweeps in which the mockingbirds switched sides smoothly like a cardinal (715 ± 266 Hz, N = 35, P<0.001, df = 3). The mean duration of overlap was significantly greater (P<0.050, N = 54, df = 3) in mockingbirds that did not switch sides smoothly (e.g., Fig 3c) than in those that did (e.g., Fig 3a), or than the cardinal tutors. Corresponding segments of mockingbird syllables with good switches between sides did not differ significantly from the cardinal tutors. Three of the 4 mockingbirds occasionally attempted to sing cardinal sweeps using only a single side of the syrinx in 5 to 29% of their sweeps (Fig 3e, Table 1).

The important influence of motor constraints on the production of linear FM sweeps is further illustrated by mockingbird copies of cardinal-like, computer-generated sweeps (Fig 3b, d and f). Four birds used a coordinated mid-syllable right-left switch in 92-100% of their copies of synthesized tutor sweep 4 (Fig 3b). When copying a synthesized upward sweeping FM, 2 of these birds always switched smoothly from left to right in mid sweep (e.g., first sweep in Fig 3d). The other 2 birds switched smoothly in 83% or 70%, respectively, of all syllables analyzed (n =55), but in other cases sang all or part of
Figure 3. Mockingbird copies of extended FM sweeps. (a) and (b) When mockingbirds used a similar motor pattern as a cardinal to produce frequency-modulated (FM) sweeps, their copy resembled the tutor most closely. Like the cardinal tutor song (top), the mockingbird switches phonation cleanly from the right to left side mid-syllable, this was true whether they mimicked a cardinal or synthesized FM sweeps. Mockingbirds used a cardinal-like motor program to sing both downward (b) and upward (first sweep in panel d) computer synthesized FM sweeps. In both cases, the change in sound production from one side to the other is well coordinated with little or no biphonation. (c) and (d) If the mockingbird continues sound production on the first side of the syrinx after starting phonation on the contralateral side, different frequencies from each side result in biphonation absent in the tutor song. (d) The more precisely a mockingbird switched sides mid-sweep, the more linear the resulting sweep, while more temporal overlap in phonation from the two sides results in increased amounts of biphonation. Differences in precision of mockingbird copies of FM sweeps, may be the result of differences in the motor skills of individual birds or to other factors including the possibility that some birds preferred the spectral complexity of biphonation over the single frequency component of the tutor syllables. (e and f) A third strategy sometimes employed was to sing the entire sweep on one side. These unilaterally produced sweeps resemble the tutor in spectral quality, but have a significantly reduced bandwidth than the tutor sweep (mean unilateral = 2.96 ± 0.715 kHz, mean bilateral = 4.7 ± 0.52 kHz. (t = 8.761, df = 38, p<0.001, n=198 sweeps).
the sweep with simultaneous airflow through both sides of the syrinx. These periods of bilateral phonation were significantly greater both in duration (P<0.001, N = 75, df = 3) and bandwidth (P=0.001, df = 2) than the overlaps present in mockingbirds with more precise, cardinal-like lateral switches and necessarily greater than the synthesized tutor sweep, which had no overlap. More importantly perhaps, the mean mid-sweep bandwidth in syllables of birds that made ‘good’ cardinal-like switches between sides (562 ± 349 Hz; e.g., Fig 3d) was not significantly different than that of the synthesized tutors (659 Hz), indicating a very precise L-R switch. Unlike the cardinal tutors, who switched sides between 3.5 and 4.0 kHz, the mockingbirds in this study switched sides between about 1.9 and 3.6 kHz.

When mockingbirds copied FM sweeps (of either cardinal or synthesized tutors) that were within the frequency range of one side of their syrinx they always produced the entire sweep on one side (Fig 3e & f), even though part of the sweep extended into the frequencies that could be produced on either side. Such sweeps had a single smoothly modulated fundamental similar to that of the tutor sounds, but their bandwidth (2.96 ± 0.72 kHz) was reduced significantly compared to sweeps produced bilaterally (4.68 ± 0.52 kHz; t = 8.761, df = 38, P<0.001 n = 198 sweeps; 4 birds).

**Canary-like long duration, high repetition rate trills**

Temporal, as well as spectral, aspects of song are subject to performance limits. Attempts by 2 mockingbirds to copy phrases of canary song having a high syllable repetition rate reveal the importance of respiratory limitations on trill production. When copying a canary trill having a duration of 4.1 to 7.7 s and sung at a repetition rate of 22 syllables s⁻¹ (Fig 4a), neither bird copied the minibreath respiratory pattern used by the canary (Fig 4c), but instead periodically interrupted the trill with a brief inspiration that divided it into clusters of notes. The notes within each cluster are produced by pulsatile expiration and separated from each other by a brief inspiration (Fig 4d). Within each note
Figure 4. (a) Wasserslager canary tutor song. (a) & (c) The canary sings this uninterrupted trill for 4 seconds. He maintains this rapid repetition of syllables (20 s⁻¹) by taking “minibreaths” (mb) between each syllable (small arrows in c). (b) & (d) The much larger mockingbird cannot achieve the canary syllable repetition rate using minibreaths, but breaks the trill into a series of short segments each containing several syllables produced by pulsatile expiration during which pressure remains positive between syllables. Each syllable is produced by briefly opening of the right syrinx (evidenced by fluctuations in the flow rate on the right). The high syllable repetition rate is achieved at the cost of depleting the air supply, forcing the mockingbird to periodically interrupt the trill by opening the left non-phonating side for a minibreath. The overall duration of the interrupted trill is 1 second shorter than that of the tutor. Bracket above the oscillographic trace of the mockingbird vocalization indicates portion of the song shown in (d). Inspiratory airflow during minibreaths is shaded. Abbreviations as in Figure 1.
cluster the trill is accompanied by a sustained positive subsyringeal pressure and each syllable is produced by briefly opening one side of the syrinx to release a puff of air. The mean duration of trill segments sung by mockingbirds using this pulsatile respiratory pattern was $0.54 \pm 0.18$ s (range 0.19 to 0.98 s), interrupted by breaths with mean duration of $0.19 \pm 0.08$ s ($N = 35$).

Although mockingbirds used a pulsatile phonation strategy to sing the rapid trills of the canary tutor, the same mockingbirds ($N = 2$) did use canary-like minibreaths when singing trills with lower repetition rates ($\sim 10$ s$^{-1}$). When using minibreaths, mockingbirds in this study were able to sing uninterrupted trills with durations as long as 9.8 seconds (mean duration trill with minibreaths $3.6 \pm 2.1$ s, $N = 25$). The duration of uninterrupted trills produced using a minibreath respiratory pattern was significantly longer than that of trill segments produced with pulsatile respiratory strategy ($t = 2.002$, df $= 57$, $p < 0.001$).

**DISCUSSION**

The mockingbirds in this study always employed a motor pattern similar to that of the tutor when they copied the tutor's song. When the mockingbird's motor pattern differed from the tutor, his vocalization also differed. Thus, during the process of trial and error motor learning, both model and mimic converged on the same motor pattern. This suggests that similar basic physical and physiological constraints on song production apply across species of songbirds and styles of song, and that the different motor patterns employed by various taxa are unique motor solutions for producing their species-specific songs.

Within a given tutor species, the accuracy with which the mimic reproduces the motor pattern of the model provides an indication of which parts of the tutor song are most difficult to produce. Despite the superficial similarity of their vocal organs, natural selection has pushed against the production constraints of each tutor species’ vocal system in one or a few ways, and the direction of selection is quite different for different species.
Thus cardinals are specialized for producing extended frequency sweeps, cowbirds for step-like frequency jumps between adjacent notes and canaries for producing long trills at high syllable repetition rates. Mockingbirds on the other hand have been selected to maximize the diversity of their vocalizations, and perhaps the quality of their ability to mimic. As vocal generalists they must avoid directional specialization of their syringeal or neural ‘fine structure’ and remain a jack of all trades but master of none. It appears that the features of the model’s songs that are the hardest for mockingbirds to mimic are the features under the strongest selection in model species, and determine the characteristic form of their species-specific songs.

A distinctive feature of cowbird song, for example, is the rapid alternation of successive frequency-stepped notes between opposite sides of the syrinx. West and King (King et al., 1980; West et al., 1981; King and West, 1983) showed that timing and intensity of low and high pitched notes in the note clusters are important in determining the ‘potency’ of a male cowbird’s song in eliciting a copulation solicitation display from the female, raising the possibility that sexual selection has favoured the motor skills required to produce them. Yearling male cowbirds sing fewer complete and shared songs, which are preferred by females, suggesting that vocal motor skills take time to develop. This developmental cost may ensure signal honesty as an indicator of male quality (O’Loghlen and Rothstein, 2003). The fact that mockingbirds, like cowbirds, achieve abrupt steps between notes by producing them on opposite sides of the syrinx, supports the hypothesis that this motor strategy evolved to avoid the time delay or frequency slur between notes caused by limitations on the speed with which labial valves gating phonation can operate and labial tension controlling fundamental frequency can be adjusted for successive notes produced on the same side of the syrinx.

A distinctive feature of cardinal song is the precision with which sound is switched from one side of the syrinx to the other to generate broadband FM syllables that often have a fundamental bandwidth sweeping smoothly over more than 2 octaves with no
perceptible interruption of the sound. It is this extended bandwidth and smoothly coordinated mid-sweep transfer of sound production from one side of the syrinx to the other that Mockingbirds have the most difficulty in copying, as judged by the accuracy of their rendition. In cardinals the two sides of the syrinx are more highly specialized to cover separate frequency ranges than in other species studied and cardinals appear to have special skills of bilateral coordination that allow them to generate a continuous sweep while switching from one sound source to the other.

Mockingbird renditions of canary trills show how production constraints on song have an important role in determining the maximum tempo or duration of trilled phrases. Female canaries prefer males with high syllable repetition rates (Vallet et al., 1998; Draganoiu et al., 2002). The mockingbird’s version of the high syllable repetition rate canary trill, differed from the tutor in both its acoustic properties and its underlying motor pattern. Instead of producing a continuous trill at the tutor’s syllable repetition rate using minibreaths, the mockingbird divided the trill up into short segments each containing several syllables produced by pulsatile expiration. Each of these segments was separated from by next by a silent interval for an inspiration.

The mockingbird’s segmentation of canary trills is likely due to a production constraint that results in an inverse relationship between body mass and the maximum rate of respiratory ventilation. During minibreaths, ventilation is driven by oscillatory motion of the thorax and abdomen that replaces the respiratory volume after each syllable. The syllable repetition rate for switching from minibreaths to pulsatile expiration (e.g., 30 s\(^{-1}\) in ~18 g canaries; 16 s\(^{-1}\) in ~40 g cardinals; 10 s\(^{-1}\) in ~50 g mockingbirds) is inversely related to body mass, and presumably to the mass of tissue that must oscillate at the respiratory frequency. We hypothesize that the larger body mass of mockingbirds precludes taking minibreaths at the tutor canary’s syllable repetition rate of 20 s\(^{-1}\) (Fig 4a). Instead the mimic was forced to resort to a pulsatile expiratory pattern in order to match the repetition rate of the tutor trill. In pulsatile expiration the respiratory volume is not
replaced between syllables, forcing the mockingbird to interrupt the trill every several syllables for an inspiration to replenish the air expelled for phonation. A similar pattern of broken syntax was observed in sparrows tutored with artificially increased syllable repetition rates (Podos, 1996). The present results indicate that these interruptions were likely also due to physical constraints on respiratory frequency.

The data do not support a possible alternative explanation that interruptions in the canary trill simply reflect the mockingbird's preference for dividing long song sequences in short bouts of syllables (Derrickson and Breitwisch, 1992). The number of syllable repetitions within these bouts is inversely related to the duration of the syllables (Derrickson, 1988), suggesting that it is bout duration rather than the number of syllables that is the salient factor determining the temporal patterning of mockingbird song. This behavioral preference hypothesis does not explain why the mockingbird uses pulsatile expiration instead of minibreaths to sing note clusters in the canary trill. Recordings from our mockingbirds show that they insert a minibreath between syllables within bouts when syllable repetition rate is $\leq 10$ s$^{-1}$. The mean length of a minibreath song bout was more than 6 times that of the pulsatile note clusters in the mockingbird's renditions of the canary trill (see Results). Using minibreaths, the mockingbirds in our study sang uninterrupted bouts that were almost 2 s longer than the longest tutor song we used.

The ability of a vocal generalist, like a mockingbird, to reproduce many of the basic motor and acoustic patterns of heterospecific song indicates that the rules for song production are shared across species. As selection pushes acoustic signals toward the individual's performance ceiling, these signals have the potential to be used as honest signals (Zahavi, 1975; Zahavi, 1977) of certain aspects of motor performance that is perhaps related to male quality. Further studies of song production from the unique perspective of vocal mimics may help us understand the role of motor constraints and special motor skills in the evolution of vocal communication.
Chapter 2

Two-voice complexity from a single sound source: Nonlinear phenomena in northern mockingbird (*Mimus polyglottos*) vocalizations
**Abstract**

Songbirds produce their diverse vocal signals with independent, but highly coordinated patterns of muscle activity. These muscles control separate sound generators on the right and left side of the duplex vocal organ, the syrinx. Some acoustic effects are intrinsic to the vocal organ such that they are not controlled by the central nervous system but are instead the result of nonlinear dynamics of the oscillating tissues within each side of the syrinx. Because of the bipartite nature of the songbird syrinx, few data have been available showing to what extent nonlinear phenomena, such as frequency jumps, subharmonics, biphonation and deterministic chaos were part of the normal repertoires of intact songbirds. The present study investigated the occurrence of such events in the repertoires of northern mockingbirds (*Mimus polyglottos*). Our data show that certain sounds that may have previously been attributed to two-voice phenomena are in fact nonlinear phenomena produced unilaterally. Patterns of subsyringeal air sac pressure or relative rates of air flow through the syrinx did not predict the occurrence of such unilaterally produced nonlinear phenomena. This is the first evidence of syringeal lateralization of nonlinear dynamics during certain types of bilaterally-produced chaotic calls. We did not find patterns of subsyringeal air sac pressure or relative rates of air flow through the syrinx were consistently associated with the occurrence of such unilaterally produced nonlinear phenomena. Finally, our data support previous hypotheses for mechanical and acoustic coupling between the two sides of the syrinx. These results will help lay the foundation upon which the function of such phenomena may begin to be understood.
INTRODUCTION

One of the fascinating aspects of songbird vocal communication is the diversity and complexity of their acoustic signals. The ability for mimetic learning and the production of increasingly complex vocal signals is thought to have played a role in allowing the radiation of the songbirds into the largest and most diverse order of birds (oscine Passeriformes - Baptista and Trail, 1992). Two well-documented functions of birdsong are territory defense and mate attraction, and there is increasing evidence that natural and sexual selection may increase vocal complexity in songbirds (see recent review by Nowicki and Searcy, 2004). Certain features of vocal performance and acoustic complexity associated with the vocal motor skills of male songbirds may be used by females during mate selection (Vallet et al., 1998; Forstmeier et al., 2002; e.g. Ballentine et al., 2004). It is evident that both the unique bipartite anatomy of the songbird vocal organ as well as its intrinsic biomechanical properties might contribute to increased acoustic complexity in songbird vocal signals.

Sources of acoustic complexity: The bipartite syrinx

The oscine vocal organ, the syrinx, is located at the caudal end of the trachea at the junction of the trachea and the two primary bronchi. Early descriptions of syringeal anatomy recognized that the syrinx was comprised of two distinct sound sources with independent nervous and muscular control, (e.g. Setterwall, 1901; Rüppel, 1933). Situated at the cranial end of each primary bronchus is a pair of vibratory labia (the medial and lateral labia) and a medially situated tympaniform membrane (MTM), which is contiguous with the medial labia (King, 1989). Recent endoscopic observation of the syrinx, along with MTM ablation experiments have shown the labia to be the primary sound sources (Goller and Larsen, 1997; Goller and Larsen, 2002). Historically, much of the acoustic complexity in birdsong has been attributed to the bipartite nature of the
syrinx, especially the presence of temporally overlapping tones that are not harmonically related (Thorpe, 1961; Grenewalt, 1968; Stein, 1968).

The lateralized use of the bipartite syrinx has been a topic of investigation for several decades. Grenewalt (1968) is credited with defining this class of sounds as “two-voice phenomena.” A decade later, Nottebohm (1971; 1976), in a series of experiments in which they denervated one side of the syrinx, described a strong pattern of syringeal lateralization for song production in Waterschlager canaries (*Serinus canarius*), a domesticated strain that has undergone intense artificial selection for certain song features, and chaffinches (*Fringilla coelebs*). The pattern of syringeal lateralization in Waterschlager canaries was corroborated in subsequent bronchial plug experiments (Hartley and Suthers, 1990). Further investigations into syringeal lateralization by measuring airflow through the right and left sides of the syrinx in other species found no prominent lateral biases (Suthers, 1990; Allan and Suthers, 1994; Suthers, 1997). In fact, extensive bilateral exploitation of the two sides of the syrinx during normal song seems to be the rule rather than the exception, even in a less-inbred strain of domestic canaries (Suthers et al., 2004).

The techniques for recording airflow through each side of the syrinx during song (Suthers, 1990) allowed for a more comprehensive investigation into the intricate syringeal and respiratory motor dynamics that birds master during song learning and production. In addition to two-voice phenomena, songbirds exploit their dual sound source to increase vocal versatility in other domains, such as increasing bandwidth, repetition rate, abrupt changes between notes, and so on (see review in Suthers and Zollinger, 2004).

*Nonlinear dynamics of the syrinx*

In addition to the coordinated neuromuscular control of the syrinx and respiratory system, there is another potential contributor to the acoustic complexity of birdsong. This alternate source of complexity arises from the passive biomechanical properties of
the syrinx, specifically the dynamic vibratory properties intrinsic to the pair of oscillators (labia) comprising each sound source. Recent experiments have demonstrated that the labia, much like the vocal folds in the mammalian larynx (Herzel et al., 1994), comprise a nonlinear physical system (Fee et al., 1998; Fee, 2002). As in any such system, the oscillating masses predictably exhibit certain traits or behaviors including abrupt bifurcations between different vibratory modes.

Four acoustic phenomena are associated with nonlinear systems (Wilden et al., 1998). These “nonlinear phenomena” (NLP) include frequency jumps, subharmonics, biphonation, and deterministic chaos. Nonlinear phenomena have been identified in vocalizations from a diverse set of species including non-songbirds such as doves (Beckers and ten Cate, 2006) and parrots (Fletcher, 2000), frogs (Feng et al., 2002), and mammals (e.g. Titze et al., 1993; Herzel et al., 1995; Riede et al., 1997; Wilden et al., 1998; Riede et al., 2000; Tokuda et al., 2002; Riede et al., 2004; Riede et al., 2007).

**Increased complexity of a two-voice system**

Spectrographic analyses alone in songbirds cannot always reliably distinguish between two voices and some kinds of NLP. For example, in mammals biphonation is traditionally defined as the simultaneous appearance of two independent frequencies (Berry et al., 1996; Wilden et al., 1998). However, the same definition was applied by Greenewalt (1968) to describe standard two-voice phenomena. The problems discerning NLP from two-voice phenomena based solely on emitted vocalizations have been further described by Laje and Mindlin (Laje and Mindlin, 2005; Mindlin and Laje, 2005), whose models of source-source and source-tract interactions in the oscine syrinx demonstrated that interactions of the two sides of the syrinx can produce acoustic effects resembling those commonly associated with nonlinear theory, such as subharmonics and biphonation. These models support earlier evidence of source-source coupling in the oscine syrinx (Nowicki and Capranica, 1986) and demonstrate that certain complex sounds typically associated
with nonlinear dynamics, such as frequency jumps, subharmonics or “biphonation”, in birdsong might also result from two-voice phenomena.

