

Two-voice complexity from a single side of the syrinx in northern mockingbird *Mimus polyglottos* vocalizations

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SUMMARY

The diverse vocal signals of songbirds are produced by highly coordinated motor patterns of syringeal and respiratory muscles. These muscles control separate sound generators on the right and left side of the duplex vocal organ, the syrinx. Whereas most song is under active neural control, there has been a growing interest in a different class of nonlinear vocalizations consisting of frequency jumps, subharmonics, biphonation and deterministic chaos that are also present in the vocal repertoires of many vertebrates, including many birds. These nonlinear phenomena may not require active neural control, depending instead on the intrinsic nonlinear dynamics of the oscillators housed within each side of the syrinx. This study investigates the occurrence of these phenomena in the vocalizations of intact northern mockingbirds *Mimus polyglottos*. By monitoring respiratory pressure and airflow on each side of the syrinx, we provide the first analysis of the contribution made by each side of the syrinx to the production of nonlinear phenomena and are able to reliably discriminate two-voice vocalizations from potentially similar appearing, unilaterally produced, nonlinear events. We present the first evidence of syringeal lateralization of nonlinear dynamics during bilaterally produced chaotic calls. The occurrence of unilateral nonlinear events was not consistently correlated with fluctuations in air sac pressure or the rate of syringeal airflow. Our data support previous hypotheses for mechanical and acoustic coupling between the two sides of the syrinx. These results help lay a foundation upon which to understand the communicative functions of nonlinear phenomena.

Key words: birdsong, mockingbird, nonlinear phenomena, song learning, vocal production.

INTRODUCTION

One of the fascinating aspects of songbirds is the diversity and complexity of their vocal signals. Two well-documented functions of birdsong are territory defense and mate attraction, and there is increasing evidence that natural and sexual selection may favour increased vocal complexity (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 (e.g. Ballentine et al., 2004; Forstmeier et al., 2002; Vallet et al., 1998). The ability for vocal learning and the production of increasingly complex vocal signals may have facilitated the radiation of the songbirds (oscine Passeriformes) into the largest and most diverse order of birds (Fitzpatrick, 1988; Vermeij, 1988), but its role in speciation is controversial (Baptista and Trail, 1992; Raikow, 1986).

Understanding the vocal mechanisms responsible for the spectral and temporal complexity of bird song can provide a valuable insight into the performance constraints and evolution of song diversity. A major source of acoustic complexity in songbirds comes from the versatility of motor control of their duplex vocal organ, but in some species the intrinsic biomechanical properties of the vibratory sound generating structures in the vocal organ may also contribute significantly to song complexity. In this paper, we attempt to assess the contribution each of these sources makes to the vocal diversity of song by the northern mockingbird.

Sources of acoustic complexity

The bipartite syrinx

The songbird's vocal organ, the syrinx, is composed of modified cartilages at the cranial end of each primary bronchus and the caudal end of the trachea. Each bronchus contains a pair of fleshy pads, the medial and lateral labia (King, 1989), which vibrate when adducted into the respiratory airflow (Goller and Larsen, 2002) and provide the bird with two independently controlled sound sources, one in each bronchus (Suthers, 1990). The acoustic properties of song generated by each pair of labia are controlled by the activity of ipsilateral syringeal muscles innervated by the tracheosyringeal branch of the hypoglossal nerve (Goller and Suthers, 1996a; Goller and Suthers, 1996b).

Spectrographic analyses of birdsong (Borror and Reese, 1956; Greenewalt, 1968; Stein, 1968; Thorpe, 1961) revealed the presence in many species of two, simultaneous non-harmonically related frequencies. Greenewalt (Greenewalt, 1968) referred to these as 'two-voice' phenomena and hypothesized the voices originated on opposite sides of the syrinx, a view supported by subsequent experiments showing varying degrees of song lateralization following unilateral section of the tracheosyringeal branch of the hypoglossal nerve (Floody and Arnold, 1997; Lemon, 1973; Nottebohm, 1971; Nottebohm and Nottebohm, 1976; Suthers, 1990; Suthers et al., 2004; Williams et al., 1992).

A more detailed understanding of the acoustic contribution each sound source makes to oscine song has come from techniques for

recording airflow through each side of the syrinx, together with syringeal and respiratory motor activity during spontaneous song with both sides of the syrinx intact (Suthers, 1990). These data show that songbirds exploit their dual sound source to increase vocal virtuosity in multiple ways, including the production of two-voice elements, switching phonation between sides to produce abrupt frequency steps between notes and taking advantage of lateralized functional specializations in the acoustic properties of each sound source (reviewed in Suthers, 1999; Suthers and Goller, 1997; Suthers and Zollinger, 2004).

Syringeal nonlinear dynamics

In addition to vocal production by coordinated neuromuscular control of the syrinx and respiratory system, there is evidence that intrinsic, passive, biomechanical properties of syrinx, particularly the dynamic vibratory properties of the paired oscillators (the medial and lateral labia) comprising each sound source, can also result in the production of complex sounds (Fee, 2002; Fee et al., 1998; Mindlin and Laje, 2005). Recent experiments have demonstrated that the labia, much like the vocal folds in the mammalian larynx (Berry et al., 1996; Herzel et al., 1994), comprise a nonlinear physical system (Fee, 2002; Fee et al., 1998). 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. In addition to the NLP recorded from excised syrinxes of zebra finches (Fee et al., 1998), NLP have been identified in the natural vocalizations of a diverse set of species, including non-songbirds such as doves (Beckers and ten Cate, 2006) and parrots (Fletcher, 2000), frogs (Suthers et al., 2006), terrestrial and marine mammals (Herzel et al., 1995; Riede et al., 2007; Riede et al., 2000; Riede et al., 2004; Riede et al., 1997; Titze et al., 1993; Tokuda et al., 2002; Tyson et al., 2007; Wilden et al., 1998).