Rapid alternation between phonation on the right and left sides of the syrinx can also be difficult to distinguish, based on spectrograms alone, from frequency jumps produced by nonlinear dynamics. For example, the introductory note of a brown-headed cowbird (*Molothrus ater*) song consists of a series of alternating high- and low-frequency tones with abrupt jumps between successive frequencies. These frequency jumps are produced by rapid alternations between left and right syringeal phonation (Allan and Suthers, 1994). Spectrographically, however, these frequency jumps are indistinguishable from frequency jumps resulting from bifurcations in a single pair of oscillators.

In this study, airflow through each side of the syrinx during song was monitored in order to determine whether complex sounds were produced bilaterally (two-voice; with airflow through both the right and left syrinx simultaneously) or unilaterally (NLP; airflow through only one side of the syrinx, while the other side is closed). This is the first experiment monitoring syringeal lateralization to evaluate the relative contribution of NLP to two-voice phenomena and song variety.

**METHODS**

**Rearing and acoustic experience of birds**

Mockingbirds were housed in individual cages as groups within a single sound attenuating chamber (Industrial Acoustics Company, Inc., Bronx, NY). Subjects in this study were 4 adult (1-3 year old) male northern mockingbirds (*Mimus polyglottos*), that had been hand-reared in the laboratory. Each bird was tutored during their first year with a wide variety of sounds including recordings of heterospecific songs from several species and computer-synthesized sounds designed to resemble different bird song types (Table 1). Because mockingbirds are vocal mimics, the individual repertoires of each
Table 1. Tutor regimes for 4 mockingbirds in this study

<table>
<thead>
<tr>
<th>Bird ID</th>
<th>Sound type</th>
<th>Tutor type&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Recordings&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Live&lt;sup&gt;b&lt;/sup&gt;</th>
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<tr>
<td></td>
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<td>CF</td>
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<td>FM “two-voice”</td>
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</tr>
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</table>

<sup>a</sup>1<sub>fo</sub>, single f<sub>o</sub> varying over time (may be pure-tonal or include upper harmonics); FJ, tutor sound contains an abrupt jump up or down in frequency; 2<sub>fo</sub>-SB, sound that contains prominent sidebands above and below a f<sub>o</sub>, visible in a narrowband spectrogram, corresponding to a second, modulating frequency (m<sub>o</sub>); 2<sub>fo</sub>-other – sounds that contain two independent fundamental frequencies, in any other combination than the sideband relationship described above (such as two-voice phenomena).

<sup>b</sup>“Recordings” refers to field recordings of naturally-produced bird songs; playback to mockingbird juveniles during tutoring was via compact disc.

“Live” tutors, were birds housed in adjacent rooms, which mockingbirds may have heard.

“Synthesized” tutors were computer-generated sounds, playback was via compact disc.


FM, frequency modulated pure-tonal sounds; CF, constant frequency pure tones; CF “tone pairs”, tones of different frequency presented in step-wise pairs; AM, amplitude modulated FM or CF tones with sidebands corresponding to the modulation frequency; FM “two-voice”, two simultaneous, independent, synthesized FM sounds.

“Tone pairs” describes abrupt step-wise jumps in frequency, however since the production patterns for these recorded birdsong elements are not known, do not necessarily represent frequency jumps due to nonlinear dynamics.
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*aNumber of individual syllables assigned to each classification category (n= 1000 syllables per bird). If a syllable contained more than one type of NLP it was counted toward totals of each, but if it contained at least one type, it was not included in “harmonic” categories (1f₀ and 2VC) regardless of the ratio of harmonic vs. nonlinear elements.

*bTotal number of discrete syllable types within the 1000 syllable sample per bird.

*cSyllables produced with flow through only one side of the syrinx. 1f₀, single f₀ sounds; FJ, frequency jumps; SH, subharmonics; CH, deterministic chaos; BP, biphonation (two independent fundamental frequencies, but air flow through only one side of the syrinx);

*dSyllables produced with flow through both sides of the syrinx during the portion of the sound containing the NLP. SB-2VC, sidebands (single carrier frequency with sidebands, but flow through both sides of the syrinx); 2SB-fixed, two f₀, each with sidebands with a fixed modulation frequency; 2SB-changing, two f₀, each with sidebands with a changing modulation frequency; 2VC, two-voice phenomena (each side of the syrinx producing a distinct, unrelated f₀).
bird were dominated by mimicries of some subset of the tutor syllables they had heard. The repertoires of the birds in this study were between ~ 90 and 120 syllable types at the time of the experiment (but repertoire sizes are seasonally variable, pers. obs.). Tutor sounds were chosen or designed for an experiment on song production (see Zollinger and Suthers, 2004 for tutoring details). While the tutor experience of these mockingbirds was not specifically designed to investigate nonlinear phenomena, the sounds were intended to expose juvenile mockingbirds to a wide variety of complex sounds, including some possible NLP. All birds had been exposed to tutor sounds containing two simultaneous unrelated frequencies, either in recordings of heterospecific song or in computer-synthesized tutor sounds. These two-frequency sounds were of two sorts, the first type consisted of two higher frequency tones (between 1-7 kHz) with independent rates of frequency modulation (FM). The second type of two-\(f_0\) sounds consisted of a single higher \(f_0\) and a lower (<1 kHz) modulating frequency, resulting in a periodic amplitude modulation (AM) of the waveform with sidebands. Some tutor sounds contained frequency jumps, consisting of abrupt step-like changes of 0.5 and 3 kHz in \(f_0\), in the frequency range between 1 and 7 kHz. None of the tutor sound recordings contained subharmonics or chaos, however mockingbirds were occasionally exposed to the song of northern cardinals (\textit{Cardinalis cardinalis}), eastern towhees (\textit{Pipilo erythrophthalmus}), zebra finches (\textit{Taeniopygia guttata}) and ring doves (\textit{Streptopelia risoria}) that were housed in adjacent rooms in the laboratory, therefore we can not rule out the possibility that mockingbirds may have heard any NLP that could have arisen spontaneously in the songs of these other species.

\section*{Surgery and Data Acquisition}

Birds were anesthetized by injection of chloropent (4.1 ul /g body weight, recipe from Fort Dodge Animal Health, Overland Park, KS) into the pectoral muscle. A silastic cannula (Dow Corning Corp, Midland, MI; ID 1.02 mm, OD 2.16 mm) was inserted
into a cranial thoracic air sac for measurement of subsyringeal pressure. The cannula was attached to a miniature piezoresistive pressure transducer (Fujikura FPM-02PG, Marietta, GA) mounted on a small backpack attached to an elastic belt fitted around the bird’s thorax.

A mid-ventral incision was made between the clavicles in order to expose the syrinx through an opening in the interclavicular membrane. The rate of airflow was recorded by a heated microbead thermistor (Thermometrics, Edison, NJ, BB05JA202) inserted into each bronchus a few semi-rings caudal to the syrinx. The interclavicular membrane was sealed around the thermistor leads, which were routed under the skin to the backpack. For more detailed surgical methods see (Suthers et al., 1994; Zollinger and Suthers, 2004). Pressure and airflow signals were transmitted from the backpack on leads that exited through the top of the cage to signal conditioning instruments (Hector Electronics, Elletsville, IN) and a multi-track digital data recorder (Metrum DataTape RSR512, Littleton, CO). Four signals (vocalization, rate of airflow through the right and left bronchi, and air sac pressure) were recorded digitally (20,000 samples s^{-1}) onto separate tracks on ½-inch magnetic tape, using the Metrum recorder. Signals were transferred from tape to microcomputer by resampling (40,000 samples s^{-1}) using a Data Translation board (DT-2821G) and an antialiasing filter (TTE, J87, St Pete Beach, FL, 8 kHz high cut-off, stopband attenuation 60 dB per 1/3 octave). An experiment lasted 7-10 days, during which the bird could move freely about its cage. Vocalizations during experiments were recorded with a directional condenser microphone (Audio-Technica AT835b, Stow, OH) positioned approximately 50 cm in front of the cage.

Two methods were used to determine what each side of the syrinx contributed to the song. The first method measured airflow through the syrinx; any air flowing through one side of the syrinx while the other side was closed indicated that the sound was produced entirely with the open side. In some recordings, the thermistors responded to air oscillations up to ~2 or 3 kHz produced by the acoustic signal from the ipsilateral side
of the syrinx. In these cases it was possible to determine the sound generated by each side when both sides were phonating (Suthers, 1990). The low frequency components of bronchial signals related to respiratory or phonatory motor patterns were removed post-recording with a digital 100 Hz high-pass filter.

Signals were analyzed with Igor Pro v. 5 (WaveMetrics Inc., Lake Oswego, OR) and with Adobe Audition v. 1.5 (Adobe Systems Inc., San Jose, CA). Statistical analysis was conducted using Igor Pro v. 5 and SigmaStat v. 2.03 (SPSS Inc., Chicago, IL). Preoperative song (100-300 minutes per bird) was recorded from adult birds (>300 days post hatching) for comparison with pre- and post-surgery repertoires (Avisoft-Recorder v. 1.7).

For each syllable that spectrographically resembled one of the four NLP, we examined the airflow and pressure recordings, and noted the acoustic contribution of each side of the syrinx. A syllable was defined as a sound in which the air sac pressure was negative prior to the sound, positive during the sound production, and negative after completion of the sound (a single expiratory pulse). Vocalizations were first examined for the occurrence of NLP through visual inspection of narrowband spectrograms (16-kHz sampling frequency, 35-ms Hanning window, 98% window overlap) and associated power spectra. Each syllable was scored for the presence of the four NLP described above. If a syllable contained more than one type of phenomenon, it was counted in each category.

Identifying Nonlinear Phenomena

Spectrographic evaluation

We examined 1000 syllables from 4 subjects for acoustic evidence of NLP (frequency jumps, subharmonics, biphonation or deterministic chaos). This initial sorting of sounds by visual spectrographic examination was not sufficient to determine the mechanism of production, but was sufficient to identify possible NLP for further investigation.

Frequency jumps are sudden changes in fundamental frequency \( f_0 \) to a higher or lower \( f_0 \) (Fig 1A). Frequency jumps are qualitatively different from continuous modulation with smooth upward or downward transitions. A frequency jump was defined as a visible,
Figure 1. Spectral properties typical of three types of nonlinear phenomena; frequency jumps, subharmonics and deterministic chaos. (A) A 3500 Hz tone with two 250 Hz frequency jumps, a power spectrum taken at arrow a shows sound energy at a single $f_0$. (B) A 3750 Hz tone, with a series of bifurcations, the first from a single $f_0$ to a $1/3$ $f_0$ subharmonic regime, then an abrupt transition to deterministic chaos, and then to a $1/4$ $f_0$ subharmonic regime. Comparing spectra at arrows a and b illustrates the difference between a single $f_0$ regime at arrow a (spectra is identical to the $1f_0$ spectra, a in Box A) and the more complex spectrum that results from the addition of subharmonic values and their harmonics (b, Box B). (C) A 10 ms section of deterministic chaos (in this case, a low-dimensional noise, generated using a Rossler attractor equation). The aperiodic nature sound waveform (V) and the sound energy fairly evenly distributed across the entire spectrum (spectrogram C, and power spectrum, c) are both indicators used to identify potential chaos in mockingbird songs. Abbreviations the same as those in Tables 1 and 2; FJ, frequency jump; SH, subharmonics; CH, deterministic chaos; $1f_0$, single sounds; V, amplitude of sound waveform in volts.
**Figure 2.** Different classes of biphonation and two-voice phenomena that might arise from a single sound source (A and B) or from a dual sound source (A-D). The spectrogram (top) and spectrum (bottom) in box (A) illustrate the spectral properties typical of a either type 1 biphonation or two-voice phenomena. This class of sounds is characterized by 2 independent fundamental frequencies that are not harmonically related. A power spectrum (bottom) taken at the midpoint of the sound (arrow), shows two distinct, non-harmonic peaks of sound energy. (B) A second kind of two-fundamental sound, when produced with a single sound source this illustrates type 2 biphonation. In this example the type 2 biphonation is evident as a 1 kHz tone with sidebands 250 Hz above and below it. This class of sounds is also the result of two non-harmonically-related frequencies. However, in this class of sounds the first $f_0$ (in this example, 1000 Hz) is not entirely independent of the second, which is evident as a low frequency (250 Hz), cyclic modulation of the amplitude envelope of the first. Spectrally, the amplitude modulation results in sidebands visible in the spectrogram (parallel bands flanking the 1 kHz tone), and also as peaks 250 Hz to either side of the 1 kHz central peak in a power spectrum (bottom) taken at the midpoint of the sound (arrow). Box C and D both illustrate bilaterally-produced biphonation of type 2. If each side of the syrinx produced a type 2 biphonic sound simultaneously, the result might be similar to the sounds illustrated. In the bilateral biphonation in box C, two unrelated fundamental frequencies produced on each side ($f_0$ and $g_0$), are each modulated by a third, lower, modulating frequency (250 Hz, $m_0$). In the illustration in box C, the modulation rate is constant (fixed) throughout the duration of the syllable, while in box D $f_0$ and $g_0$ are the same as in box C, but $m_0$ varies over time. BP, biphonation 2VC, two-voice phenomena; 2SB-fixed, two fundamentals, each with sidebands with a constant modulation frequency; 2SB-changing, two $f_0$, each with sidebands with a changing modulation frequency. 
instantaneous step-change in $f_0$ (“instantaneous” was defined as a silent interval of <5 ms in duration between adjacent frequencies, as measured from the time waveform from each vocalization). In narrowband spectrograms, sounds before and after the jump often appeared to have a slight temporal overlap.

Subharmonics (Fig 1B) are additional spectral components at integer fractional values of $f_0$ (e.g., $f_0/2, f_0/3$, etc.). They appear at evenly spaced intervals below $f_0$ and between adjacent harmonics throughout the frequency spectrum.

Biphonation refers to the occurrence of two simultaneous but independent $f_0$ that are generated by a single sound source (e.g. one pair of vibrating tissues). We grouped at least two types of phenomena under this term. We assume a primary oscillator producing a $f_0$. In the first type of biphonation, a second independent frequency ($g_0$) also exists, which shows no obvious interaction with $f_0$ (Fig 2A). In the second type, we observe a primary fundamental frequency ($f_0$) and an additional, much lower, modulating frequency ($m_0$). The narrowband spectrogram of this type is characterized by sidebands that are above and below $f_0$ and its harmonics (Fig 2B). These sidebands are associated with the frequency of the cyclic amplitude fluctuations in the waveform. Because of the presence of two sound sources in the oscine syrinx, biphonation may be unilateral or bilateral. For example, bilateral biphonation might be characterized spectrographically by two independent frequencies ($f_0$ and $g_0$), each with sidebands corresponding to a low fundamental frequency ($m_0$) (Fig 2, C and D).

Deterministic chaos is technically distinguishable from stochastic noise by the number of dimensions needed to describe it (Tokuda et al., 2002). However, the distinction can also be made based on telltale characteristics visible in narrowband spectrograms (discussed by Wilden et al., 1998), including preceding subharmonics (e.g, Fig 1B) and the presence of harmonic “windows” in otherwise noisy segments. We classified sounds as “deterministic chaos” if we observed a broadband, noise-like segment in the spectrogram, a predominantly aperiodic waveform (Fig 1C), and by additional indications, such as
preceding subharmonics or harmonic windows within the noise.

Mechanism of vocal production

For each putative instance of NLP observed spectrographically, we then examined concurrent airflow through the right and left sides of the syrinx, along with subsyringeal air sac pressure. This analysis allowed us to determine if the occurrence of such sounds could be explained by independent phonation on the two sides of the syrinx, or if they were produced by a single source.

In order to test whether the relationships between the occurrence of frequency jumps or subharmonics and changes in either air sac pressure or bronchial airflow were significant, we investigated changes in rates of air flow immediately prior to the bifurcation and at an earlier point in the same syllables. Temporal resolution of the time series was 0.025 ms. The signal was examined over two 5-ms time intervals (20 – 25 and 5 - 0 ms) prior to the bifurcation and 0-5 ms after the bifurcation. Air sac pressure or air flow through the syrinx was normalized to percentage of maximum flow rates or pressure, and then regressed against distance to the point of bifurcation. Slopes of regressions between groups were then tested for differences in variance using SigmaStat 3.11 (Systat Software Inc). Because most examples of chaos occurred either for the entire duration of the syllable, or immediately following a period of subharmonics, similar analyses of flow and pressure prior to the onset of chaos were not conducted. Similarly, biphonation usually had a gradual onset and often lasted the entire duration of the syllable, precluding a meaningful analysis of flow and pressure fluctuation associated with the bifurcation in these cases.

RESULTS

Unilaterally-produced acoustic phenomena typical of nonlinear systems, including frequency jumps, subharmonics, deterministic chaos and biphonation, were observed
in 8.5% of syllables analyzed across individuals (1000 syllables each from 4 birds, individually: m108, 5.8%; m123, 4.3%; m130, 7.2%; m152, 16.5%) (Table 2). “Unilaterally-produced” means that there is airflow through only one side of the syrinx for the duration of the sound in question. The pre-operative occurrence of sounds resembling NLP was not different from the post-operative occurrence (Wilcoxin Signed-Rank test: W= 4.000, T+ = 7.000, T-= -3.000, P(exact) = 0.625). We did not find any vocalizations that were produced during inspiration.

**Frequency jumps**

*Occurrences of Frequency Jumps*

Unilaterally-produced frequency jumps (Fig 3) occurred in 1.2% of syllables overall (mockingbird m108, 0.8%; m123, 1.2%; m130, 1.5%; m152, 1.3%) bilateral frequency jumps were observed in 4.9% of all syllables (m108, 3.3%; m123, 3.0%; m130, 6.8%; m152, 6.5%). In unilaterally-produced frequency jumps, the fundamental frequency shifts abruptly up or down with a silent interval <5 ms between adjacent frequencies. During the jumps there is airflow through only one side of the syrinx the other side being closed. The change in frequency due to the jump ranged from ~45-450 Hz. Both jumps from a higher to lower frequency and lower to higher frequency were observed (47.9% down-jumps, 52.1% up-jumps). Mimicked copies of tutored frequency jumps between tone-pairs spectrographically resembled the abrupt bifurcations commonly observed in nonlinear systems, however the production of these very large steps in frequency were always produced bilaterally, by alternating phonation between the two sides of the syrinx for each $f_0$ (see Zollinger and Suthers, 2004).

*Physiology and Production of Frequency Jumps*

No significant differences in subsyringeal air sac pressure accompanied the production of frequency jumps. Airflow through the bronchus producing the frequency jump often, but not always, occurred concurrently with a transient (5-10 ms) change in rate
Figure 3. Examples of frequency jumps and subharmonics in mockingbird song (bird m123). (A) Frequency jumps occurred with airflow through only the right (a) or left (c) side of the syrinx. Arrow b indicates a shift from a $\frac{1}{2}f_0$ to $\frac{1}{4}f_0$ subharmonic regime. Arrow c indicates a shift between $f_0$ and $\frac{1}{2}f_0$ regime. (B) Expanded views of the sound waveform at each arrow in spectrogram (A), showing the abrupt changes in oscillation patterns at the onset of the frequency jumps and subharmonic regimes. (C) Power spectrum taken at arrow b. Spectral peaks show sound energy at $f_0$ and it’s harmonics ($2f_0$, $3f_0$, etc), as well as at fractional integer values corresponding with a $\frac{1}{4}f_0$ subharmonic, and it’s harmonics. FL and FR, rate of airflow through left and right bronchus, respectively. Airflow associated with positive pressure is expiratory, and that associated with negative pressure is inspiratory. P, pressure in the cranial thoracic air sac; V, oscillogram of vocalization (sound waveform). Horizontal lines indicate ambient pressure or zero air flow.
Figure 4. Normalized rates of bronchial airflow 25 ms before to 5 ms after a frequency jump (A) or the onset of subharmonics (B). Bifurcations occurred at time 0. Slopes of linear regressions over three different 5 ms periods were measured (25-20 ms before, 5-0 ms before, and 0-5 ms after bifurcation points, indicated by vertical lines). Rates of bronchial airflow (A) show greater variance in their slope 0-5 ms before and 0-5 ms after a frequency jump than at an earlier point in the syllable, where no NLP were observed (failed Levene’s test of equal variances below the 5% level, P<0.05. Variance at 25-20 ms prior to bifurcation, $\sigma^2 = 0.8$; 5-0 ms prior, $\sigma^2 = 7.7$; 0-5 ms after, $\sigma^2 = 7.2$). Airflow was normalized to percent of maximum flow rate during syllable. Grey lines = upward jump in frequency; black lines – downward jump. (B) Rate of bronchial airflow 25-20 ms prior, 5-0 ms prior and 0-5 ms after onset of subharmonics did not show significant differences in slope (passed Levene’s test for equal variances well above the 5% level, P = 0.21).
of airflow (only those jumps produced with airflow through a single side of the syrinx
were investigated). The slope of standardized rates of air flow regressed against time
immediately before and after the bifurcation (Fig 4A) had greater variance immediately
before the frequency jumps (0-5 ms prior to bifurcation, mean slope -0.28 ± 2.773 SD,
variance 7.7) than at an earlier point in the syllable where no nonlinear phenomenon
was observed (20-25 ms prior to bifurcation, mean slope -0.26 ± 0.896 SD, variance 0.8).
While the mean slope of the normalized rate of airflow at 20-25 ms before bifurcations
was not significantly different than that immediately before the bifurcation, the variance
was significantly higher in the 5-0 ms before a frequency jump (Levene’s test of equal
variances, P < 0.050), and thus we reject the null hypothesis that the variances between
the two groups are the same. Changes in rate of air flow occurred immediately before a
frequency jump more often than at times during the same syllable where no jump was
observed. However, detectable changes in flow were not always found, and therefore
cannot be considered a necessary condition for the production of this type of bifurcation.
When airflow changed during a jump, the change was not consistent in either magnitude
or direction. Jumps were observed concurrently with increases, decreases or no change
in direction of rate of flow, regardless of the direction of the jump (increase or decrease in
frequency). Frequency jumps also occurred when the flow rate was not changing (slope ≈
0).

Subharmonics

Occurrences of Subharmonics

Unilaterally-produced subharmonics were observed in 1.3% of syllables analyzed
(m108, 0.4%; m123, 1.0%; m130, 1.8%; m152, 1.8%). Subharmonics occurred both alone
(Fig 3), or preceding or following chaotic regimes (Fig 5). We found subharmonics in the
$f_o$/2 mode (Fig 3 arrow a, and Fig 5), with subharmonic frequency bands occurring at 0.5 $f$
$\approx$ 1.5 $f_o$, 2.5 $f_o$, etc., and also in the $f_o$../3 and $f_o$../4 mode (Fig 3, arrows c and b, respectively).
Figure 5. Unilaterally-produced subharmonics and deterministic chaos (mockingbird m152). (A) The first syllable in this pair contains an abrupt transition from a harmonic vocalization to a chaotic sound. The chaotic sound (arrow a) is followed by a period of subharmonics (arrow b) as the vocalization returns to a periodic state. (B) A 25 ms segment of the sound waveform showing the abrupt transition from periodic to aperiodic oscillation. Arrows in spectrogram (A) and waveform (B) indicate points of transition between vibratory modes. (C) Power spectrum taken at arrow b (spectrogram, A). Spectral peaks show sound energy at $f_0$ and associated harmonics ($2f_0$, $3f_0$, etc) as well as at $0.5f_0$ and related harmonics ($1.5f_0$, $2.5f_0$, $3.5f_0$, etc.) Abbreviations as in Fig 1.
The example in Fig 3 shows shifts between three different subharmonic modes within two syllables. In the $f_0/2$ mode (immediately to the right of arrow a, Fig 3), the fundamental frequency is 1720 Hz, with subharmonics at 860 Hz (0.5 $f_0$), 2580 Hz (1.5 $f_0$), 4300 Hz (2.5 $f_0$). Another period doubling (Fig 3, arrow b), produces subharmonics in the $f_0/4$ mode, with the fundamental frequency at 1763 Hz, and subharmonics visible at 2203 Hz (1.25 $f_0$), 2645 Hz (1.5 $f_0$), 3085 Hz (1.75 $f_0$), etc.

**Physiology and Production of Subharmonics**

The occurrence of subharmonics in mockingbird song did not correlate with regular changes in rates of bronchial air flow or pressure (Fig 4B). Rates of airflow (described as slope, or rate of change, normalized to maximum flow for that syllable) were not significantly different either in mean or in variance just prior to the onset of subharmonics, than 5 ms after onset or 25 ms prior to onset, (25 ms prior, mean 0.33 ± 0.929 SD, variance 0.86; 5 ms prior, mean 0.79 ± 1.287 SD, variance 1.66; 5 ms post, mean 0.41 ± 0.736 SD, variance 0.54). Differences between groups were not significant (one-way ANOVA, df = 2, SS = 2.74, MS = 1.37, F = 1.34, P = 0.268). Airflow could either increase or decrease and the magnitude of these changes varied. While many of the instances of subharmonics coincided with an increasing rate of airflow (43.5% of cases), subharmonics also occurred during periods of decreasing or constant flow rates (30.4% and 26.1% of cases, respectively) and so these conditions are not necessary for production of such phenomena.

**Biphonation and two-voice phenomena**

**Occurrences of Biphonation and Two-Voice Phenomena**

The simultaneous presence of two or more independent frequencies was common in the acoustic signals of these mockingbirds (68.0 % of all syllables; individually: m108, 69.6%; m123, 62.1%; m130, 94.4%; m152, 45.8%). In most cases the production of such
sounds coincided with simultaneous airflow through both sides of the syrinx (63.7% of total syllables, 93.7% of sounds with ≥2 fundamental frequencies). Mockingbirds also produced biphonation, i.e., two harmonically-unrelated sounds using only a single sound source as indicated by airflow through only one side of the syrinx, the other side being closed (4.3% of total syllables, 6.3% of sounds with ≥2 $f_0$). Biphonation can appear in a spectrogram as two “types”. In the first type, two autonomous fundamental frequencies are present (Fig 2A). In the second type, the two fundamental frequencies are observed spectrographically as sidebands adjacent to the fundamental frequency (Fig 2B). We found both type 1 (Fig 6) and type 2 (Fig 7, arrow a) biphonation produced unilaterally in mockingbirds.

In oscines, biphonation might also be produced simultaneously by each side of the syrinx, resulting in “bilateral biphonation” (Fig 2, C and D). Mockingbirds produced type 2 biphonation bilaterally (Fig 7, arrow b and Fig 8), but we did not find examples of type 1 biphonation produced simultaneously on each side of the syrinx. Type 2 bilateral biphonation (e.g. two fundamental frequencies each modulated by a third independent frequency) represented between 0.8 and 15.1% of syllables examined per bird (mean 7.1% ±6.35 SD). In every case of bilateral biphonation, $m_o$ was the same for both right and left-produced carrier frequencies.

**Physiology and Production of Biphonation and Two-Voice Phenomena**

Figure 6 (arrows a and b) shows examples of type 1 biphonation. In this sound only one side of the syrinx is open, but the bird produces two autonomous frequencies that are independently modulated, i.e. not harmonically related. A power spectrum of the sound at arrow b shows the first fundamental frequency ($f_0$) at 946 Hz and a second fundamental frequency ($g_0$) at 1505 Hz. Second harmonics of $f_0$ and $g_0$ are visible at 1892 Hz and 3010 Hz, respectively. Other peaks present represent linear combination products of $f_0$, $g_0$, as marked in the figure. At arrow a, the lower frequency ($f_0$) is 990 Hz, and the higher frequency is 1505 Hz (sound energy is also visible in the spectrogram at upper harmonics
Figure 6. Biphonation in mockingbird song. (A) Two independent frequencies produced by a single side of the syrinx. Two examples of this syllable type were found to contain biphonation. Arrows a and b indicate biphonic sounds concurrent with airflow through only the left side of the syrinx. At arrow a, sound energy is present at 990 Hz ($f_0$) and 1505 Hz ($g_0$), and their harmonics, $2f_0$ (1980 Hz) and $2g_0$ (3010 Hz). (B) An expanded view of the sound waveform at arrow a (spectrogram, A), showing a change from the biphonation event to a single $f_0$ tone. (C) Power spectrum taken at arrow b, in spectrogram (A), showing the two fundamental frequencies ($f_0$ and $g_0$), as well as sound energy at various linear combinations of the two fundamentals. Abbreviations as in Fig 1.
Figure 7. Unilateral and bilateral biphonation in mockingbird song. (A) Spectrogram of two syllables produced in sequence by mockingbird m108. The first syllable in the pair (a) is an example of unilateral biphonation. This syllable is produced with the left side only, but two independent frequencies are present, the fundamental frequency \( f_0 \) at \( \sim 1800 \) Hz, and a lower, modulating frequency \( m_0 \) visible as sidebands \( \sim 115 \) Hz above and below \( f_0 \). The bird adds phonation from the right side of the syrinx in second syllable (b), and a second fundamental \( g_0 \) appears, also with sidebands 115 Hz above and below, indicating that \( g_0 \) is also modulated by \( m_0 \). (B) Expanded view of the sound waveform at arrows a and b in spectrogram (A), showing the AM pattern on the waveforms at a rate of \( \sim 115 \) Hz (period of one modulation cycle \( \sim 11.5 \) ms) both during unilateral flow (a) and bilateral flow (b). In addition to the 115 Hz modulation pattern, the two-voiced sound exhibits a second pattern in the waveform which is likely the result of beating between \( f_0 \) and \( g_0 \). A beat frequency is equal to the difference between \( f_0 \) and \( g_0 \), in this example, the second modulation rate in b is approximately equal to 550, which corresponds with the difference frequency between \( g_0 \) and \( f_0 \) (2695 – 2135 Hz). (C) Power spectra taken at arrows a and b in panel (A). Peaks labeled correspond with fundamental frequencies as well as the sidebands resulting from the interaction of modulating frequency \( m_0 \) with the carrier \( f_0 \) in a, and with the two carrier frequencies \( f_0 \) and \( g_0 \) in b. Abbreviations as in Fig 1.
Figure 8. Biphonation concurrent with two-voice phenomenon. (A) The sound at the arrow consists of two fundamental frequencies \( f_0 \) and \( g_0 \), both simultaneously modulated by a third frequency \( m_0 \). Although \( f_0 \) and \( g_0 \) are modulated in opposite patterns in the frequency domain (one downsweeping and the other upsweeping in frequency), \( m_0 \), or the rate of amplitude modulation frequency is the same (approx 250 Hz) for both, as evidenced by evenly spaced sidebands the same distance from both \( f_0 \) and \( g_0 \). (B) An expanded view of the sound waveform showing the pattern of amplitude modulation. (C) Power spectrum taken at arrow a in spectrogram (A). Abbreviations as in Fig 1.
of $f_0$ and $g_0$).

An example of type 2 biphonation is shown in Fig 7. Across our sample, the modulating frequency ($m_0$) in type 2 biphonation events ranged from 57 to 540 Hz. For type 2 unilateral biphonation, such as the first syllable in Fig 7, the spacing of the sidebands in the frequency domain corresponds to the rate of AM in the sound waveform. Examination of the waveform during the first syllable (top trace, Fig 7B) shows the period of the AM pattern is approximately 11.5 ms, and sidebands are evident as sound energy peaks 115 Hz above and below $f_0$ in a power spectrum (Fig 7C, $f_0 - m_0$ and $f_0 + m_0$).

Examples of bilateral biphonation are shown in Fig 7 and Fig 8. At the start of the second syllable the bird opens the right side of the syrinx as well to produce a two-voice syllable in which each side generates independent fundamental frequencies, and both fundamentals ($f_0$ and $g_0$) are flanked by sidebands. In this second syllable, the sidebands are equal distance from both $f_0$ and $g_0$, and the modulating frequency ($m_0$) is the same for both. Comparing 35 ms segments from the center of each syllable in the pair (Fig 7B), a 115 Hz modulation pattern is apparent in both. However, compared with the waveform of the unilaterally-produced syllable (Fig 7B, top trace), addition of a second fundamental ($g_0$), and airflow through the second side of the syrinx, results in an additional AM pattern on the sound waveform of 550 Hz (Fig 7B, bottom trace). This 550 Hz modulation during the bilateral syllable is likely the result of beating (sinusoidal oscillations in amplitude resulting from the linear interaction of two similar frequencies). Beat notes resulting from the acoustic interaction in the vocal tract of the sound from each side of the syrinx during two-voiced syllables have been described in close relatives of the northern mockingbird (grey catbirds, *Dumetella carolinensis* and brown thrashers, *Toxostoma rufum*) (Suthers et al., 1994). In mockingbirds, as in thrashers and catbirds, the observed frequency of AM in the waveforms is equal to the difference in frequency of $g_0 - f_0$ (in this example 2695-2145 Hz).

In another example of bilateral biphonation (Fig 8), the two carrier frequencies ($f_0$
and $g_0$) are frequency modulated (FM) at different rates. In the first 50 ms of the syllable shown in Fig 8A, both the right and left sides of the syrinx are open and the bird sings two converging FM sounds, each with sidebands. Unlike the second syllable in Fig 7, the bilateral biphonation during the first part of the syllable in Fig 8 does not result in the appearance of a pronounced beating pattern in the waveform. However, as in all cases of bilateral biphonation, $m_0$ was the same $f_0$ and $g_0$ at any point in time, even though the FM of $f_0$ and $g_0$ moved in opposite directions (upsweeping or downsweeping, respectively). The source of $m_0$ in mockingbirds is not known.

**Deterministic chaos**

**Occurrences of Deterministic Chaos**

Syllables containing apparent deterministic chaos were present in 8.3% of syllables (individually, m108, 6.3%; m123, 5.0%; m130, 6.7%, m152; 15.3%). Chaotic or aperiodic sounds occurred in vocalizations accompanied by unilateral airflow (Fig 5) as well as those produced during bilateral airflow (Fig 9). Most examples of deterministic chaos in the repertoires of these birds were produced with bilateral syringeal airflow (m108, 2.9%; m123, 4.5%; m130, 5.9%; m152, 13.2% of syllables sampled), however, examples of unilaterally produced chaotic sounds were also present (1.7% of all syllables sampled. Individually: m108, 3.4%; m123, 0.5%; m130, 0.8%; m152, 2.1%). In each case, the apparent chaos took the form of broadband noise with a sudden onset. Chaotic segments were sometimes preceded by or followed by subharmonics (Fig 5), and harmonic windows within the chaotic segment (Fig 9, arrow b) were commonly observed.

**Syringeal Lateralization of Chaotic Sound Production**

At least three types of unlearned mockingbird calls contain chaos, including “loud hews” (Fig 9), “soft hews” and “chat” calls. Male mockingbirds are known to sometimes include unlearned calls in their learned song repertoire (Derrickson and Breitwisch, 1992). During a singing bout mockingbirds may include several repetitions of loud and
Figure 9. Contribution of right and left sides to bilaterally produced chaos. Chaotic sounds often contain harmonic windows, or brief moments of periodic oscillation, such as that seen around arrow b. Mockingbird “hew” calls (A) are always produced with flow through both sides of the syrinx for the entire duration of the call. In most cases (56 of 67 calls) one side alone appears to contribute the majority of the aperiodicity in the call, while the contribution of the other side is more pure-tonal. (B) The difference in aperiodic behavior of the two sides as seen in spectrograms of the sound recorded inside the right and left bronchus, and cranial thoracic air sac (obtained by high-pass filtering and amplifying thermistor and pressure transducer outputs). (C) 20 ms segment of the sound waveform, at the time indicated by arrow a in the spectrogram, illustrating the aperiodic nature of the oscillation. (D) Power spectrum of the sound taken at arrow a in the spectrogram (A). Additionally, the air flow in the right side (FR) shows an aperiodic, rapid modulation, which not present in the flow on the left (FL). Other abbreviations as in Fig 1.
soft hews and chat calls in addition to the mimicked syllables learned from tutors. Loud hew calls have a duration between 214 – 600 ms (mean = 359.7 ±110.03 ms, N=61) broadband sounds with abrupt on- and offsets. Loud hew calls were always produced bilaterally, but quiet hew calls were typically produced unilaterally. Soft hews are not only quieter than loud hews, but were more restricted in bandwidth. Chat calls are short (ranging between 34 – 88 ms mean = 56.3 ±17.37 ms, N=30) broadband explosive sounds, produced bilaterally.

All four of the birds in this study included hew calls as part of their song repertoires. We examined the rate of airflow and sound recorded in each bronchus for 67 hew calls from the 4 birds in this study (to increase sample size, we used an additional 50 hew calls that not in the 4000 syllables used for NLP count). Although always produced with airflow through both sides of the syrinx, the chaotic nature of the hew calls are often the result of chaotic oscillations from a single side of the syrinx. Figure 9 shows the contribution to sound from the right and left sides during hew calls produced by mockingbird m130, as recorded in the right and left bronchus by the thermistors. The frequency response of the thermistors rolls off at about 3 or 4 kHz, so it is not possible to completely rule out a chaotic signal at higher frequencies on the left side. However, the presence of rapid fluctuations in the air flow rate through the right side (F_{r} in Fig 9a) and their absence in the flow rate on the left side (F_{l} in Fig 9a) suggests that the two sides are behaving differently when producing these chaotic sounds. In most hew calls (51 of 67) the right side alone appeared responsible for most of the aperiodicity, while the left side's contribution was more tonal. In these 51 cases, the rate of air flow in the right side shows an aperiodic, rapid modulation, which is not present in the flow on the left. In 5 of 67 calls, the left side appeared responsible for most of aperiodicity, and a strong aperiodic fluctuation in left flow rate throughout the duration of the call, while the flow rates on the right side were more constant. In 11 of 67 calls, the two sides appeared to contribute equally, or the relative contribution of the right and left sides could not be determined
DISCUSSION

The data presented here contribute several important new findings to current understanding of the oscine vocal system. We show that all four classic acoustic phenomena associated with nonlinear theory are present in unilaterally-produced vocalizations of intact mockingbirds, that each side of the syrinx can produce NLP, some of which may have been previously misidentified as two-voice phenomena. We also provide the first evidence for lateralization of certain NLP to one side of the syrinx in bilaterally-produced chaotic calls. In addition, we provide evidence from bilaterally produced biphonation involving source-source coupling between the two sides of the syrinx. Finally, we did not find air sac pressure or air flow alterations that were consistently associated with, or necessary for production of NLP.