Identifying the source of acoustic complexity in a two-voice vocal system

Because their vocal organ contains two independent sound sources, spectrographic analyses alone in songbirds cannot always reliably distinguish between two voices and some kinds of NLP. Frequency jumps produced by rapidly switching phonation from one side of the syrinx to the other (see Allan and Suthers, 1994) may be indistinguishable from frequency jumps resulting from bifurcations due to the nonlinear dynamics of a single pair of oscillators.

In mammals, biphonation is traditionally defined as the simultaneous appearance of two independent frequencies (Berry et al., 1996; Wilden et al., 1998). The same definition was applied by Greenewalt (Greenewalt, 1968) to describe standard two-voice phenomena in songbirds, but it is now clear that though both examples contain simultaneous harmonically unrelated frequencies, their physical basis is quite different. In two-voice phenomena each voice is generated by a separate set of paired oscillators whereas in biphonation harmonically unrelated frequencies are generated by the nonlinear properties of a single set of oscillators (Suthers et al., 2005).

Additional problems in discerning NLP from two-voice phenomena based solely on emitted vocalizations were described by Laje, Mindlin and colleagues (Laje and Mindlin, 2005; Laje et al., 2008), whose models of source–source and source–tract interactions in the oscine syrinx demonstrate 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. Their 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 acoustic interactions within the syrinx and trachea of sounds produced on the two sides.

Here we investigate the occurrence of the nonlinear characteristics in spontaneous song of the northern mockingbird, a vocal mimic. By monitoring subsyringeal pressure and airflow through each side of the syrinx we can determine if these nonlinear features are lateralized to one side of the syrinx or produced bilaterally and distinguish them from superficially similar two-voice vocalizations, in order to more accurately estimate their contribution to song complexity.

MATERIALS AND 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, USA). Subjects were four adult (1–3 year old) male northern mockingbirds *Mimus polyglottos* L. 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 replicate certain distinctive acoustic features of different song types (Table 1). Because mockingbirds are vocal mimics, the individual repertoires of each bird were dominated by mimicries of some subset of the tutor syllables they had heard. The repertoires of the birds in this study varied seasonally but contained between ~90 and 120 syllable types at the time of the experiment. Tutor sounds were chosen or designed for an experiment on song production [tutoring details are given elsewhere (Zollinger and Suthers, 2004)]. 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. Sounds containing two independent frequencies were of two general types. The first type consisted of two distinct tones (between 1 and 7 kHz) with independent rates of frequency modulation (FM), e.g. Fig. 1A. The second type consisted of a single high fundamental frequency f_0 accompanied by a lower (<750 Hz) modulating frequency (m_0), resulting in a periodic amplitude modulation (AM) of the waveform with sidebands (e.g. Fig. 1B). 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 *Cardinalis cardinalis*, eastern towhees *Pipilo erythrophthalmus*, zebra finches *Taeniopygia guttata* and ring doves *Streptopelia risoria* that were housed in adjacent rooms in the laboratory, therefore we cannot rule out the possibility that mockingbirds heard NLP that may have been present in the songs of these other species.

Surgery and data acquisition

Birds were anesthetized by injection of chloropent (4.1 $\mu\text{l g}^{-1}$ body mass; recipe from Fort Dodge Animal Health,

Table 1. Tutor regimes for four mockingbirds in this study

Bird ID	Sound type ^a	Tutor type ^b		
		Recordings ^c	Live ^c	Synthesized ^d
m108	1 _f ₀	NOMO, WOTH	NOCA	FM CF
	FJ	WOTH tone pairs ^e	—	CF tone pairs
	2 _f ₀ -SB	NOMO	—	AM
	2 _f ₀ -other	NOMO, WOTH	—	FM 'two-voice'
m123	1 _f ₀	NOCA, BRCO, canary	NOCA	—
	FJ	BRCO tone pairs	—	—
	2 _f ₀ -SB	EATO	—	—
	2 _f ₀ -other	—	—	—
m130	1 _f ₀	NOMO, NOCA, canary, WOTH	NOCA	FM CF
	FJ	WOTH tone pairs	—	CF tone pairs
	2 _f ₀ -SB	EATO	—	AM
	2 _f ₀ -other	NOMO, WOTH	—	FM 'two-voice'
m152	1 _f ₀	NOMO, NOCA, canary, WOTH, WAVI	NOCA	FM CF
	FJ	BLJA, WOTH and HETH tone pairs	—	CF tone pairs
	2 _f ₀ -SB	EATO	—	AM
	2 _f ₀ -other	NOMO, WOTH	—	FM 'two-voice'

^a1_f₀, single f_0 varying over time (may be pure-tonal or include upper harmonics); FJ, tutor sound contains an abrupt jump up or down in frequency; 2_f₀-SB, sound that contains prominent sidebands above and below a f_0 , visible in a narrowband spectrogram, corresponding to a second, modulating frequency (m_0); 2_f₀-other, sounds that contain two independent fundamental frequencies, in any other combination than the sideband relationship described above (such as two-voice phenomena).

^b'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.

^cRecorded and Live tutor species, with the exception of 'canary' (Waterschlager canary *Serinus canarius*), are listed by standard American Ornithological Union 4-letter abbreviations as follows: NOMO, northern mockingbird (*Mimus polyglottos*); WOTH, wood thrush (*Hylocichla mustelina*); NOCA, northern cardinal (*Cardinalis cardinalis*); BRCO, brown-headed cowbird (*Molothrus ater*); EATO, eastern towhee (*Pipilo erythrophthalmus*); WAVI, warbling vireo (*Vireo gilvus*); BLJA, blue jay (*Cyanocitta cristata*); HETH, hermit thrush (*Catharus guttatus*).

^dFM, 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.

^e'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 non-linear dynamics.