Identification of nonlinear phenomena

Nonlinear phenomena have been described in a handful of bird species with single sound sources (tracheal syringes), such as doves and parrots (Lavenex, 1999; Fletcher, 2000; Beckers et al., 2003). In contrast to these species, birds with tracheobronchial syrinxes, such as the oscine songbirds, have two independent sound sources, making it risky to identify most kinds of NLP on the basis of the vocalization alone.

By recording respiratory dynamics of vocalization on each side of the syrinx of intact, singing mockingbirds, we found unilaterally produced NLP in about 8% of all syllables, representing only about one-sixth of the sounds that appeared to contain biphonation, chaos, jumps in frequency or subharmonics based on spectrographic analysis alone (48.7%). The relatively small ratio of NLP to harmonic sounds in our sample suggests that while the exploitation of the passive biomechanical properties of the syrinx is a possible strategy for production of complex sounds, mockingbirds rely more heavily on their
bipartite vocal organ for the rich diversity of complex sounds in their repertoires. Acoustic analysis of NLP in mockingbird song, along with bronchial airflow and subsyringeal pressure provide an insight into how songbirds might exploit the inherent biomechanical properties of their nonlinear vocal systems to produce such complex sounds as those described by Thorpe (1961).

Production of nonlinear phenomena in songbirds

We hypothesize that the occurrence of NLP in songbirds is sometimes under voluntary control, and is in other cases potentially the result of instabilities of the vocal system. While it has been proposed that NLP in mammalian vocalizations could be the result of the animal driving the vocal system towards its limits (Riede et al., 2007), and their occurrence has been shown to increase as sound amplitude or frequency increase, it may be that these phenomena occur at different threshold points which mark boundaries between stable vibratory modes.

Fee et al. (1998) demonstrated that the zebra finch syrinx ex vivo behaves as a nonlinear system, in which a linear increase in subsyringeal pressure results in nonlinear jumps between different vibratory modes. The absence of a consistent relationship between the occurrence of NLP and a detectable increase in \( f_0 \), rates of bronchial air flow or subsyringeal air sac pressure in our mockingbirds may reflect the availability of more complex control mechanisms involving activity of respiratory, syringeal and upper vocal tract muscles that were not included in Fee's ex vivo preparations. While we did not observe a consistent pattern in bronchial airflow rates or subsyringeal pressure related to the occurrence of frequency jumps or subharmonics, frequency jumps were often concurrent with periods of change in the rate of bronchial airflow, and subharmonics often, but not always, were associated with linear increases in airflow. The association of increased variation in rates bronchial air flow and nonlinear jumps in vibration rate could be important if it describes a condition where there is relationship between vocal
“mistakes” (such as an unplanned period of “roughness” or a less perfect copy of a tutor sound) and a production “mistake” (such as imprecise control of the respiratory system during phonation). However, these periods of rapid change in flow rates were not always present before or after bifurcations, and therefore cannot be a necessary precursor in all cases.

While we did not find that particular patterns or changes in airflow or pressure were correlated with NLP, we cannot rule out the role of these parameters in the occurrence of bifurcations. Nonlinear theory suggests that even very small changes in parameters such as subglottal pressure can result in production of NLP. Further, there are many parameters which are or could be involved in producing and regulating oscillatory patterns within the syrinx. In addition to subglottal pressure and air flow, the mass and tension of the vibrating tissues are dynamic variables in even the simplest models of syringeal mechanics. Finally, the air flow measurements we recorded at the location of the thermistors (3-8 mm caudal from the labia) may not detect fine changes in the flow rate or turbulence that could occur at the surface of the vibrating tissues as the result of shape changes of the constriction caused by the oscillation.

**Biphonation vs. two-voice phenomena**

We found unilateral biphonation of two types in mockingbird song. First, biphonation can occur as harmonically-unrelated fundamental frequencies, each independently modulated (Fig 6), or as a \( f_0 \) modulated by a second, lower frequency, which appears as sidebands parallel to the \( f_0 \) in a narrowband spectrogram (Fig 7). While sidebands indicate the occurrence of two independent frequencies, there are several ways in which they may be produced. In biphonation, sidebands result from one \( f_0 \) modulated by a second, lower frequency (Greenewalt, 1968; Lavenex, 1999). Experiments with an excised larynx or computer modelling have shown that the mammalian vocal folds, vibrating asymmetrically, can produce AM with accompanying sidebands that are the result of
linear combinations of the two fundamentals (e.g. \(2g_0 - f_0\), \(2f_0 - g_0\)) (Herzel et al., 1995; Mergell and Herzel, 1997; Giovanni et al., 1999; Neubauer et al., 2001). In such cases, the two vocal folds oscillate at slightly different frequencies, each producing a separate sound pressure wave, which are close to each other in fundamental frequency. If the same phenomenon can occur during oscillation of the medial and lateral labia in songbirds, biphonic vocalizations might be the result of either a higher \(f_0\) with a lower modulating frequency (e.g. Fig 2B), or to the interaction of two higher tones, which are close in fundamental frequency (Fig 2A). In either case, biphonation (i.e., the production of two independent frequencies by a single side of the syrinx), has not been previously described in intact songbirds.

**Complications of two voices for sound analysts**

Because songbirds have two independently controlled vocal sources, there is the potential for increased complexity of sounds as compared to vertebrates with single sound sources (such as mammals and some non-songbirds). In mockingbirds, examples of such increased complexity include biphonation by both sides of the syrinx, which could result in the appearance of at least four independent frequencies. We found several cases of airflow through both sides of the syrinx generating three independent frequencies, appearing as two distinct fundamental frequencies, each with sidebands corresponding to a third modulation frequency. Nowicki and Capranica (1986) reported evidence for a source-vocal tract coupling in the amplitude-modulated calls of black-capped chickadees (*Parus atricapillus*), and speculated on possible source-source (acoustic or mechanical) coupling. Our observation that in every case of bilateral biphonation the frequency of the amplitude modulation (\(m_0\)) was the same for both the left- and right-produced fundamental frequencies lends further support to their hypothesis of a source-source coupling in the oscine syrinx. The possible mechanisms of source-filter and source-source interactions were investigated recently with a simple model (Laje and Mindlin, 2005),
which demonstrated that such interactions could indeed produce the complex, multi-frequency sounds observed in birdsong. The results presented by Laje and Mindlin are relevant to the findings of this study since they show how sounds previously presumed to be NLP in intact songbirds such as zebra finches (e.g. Fee, et al., 1998), could alternatively be explained by the interactions between the two sides. Nelson (2004) describes how rapid FM within a song element in eastern towhees can produce an AM-like sideband pattern in narrowband spectrograms, and further speculated on as yet unidentified third independent modulator in the syrinx, but further evidence for the identity or existence of such a structure is lacking.

Mindlin and Laje (2005) have offered an avian-specific computational simulation of a possible nonlinear relationship between source and filter, such as has been described in studies of simulated interactions between the larynx and vocal tract (Mergell and Herzel, 1997; Titze, 2004). A highly variable vocal tract system involving a complicated motor pattern has been demonstrated in songbirds (Fletcher et al., 2006; Riede et al., 2006), and thus the coordination of such a system may add to the costs involved in the production of tonal sounds free from involuntary NLP.

Deterministic Chaos in Calls and Song

Mockingbird “hew” and “chat” calls are broadband, chaotic sounds, produced with flow through both sides of the syrinx. This is in stark contrast to the more predominantly tonal sounds that comprise their songs (Derrickson and Breitwisch, 1992). Periods of deterministic chaos can theoretically occur in any system of coupled oscillators, such as the paired labia within each side of a songbird syrinx. Whereas chaos may or may not be a common feature of learned song, the unlearned calls of many songbirds, such as alarm calls, contact calls and aggressive calls, are often characterized by broadband, noisy, “buzzy” or “harsh” sounds (Marler, 2004).

Although our data show that mockingbirds have some control over the respiratory and
syringeal parameters necessary to allow the production of chaotic sounds, as evidenced by the chaotic nature of three very common call types, aperiodic vibratory modes are also presumably induced involuntarily at times. Chaos was found within a small number of otherwise harmonic or pure-tonal song elements. These erratic occurrences of chaos likely represent cases more like those described in the mammalian literature, which are often attributed to pathologies (Mende et al., 1990; Herzel et al., 1994), instabilities in the vocal system (Mergell et al., 2000), as results of increasing, or maximizing frequency or amplitude levels (Berry, 2001; Brown et al., 2003; Riede et al., 2007) or the abrupt desynchronization of the vibrating labia (Neubauer et al., 2001). Instances of chaos within more tonal mockingbird sounds were likely involuntary, as they rarely occurred in the same syllable sung by the same bird more than once (e.g. chaos and subharmonics are present for a brief period in the first, but not second repetition of the same syllable type illustrated in Fig 5).

The conditions under which chaotic regimes occurred also differed between calls and songs. In hew calls, the right side of the syrinx appears to contribute all or most of the aperiodicity, while the left side contributes a more narrowband, or even pure-tonal, sound. During a hew call, the airflow through the right side shows large, aperiodic oscillations in rate of flow, while the flow throughout the left side is typically constant through the duration of the call. In cases where chaos occurred within a unilaterally-produced song syllable, however, no pattern of modulation in the flow rate similar to that present in the flow rate on the right side during hew calls was observed. So while these oscillation patterns in the airflow during calls appear to be important in the production of the chaos, they are not necessary for its appearance in song.

Possible Communicative Roles of Nonlinear Phenomena

Several communicative functions of NLP have been hypothesized. It has been suggested that increased vocal “roughness” may be an honest indicator of poor
reproductive fitness (Goller, 1998) or health status (Herzel et al., 1994; Riede et al., 1997). A preference for pure-tonal over harmonic or aperiodic vocalizations has been shown for some songbirds (Strote and Nowicki, 1996). An alternative, seemingly contradictory, hypothesis suggests that animals might exploit the nonlinear properties of their vocal systems to increase vocal complexity, and that NLP could aid in individual recognition in some species (Fee et al., 1998; Wilden et al., 1998; Fitch et al., 2002). While it is still not clear what, if any, adaptive advantages or selective pressures are associated with NLP in animal vocalizations, the literature is becoming increasingly rich with examples of these phenomena in an ever widening range of taxa.

Bifurcations occur in two kinds of situations within mockingbird repertoires. In many cases the NLP occurred unpredictably within normally pure-tonal or harmonic song elements, but in other cases, a particular nonlinear phenomenon was always present in a particular vocalization (e.g. chaos in hew calls). The different situations may represent cases where each of the above proposed hypotheses for a role of NLP in communication, might find support. In the case of song, if “roughness” is perceived as interruption or mistake, NLP could be used as a measure of a singer’s quality. However, since calls function in a different communicative capacity than song, the selective pressures on the occurrence of nonlinearities in calls might be quite different. In that communicate danger, alarm, food sources or other information critical to survival, NLP may provide an evolutionarily “cheap” way to increase signal diversity or complexity. However, the extent to which birds, such as mockingbirds, use nonlinear phenomena, or exploit the passive biomechanical properties of their vocal system voluntarily to enhance the complexity of their songs is in need of further examination.
Chapter 3

Limits on the independent vocal behavior of the right and left syrinx during two-voice phenomena in northern mockingbirds (Mimus polyglottos)
Abstract

Birdsong, like human speech, is a complex and learned acoustic signal, the control of which is lateralized both centrally and peripherally. The rich variability observed in birdsong is due in part to the complexity of the peripheral vocal production system of oscine songbirds. The vocal organ in songbirds is a bipartite tracheobronchial syrinx, with an independently innervated sound source at the cranial end of each primary bronchus. Syringeal innervation and musculature is lateralized, and in all species of songbirds, the syrinx has been demonstrated to have the capacity for varying degrees of bilateral independence during song production. However, the extent to which the two sides of the syrinx are independent in their phonatory capacity is not well understood. Several putative peripheral and central constraints could limit a songbird’s ability to produce different, unrelated sounds simultaneously from the two sides of the syrinx. In this study we exploit the propensity for heterospecific mimicry in northern mockingbirds to test assumptions about the independent control of the two sides of the syrinx. We tutored juvenile mockingbirds with computer-synthesized “two-voice” sounds designed to test the limits of two-voice vocal abilities. Our data show that although the phonatory behavior of the two sides of the syrinx is theoretically independent, two-voice song production in mockingbirds is severely limited both in the absolute frequency difference and the degree to which the two voices can be independently modulated, as compared to the capacity of either side when phonating alone.
INTRODUCTION

The diversity and complexity observed in the vocal signals of oscine songbirds may arise from numerous sources. Most notably, songbirds are vocal learners, and must learn their songs by listening to and mimicking tutors (typically conspecific adult males). Sensory and sensorimotor learning stages during development in songbirds are controlled by several interconnected neural pathways comprised of multiple specialized brain and spinal cord nuclei. Vocal learning allows birds an increased aptitude for developing more complex songs during their lifetime, or evolving more complex signals as a species over time. But in addition to the neural pathways and central control of song learning and production, songbirds have evolved an equally specialized and complex peripheral vocal production system, which contributes many additional sources for increased acoustic complexity.

Peripherally, songbird vocal signals are produced and modified by precisely choreographed motor patterns to the muscles of the syrinx and respiratory system (Suthers et al., 1999), dynamic modification of the upper vocal tract (Podos et al., 1995; Nelson et al., 2005; Riede et al., 2006), and nonlinear dynamics of the syrinx (Fee et al., 1998; Fee, 2002). To make the equation even more difficult, the syrinx of oscine songbirds is comprised of two independently-controlled sound sources. Located at the intersection of the trachea and two primary bronchi, the left and right bronchus each house a pair of vibratory tissues (the lateral and medial labia), and a medio-situated vibratory membrane (the medial tympaniform membrane) that is continuous with the caudal edge of the medial labium (Fig 1). The extrinsic muscles of the syrinx control the tension and position of the labia, moving them into the path of airflow from the lungs and setting them into vibration, which produces the sound pressure waves. The muscles and descending neural control of the right and left sides of the syrinx are lateralized and independent, allowing for each side to behave, in principle, as an independent sound
source.

Though the independent use of the two sides of the syrinx has been postulated since the 1950s (Borror and Reese, 1956; Thorpe, 1961; Greenewalt, 1968), the details of motor control, lateralization and sound production are still not fully understood. Some of the first experimental evidence that the two sides could indeed function autonomously came from disabling one side of the syrinx by unilateral nerve cuts or bronchial plugs (Lemon, 1973; Nottebohm and Nottebohm, 1976; Nottebohm et al., 1979; Seller, 1979; Hartley and Suthers, 1990; Williams et al., 1992), which found highly lateralized contributions of the right and left syrinx to song in a variety of species. Direct evidence for the independent control of the two sides of the syrinx was obtained by directly measuring bilateral syringeal airflow in singing brown thrashers (Toxostoma rufum) and grey catbirds (Dumetella carolinensis) (Suthers, 1990). It is now well understood from a variety of species, that the bilateral and independent use of the two sources is most likely the rule, rather than the exception (Suthers, 1990; Allan and Suthers, 1994; Suthers, 1998; Suthers et al., 2004; Zollinger and Suthers, 2004).

But are the two-voice songs in songbirds simply the sum contribution of two completely independent sound sources? There is a variety of evidence to suggest that the right and left sides may be limited in the extent to which they can produce simultaneous autonomous sounds. Suthers et al. (1994), found that in thrashers and catbirds, the fundamentals produced on the right and left sides during two-voice syllables averaged closer together in frequency than comparisons of unilaterally produced sounds on the right or left. This observation might suggest a constraint on how different the tension between the two sides can be at the same time. The constraint might also be due to limitations of the suprasyringeal filter, in that if the two sides simultaneously produce two very different frequencies, the bird likely can not tune the resonant properties of his upper vocal tract broadly enough to efficiently pass both frequencies. While there are two sound sources, both sounds must pass simultaneously through the same suprasyringeal
vocal tract. Indeed, Riede, et al.(2006) found that northern cardinals (*Cardinalis cardinalis*) adjust the volume of their oropharyngeal-esophageal cavity (OEC) to support the fundamental frequency of their song. By adjusting the volume of their vocal tract as the $f_0$ of their song changes, the birds create in essence a narrow passband filter, through which only frequencies at or around the peak resonant frequency are effectively passed.

Two smaller peaks related to the resonant properties of the trachea are also predicted by their model, but since the trachea is essentially fixed in length, these smaller peaks are relatively fixed. Therefore, if the two sides of the syrinx were to produce two very different frequencies, the bird must choose one or the other frequency to which to tune their OEC, and unless the frequency of the second voice's contribution happens to match one of the smaller tracheal resonant frequencies, it is unlikely that both frequencies could be supported.

Increasing evidence of coupling (Nowicki and Capranica, 1986; Nowicki and Capranica, 1986; Laje and Mindlin, 2005; Zollinger, Riede and Suthers, Chapter 2 this volume) between the two sides of the syrinx suggest that the two sides, though separately innervated by ipsilateral brain nuclei, and controlled by lateralized syringeal muscle groups, may not be completely independent during two-voice sounds. Nowicki and Capranica (1986) found evidence of a physical coupling between the two sides during bilaterally-produced vocalizations of black-capped chickadees (*Parus atricapillus*).

Results from unilateral nerve cuts to the syrinx showed that the right and left sides each contributed independent tones with associated second and third harmonics, but that the song from intact birds (presumably phonating bilaterally) contained frequencies that were not related to either $f_0$ or $g_0$ from the left and right sides. Nowicki and Capranica postulated that these additional frequencies present in the vocalizations of intact birds were the sum and difference frequencies (heterodyne frequencies) resulting from a cross-modulation between the two phonating sides. They found that birds with unilateral nerve cuts managed to restore some structure of their normal song after 10 days, too soon for
**Figure 1.** Frontal section through syrinx of a northern mockingbird, showing the bilateral nature of the vocal organ and the placement of the thermistors (Th) implanted in the right and left bronchus to record airflow. While the right and left sets of vibratory tissues (medial and lateral labia) are located at the cranial end of each primary bronchus, and independently innervated by the ipsilateral side of the brain, it is important to note that the two sides are not entirely mechanically isolated. Between the right and left medial labia and medial tympaniform membranes is an air pocket, the interbronchial foramen, bordered on the dorsal side by the esophagus, to which the syrinx is attached. A thin interbronchial ligament attaches the two bronchi just caudal to the medial tympaniform membranes. The bony pessulus and semilunar membrane atop it elongate the septum between the two bronchi cranially into the trachea.
neuronal regeneration, which strongly supports a passive physical interaction between sources, rather than simply the production of beat frequencies by the two fundamentals after they are emitted from the vocal tract.

A consideration of syringeal anatomy may provide a possible morphological basis for a mechanical coupling between the two sides. The syrinx (and most of the descending trachea) is attached dorsally to the esophagus. The two sides of the syrinx (Fig 1) are separated by a small air pocket, the interbronchial foramen (IBF), which is bordered laterally by the medial tympaniform membranes (MTMs) and medial labia, cranially by the pessulus, dorsally by the esophagus, and caudally by the interbronchial ligament (IBL), a thin ligament stretching between the two bronchi. The IBL connects the two primary bronchi, inserting on each side just caudal to the medial tympaniform membranes connects the two sides of the syrinx (King, 1989). The role, if any, of the IBL or IBF in phonation is not known, but the placement of the IBL and its attachment to both medial surfaces of the MTMs might be such that it could have a role in a putative mechanical coupling. Likewise, the IBL serves to almost enclose the air pocket between the two medial labia and tympaniform membranes (the IBF), with only a narrow opening at the caudo-ventral edge of the syrinx into the air sac system, may create in essence a two-headed drum between the two medial vibratory surfaces of the syrinx and could contribute to crosstalk between the two sides when either is vibrating.

While two sides of syrinx are controlled by independently innervated muscles on the right and left, activity of the respiratory muscles that regulate phonation is not lateralized (Goller and Suthers, 1998), therefore, the subsyringeal pressure is presumably the same in each bronchus. Two sounds with very different rates or patterns of frequency modulation (sounds that require the bird to modulate frequencies in very different directions simultaneously, or to sustain a steady oscillation rate on one side, while the other side fluctuates between dramatically different tensions and air flow rates) would require the bird to both be able to control the respiratory and phonatory muscle groups.
of the two different sides to accurately produce the desired FM sound, but then to also respond to dynamically fluctuating pressure and airflow resulting from the modulation of the opposite side of the syrinx. However, birds may be adapted to deal with this problem, by using somatosensory feedback to allow rapid corrections for abrupt changes in subsyringeal pressure. Suthers et al. (2002) found a compensatory decrease in the activity of the abdominal expiratory muscles in northern cardinals in response to abrupt brief perturbations to their subsyringeal air sac pressure during song. These real-time adjustments of the respiratory system in response to unexpected fluctuations in the subsyringeal pressure in both hearing and deafened birds indicate that birds can use somatosensory feedback signals to stabilize the control of song output, even during unstable moments of changing pressure or airflow. It is possible that songbirds might also use somatosensory feedback to the expiratory muscles to quickly adjust for fluctuations in subsyringeal pressure resulting from the opening and closing of one side of the syrinx or the other or both. However, because control of the expiratory muscles used for controlling phonation are not lateralized (Goller and Suthers, 1996), the role that somatosensory feedback would play in regulating two-voice songs is not known.

The present study was designed to test the limits to two-voice independence and complexity in northern mockingbirds (Mimus polyglottos). We chose mockingbirds for this study because they are closely related to the thrashers and catbirds (family Mimidae), which both have vocal repertoires rich in two-voice phenomena. However, northern mockingbirds are the most conspicuous heterospecific mimics of the family (Derrickson, 1985; Merritt, 1985; Derrickson and Breitwisch, 1992), their Latin name translates to “many-throated mimic”, and have been shown in earlier lab studies (Zollinger and Suthers, 2004) to readily learn and attempt to copy a wide variety of heterospecific birdsongs and even computer-synthesized birdsong-like sounds. Because of this propensity for vocal imitation, mockingbirds make exceptionally good models for the study of vocal motor constraints.
We tutored mockingbirds with a collection of computer synthesized sounds, each containing two distinct tonal elements, each with an independent frequency that was not harmonically related to that from the other side of the vocal organ, and with different patterns of frequency modulation (FM).

**METHODS**

*(a) Collection and Rearing of Birds*

Data in this study were collected from 8 male and 1 female adult mockingbirds, across 3 years (2001-2004). We collected nestling mockingbirds aged 2-7 days from nests in North Carolina (2001), South Carolina (2004), Florida (2004) and Indiana (2001-2004), and hand-reared them in the laboratory. Nestling birds were sexed by laprotomy in the lab or field under isoflurane anesthesia (Halocarbon Laboratories, River Edge, NJ). Nestling birds from each year’s cohort were housed during their first year in individual cages in group rooms, where they could hear each other as well as the tutor recordings (Table 1). Birds were tutored with a collection of computer-synthesized sounds designed to test the independence of the two sides of the syrinx, or to investigate constraints or limits on the vocal registers of the right and left sides, and determine the acoustic parameters that cause the bird to use one side vs. the other when producing sounds that may move in and out of the “normal” frequency range for a particular side.

Although birds were housed in sound-attenuating chambers (Industrial Acoustics, model 102318) they were at times exposed to songs of northern cardinals (*Cardinalis cardinalis*) and eastern towhees (*Pipilo erythrophthalmus*) and zebra finches (*Taeniopygia guttata*) in adjoining rooms. As adults (>300 days post-hatch), birds were often also exposed to mockingbirds from previous years’ cohorts, that might have been singing song syllables not previously heard by experimental birds.
Table 1: Mockingbirds Used in This Study

<table>
<thead>
<tr>
<th>BIRD ID#</th>
<th>SEX</th>
<th>DATE</th>
<th>AGE</th>
<th>T-IMPLANT</th>
<th>TUTOR</th>
<th>PHYS. DATA RECORDED</th>
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<td>U,V,W</td>
<td>R,P,V</td>
</tr>
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<tr>
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<td>R,P,V</td>
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<td>L,R,P,V</td>
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<tr>
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<td>413</td>
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<td>S,T,Z</td>
<td>L,R,P,V</td>
</tr>
<tr>
<td>M148</td>
<td>M</td>
<td>4/14/04</td>
<td>668</td>
<td>N</td>
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<td>Y</td>
<td>S,T,X,Y</td>
<td>L,R,P,V</td>
</tr>
</tbody>
</table>

1 Date of surgery. Data were collected over a 2-14 day period after date of surgery.
2 Approximate days post-hatch at time of surgery
3 A 12.5 mg testosterone propionate pellet was implanted subcutaneously 7-14 days prior to surgery to stimulate singing behavior
4 Subset of tutor syllables presented to bird during first 300 days post-hatch, see tutor syllable descriptions in Table 2.
5 V, vocalization; L, left bronchial airflow; R, right bronchial airflow; P, subsyringeal air sac pressure.
Table 2. Synthesized “Two-voice” Tutor Syllables

<table>
<thead>
<tr>
<th>Tutor Sound</th>
<th>LOWER COMPONENT</th>
<th>UPPER COMPONENT</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DURATION (ms)</td>
<td>MIN KHz</td>
</tr>
<tr>
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<td>110</td>
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</tr>
<tr>
<td>S₂</td>
<td>120</td>
<td>1.5</td>
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</tr>
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</tr>
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<td>200</td>
<td>2</td>
</tr>
<tr>
<td>T₂</td>
<td>200</td>
<td>2</td>
</tr>
<tr>
<td>T₃</td>
<td>200</td>
<td>2</td>
</tr>
<tr>
<td>T₄</td>
<td>200</td>
<td>2</td>
</tr>
<tr>
<td>U₁</td>
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<td>1.5</td>
</tr>
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<td>U₂</td>
<td>50</td>
<td>1</td>
</tr>
<tr>
<td>U₃</td>
<td>100</td>
<td>1.5</td>
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<td>100</td>
<td>1.5</td>
</tr>
<tr>
<td>V₂</td>
<td>50</td>
<td>1</td>
</tr>
<tr>
<td>V₃</td>
<td>100</td>
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</tr>
<tr>
<td>W</td>
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<td>1.5</td>
</tr>
<tr>
<td>X</td>
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</tr>
<tr>
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</tr>
<tr>
<td>Z*</td>
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</tr>
<tr>
<td>Z*</td>
<td>250</td>
<td>2</td>
</tr>
</tbody>
</table>

*See Fig 9, and text for explanation of the 2 interpretations of tutor sound Z.
(b) Tutor sound synthesis and presentation

Synthetic tutor sounds were generated using the dialogue synthesizer and sine wave generator in Avisoft SASLab software (Avisoft Bioacoustics, Berlin Germany), with a sample rate of 44.1 kHz. Each tutor sound consists of 2 independently-synthesized pure-tonal components mixed together digitally so as to overlap temporally. Details of the upper and lower components for each synthesized tutor sound are given in Table 2.

Tutor design rationale

Tutor sounds were designed to test the limits of right/left syringeal independence and vocal registers during the production of two-voice sounds. When designing tutor sounds, we analyzed 3 hours of mockingbird song recorded in Ohio, Indiana and North Carolina (Borror Laboratory of Bioacoustics, Columbus, OH) to determine the maximum and minimum fundamental frequencies of typical mockingbird song in the field. We also referred to data from an earlier study (Zollinger and Suthers, 2004) describing the frequency range produced on the right and left sides by adult mockingbirds hand-reared under similar conditions. Specifically, in mockingbirds, sounds below about 1.9 kHz (± 0.33 kHz, n=8 males) were produced on the left side, while sounds above 2.9 kHz (± 1.32 kHz, n = 8 males) were produced on the right. Note that the range of frequencies produced by the right and left side overlap, and that either side might produce frequencies that fall between 1.9 and 2.9 kHz. Tutor sounds were designed using these baseline parameters to push mockingbirds to use the right and left sides to produce sounds outside their normal vocal ranges.

Tutor sound descriptions

Tutor series sounds S₁-S₄ (Fig 2A) were designed to determine how different in frequency simultaneously-produced sounds from the right and left sides can be. Each of the S-series were 120 ms pairs of approximately parallel FM sweeps with fundamental
frequencies that are not harmonically related ($g_0$ values do not correspond with integer multiples of $f_0$ or vice versa) and which are both within the overlap range ($S_1$), above and below ($S_2$), both above ($S_3$), or both below ($S_4$) the overlap range of the right and left sides for most of the bandwidth of the sweeps.

Tutor sounds T - V were designed to test the mockingbirds’ ability to produce two sounds that are frequency modulated in opposite directions (such as two simultaneous up- and down-sweeps). The $T_1$ – $T_4$ tutor series sounds (Fig 5A) consist of two short (200 ms) converging FM sweeps, the top sweep decreasing in frequency over time, and the lower sweep increasing in frequency. The lower, upswept component in each of the T-series sounds was entirely within the overlap range (2-2.5 kHz), and the upper downsweeps varied in frequency deviation, but always originated within the range of the right side (start frequencies of upper components were between 3.5 and 5 kHz).

Tutor sounds U and V (Fig 6A and B), like the T-series sounds, contained simultaneous up- and down-sweeps, but were designed to push mockingbirds to attempt to produce more extreme differences in both $f_0$ and degree of FM than the T-series (Fig 5A). The first element in both U and V is a 100 ms pair of converging linear FM sweeps that were much wider bandwidth than any of the T-series sounds. The third element in U and V is identical to the first, but reversed so that the upper and lower sweeps diverge in frequency. The lower sweeps in U and V extend from 1.5 kHz through the entire overlap range to 3.5 kHz. The middle components ($U_2$ and $V_2$) are 50 ms shallowly FM tones that differed in absolute difference frequency ($\Delta f$). Tutor sound $U_2$ has a max $\Delta f$ of 1.1 kHz, and $V_2$ had a max $\Delta f$ of 4.3 kHz.

Tutor sounds W – Z (Figs 8 and 9 – 11) were designed to test the degree to which mockingbirds could independently modulate frequencies on the right and left during two-voice sounds. Tutor sounds W, X and Y each consist of a sinusoidally frequency modulated “warble” paired with a lower constant frequency tone (W) or a higher FM sweep (X and Y). The duration, frequency excursion and rate of the sinusoidal FM
also differed between the three. Sound W (Fig 8A) consists of a 50 ms, 2 kHz constant frequency (CF) tone, followed by a 550 ms, 1.5 kHz tone. The upper component of W is a 800 ms “warble” with a 10 Hz sinusoidal frequency modulation, and a 700 Hz frequency excursion (max 3.2 kHz – min 2.5 kHz). Tutor sounds X (Fig 9A) and Y (Fig 10A) have an upper component of a shallow, 350 ms FM sweep (3 – 3.5 kHz). The lower frequency component in sound X was a 325 ms sinusoidal warble with a 10 Hz modulation frequency and a 1 kHz frequency deviation (500 –1500 Hz). The lower warble in tutor sound Y had a slower modulation rate (3.3 Hz), a 1 kHz frequency deviation, but a different frequency range (800 – 1800 Hz).

Tutor sound Z (Fig 11A) was designed to pose the greatest challenge of all the tutor sounds in the experiment, to test the mockingbirds’ ability to simultaneously produce complex FM sounds on the right and left side of the syrinx. Sound Z was synthesized by combining two 2-5 kHz FM sweeps, each with a second, 10 Hz sinusoidal frequency modulation, and with the cycles of the sinusoidal FM patterns of the two overlapping sweeps 180° out of phase from each other.

Tutor sound presentation

Tutor sounds were copied onto compact disc for playback from a compact disc player (TEAC, model CD-P1120) and an amplified monaural speaker (Yamaha, model MS101II). Tutor sounds were presented to the birds for ca. 2 h a day from post-hatch day 14 to 160, and then 1 h daily until birds were 1 year old. Each tutor “song” was ca. 60 s in duration, and consisted of several repetitions (5-20, depending on the duration of the tutor syllable) of a syllable or motif with silent pauses between. Daily tutor regimes consisted of a randomized presentation of tutor songs, with 5-10 repetitions of each during the 1-2 hour tutoring session.

Adult mockingbirds (>300 days post-hatch) were moved into smaller recording cages, and their songs monitored. Preoperative song (100-300 minutes per bird) was recorded from adult birds (>300 days post hatching) for comparison of pre and post-surgery
repertoire (Avisoft-Recorder v. 1.7, Avisoft Bioacoustics, Berlin Germany).

(c) Surgery and Physiological Recordings.

Birds were anesthetized by injection of chloropent (4.1 µl/g body weight, recipe available from Fort Dodge Laboratory) into the pectoral muscle. A silastic cannula (Dow Corning Corp., ID 1.02 mm, OD 2.16 mm) was inserted into a cranial thoracic air sac for measurement of subsyringeal pressure. Pressure in the air sac was measured by attaching the cannula to a miniature piezoresistive pressure transducer (Fujikura FPM-02PG), which was mounted on a backpack held in place by an elastic belt around the bird's thorax. The syrinx was exposed by mid-ventral incision between the clavicles, and a small opening in the interclavicular membrane. Microbead thermistors (Thermometrics, BB05JA202) were inserted into each bronchus between cartilaginous semi-rings, several rings caudal to the syrinx. Thermistor leads were routed out of the thoracic cavity and under the skin to the backpack. The interclavicular membrane was sealed around the thermistor leads with a suture and tissue adhesive. For more detailed surgical methods see (Suthers et al., 1994). Pressure and airflow signals were transmitted from the backpack on leads exiting through the top of the cage to signal conditioning instruments and a digital data recorder (Metrum DataTape, model RS512). During an experiment, which typically lasted 7-14 days, the bird could move freely about the cage. Pre and post-operative song was recorded with a directional microphone (Audio-Technica, AT835b) positioned approximately 50 cm in front of the cage.

We used two methods to determine which side of the syrinx produced which sounds. Airflow through one side while the other side was closed (zero airflow), indicates definitively that a sound is produced on the “open” side. In some recordings, the thermistors responded to air oscillations up to ~2 or 3 kHz produced by the acoustic signal from the ipsilateral side of the syrinx. In these cases it was possible to determine the sound generated by each side when both sides were phonating. Because of this
response in the thermistors it is also possible, to some degree, to determine the frequency contributions to vocalizations from the right and left sides.

Acoustic and physiological signals were analyzed with Igor Pro v. 5 (WaveMetrics Inc., Lake Oswego, OR), Sound Analysis Pro (v. 1.04a, Free Software Foundation, Inc., Boston, MA), and Adobe Audition v. 1.5 (Adobe Systems Inc, San Jose, CA.). Statistical analyses were conducted using Sound Analysis Pro v. 1,04a and SigmaStat v. 2.03 (SPSS Inc., Chicago, IL). Data presented as mean ± standard deviation, unless otherwise noted.

RESULTS

Short duration, parallel FM, two-voice sounds (S series tutor)

Tutor sounds S1-S4 (Fig 2) consisted of pairs of short (110-120 ms) FM sweeps with different, non-harmonically related, fundamental frequencies, and with similar or parallel directions and rates of frequency modulation. The fundamental frequencies of the upper and lower components in the tutor sounds (g0 and f0, respectively) ranged from 1.5 to 6.5 kHz, and the difference frequency (Δf = g0 – f0), ranged from 0.5 to 4.25 kHz.

Tutor sound S1 consisted of two parallel, cosine-shaped FM upsweeps, which were separated by only 0.5 kHz in fundamental frequency throughout the duration of the syllable. When attempting to mimic S1, mockingbirds were rarely able to maintain parallel rates of frequency modulation on the right and left sides of the syrinx throughout the syllable. Consequently, g0 and f0 would often overlap (10 of 13 examples), so that the frequency contour across the syllable did not match that of the tutor sound (Fig 2B).

Tutor sound S2 consisted of two FM upsweeps that were very far apart in fundamental frequency (Δf = 4.25 kHz). We did not find any examples of mockingbirds successfully copying both the high and low frequency components of S2. Four mockingbirds (m130, m138, m148 and m152) sang only the lower portion of S2 (Fig 2C), in each case using the left side of the syrinx only (zero airflow through the right side of the syrinx). None of the mockingbirds tutored with S2 sang only the higher frequency component alone during the
Figure 2. Two-voice syllables with parallel patterns of frequency modulation (FM). A) Tutor series S_1-S_4 are pairs of 110 - 120 ms FM upsweeps with difference frequencies (Δf) between 0.5 and 4.25 kHz, and essentially parallel FM. B) Mockingbird copy of tutor sound S_1. Mockingbirds had difficulty maintaining the 500 Hz difference frequency between the upper and lower component of S_1, often the two sweeps converged during the beginning of the syllable as in the case in this example. C) Mockingbird m130 copies of S_2, S_3 and S_4. Tutor syllable S_1 has a Δf of 4.25 kHz, none of the mockingbirds in this study copied this syllable successfully, and instead sang only the lower frequency component of the tutor sound (S_1 in C) on the left side (zero flow through the left side of the syrinx, LFL). Mockingbird m130 sang syllable S_3 by producing higher sweep with the right side of the syrinx and the lower on the left, almost 2 kHz higher than the highest previously recorded left-produced tone for a mockingbird. Bird m130 copied tutor sound S_4 by producing the lower sweep on the left side of the syrinx and the higher sweep on the right. The right side contribution is at the lowest range of what the right side typically produces in mockingbirds. The sweep produced by the right side in this case lacks the pure-tonal quality of the tutor, or the sweep produced on the left, and the rate of airflow through the right side has a pronounced modulation pattern (arrow, RFL in C).

D) Mockingbird m129 used a different strategy to copy sounds S_3 and S_4. Unlike m130, bird m129 sang a sweep at approximately half the fundamental (2 – 2.25 kHz, arrow in spectrogram D), but then configured his vocal tract to attenuate the fundamental and instead support the second harmonic, which matches more closely the tutor sound. The right side of the syrinx produced the higher frequency sweep. The method used by m129 to sing syllable S_4 also differed from m130 (dashed box). In this example the higher frequency component (~2 - 2.5 kHz) is produced on the left side, while the right side contributes the lower frequency tone. LFL and RFL, rate of airflow through the left and right sides of the syrinx, respectively; P, pressure in the cranial thoracic air sac. Airflow concurrent with positive pressure is expiratory, while airflow associated with negative pressure is inspiratory. V, waveform of the vocalization recorded 0.5 m in front of the bird.
Figure 3. Expanded view of mockingbird m129 syllable S4 (dashed box in Figure 2C). Spectrograms of the vocalization (A) sound in the left (B) and right (C) bronchus (obtained by high-pass filtering the amplified thermistor output at 100 Hz). The left side produces the higher of the two predominant frequency components in the sound (~2 kHz), while the right side (C) produces a very low frequency (~500-800 Hz) sound which does not appear in the emitted vocalization (A). However, the sound recorded in right bronchus is also present in the sound recorded in a subsyringeal (cranial thoracic) air sac, as well as additional spectral components that do not appear in either the emitted vocalization or the sounds recorded in either bronchus (e.g. a ~700-1000 Hz FM sweep between the contributions of the left and right sides).
experimental period.