Overland Park, KS, USA) into the pectoral muscle. A silastic cannula (Dow Corning Corp, Midland, MI, USA; i.d. 1.02 mm, o.d. 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, USA) 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, USA, 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. Surgical methods are described in more detail elsewhere (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 Engineering, Ellettsville, IN, USA) and a multi-channel digital data recorder (Metrum DataTape RSR512, Littleton, CO, USA). Four signals (vocalization, rate of airflow through the right and left bronchi, and

air sac pressure) were recorded digitally (40 000 samples s⁻¹ channel⁻¹) onto separate tracks on S-VHS 1/2" magnetic tape cassettes (Maxell ST-31BQ SVHS, Fair Lawn, NJ, USA) using the Metrum recorder. Signals were transferred from tape to microcomputer using a Data Translation board (DT-2821G) and an antialiasing filter (TTE, J87, St Pete Beach, FL, USA; 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, USA) 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 Hanning high-pass filter.

Signals were analyzed using Igor Pro v. 5 (WaveMetrics Inc., Lake Oswego, OR, USA) and Adobe Audition v. 1.5 (Adobe Systems Inc., San Jose, CA, USA). Statistical analysis was conducted using Igor Pro v. 5 and SigmaStat v. 2.03 (SPSS Inc., Chicago, IL, USA). Preoperative song (100–300 min per

bird) was recorded from adult birds (>300 days post-hatching) for comparison with pre- and post-surgery repertoires (Avisoft-Recorder v. 1.7, Avisoft Bioacoustics, Berlin, Germany).

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 (1024 points at 40 000 samples s⁻¹, frame duration 25.6 ms, window duration 75%, Hanning window type) 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 NLP it was counted in each category.

Identifying nonlinear phenomena

Spectrographic evaluation

We examined 1000 syllables each from four subjects for acoustic evidence of NLP (frequency jumps, subharmonics, biphonation or

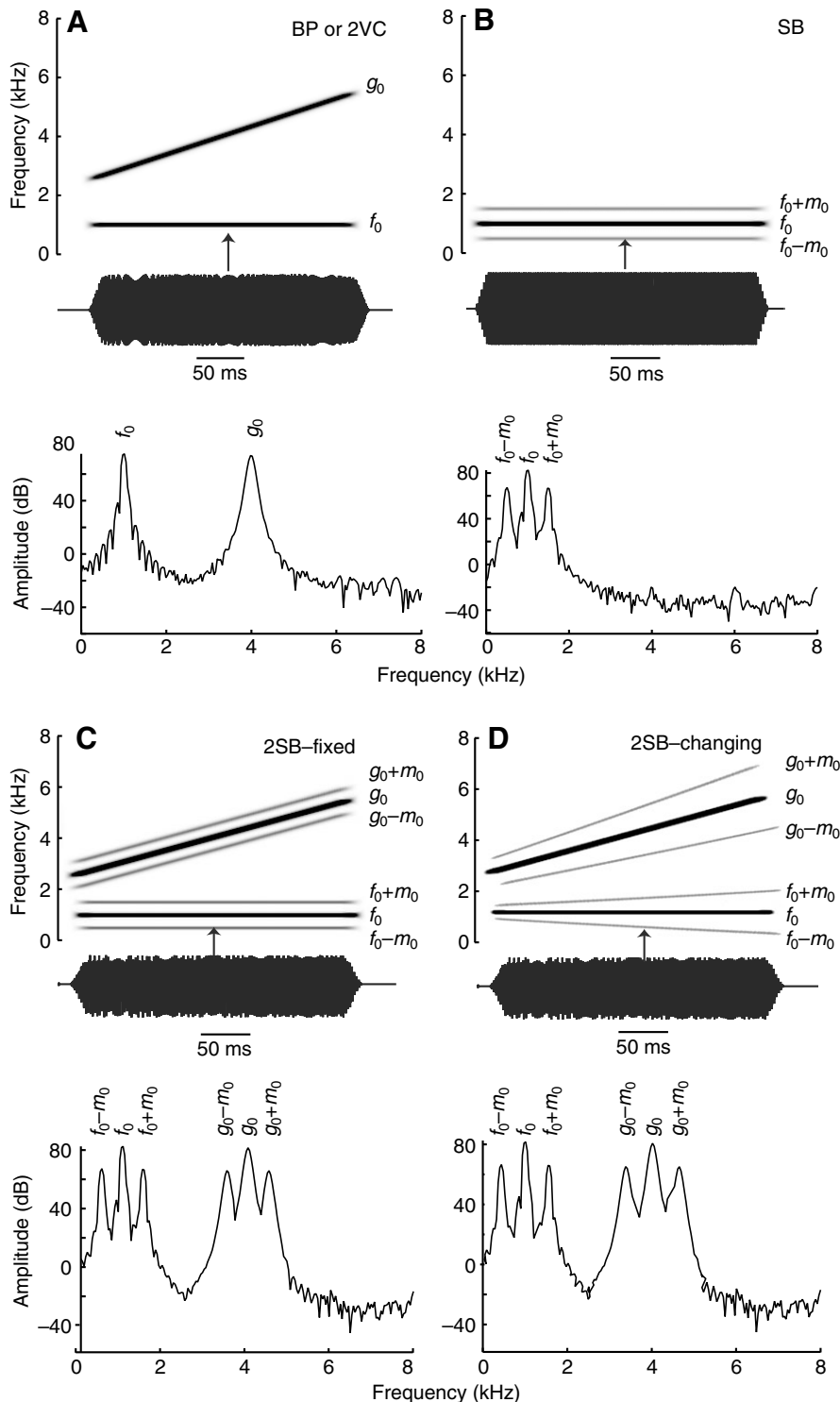


Fig. 1. Synthesized examples illustrating four types of biphonation and two-voice phenomena observed in mockingbird songs. (A) The spectrogram (top) and spectrum (bottom) illustrate the spectral properties typical of both 'type A' biphonation and two-voice phenomena, consisting of two independent frequencies, f_0 and g_0 . (B) 'Type B' biphonation consists of a fundamental frequency and sidebands. In this synthesized example, f_0 is a 1 kHz tone. The second frequency is a 250 Hz modulation frequency, m_0 , which appears spectrographically as sound energy 250 Hz above and below f_0 . (C) A synthesized example of 'dual biphonation' similar to the type observed in mockingbird vocalizations. Each side of the syrinx produces 'type B' biphonation simultaneously. In this example, two unrelated fundamental frequencies (f_0 and g_0), originate from opposite sides of the syrinx. The two 'voices' are each modulated by an unrelated, lower modulating frequency (250 Hz, m_0). (D) A synthesized example of 'dual biphonation' similar to C, but in this case m_0 is also frequency modulated, resulting in sidebands that are not parallel to f_0 or g_0 . BP, biphonation; 2VC, two-voice phenomena; SB, sidebands; 2SB, dual biphonation (two f_0 values, each with sidebands).

deterministic chaos). This initial sorting of sounds by visual spectrographic examination is not sufficient to determine the mechanism of production, but was done to identify potential NLP for further investigation.

Frequency jumps are sudden changes in fundamental frequency (f_0) to a higher or lower f_0 (Fig. 2A). A frequency jump was defined as a visible, instantaneous (<5 ms silent interval between adjacent frequencies, as measured from the time waveform) step-change in f_0 .

Subharmonics (Fig. 2B) are additional spectral components at integer fractional values of f_0 (e.g. $0.5f_0$, $0.33f_0$, etc.). They appear at evenly spaced intervals below f_0 and between adjacent harmonics throughout the frequency spectrum.

Deterministic chaos (low-dimensional noise) is technically distinguishable from stochastic noise (high-dimensional chaos) 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 (Wilden et al.,

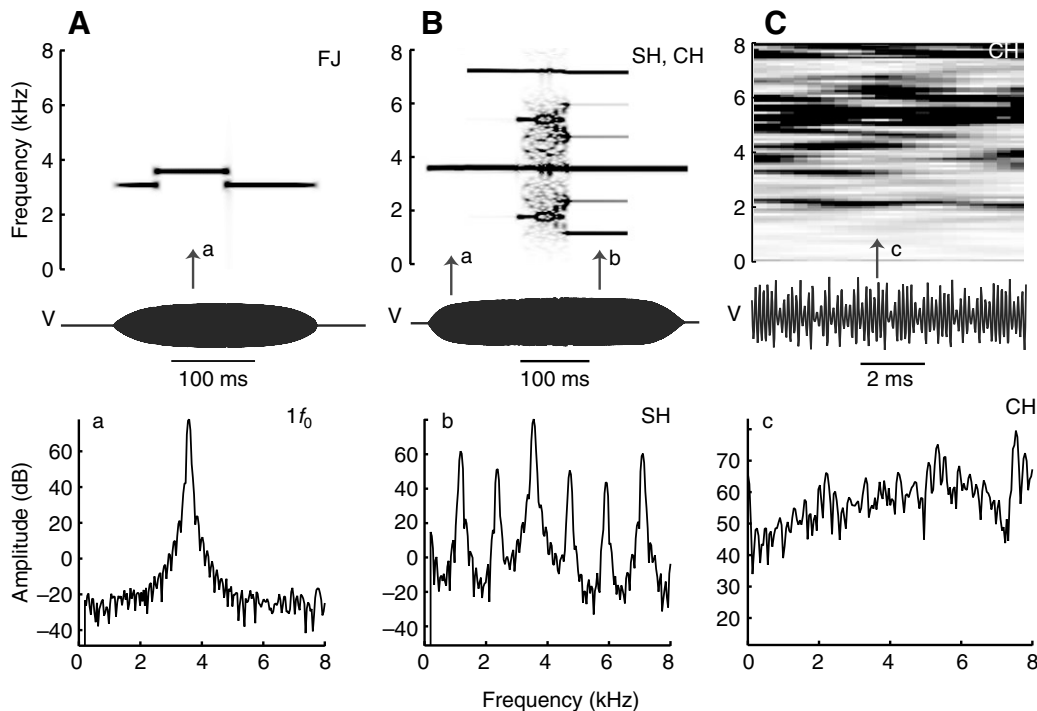


Fig. 2. Spectral properties typical of three types of nonlinear phenomena; frequency jumps, subharmonics and deterministic chaos. (A) A 3500 Hz tone with two 250 Hz frequency jumps. A power spectrum (a) taken at arrow a shows a single peak of sound energy corresponding to f_0 . (B) A 3750 Hz tone, with a series of bifurcations, the first from a single f_0 to a $0.5f_0$ subharmonic regime, then an abrupt transition to deterministic chaos, and then to a $0.33f_0$ subharmonic regime. Comparing spectra a and b illustrates the increase in spectral complexity resulting from the addition of subharmonic values and their harmonics (b in B). (C) A 10 ms section of deterministic chaos (in this case, a low-dimensional noise, generated using a Rossler attractor equation). The aperiodicity of the sound waveform (V) and the sound energy fairly evenly distributed across the entire spectrum (spectrogram C, and power spectrum, c) are indicators used to identify potential chaos in mockingbird songs. Abbreviations as in Tables 1 and 2; FJ, frequency jump; SH, subharmonics; CH, deterministic chaos; $1f_0$, single frequency sounds; V, amplitude of sound waveform.

1998), including preceding subharmonics (e.g. Fig. 2B) and the presence of harmonic 'windows' in otherwise noisy segments. We classified sounds as 'deterministic chaos' if we observed a broadband, noisy segment in the spectrogram (Fig. 2C), plus at least two additional indications, such as a sudden onset of the noise, preceding subharmonics or harmonic windows within the noise.

Biphonation refers to the occurrence of two simultaneous but independent fundamentals that are generated by a single sound source (e.g. one pair of vibrating tissues). We include 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. 1A). In the second type, we observe a primary fundamental frequency (f_0) and an additional, much lower, modulating frequency (m_0). Spectrographically, this type of biphonation is characterized by sidebands that are above and below f_0 and its harmonics (Fig. 1B). 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 or 'dual biphonation' (biphonation produced by both 'voices' simultaneously) 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. 1C,D).