Tutor sounds $S_3$ and $S_4$ were pairs of parallel linear upsweeps that were designed so that both sweeps were within the normal range of the right side ($S_3$), or both in the range of the left side ($S_4$) for at least some portion of the syllable duration. Using the sound recorded in the bronchi to determine the frequency contribution of the two sides, we discovered that mockingbirds produced $S_3$ in two different ways. Because the lowest frequencies in this tutor sound were still well above the normal range for the left side, mockingbirds appeared to have some difficulty matching the two sweeps accurately. Mockingbird m130 (Fig 2C) managed to sing the frequency sweep of the lower component on the left side, but did not match the fundamental frequency of the tutor; producing instead a sweep approximately 400 Hz lower (3.7 kHz ± 0.02 to 4.1 kHz ± 0.11, n = 6 syllables). Interestingly, m130 maintained the same inter-syllable distance between the lower left side and the sweep on the right, singing the upper component about 400 Hz lower than the tutor as well (4.6 kHz ± 0.12 to 5.2 kHz ± 0.21, n = 6 syllables).

Mockingbird 129 found another way to reproduce syllable $S_3$ (Fig 2D). Rather than pushing the left side to sing above its normal range, m129 instead produced a parallel sweep on the left with $f_0$ of one half the desired frequency (Fig 2D, arrow), but the relatively low amplitude in the omitted sound of the $f_0$ compared to $f_2$ suggests that the bird configured his vocal tract resonance filter (Riede et al., 2006) to attenuate the fundamental, and instead support the 2nd harmonic, which ranged in frequency from 3.8 kHz ± 0.02 to 4.3 kHz ± 0.11 kHz (n = 8 syllables). The right side of the syrinx in m129 produced the upper component but never quite reached the maximum frequency of tutor sound (right-produced $S_3$ upper sweeps mean frequency 4.6 kHz ± 0.106 to 5.2 kHz ± 0.203, n = 8 syllables).

Syllable $S_4$ posed the opposite problem to mockingbirds, compared to syllable $S_3$, in that both of the FM sweeps originate outside the normal range for the right side of the syrinx (upper component 2 – 2.5 kHz, lower 1.5 – 2.25 kHz). Again, examination of the
sound recorded by the thermistors in the right and left bronchi reveal that mockingbirds produced these two low frequency parallel tones in two ways. Mockingbird m130 (Fig 2C) produced the upper component on the right side of the syrinx, and the lower component on the left. However the sound produced on the right side was lacking the pure-tone quality of the tutor sound (or the contribution from the left side). The rate of airflow through the right side during the production of the lower frequency sweep was heavily modulated (Fig 2C, RFL arrow), which is not present in the flow rate through the left side (LFL, Fig 2C). Mockingbird m129, in contrast, appeared to produce the higher of the two components in S₄ on the left side, a rare example of a songbird using the left side to sing a higher frequency than the right during two-voiced song. Interestingly, the $f_0$ of the upper component produced on the left in S₄ was essentially the same as the $f_0$ produced immediately before for the lower component of S₃, but was apparently attenuated in the previous syllable by the configuration of the vocal tract filter. In syllable S₄, the amplitude of the $f_0$ is greater than that of the second harmonic $2f_0$, although $2f_0$ is not entirely attenuated in S₄. The production mechanism for S₄ in m129 is not clear, as sound recorded by the thermistor in the right bronchus reveals a ~500-800 Hz tone (Fig 3C), which does not correspond harmonically or in frequency contour to any of the sound energy peaks present in the emitted sound.

The mockingbirds’ varied attempts to copy the S-series tutor sounds show that in two-voice sounds with similar FM rates and bandwidth, mockingbirds were limited by both difference frequency as well as the relative fundamental that could be produced by the right and left sides. The maximum $\Delta f$ produced simultaneously on the right and left sides in mockingbirds did not exceed 2.1 kHz. Individually, the upper and lower sweeps of each pair in the S-series sounds were within the range of frequencies normally produced by mockingbirds during unilateral phonation. However, when phonating simultaneously in two-voice sounds, the frequency each side can produce is reduced (Fig 4, Table 3).
Figure 4. Maximum and minimum frequency (mean ± standard error) produced on the left and right sides of the syrinx during unilateral (black boxes) or bilateral (red boxes) phonation. Overall high and low frequencies mean from 4 birds, mean scores from individual birds presented in Table 3.
Table 3: Frequency Range of the Right and Left Syrinx in Unilateral and Two-Voice Syllables

<table>
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<tr>
<th>Bird</th>
<th>Left (Unilateral)</th>
<th>Left (Two-Voice)</th>
<th>Right (Unilateral)</th>
<th>Right (Two-Voice)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Max. (Hz)</td>
<td>Min. (Hz)</td>
<td>Max. (Hz)</td>
<td>Min. (Hz)</td>
</tr>
<tr>
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<td>2673.6 ± 532.42</td>
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<td>M130</td>
<td>2270.7 ± 565.83</td>
<td>1287.5 ± 393.17</td>
<td>4209.1 ± 1616.32</td>
<td>1688.8 ± 556.48</td>
</tr>
<tr>
<td>M138</td>
<td>1972.7 ± 147.89</td>
<td>1230.5 ± 383.4</td>
<td>3177.1 ± 742.63</td>
<td>2287.9 ± 816.36</td>
</tr>
<tr>
<td>M148</td>
<td>2281.3 ± 586.72</td>
<td>1445.3 ± 221.74</td>
<td>3183.6 ± 911.34</td>
<td>2161.5 ± 934.78</td>
</tr>
</tbody>
</table>
Within a narrow range of frequencies, and for short durations, mockingbirds were able to accurately mimic sounds consisting of very different simultaneous FM patterns or directions.

Mockingbirds attempted to copy a series of tutor sounds consisting of two short converging frequency sweeps (a simultaneous upsweep and downsweep). The T-series sounds (Fig 5A) each have a 200 ms lower component with frequencies entirely within the normal range of the left side, with a simultaneous, 200 ms, higher frequency downsweeps of varying bandwidth.

The two sweeps in syllable T$_1$ have an initial $\Delta f$ of 1500 Hz, and converge to a $\Delta f$ of 500 Hz at the end of the syllable. Mockingbirds could accurately copy the upper and lower components of T$_1$, but did not match the pure-tonality of the tutor sounds as the two sweeps converged. Mockingbirds always sang the higher frequency component of T$_1$ on the right side of the syrinx, and lower on the left. (n = 23 examples from 4 birds: m129, m130, m138, m148). At the start of the syllable, the contribution from each side was a good match to the tutor sound (Fig 5B), but as $g_0$ and $f_0$ converge in frequency, the birds mimicry becomes less tonal, the bandwidth of its components becomes wider and strong sidebands appear in the spectrogram. Amplitude modulation (AM) appears in the envelope of the sound’s waveform. However, it is unlikely that the additional spectral components that arise as the two sweeps converge in mockingbird copies of T$_1$ are simply the heterodyne or difference frequency of the two fundamentals, because the frequencies of the sidebands do not correspond with the difference frequency between $g_0$ and $f_0$. Additionally, if the sidebands present in the sound were the result of difference frequencies, the difference frequency would be decreasing throughout the duration of the syllable, since the two sounds converge in frequency, the resulting sidebands would become closer and closer to the fundamental. However, the sidebands present in T$_1$ remain essentially parallel to $f_0$ and $g_0$ from their onset throughout the syllable. The $\Delta f$ at
Figure 5. Tutor series $T_1 - T_4$ (A), two-voice linear FM sweeps with converging fundamental frequencies. B) Three repetitions of $T_1$ by mockingbird m130. When the final $\Delta f$ of the bird’s copy is larger (the first of the three syllables in B), the two sweeps are closer matches to the pure-tonal quality of the tutor sounds than when the mean frequency contour of the two sides more closely match the upper and lower sweeps of the tutor (as in the second and third syllables). C) Three repetitions of $T_2$ by m130. While the initial $\Delta f$ of $T_2$ is greater than that of $T_1$, the final $\Delta f$ is the same. The contribution of the two sides is again more pure-tonal if the bird at the expense of a larger final $\Delta f$ than the tutor sound (first syllable in the spectrogram C). However, when the mean $f_0$ of the two sides converge to a $\Delta f$ of less than 700 Hz, there is a strong sideband pattern at ~100 Hz intervals above and below the two fundamental frequencies (arrows, B and C). Arrows also mark the onset of a pronounced modulation of the rate of airflow through the right bronchus (RFL).

Three repetitions of $T_3$ produced by m129 (D). None of the mockingbirds reproduced the 3 kHz difference frequency at the beginning of tutor sound $T_3$. The right side of the syrinx in this case produces the upper sweep, but the left side does not join in until ~30 ms later, when the $\Delta f$ is only ~2 kHz. E) Attempts of 3 mockingbirds to copy tutor sound $T_4$. The first bird (m129) reproduced fairly pure-tonal linear sweeps that intersected as the frequency contribution of the right and left sides moved in opposite directions. The attempts of m130 and m138 were less successful, and as the right and left sides approached each other in fundamental frequency, the FM rate approached zero and sidebands or occasional aperiodicity appears in the resulting sound. Abbreviations as in Fig 2.
which sidebands typically appeared was around 1kHz (mean 1030 Hz ± 52.4 SD, n = 25 syllables). Mockingbirds minimized the occurrence of sidebands by maintaining a larger difference frequency across the syllable (first syllable in Fig 5B, max $\Delta f$ 800 Hz).

Tutor sound $T_2$ had an identical lower frequency component, and the same ending $\Delta f$ as the tutor sound $T_1$, but the initial frequency of the upper sweep was 500 Hz higher, resulting in an initial $\Delta f$ of 2 kHz rather than 1.5 kHz. As with tutor $T_1$, mockingbirds had difficulty reproducing pure-tonal sweeps at $\Delta f$ values smaller than ~1 kHz, but because the initial $\Delta f$ of syllable $T_2$ was greater, the onset of sidebands occurred later in the syllable than it did in $T_1$. Again, pronounced sidebands were avoided when mockingbird sang the two sweeps further apart in frequency than the tutor (Fig 5C, first syllable). The frequency of the modulation associated with the sidebands averaged 100.9 Hz ± 20.83 (n = 32 syllables), while the difference frequency between $g_0$ and $f_0$ at which sidebands were present ranged from 1359 Hz to 489 Hz $\Delta f$. Mockingbirds can closely match the high and low frequency of the upper and lower sweeps (upper sweep mean maximum $f_0$ 4.0 kHz ± 0.14, min $f_0$ 2.7 kHz ± 0.12; lower sweep min $f_0$ 1.9 kHz ± 0.34, max $f_0$ 2.6 kHz ± 0.37).

The upper and lower components of tutor syllable $T_3$ (Fig 5A) were the most different of the T-series tutor sounds in both absolute frequency difference (3 kHz at beginning of tutor syllable), and in the bandwidth of FM (the rate of change in $f_0$ of the upper sweep was 3 times greater than the lower). Mockingbirds could not copy the most extreme frequency difference (3 kHz) at the beginning of the syllable, rather initial frequency of the upper (right side) component was lower than the tutor (tutor sound max $f_0$ 5 kHz, mockingbird max $f_0$ in $T_3$ 4.8 kHz, mean 4.5 ± 0.25 kHz), and the contribution of the left side did not begin until later in the syllable when the $\Delta f$ between the two sweeps was less than 2 kHz (mean $\Delta f$ produced in $T_3$ by mockingbirds 1.8 ± 0.22 kHz). In all 3 mockingbirds that sang syllable $T_3$, the right side contribution was longer than that of the left (duration of right side prior to onset of left mean 86.2, ± 43.28 ms, overall duration of right side sweep mean 188.5 ± 48.09 ms). The left side’s contribution was shorter duration
(mean duration left upsweep 125.4 ± 32.04 ms), and was often closer to a CF tone, than the FM upsweep of the tutor.

T\textsubscript{4} tutor syllable consisted of a 4-2.5 kHz downsweep and a simultaneous 2 – 2.5 kHz upsweep which crosses the lower sweep at 2.4 kHz and the two sweeps continue past the intersection point for 35 ms, ending with a 500 Hz frequency deviation. While the mockingbirds often seemed to have difficulty with reproducing the pure-tonality of converging sweeps in tutor sounds T\textsubscript{1} and T\textsubscript{2}, two mockingbirds (m152 and m129) produced the T\textsubscript{4} upper and lower sweeps without the onset of sideband frequencies, and even were able to mimic the crossing FM sweep pattern of the tutor sound (Fig 5D). Two other birds (m130 and m138) had more difficulty with the task, and as the right and left sides converged in frequency, the mockingbird copies became heavily modulated and rather than the frequency sweeps crossing as they do in the tutor sound, the slopes of the sweeps decrease as they approach each other becoming essentially parallel CF tones. In both m130 and m138, the CF portions are heavily modulated, with sidebands or occasionally aperiodic segments (Fig 5D).

Overall, we found that when mimicking the T-series sounds, that there was an apparent tradeoff between reproducing the linear, pure-tonal quality of the tutor FM sweeps, and matching the mean frequency of the upper and lower components. As the upper and lower frequency sweeps converged, a pronounced AM of the sound waveform was often present. However, the rate of the AM did not correspond with the difference frequency of the upper and lower components, and so do not appear to be the result of beating. Additionally, a $\Delta f$ below 1000 Hz was not always correlated with an amplitude modulation, suggesting that small $\Delta f$s are not necessarily the cause of the AM in the production of converging linear FM sweeps.

**Extreme frequency differences and opposite directions of FM – (U and V series tutor)**

The tutor series U and V consist of three pairs of two-$f_0$ sounds (Fig 6A and B). The
Figure 6. Tutor series U and V each consist of 3 different two-voice sounds. Tutor sounds U₁ and U₃ were identical to V₁ and V₃ (A and B, respectively), and consist of 100 ms, wide bandwidth, linear FM sweeps in opposite directions, with the frequency of the upper and lower sweeps converging in U₁ and V₁, and diverging in U₃ and V₃. The middle components of the tutor sounds (U₂ and V₂) were 50 ms pairs of shallowly FM tones with max Δf's of 1.2 kHz and 4.3 kHz, respectively. C) Mockingbird m108 copies of tutor series U and V. The contributions of the right and left sides are labeled for easy in identification. None of the mockingbirds tutored with U and V copied the higher frequency components of U₁, U₃ or the V series sounds. However, the right side of the syrinx typically contributed a short (~28 ms) higher frequency two-voice component during the last third of syllables U₁ and V₁. Interestingly, while the 1.5 – 3.5 kHz lower sweep in U₁ and V₁ was always produced on the left side of the syrinx by the mockingbirds, the same bandwidth downsweep in U₃ and V₃ was produced by the right side, with only brief, lower frequency contributions from the left side. Abbreviations as in Fig 2.
first and third sounds in both U and V are similar to the T-series sounds, in that they were two linear FM sweeps in opposite directions (a simultaneous upsweep and downsweep), although they are similar in duration to the T-series (Table 1), they have a greater rate of FM and total bandwidth. Mockingbirds did not accurately copy the higher frequency components in U₁ and U₃, nor in any of the three V-series sounds and in many cases completely omitted any two-voice component in their copies (Fig 6C). However, the lower frequency components of U₁ and V₁ were not produced the same way as those of syllables U₃ and V₃, despite having the same duration, FM rate and bandwidth. Mockingbirds produced the lower components of tutor syllables U₁ and V₁ on the left side of the syrinx (L in Fig 6C)(n=18 syllables from 3 birds: m102, m103, and m108). But when singing a sweep of the same bandwidth in the reverse direction (lower frequency component of U₃ and V₃) mockingbirds began phonation the syllable on the right side, in most cases singing the entire downswept lower component on the right. In most examples, the right side contributes a small two-voice component at the very end of the intro-notes (R in U₁ and V₁, Fig 6C), but the duration of the relatively low amplitude contribution from the right was only 30.6% of the total duration of the tutor syllable (mockingbird total duration syllable U₁ 93.3 ms ± 10.08; mockingbird right side duration 28.6 ms ± 9.09) and was absent in the tutor syllable. When the downswept lower frequency components of these syllables (U₃ and V₃) begins within the normal frequency range of the right side, birds sang these sweeps on the right side, or by starting phonation on the right and switching mid-sweep to the left side for the remainder of the sweep (using the same strategy as northern cardinals (Cardinalis cardinalis) use to produce wide bandwidth FM sweeps).

Shorter middle two-voice components (U₂ and V₂) differ in their Δf between the upper and lower components. In U₂ the maximum Δf is 1.2 kHz, while in V₂ the max Δf is more than three times that (4.5 kHz). Mockingbirds sang both the upper and lower components of U₂, but never produced the higher frequency component of V₂. Instead they sang the lower component on the left side and kept the right side of the syrinx closed.
Figure 7. Wood thrush song element consisting of a CF tone concurrent with a quasi-sinusoidal FM higher frequency component. The syringeal lateralization or production mechanism of the wood thrush is not known. Song obtained from the Stokes Field Guide to Bird Songs: Eastern Region. Lang Elliott et al., 1997. Audio CD, Little, Brown & Company, publisher.
**Two different FM patterns, a lower CF tone and upper FM warble – (W tutor)**

Mockingbird tutor sound W was modeled after a common two-voice wood thrush (*Hylocichla mustelina*) song element (Fig 67), and consists of a long constant frequency tone concurrent with a higher frequency, sinusoidal FM “warble”. The synthesized tutor sound (Fig 8A) was lower in overall frequency compared to the wood thrush song. The two lower CF tones (Table 2) were in the range of the mockingbirds left side (1.5 and 2.0 kHz), and the warble component was modulated between 2.5 and 3.2 kHz, which is in the range of the mockingbird right side (Table 3).