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 25 μ s. 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 and rate of airflow through the syrinx were normalized to a percentage of maximum flow rate or pressure. The normalized pressure or rate was then regressed against distance (time) to the point of bifurcation. Slopes of these regression lines were tested for differences in variance between groups using SigmaStat 3.11 (Systat Software Inc., San Jose, CA, USA). 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 or 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

Table 2. Number of nonlinear phenomena, two-voice phenomena and harmonic vocalizations present in the vocal repertoires of the mockingbirds in this study^a

(A)		Unilateral flow classification categories ^c				
Bird ID	Repertoire size ^b	1 _f ₀	FJ	SH	CH	BP
m108	121	171	8	4	34	12
m123	60	258	12	10	5	16
m130	73	166	15	18	8	31
m152	102	309	13	18	21	113
Mean ± s.d.	89±27.63	226±69.62	12±2.94	12.5±6.81	17±13.29	43±47.38

(B)		Bilateral flow classification categories ^d						
Bird ID	1 _f ₀	FJ	SH	CH	SB-2VC	2SB-fixed	2SB-changing	2VC
m108	38	33	30	29	28	26	64	566
m123	2	30	9	45	35	13	21	536
m130	0	68	75	59	96	113	38	666
m152	13	65	10	132	40	6	2	297
Mean ± s.d.	13.3±17.46	49±20.28	31±30.89	66.25±45.51	49.75±31.22	39.5±49.70	31.25±26.32	516.25±156.38

^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 (1_f₀ 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. 1_f₀, single *f*₀ 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); since there was flow through both sides of the syrinx during these sounds, we did not classify them as NLP; 2SB-fixed, two *f*₀, each with sidebands with a constant modulation frequency (parallel to *f*₀); 2SB-changing, two *f*₀, each with sidebands with a changing modulation frequency (not parallel to *f*₀); 2VC, two-voice phenomena (each side of the syrinx producing a distinct, unrelated *f*₀).

chaos and biphonation, were observed in 8.5% of syllables analyzed across individuals (1000 syllables each from four birds, individually: m108, 5.8%; m123, 4.3%; m130, 7.2%; m152, 16.5%) (Table 2). 'Unilaterally produced' means that there was 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 jumps ranged from ~45 to 450 Hz. Jumps from both 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 could spectrographically resemble frequency jumps resulting from nonlinear dynamics; however, these large steps in frequency (~500–4500 Hz) were always produced bilaterally, by alternating phonation between the two sides of the syrinx, rather than unilaterally (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 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, slope -0.28 ± 2.773 (mean ± s.d.), 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 (s.d.), 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 the slope of the rate of airflow occurred immediately before a frequency jump more often than at times during the same syllable 25 ms before or after the jump. 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 the absolute magnitude or in an increase or decrease in flow rate. Jumps were observed concurrently with increases, decreases or no detectable change in the 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

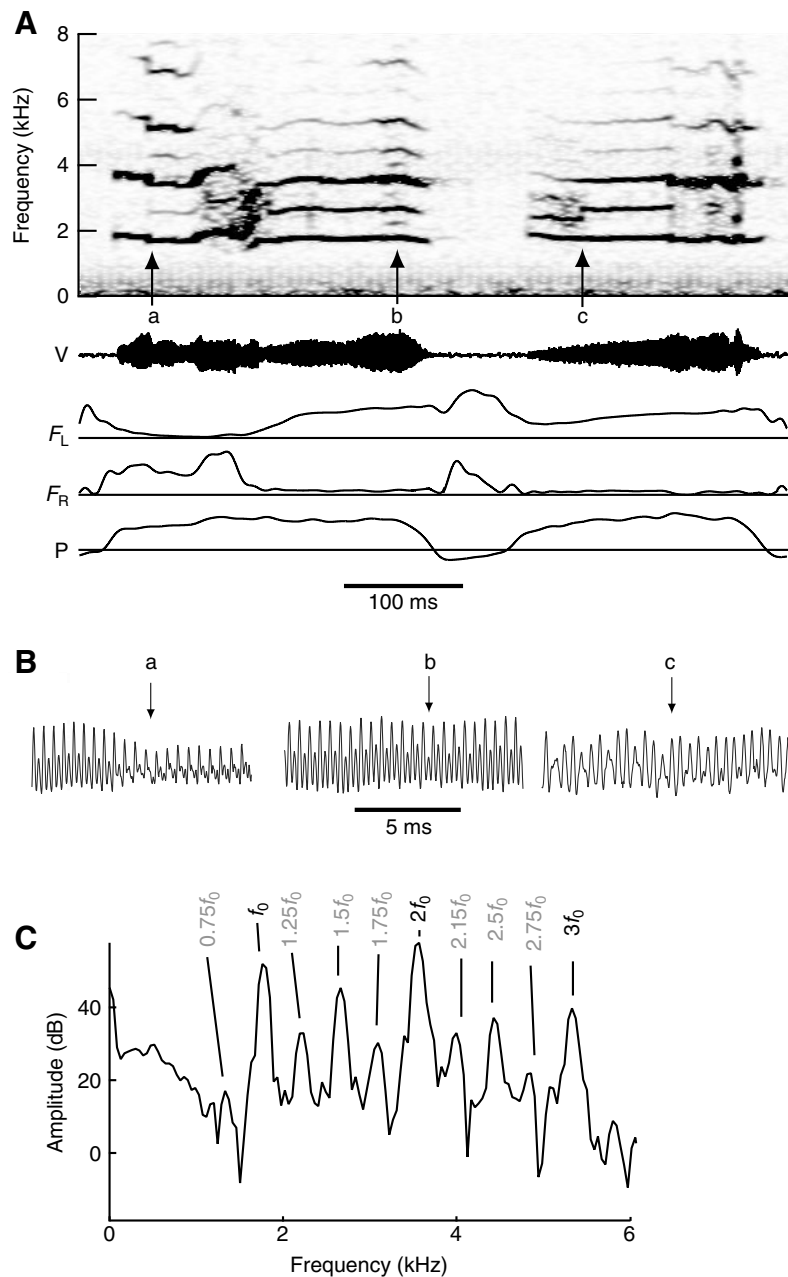


Fig. 3. Examples of frequency jumps and subharmonics in mockingbird song (bird m123). (A) Frequency jumps occurred with airflow through only the right (arrow a) or left (arrow c) side of the syrinx. Arrow b indicates a shift from a $0.5f_0$ to $0.25f_0$ subharmonic regime. Arrow c indicates a shift between a $0.33f_0$ and $0.5f_0$ subharmonic regime.