Birds m102 (Fig 8D), m103 (Fig 8E) and m108 (Fig 8B and C) each attempted to sing this syllable, however, none of the three birds sang the CF and warbled two-voice elements simultaneously like a wood thrush. Mockingbirds m102 and m103 sang only the first introductory CF tone, and then the warble, without the lower concurrent CF tone, or with a very brief (11-56 ms duration, n = 18 syllables) contribution from the second side during the first 50 ms of the 800 ms warble (Fig 8D, E). Mockingbird m108 used a different strategy than the other 2 birds to try and replicate syllable W. His imitations included both CF lower tones, but rather than starting the warble component after 50 ms of the 1.5 kHz tone, he continued the tone alone for a longer duration using the left side, with the right contributing a shortened version of the upper FM warble. In some cases, he would almost completely close the left side of the syrinx when the right-produced warble began (Fig 8C), but in other cases he attempted to continue the CF tone on the left throughout the rest of the syllable. However, whenever m108 phonated on the left during the right side warble, he was not able to maintain a constant tone, but instead the contribution from the left was segmented into staccato-like bursts of phonation. Furthermore, the tones that were produced on the left were not constant in frequency like the tutor, but were frequency-modulated in a quasi-sinusoidal pattern that were parallel (or corresponded temporally and directionally) with the peaks of the warble on the right
Figure 8. Tutor sound W (A) was created as a synthesized version of a common wood thrush (*Hylocichla mustelina*) song (Fig 7), and consists of a 50 ms 2 kHz CF introductory note followed by a 550 ms 1.5 kHz CF tone. The onset of a second, higher frequency, FM “warble” is 100 ms from the start of the first CF tone. The warble is a sinusoidally FM tone with min and max frequencies of 2.5 – 3.2 kHz. B) A copy of tutor W by mockingbird m108. None of the mockingbirds in this study were able to maintain the 1.5 CF tone during the production of the higher frequency warble. M108 attempted (arrow, B) to produce the 1.5 tone on the left while singing the sinusoidal FM pattern on the right side, but only manages to phonate in short bursts on the left, and is not able to maintain a constant frequency, but rather the contributions from the left side appear to be modulated in a sinusoidal pattern phase-locked with the FM pattern being produced on the right side. C) In other examples, the same bird would simply extend the duration of the 1.5 CF tone for an additional ~50 ms, and then silence the left side completely when the right side began phonation of the warble, with little or no two-voice overlap. Mockingbirds m102 (D) and m103 (E) sang the 2 kHz intro-note on the left side (the thermistor in the left bronchus of each of these birds was non-functioning at the time of recording. Phonation on the left side can be assumed when airflow was zero through the right side of the syrinx, and pressure was positive, indicating expiratory airflow), but the 1.5 CF tone was omitted. Unlike m108 and m103, mockingbird m102 sang the higher frequency warble on the left side, using the right side only for a minibreath between the intro-note and the onset of the warble (arrow, D). Mockingbird m103 switched to the right side of the syrinx to produce the warble, and appears to include an attempt at the 1.5 kHz CF tone during the first 50 ms of the warble (arrow, E), but without airflow through the left side of the syrinx, the origin of this lower tone can not be verified as coming from the left side. Abbreviations as in Fig 2.
side (Fig 7B). The overall durations of W syllables sung by mockingbirds were significantly shorter than the duration of the tutor sound (ANOVA on ranks with Dunn’s method for comparisons vs. control (tutor) group: m102 mean duration 687 ms ±70.6 ms SD, Q(1, 11, 13) = 3.330, P<0.05, n = 12; m103 mean duration 466 ms ±28.1 ms SD, Q(1, 7, 13) = 5.376, P<0.05, n = 8; m108 mean duration 623 ms ±80.7 ms SD, Q(1, 13, 13) = 4.421, P<0.05, n = 28).

*Lower FM warble with an upper FM sweep – (X and Y tutor)*

Syllables X and Y (Figs 9 and 10) were designed to pose the opposite challenge as that of the W syllable. In syllables X and Y the sinusoidal FM pattern was presented as the lower component (which would presumably be produced on the left) and a simpler FM pattern as the higher (right side) component. The lower component in syllable X was a FM warble with a modulation rate of 10 Hz, and frequency bandwidth of 500 - 1500 Hz. The warble in the lower component of syllable Y had a lower FM rate (3.3 Hz), and a slightly higher fundamental frequency throughout (Table 2). The higher component both X and Y was not a CF tone as in sound W, but rather a slight upsweep, making the overall syllable presumably more difficult to produce, as it would require both sides to modulate their $f_0$ at different rates over the duration of the syllable. None of the mockingbirds tutored with either X or Y accurately mimicked these two-voice tutor sounds. The production strategies employed by mockingbirds attempting to sing X and Y were unlike those used to sing the W syllable. Rather than choosing to sing either the upper or lower frequency component, as they did with syllable W, for both X and Y, mockingbirds produced a two-voice sound that was intermediary to both the upper and lower FM component of the tutor sound.

In both mockingbirds that attempted to sing syllable X (m148 and m152), both the right and left sides contributed a sinusoidal FM signal, neither of which matched the $f_0$ of the FM warble of the tutor, nor a harmonic of it (Fig 9B). However, the higher frequency
A Tutor file X Tutor X (blue) with difference frequency (red)

B m148

C m148 (black) tutor sound (blue), and tutor difference frequency (red)
Figure 9. Tutor sound X (A) was designed to test mockingbirds on the opposite lateralization task as that posed by tutor sound W (Fig 8A). Tutor X was composed of a 350 ms, shallowly FM (3 – 3.5 kHz) sweep above a sinusoidally modulated FM warble (0.5 – 1.5 kHz, 10 Hz modulation frequency). The red plot in the second spectrogram (A) is a plot of the difference frequency between the upper and lower component, light blue outlines the peak frequency of the upper and lower components of the tutor sound. Mockingbird m148’s copy of tutor sound X (B) was unlike either the upper or lower component of the tutor, but consisted of two FM warbles, one contributed from each side of the syrinx and essentially parallel in frequency contour. The FM warble produced on the right side had a similar overall bandwidth and frequency range as the upper FM sweep (mean frequency range of mockingbird right-produced warble 2.8 ± 0.12 kHz – 3.8 ± 0.15 kHz). The average contribution from the left side ranged in frequency from 1.8 – 2.9 kHz (SD ± 0.14 – 0.35 kHz, respectively), which is similar in frequency range to the difference frequency between the upper and lower components of the tutor sound (red plots, A and C). C) The same copy of the tutor by m148 with the peak frequencies of the upper and lower tutor sounds (blue) and the difference frequency of the tutor sound (red) superimposed on top for ease of comparison. Abbreviations as in Fig 2.
Figure 10. Tutor sound Y (A) consists of a 3 – 3.5 kHz upsweep and an 800 – 1800 Hz sinusoidally FM tone, with a 3.3 Hz modulation frequency. B) Mockingbird m148 approximated this tutor sound by singing a sound with a 10 Hz sinusoidal modulation frequency that was intermediate to the upper and lower components of the tutor in mean frequency. The mockingbird superimposed a secondary frequency modulation on top of the 3.3 Hz “warble” FM with a modulation rate of approximately 85 Hz, and a frequency deviation of ~750 Hz. The peak frequencies of the mockingbird’s copy are plotted on top of the tutor sound (red trace on spectrogram, A), to facilitate comparison of the overall frequency bandwidth of the mockingbirds copy and the tutor sound. Abbreviations as in Fig 2.
warble that mockingbirds produced on the right side actually spanned a frequency range that matched that of the upper FM sweep component in the tutor sound (tutor upper FM sweep, 3 - 3.5 kHz; mockingbird upper warble mean min – max frequency 2.8 kHz ± 0.12 – 3.7 kHz ± 0.14, n = 32 syllables). Interestingly, the contribution of the left side of the syrinx did not match the frequency range of the lower component of the tutor sound, but rather matched the difference frequency between the upper and lower components of the tutor (red plot superimposed on the tutor spectrogram, Fig 9B, and lower mockingbird spectrogram 9C). The warbles from the right and left sides were essentially parallel in frequency contour, so that the sinusoidal modulations were always in phase with each other.

Two birds (m148 and m152) attempted to sing syllable Y (Fig 10). Like syllable X, neither of the birds sang syllable Y by matching either the upper or lower FM component, but rather produced a syllable intermediate in frequency to both. Unlike the strategy used to copy syllable X, where the right and left side both sang FM warbles that matched the modulation pattern of the difference frequency of the tutor, mimicries of syllable Y had a single \( f_0 \) through much of the syllable, with a relatively low intensity higher two-voice component only occasionally evident. Rather than choosing the higher or lower frequency component of the tutor to reproduce, the mockingbirds sang a hybrid syllable of sorts. The mockingbird copies of syllable Y have the same overall 3.3 Hz FM rate as the lower component of the tutor (mean modulation period 306 ms ±31.7 SD. Mann-Whitney Rank Sum Test, \( T= 42.000, n =18, P = 0.766 \)), but with an additional, shallower frequency modulation pattern superimposed on top throughout the syllable with an average modulation depth of (756.8 ±180.276 Hz, \( n =18 \)), and an average FM rate of 84.7 Hz (±5.284, \( n =18 \)).

**Two upswept sinusoidal warbles, 180 degrees out of phase – (Z tutor)**

Tutor sound Z was synthesized from two overlapping 2-5 kHz upsweeps, each with a
secondary sinusoidal frequency modulation of 20 Hz (peak to peak period 50 ms), and frequency deviations of 1.5 kHz per cycle (Fig 11A). The two overlapping sinusoidal sweeps were 180° out of phase, so that the modulation of the warble was in opposite directions, intersecting at the zero-crossing of each cycle.

Frequency deviation of the right and left sides vs. overall deviation

Three of four mockingbirds in our study did not copy the overlapping 1.5 kHz frequency deviation sweeps of the tutor sound. Rather, these birds used the right and left sides of the syrinx to produce upper (right) and lower (left) non-overlapping FM warbles with a smaller frequency deviation (Fig 11C) (frequency deviation upper warble 989.9 Hz ± 293.73; lower warble 675.6 Hz ± 220.97), which rarely overlapped or met in frequency, but instead were typically separated by a frequency gap of ~ 335 Hz (max Δf 1015 Hz, min Δf 0 Hz, mean 334 Hz ± 274.23, n = 38 syllables from 3 birds), m127, m129, m130). However, if we compare the overall bandwidth of the mockingbirds’ two FM warbles to that of the tutor sound, the overall bandwidth of the fundamental frequency was not significantly different (measured from the peak of the upper warble to the trough of the lower warble, measurements taken at 3 different times across the syllable: 25, 50 and 75% of the total duration. (One-Way ANOVA, using the Holm-Sidak method for comparison against the tutor. Tutor sound bandwidth (BW) 1.5 kHz, m130 mean overall BW 1.8 ± 0.32 kHz, t = 1.131, P = 0.271; m127 mean overall BW 1.8 ± 0.38 kHz, m129 mean overall BW 1.5 ± 0.36 kHz, t = 0.252, P = 0.802).

One of the 4 mockingbirds (m148) attempted to sing this syllable (Fig 11D) with contributions from each side having a bandwidth of the sinusoidal FM closer to the 1.5 kHz frequency excursion of the tutor sound, than to the upper and lower relatively narrowband FM components produced by the other 3 birds (mean BW right side 922 ± 95.7 Hz, mean BW left side 869 ± 101.3 Hz) However, The resulting syllable was unlike the crisscrossing pattern of frequency modulation found in the tutor sound, and instead the two sinusoidal warbles produced by the bird were in phase for most of the duration of the
Figure 11. Tutor sound Z (A) was created from two, 180° out of phase, temporally-overlapping sinusoidally FM 2 – 5.5 kHz upsweeps, with 20 Hz modulation frequency and a 1 kHz frequency deviation per cycle. B) Perceptually, the tutor sound might also be interpreted as higher (red) and lower (green) non-overlapping upswept quasi-sinusoidal “warbles” with half the frequency deviation and double the modulation frequency (500 Hz frequency deviation, 40 Hz FM rate), with the upper and lower warbles 180° out of phase with each other. C) Mockingbird m130 copy of tutor sound Z, m130 and two other mockingbirds (m129 and m138) sang sound Z by producing two non-overlapping warbles with frequency deviations between ~500 – 1000 Hz, and modulation rates between ~52 and 75 Hz). Unlike the tutor sound, the sinusoidal modulations produced on the right and left sides of the syrinx in mockingbirds were in phase for most of the syllable. In some cases the mockingbird would begin the syllable with the direction of the FM on the right and left sides moving in opposite directions, but the two sides were always phase-locked by the end of the third cycle of modulation (between two red lines in spectrogram, C). One bird (m148, D) copied tutor sound Z by producing two overlapping FM sinusoidal warbles with a frequency deviation (ranged between ~850 – 1800 Hz) closer that of the 1.5 kHz frequency deviation of the tutor sound. Red lines in spectrograms ease comparison of the phase of modulation between the upper and lower components of tutor and mockingbird sounds. Abbreviations as in Fig 2.
sound, with occasional cycles when the two sides moved out of phase (e.g., arrow in Fig 11D).

**Period of FM warbles**

The tutor sound Z was created by overlapping two sinusoidal FM sweeps, each with a 50 ms period of modulation, however, the tutor sound could be interpreted as two non-overlapping (but contiguous) FM warbles of smaller bandwidth. In this case, the upper and lower components (red or green portions in Fig 11B, respectively) are each a quasi-sinusoidal FM warble with half the period (25 ms), and half the frequency excursion (750 Hz), but with the two warbles still 180° out of phase with each other. Mockingbird copies differed from the tutor not only in frequency excursion of the right and left side but the period of the sinusoidal modulation was shorter than in the tutor sound (mean period 17.1 ± 4.69 ms). Mockingbirds m127, m129 and m130 may have been attempting to sing the portions of the tutor above or below the intersection point of the two larger warbles on the two sides of the syrinx, rather than the entire overlapping 1.5 kHz frequency deviation on each side (as m148 seemed to have been trying to do). The period of the upper and lower warbles produced by mockingbirds ranged from 14 – 28 ms, but was on average much shorter than either the period of the 20 kHz FM warbles used to create the tutor, or the period of the upper or lower quasi-sinusoidal warbles above or below the intersection frequency (mean period 20.1 ± 3.69 ms).

**Phase-locking of bilateral FM warbles**

In all four mockingbirds, the contributions of the right and left side, regardless of the bandwidth or period, were frequency modulated in the same direction (in phase with each other) with few exceptions. In some cases (m127, 2 of 19 syllables; m129, 3 of 11 syllables; m130, 3 of 21 syllables and m148 4 of 10 syllables) mockingbirds would start the syllable with the FM on the right and left sides moving in opposite directions (as they would when the two sine waves are out of phase), but by the end of the second or third cycle of the modulation (between red lines in Fig 11D), the right and left sides were phase locked with
each other, and remained in phase for the remainder of the syllable (Fig 11D), with the exception of m148, in which the two sides would periodically move slightly in and out of phase during the syllable, but were never 180° out of phase for more than one cycle of the modulation.

**DISCUSSION**

Our data show that while mockingbirds can and do produce various two-voiced sounds that are not harmonically related, the extent to which these two sounds can be independently modulated during bilaterally-produced vocalization is seriously limited. Both the absolute difference in fundamental frequency and the degree and control of frequency modulation produced by the two sides was greater when comparing the acoustic output of each side during unilateral phonation with output of each side during bilateral phonation (Table 3).

**Limits on fundamental frequency during two-voice phenomena**

*Very large Δf*

Tutor syllables in which $g_0$ and $f_0$ were separated by more than 2.25 kHz were rarely mimicked by mockingbirds. In cases where mockingbirds did attempt to copy sounds with a $Δf$ greater than 2.25 kHz, the higher frequency component was often omitted completely (e.g. S₂, U and V, Figs 2 and 6). The largest frequency difference mockingbirds produced simultaneously with the two sides of the syrinx was 2.18 kHz. The reasons for a constraint on difference frequency are not known, however several possibilities exist. Since the two sides of the syrinx are physically linked, the degree to which a bird can adjust the tension of the labia on opposite sides may be constrained mechanically. Increasing labial tension on one side might distort the cartilaginous framework of the syrinx in a way that also affects tension on the contralateral side. Beyond a direct physical connection, the vibratory behavior of one side of the syrinx could interfere with the
independent vibration of the other simply by nature of their close proximity to each other. An oscillation of the labia and/or MTMs on one side of the syrinx creates pressure waves that could, in theory, set the vibratory tissues of the other side into sympathetic vibration at the same rate. During bilateral phonation, this acoustic “cross-talk” between the two sides may limit the absolute Δf which a bird can produce between the two sides simultaneously.

Another potential constraint on how different the $f_0$ from the two sides could be tuning of the suprasyringeal vocal tract filter. Riede et al. (2006) found that northern cardinals dynamically modulate the resonance of their upper vocal tract by rapidly changing the volume of their oropharyngeal-esophageal cavity (OEC) to support the changing $f_0$ of their song during FM sweeps (Fletcher et al., 2006). Since both sides of the syrinx share the same suprasyringeal vocal tract filter, the pass band of the filter will limit the extent to which $f_0$ and $g_0$ can differ in frequency and still be transmitted through the vocal tract.

*Very small $\Delta f$ – beat frequencies*

When producing two sounds very close in frequency, two-voiced mockingbird songs often contained pronounced beat frequencies. Beating occurs when two slightly different frequencies interfere with each other, resulting in periodic modulation of the amplitude envelope with a modulation rate that is the difference between the two frequencies (Greenewalt, 1968; Banta-Lavenex, 1999). Interestingly, while two-voiced mockingbird vocalizations that were close in frequency often exhibited beating or amplitude modulation (e.g. Fig 5, B and C), there were also instances where beating was not observed (e.g. Fig 2B). Beating is often absent if both frequencies are not at high (or similar) intensities. However, the rate of the amplitude modulation of the sound waveform in many instances could not be attributed to sum or difference frequencies of the two fundamentals, suggesting that the source of this modulation was not simply the production of heterodyne frequencies. The source of these additional frequency
components is not clear; however they often corresponded with a periodic modulation of the rate of airflow through the right (and sometimes left) side of the syrinx, indicating that the production of the modulation frequency could originate in the right side of the syrinx. In brown thrashers and grey catbirds, close relatives of the northern mockingbird, the right side of the syrinx often produces a rapid amplitude modulation by the rapid, cyclical abduction of the labia (Suthers, 1994; Goller and Suthers, 1996). In thrashers and catbirds, these rapid AM syllables are a regular acoustic feature of some syllables, and our observation of a similar acoustic phenomena associated with a rapid, cyclic modulation in the right airflow may indicate a similar predilection in mockingbird vocalizations. Alternatively, if a beating pattern was detected perceptually by the mockingbirds when listening to tutor sounds with two similar fundamental frequencies, the production of the sidebands might be an attempt by the mockingbird to replicate the “roughness” perceived in the tutor. In either case, mockingbirds may have some control over the intensity or occurrence of interactions between similar two-voice frequencies either at the source or by filtering in the vocal tract. The mechanism, if any, by which birds might isolate the frequencies produced on each side of the syrinx from crosstalk (acoustically or mechanically) requires further investigation.

Both $g_0$ and $f_0$ beyond the frequency range of one side

Besides limitations on the absolute difference in fundamental frequency the two sides can simultaneously produce, one might predict that the contribution from each side will be constrained by the maximum and minimum oscillation frequency sustainable on that side. For instance, in a previous study of syringeal lateralization in mockingbird mimicries, Zollinger and Suthers (2004), found that the highest frequency produced by the left side of the syrinx was ~ 3.2 kHz, and the lowest frequency produced by the right side was ~ 1.8 kHz (Table 3), different mockingbirds in our study tried different strategies to copy sounds above or below their normal range. Mockingbird m130, when copying a
tutor sound with both the upper and lower component out of the normal range for the left side \( (S_3, \text{Fig 2}) \), pushed the left side to produce the lower of the two frequency components both of which were higher than those normally sung on the left side. In comparison, m129 sang the same tutor sound by producing a sweep at one-half the tutor frequency, but then achieved a close match to the tutor frequency by selectively tuning his vocal tract to support the second harmonic and attenuate the fundamental.