(B) Expanded views of the sound waveform at each arrow in spectrogram (A), showing the abrupt changes in oscillation patterns at bifurcation points. (C) Power spectrum taken at arrow b, showing spectral peaks at f_0 and its harmonics ($2f_0$, $3f_0$, etc.), as well as at fractional integer values corresponding with a $0.25f_0$ subharmonic, and its harmonics. F_L and F_R , 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 in (A) indicate ambient pressure or zero airflow.

following chaotic regimes (Fig. 5). We found subharmonics in the $f_0/2$ mode (Fig. 3, arrow a, and Fig. 5), with subharmonic frequency bands occurring at $0.5f_0$, $1.5f_0$, $2.5f_0$, etc. and also in the $0.33f_0$ and $0.25f_0$ mode (Fig. 3, arrows c and b, respectively). The example in Fig. 3 shows shifts between three different subharmonic modes within two syllables. In the $0.5f_0$ mode (immediately to the right of arrow a, Fig. 3), the fundamental frequency is 1720 Hz, with subharmonics at 860 Hz ($0.5f_0$), 2580 Hz ($1.5f_0$), 4300 Hz ($2.5f_0$). Another period doubling (Fig. 3, arrow b), produces subharmonics in the $0.25f_0$ mode, with the fundamental frequency at 1763 Hz, and subharmonics visible at 2203 Hz ($1.2f_0$), 2645 Hz ($1.5f_0$), 3085 Hz ($1.75f_0$), etc.

Physiology and production of subharmonics

The occurrence of subharmonics in mockingbird song did not correlate with predictable changes in rates of bronchial airflow or pressure (Fig. 4B). Rates of airflow were not significantly different,

either in their mean or variance, just prior to the onset of subharmonics, from these values 5 ms after onset or 25 ms prior to onset, (25 ms prior, mean 0.33 ± 0.929 s.d., variance 0.86; 5 ms prior, mean 0.79 ± 1.287 s.d., variance 1.66; 5 ms post, mean 0.41 ± 0.736 s.d., variance 0.54). Differences between groups were not significant (one-way ANOVA, d.f.=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. Whereas 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).

Biphonation and two-voice phenomena

Occurrences of biphonation and two-voice phenomena

The simultaneous presence of two or more independent frequencies was very common in the acoustic signals of these mockingbirds (68.0% of all syllables; individually: m108, 69.6%; m123, 62.1%;

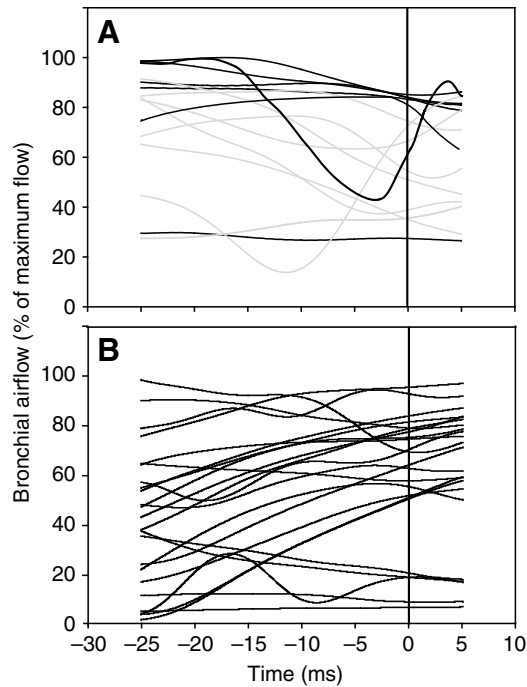


Fig. 4. Normalized rates of bronchial airflow 25 ms before to 5 ms after a frequency jump (A) or the onset of subharmonics (B). Bifurcations occurred at time 0. Slopes of linear regressions over three different 5 ms periods were measured (25–20 ms before, 5–0 ms before, and 0–5 ms after bifurcation points, indicated by vertical lines). (A) Rates of bronchial airflow 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, $P = 0.21$).

m130, 94.4%; m152, 45.8%). Sounds containing two independent frequencies were often produced during bilateral vocalization indicated by simultaneous airflow through both sides of the syrinx (63.7% of total syllables, 93.7% of sounds with ≥ 2 independent frequencies), and therefore meet the traditional definition of two-voice phenomena. When a single f_0 with sidebands was observed concurrent with bilateral airflow, we did not count these as NLP since the contribution of the two voices to the sound was not clear (Table 2, SB-2VC column).

Mockingbirds also produced biphonic sounds, i.e. two harmonically unrelated sounds using one side of the syrinx, the other side being closed (4.3% of total syllables, 6.3% of sounds with ≥ 2 independent frequencies). We found unilateral biphonation of both types illustrated in the synthesized examples (Fig. 1A,B). Examples of 'type A' biphonation (Fig. 6) were less common than 'type B'

biphonation (Fig. 7, arrow a), but both were observed in mockingbird vocalizations.