At the opposite extreme, when the two components of the tutor sound were both below the normal frequency range for the right side, mockingbirds again attempted to mimic the sound using two different vocal strategies. Mockingbird m130 sang the higher of the two low frequency sweeps in tutor sound \( S_4 \) with the right side of the syrinx (Fig 2C), however the contribution of the right side lacked the pure-tonal quality of the tutor sound or of the sound produced on the left. In mammals, (Mende et al., 1990; Gerratt and Kreiman, 2001; Brown et al., 2003; Peters et al., 2004; Riede et al., 2007), there is evidence that vocalizing at the upper or lower limits of one’s frequency or amplitude range results in an increased incidence of nonlinear phenomena, such as subharmonics, biphonation, frequency jumps or deterministic chaos. Similarly in mockingbirds, the “roughness” observed in m130’s low frequency sweep from the right side in syllable \( S_4 \) may indicate a loss of control over the regular periodic oscillation of the vibrating sound source. The strategy used by mockingbird m129 was surprising in that the apparent contribution of the right side of the syrinx was even lower than that of m130. By examining the sound recorded within each bronchus by the thermistors, we can see that m129 sings the higher of the two low frequency sweeps on the left side of the syrinx (Fig 3), and that the apparent contribution from the right side was a much lower (~500 Hz) tone, which does is not obviously related (either harmonically or in frequency contour) to any of the frequencies present in the emitted sound. This low frequency sound on the right side may be the result of a very low frequency pulsatile phonation pattern that can result when the oscillating tissues become so slack that the air flows slowly past them in a low frequency
and often aperiodic manner. The equivalent phenomena occurs in human phonation, commonly referred to as vocal fry, and may be a regular component in the vocal repertoires of hooded crows (*Corvus cornix*) (Jensen et al, In Press)

**Limits on the control or degree of FM during two-voice phenomena**

*Linear sweeps with opposite directions of FM*

Within their normal frequency range, the ability of mockingbirds to produce bilateral FM sweeps with opposite (converging) modulation patterns appears to be constrained both by the absolute difference frequency between the two sounds and the rate of FM of each sweep. Above a maximum difference frequency (~2 kHz), mockingbirds omit the higher (e.g. Fig 2C and 6C) or lower (Fig 5D) frequency component of the tutor sound. Very different rates of modulation were also not accurately mimicked. For instance, in tutor syllable T₃, the bandwidth of the upper sweep was matched by the mockingbirds, but the bandwidth of the lower sweep was smaller than the bandwidth of the lower sweeps in tutor syllables T₁ or T₂, in which the lower tutor sweep was the same as that in T₃, but the upper sweeps were more restricted in bandwidth than that of T₃. The result is a left side contribution closer to a CF tone than the FM sweep of the tutor.

*Production of different bilaterally complex FM patterns*

We found that mockingbirds were limited in the extent to which the FM patterns of the two sides can differ. When the modulation pattern of one side became more complex (such as a sinusoidal modulation pattern), mockingbirds were not able to produce a CF tone, FM sweep or any FM pattern that was not approximately parallel to the frequency contour of the first side. While this type of sound was not successfully produced by mockingbirds in this study, it is a regular feature of wood thrush song (Fig 7[Borror and Reese, 1956; Greenewalt, 1968; Titze, 1994; Roth et al., 1996]). While the production pattern used by the wood thrush to produce this song type is not known, the syrinx of the
wood thrush is not known to be significantly different than that of other songbird species (Ames, 1971). Although subtle morphological difference in the two sides of the wood thrush syrinx cannot be excluded, their ability to simultaneously execute very different motor patterns mostly like depends on central specializations. Comparative studies of song production suggest that different species have likely evolved species-specific specializations in how they use their bilateral vocal organs. While mockingbirds may have vocal production systems adapted for an increased plasticity allowing for mimicry of a wide range of heterospecific song types, wood thrushes have likely been subject to different selective pressures.

Central control of bilateral motor coordination

Song is controlled by an interconnected, bilaterally parallel network of vocal control nuclei in both cerebral hemispheres and the brainstem (Wild et al., 2000). Motor control of the syrinx is lateralized, but in order for songbirds to produce the precisely coordinated output necessary for complex singing behavior, the bilaterally-produced motor commands must be tightly coordinated (Wild et al., 2000; Schmidt, 2003; Schmidt et al., 2004). While the song system anatomy in the two hemispheres is essentially parallel, they are functionally lateralized, with independent contributions to the production of song from the ipsilateral side of the syrinx (Nottebohm et al., 1976; Williams et al., 1992; Halle et al., 2003). In bilaterally-produced song, motor commands in HVC (a key song control nucleus in the forebrain) are coordinated by precisely timed inputs linked to the onset of syllables, despite a lack of bilateral projections within the forebrain, suggesting that bilateral circuits in the midbrain or brainstem may instruct higher-order song features such as timing, order, duration and possibly structure of frequency modulated syllables (Schmidt et al., 2004). Lesions of nucleus uvaeformis (Uva), one of the few sites of interhemispheric projections within the song system, suggests it plays a critical role in coordinating song control bilaterally (Williams and Vicario, 1993; Foster and Bottjer,
Additionally, contralateral projections and coordination in the descending motor control of vocal and respiratory structures are likely required for production of bilateral syllables (Wild et al., 2000). The degree of interhemispheric coordination necessary and the precision of motor sequences and timing that would be required for the simultaneous production of two very different motor patterns on the two sides of the syrinx make constraints at the central level very possible. In humans, learning and production of coordinated bilateral movements seems to be limited by mirror-symmetry constraints (Swinnen et al., 1998; Mechsner et al., 2001; Lee et al., 2002; Temprado et al., 2007). A similar constraint toward symmetry may be present in the motor control of the syrinx in songbirds. However, while the spontaneous tendency toward mirror symmetry in voluntary bilateral limb or digit movements has been traditionally interpreted as a muscle grouping constraint (a tendency toward activation of homologous muscle groups) (Kelso, 1984; Swinnen et al., 1998), a recent study using altered visual feedback suggests that the constraints on asymmetrical movements may be entirely perceptual (Mechsner et al., 2001). The study of Mechsner et al (2001), provides evidence that bimanual coordination is more independent of motor system constraints than is often thought, and if the control of bilaterally asymmetrical syringeal motion is similarly free from constraints of the descending motor control, it is likely that observed constraints in mockingbird song learning may be more peripheral in origin.

Conclusions and future directions

For mockingbirds, renowned heterospecific mimics, improvisation and creativity in vocal production strategies may allow for increased ability to mimic a wide range of sounds, including those of species whose songs may have evolved under very different production constraints. While the two sides of the syrinx in mockingbirds are remarkably variable in the range of frequencies and patterns of modulation and complexity they produce unilaterally, the degree to which they two sides can differ in bilaterally-produced
song appears to be under stronger constraints. The source(s) of these constraints is not yet identified, but our data suggest that the limitations on the independence of bilateral sound production can come from multiple sources including, but not limited to, a physical coupling of the two sides, coordination of the central motor control, and the absolute frequency limits resulting from the vocal range of each side.
GENERAL DISCUSSION

While the songbird syrinx is remarkably similar in morphology across species, the diversity of vocalizations produced by songbirds is staggeringly vast. A noteworthy example of extreme repertoire size and song diversity, the northern mockingbird (Mimus polyglottos) nonetheless possesses a syrinx lacking any observed specializations in morphology or proportion compared with songbirds with more homogenous or limited song repertoires (Ames, 1971; Warner, 1972 and Personal observation). The experiments in this dissertation were designed to identify and describe both new sources of complexity and putative constraints of the songbird peripheral vocal production system. Previous studies of syringeal motor patterns and lateralization in a variety of songbird species suggested that different birds might have evolved specialized motor strategies in order to exploit the duplex nature of their vocal organ to achieve their diverse specialized vocal effects. The study presented in Chapter 1 tested the hypothesis that the different respiratory and syringeal motor patterns employed by different songbirds are necessary for the efficient production of their species-specific songs. The results of this study show that in order for mockingbirds to make accurate copies of heterospecific songs, they must use the same patterns of syringeal lateralization and breath control as the model species.

Physiological or morphological differences between species can constrain mockingbirds from the option of using a similar vocal motor strategy as the model species they are trying to mimic. For instance, when attempting to copy song made by birds with much smaller body size (such as canaries), the larger mockingbird can not oscillate their body wall as rapidly as a small bird, and so are not capable of taking minibreaths at a high enough repetition rate to accurately copy the long duration, high repetition-rate trills of canaries. Mockingbirds attempted to get around this putative biomechanical constraint by using a different respiratory strategy to copy the canary trill rate, but by doing so ran
quickly out of phonatory air, and could not match the duration of the canary tutor sound.

Mockingbirds also could not match the extremely high and low frequency components of brown-headed cowbird song, simply omitting the low frequency sounds, and singing the higher frequency parts at much lower frequencies than the tutor. The reduced frequency range of mockingbirds compared with cowbirds might also represent a biomechanical constraint, at the syringeal level in this case. Preliminary data on cowbird syringeal anatomy (Zollinger and Riede, personal obs.), indicate that cowbirds have a unique syringeal structure that may be the key to explaining the production of such unusually low frequencies from a bird of their size. Further investigation of cowbird syringeal anatomy is necessary to know if a similarly unique morphological adaptation is present in the right side of the cowbird syrinx that could explain the production of their extremely high frequencies as well.

A third example of production constraint is described in Chapter 3. The mockingbird could not reproduce a two-voice song of a wood thrush (or a computer-synthesized song that was similar), which requires extremely different patterns of frequency modulation on the right and left side of the syrinx. This inability on the part of the mockingbird to faithfully reproduce the complex two-voice “vocal gymnastics” of the wood thrush is further evidence that the song system and peripheral vocal production system in different species of songbirds have likely evolved in response to very different performance constraints.

As heterospecific vocal mimics, mockingbirds must be considered vocal generalists, and presumably the selective pressures that drove the evolution of their syringeal and respiratory systems were quite different than in species for which natural or sexual selection (or even, in the case of the Wasserschlager canaries, artificial selection) may have favored a highly specialized production system or a specialized style of acoustic or temporal song complexity. For mockingbirds, the evolution of heterospecific mimicry may have been a way to increase vocal diversity or repertoire size (Baylis, 1982). There is a
growing body of evidence that song quality may be an honest indicator of genotypic and/or phenotypic quality (Nowicki et al., 1998; Nowicki et al., 2000), and thus mockingbirds potentially demonstrate their fitness by showcasing an extreme talent for vocal imitation and learning.

Many features of acoustic communication (such as fundamental frequency, temporal patterning, modulation of frequency and amplitude, etc.), are under the direct voluntary control of the bird. The control of syrinx and respiratory system during song involves a series of interconnected forebrain, midbrain and brainstem nuclei known collectively as the “song system”. Each side of the syrinx is controlled by the ipsilateral side of the brain, with independent control of separate syringeal muscle groups, creating a system with potential for production of two harmonically unrelated sounds, simultaneously, and therefore with increased complexity compared with birds (or other taxa) with only single sound sources. However, the application of nonlinear theory to the analysis of animal vocalizations shows that even a single sound source (such as the mammalian larynx or the tracheal syrinx of doves or pigeons) has the capacity to produce surprisingly complex sounds. The results presented in Chapter 2 show that some of the complexity which might have been previously misattributed to the presence of two independent sound sources is sometimes instead the byproduct of passive nonlinear dynamics within a single side of the syrinx.

The extent to which nonlinear phenomena such as biphonation, deterministic chaos, subharmonics and frequency jumps are part of the normal vocal repertoires of songbirds was not known. I found that nonlinear phenomena were present in about 8% of unilaterally-produced mockingbird song and that in some cases both sides of the syrinx apparently exhibit nonlinear phenomena simultaneously, resulting in sounds containing more than two simultaneously unrelated frequencies. For songbirds the presence of two different sound sources gives, in theory, the potential to further increase the complexity of the sounds they produce. However, while the potential exists for such complexity,
examination of two-voice sounds where the contribution of both sides contained biphonation found that the modulating frequency on both sides of the syrinx is always the same. The results presented in Chapters 2 and 3 of this thesis support hypotheses that the two sound sources are not entirely free from cross-talk or interactions during two-voice phonation.

Whether the occurrence of nonlinear phenomena in songbird vocalizations should be viewed as evidence of constraints on the system, pathologies, and/or indicators of poor vocal performance, or whether songbirds might use nonlinear phenomena as a normal, healthy component of vocal signaling is not known. Although certain stereotyped vocalizations of some birds, including mockingbirds, regularly contain apparent nonlinear phenomena, the degree of voluntary control birds have over the production of the nonlinear components within these sounds is not known. An insight into this problem comes from analysis of mockingbird attempts at imitating tutor sounds containing nonlinear phenomena. I tutored mockingbirds with a computer-synthesized version of a common eastern towhee (*Pipilo erythrophthalmus*) call consisting of a 3.5 – 4.5 kHz FM sweep with a 500 Hz modulation of the amplitude waveform, resulting in sidebands at 500 Hz above and below the fundamental in the sound spectrogram (Fig 1A) and as slightly lower amplitude peaks on either side of f0 in a power spectra (Fig 1B). Towhees regularly produce AM calls similar to this (with 500 Hz AM rate) on a single side of the syrinx, mockingbirds rarely had an AM rate in their biphonic calls greater than 280 Hz. When mockingbirds attempted to copy the "towhee" call (Fig 1C) they could not reproduce the 500 Hz AM using biphonation from a single sound source as towhees do. Instead, the mockingbirds "cheated" and sang the fundamental frequency on the right side of the syrinx, and the lower sideband on the left side. Interestingly, when the two voices of the mockingbird are close to 500 Hz apart, a strong beating pattern arises between the two fundamentals, creating a sideband pattern that is quite close spectrally (Fig 1F) to the 3-peaked spectrum of the tutor sound. However, when the frequencies from the right
Figure 1. Time-frequency spectrogram (A) and spectra (B) of a computer-synthesized eastern towhee call. The 210 ms tutor syllable consists of a 2.5 – 4.5 kHz frequency-modulated upsweep (1.1 kHz sinusoidal FM rate), which was amplitude modulated with a modulation frequency (AM rate) of 500 Hz and modulation depth of 20%. C) Three examples of mockingbird m108 copying the tutor sound. In each of the three examples, the right side of the syrinx produces the higher frequency fundamental, and the left side sings the lower fundamental. During each successive attempt in the series, the contribution of the right and left side gets closer together in frequency. When the difference frequency of the right and left side is closest to the 500 Hz modulation frequency in the tutor sound (F), strong heterodyne frequencies appear in the spectra which closely resemble the sideband pattern in the tutor sound, despite having a very different sound production mechanism ($f_0 \sim 3.5$ kHz, $g_0 \sim 4.0$ kHz at the arrow, vs. tutor sound $f_0 = 4.0$, $g_0$ (modulating frequency) $\sim 0.5$ kHz). Spectra (B, D-F) extracted over 10 ms window centered on arrows in spectrograms labeled with corresponding letters. As the fundamental frequencies produced on the right and left diverge in frequency (D and E) the mockingbird’s copy of the sound becomes different spectrally, with less pronounced heterodyne frequencies spectrally. FL and FR, rate of airflow through left and right bronchus, respectively. Airflow associated with positive pressure is expiratory, and that associated with negative pressure is inspiratory. P, pressure in the cranial thoracic air sac; V, oscillogram of vocalization (sound waveform). Horizontal lines indicate ambient pressure or zero air flow.
and left sides are further apart (Fig 1D and E), the beating pattern is not as strong and the spectral similarity declines. This example provides evidence that while nonlinear phenomena increase acoustic complexity, it is not likely that animals can control their occurrence in most cases.

The innovation mockingbirds use to avoid the constraints of their vocal apparatus, such as the example presented in Figure 1, demonstrates the adaptive advantage that vocal learning can give a species. While the evolution of two separate, independently controlled sound sources certainly gives songbirds a huge advantage for increased vocal complexity compared to animals with single sound sources, the results presented in Chapter 3 show that the extent to which the two sources are truly independent is limited in both how similar or different the fundamental frequency can be on the two sides, but also in the amount, direction or rate of frequency modulation each can produce during two-voice song.

The results presented in Chapter 3 also contributed surprising new knowledge to the current understanding of the vocal registers of the right and left sides of the syrinx. In all songbirds heretofore studied, the right and left sides do not contribute equally to song. In every species tested, the right side of the syrinx produces higher frequency sounds than the left, typically with some narrow band of mid-range frequencies in which either side of the syrinx might sing the note. However, when pushed to sing sounds outside the “normal” frequency range on either the right or left side, mockingbirds occasionally produced sounds more than 2 kHz above or below what had been previously observed as the upper or lower limit for that side! Similarly surprising results were found by Dagley, et al. (2005), who chronically denervated one side of the syrinx in northern cardinals during their entire vocal development period. They found that as adults, these cardinals were able to produce the entire frequency bandwidth with either the right or left side alone, that control (sham lesion) birds produced using both sides.

While the Dagley et al. study is still in the preliminary stages of analysis and had a very
small sample size, their finding, in combination with our observation of mockingbirds pushing their vocal ranges beyond what is normal, begs the question: if birds can sing a wider frequency range on either side of the syrinx, why don't they normally do so? One potential hypothesis is that there are consequences for vocalizing at the extremes of the vocal range. Research on human singers and speakers suggest that vocalizing at very low frequencies can result in both physiological costs (increased occurrence of vocal nodes) and also in potential communicative “costs” such as decreased control of pitch, more chaotic and “noisy” components (vocal fry), and decreased sound pressure levels and efficiency (Titze, 1988; Titze, 1994; Verdolini et al., 1999). Likewise, vocalizing at the highest limits of your production system can result in decreased sound pressure levels, vocal fatigue, and significantly increased air consumption (resulting in shorter duration vocal output between breaths) (Titze, 1994; Welham and Maclagan, 2003). Because the communicative potential of birdsong often depends on broadcasting the signal across large distances, and to the largest number of potential mates or rivals, the “costs” of a decrease in sound amplitude could be quite serious. If the fitness of a singer is judged by the acoustic quality of its song, then production decisions that increase potential flaws or reduce the perceived “virtuosity” of the singer will likely be selected against. So while songbirds might be physiologically capable of singing outside their typical vocal ranges, it may simply reduce their success to choose to do so.

Adaptive creativity and plasticity by mockingbirds during song learning and production allows them to circumvent some of the apparent constraints of their vocal production system. The ability for improvisation in vocal learners, in a broader sense, would allow an individual to quickly respond to dynamically changing environmental and social situations. This benefit is surely one of the selective forces driving the evolution of mimetic vocal learning in social animals. Humans, like songbirds, rely on a highly evolved integrated system of auditory, sensorimotor, visual, behavioral and somatosensory feedback to finely tune their vocalizations to maximize their effectiveness.
as communication signals. Because of the talent for vocal imitative learning that mockingbirds and humans share, an increased understanding of the sources of vocal complexity and diversity as well as performance and learning constraints in mockingbirds can enlighten our understanding of the evolutionary and developmental processes that shape and limit human speech.


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Teaching Experience
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L313, Cell Biology Laboratory
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Publications

Papers presented at scientific meetings

Invited Talks

Symposia Presentations


Academic Service
Indiana University Animal Behavior Conference Co-Chair. Indiana University, Bloomington IN. Helped organize the 2003, 2004 and 2005 IU Animal Behavior Conference hosted by the Center for the Integrative Study of Animal Behavior. Duties included arranging conference accommodations, catering, speakers and poster session schedules, inviting participants, publicity, keynote speaker's schedule and conference audio-visual set-up.

Steering Committee Student Representative. Center for the Integrative Study of Animal Behavior (CISAB), 2004-2005. As the student representative to the CISAB steering committee, I helped make decisions on funding, changes to curricula, invited seminar speakers, acted as a liaison between the graduate student members of CISAB and its faculty, and participated in setting yearly goals and voted on induction of new faculty members to the center.

Judge, Von Humboldt Public School, Chicago IL, 2004. Volunteered to judge 6th grade science projects for the Von Humboldt Public School Science Fair. As a judge, I interviewed students, assessed and scored each project for scientific merit and presentation quality.

Graduate recruitment weekend committee member. Department of Biology, Indiana University, Between 2000 and 2006, I served on various committees to organize and run the annual graduate recruitment weekend for the Department of Biology. I have been responsible for planning transportation of prospective students, planning and conducting tours of CISAB and Biology facilities, arranging accommodations and group activities for prospective students.

Scientific Organization Affiliations:
Society for Neuroscience
International Society for Neuroethology
Acoustical Society of America
National Association of Science Writers