Since oscines have two theoretically independent sound sources (a pair of vibratory tissues within each side of the syrinx) we looked for examples of two simultaneous biphonic sounds, or 'dual biphonation' such as illustrated in Fig. 1C,D. Mockingbirds did produce dual biphonation, or two-voice syllables in which each 'voice' was biphonic (Fig. 7, arrow b and Fig. 8). Type B 'dual biphonation' (e.g. each side producing a different biphonic sound, each consisting of a fundamental frequency and an independent modulating frequency) represented between 0.8 and 15.1% of syllables examined per bird ($7.1 \pm 6.35\%$, mean \pm s.d.). Interestingly, in every case of bilateral biphonation, the modulating frequency (m_0) of the two voices was the same for both right- and left-produced carrier frequencies (i.e. voices), even when m_0 was itself frequency

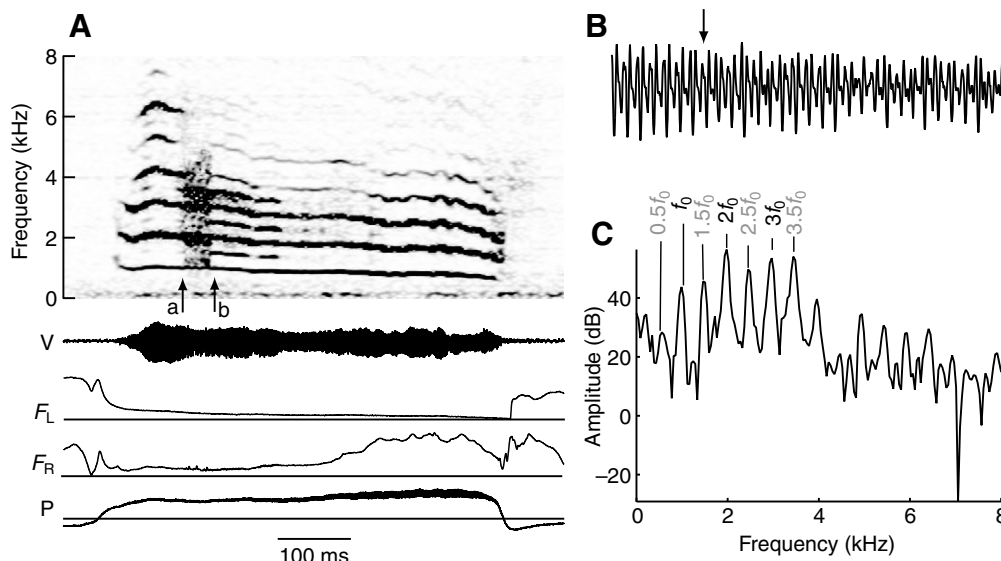


Fig. 5. Unilaterally produced subharmonics and deterministic chaos (mockingbird m152). (A) Arrows indicate abrupt transitions from a harmonic vocalization to a chaotic sound. The chaotic region is followed by a period of subharmonics (arrow b) after which the vocalization returns to a periodic state. (B) A 25 ms segment of the sound waveform. The arrow indicates an abrupt transition from a periodic to aperiodic oscillation. (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. 3.

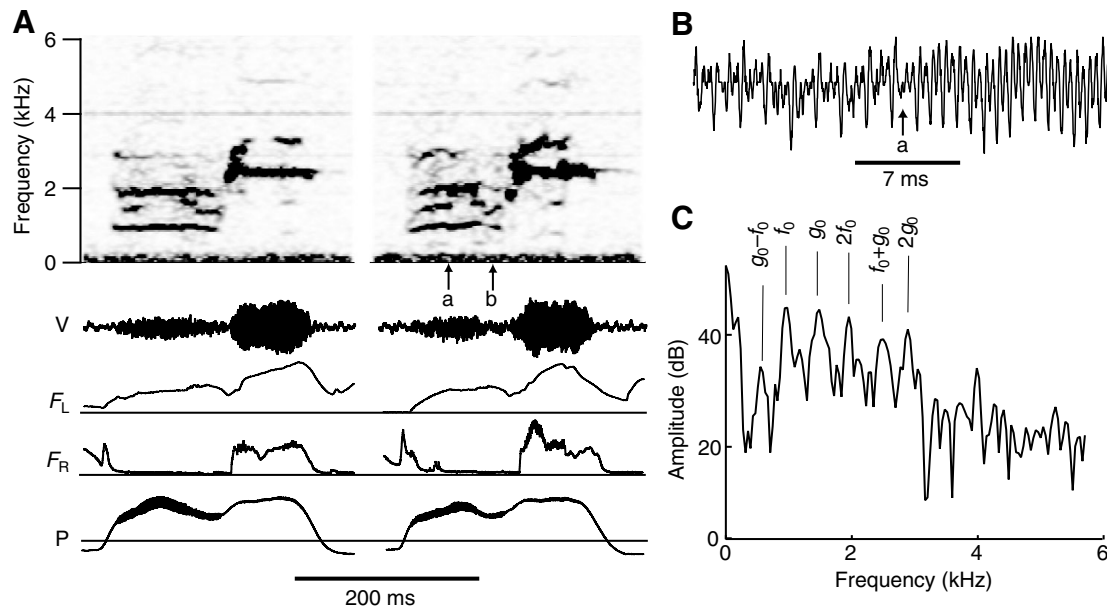


Fig. 6. Unilateral biphonation in two syllables produced by mockingbird m130. (A) Two independent frequencies produced by a single side of the syrinx. Arrows a and b indicate biphonic sounds concurrent with airflow through only the left side of the syrinx. Similar, but less dramatic, biphonation events also occur during the first syllable in A. 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. 3.

modulated. We did not find any examples of simultaneous bilateral production of type A biphonation.

Physiology and production of biphonation and two-voice phenomena

Examples of type A biphonation produced with airflow through only a single side of the syrinx are shown in Fig. 6, arrows a and b. 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 correspond to linear combination products of f_0 and g_0 , as labelled. At arrow a, the lower frequency (f_0) is 990 Hz, and the higher frequency is 1505 Hz.

An example of type B unilateral biphonation is shown in Fig. 7 (first syllable). Across our sample, the modulating frequencies (m_0) in type B biphonation ranged from 57 to 540 Hz. For type B unilateral biphonation, 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 115 Hz above and below f_0 in a power spectrum (Fig. 7C).

Examples of two-voice biphonation are shown in Fig. 7 (second syllable) and Fig. 8. At the start of the second syllable in Fig. 7 the bird opens both sides of the syrinx 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 two-voice syllable is likely the result of beating (sinusoidal oscillations in amplitude resulting from the linear interaction of two similar frequencies). The observed frequency of 550 Hz amplitude modulation is equal to the difference in frequency of $g_0 - f_0$ (2695–2145 Hz in Fig. 7).

In another example of two-voice biphonation (Fig. 8), the two carrier frequencies (f_0 and g_0 ; representing the left and right voice, respectively) are frequency modulated (FM) in opposite directions. During the first 50 ms of the syllable 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 two-voice 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, in all cases of two-voice biphonation, m_0 was always the same on the two sides of the syrinx, even if the FM pattern of f_0 and g_0 were opposite (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 sounds occurred in vocalizations accompanied by unilateral airflow (Fig. 5) as well as those produced during bilateral airflow (Fig. 9). Most examples of 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 aperiodic sounds were also present (1.7% of all syllables sampled for all birds. Individually: m108, 3.4%; m123, 0.5%; m130, 0.8%; m152, 2.1% of syllables sampled). 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 'noisy' segment (e.g. Fig. 9A, arrow b) were commonly observed.

Syringeal lateralization of chaotic sound production

At least three types of unlearned mockingbird calls contain chaotic sounds, including 'loud hews' (Fig. 9), 'soft hews' and 'chat' calls. Male mockingbirds are known to sometimes include calls in their song repertoire (Derrickson and Breitwisch, 1992). During a singing bout mockingbirds may include several repetitions of loud and soft hews and chat calls in addition to the mimicked syllables learned from tutors. Loud hew calls are broadband sounds with an abrupt onset and offset, and a duration of 214–600 ms

(mean = 359.7 ± 110.03 ms, $N=61$). 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 are 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 'loud hew' calls in their song repertoires. We examined the rate of airflow and sound recorded in each bronchus for 67 loud hew calls from the four birds in this study (to increase sample size, we used an additional 50 loud hews that were 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 often appeared to be the result of chaotic oscillations from only a single side of the syrinx.

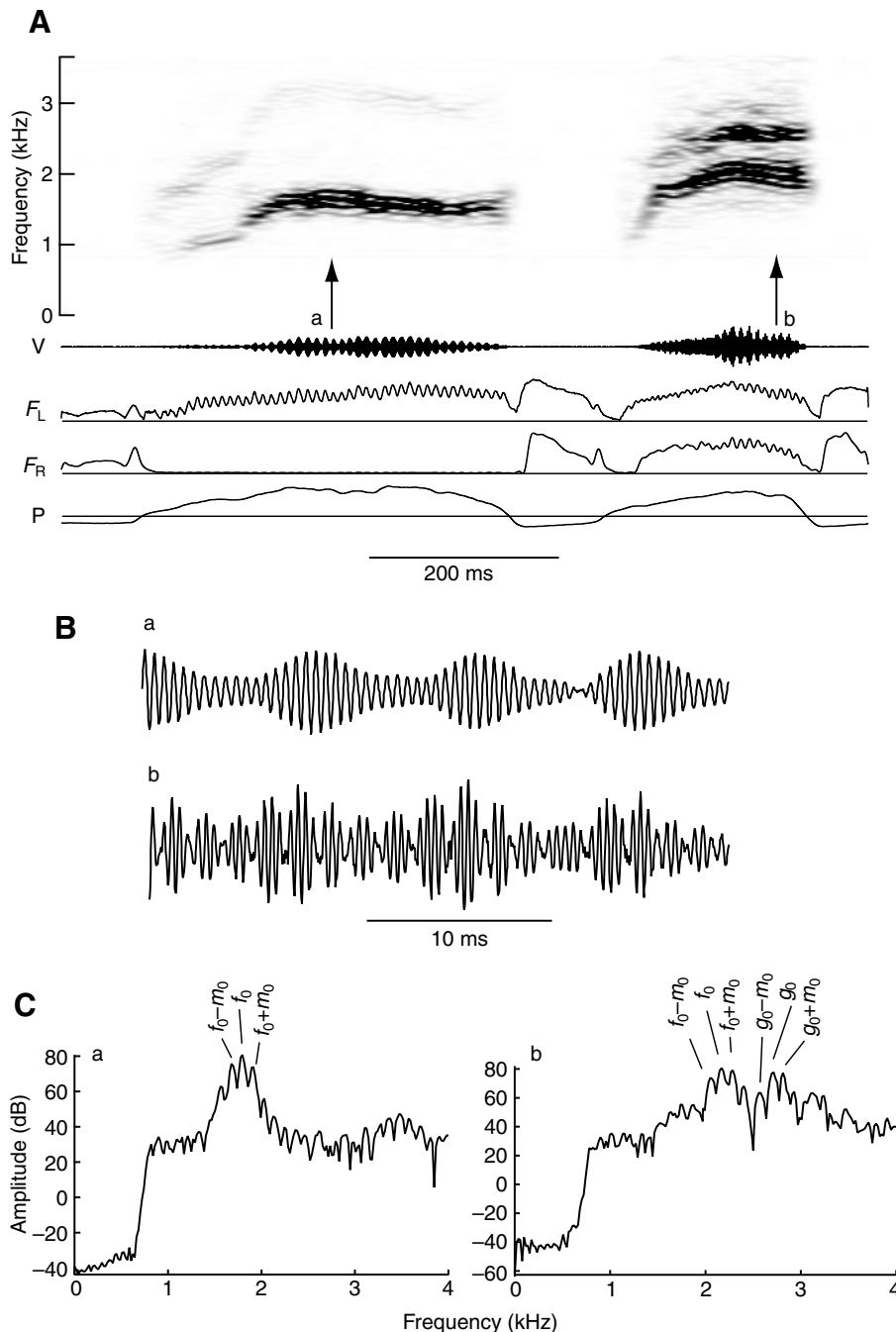


Fig. 7. Unilateral biphonation and 'dual biphonation' in mockingbird song.

(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 ~1800 Hz, and a lower, modulating frequency (m_0) visible as sidebands ~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 . This is a two-voiced syllable in which each voice is biphonic. (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 ~115 Hz (period of one modulation cycle ~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 (A). Sound was filtered with a digital 800 Hz Hanning shape high pass filter. 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. 3.

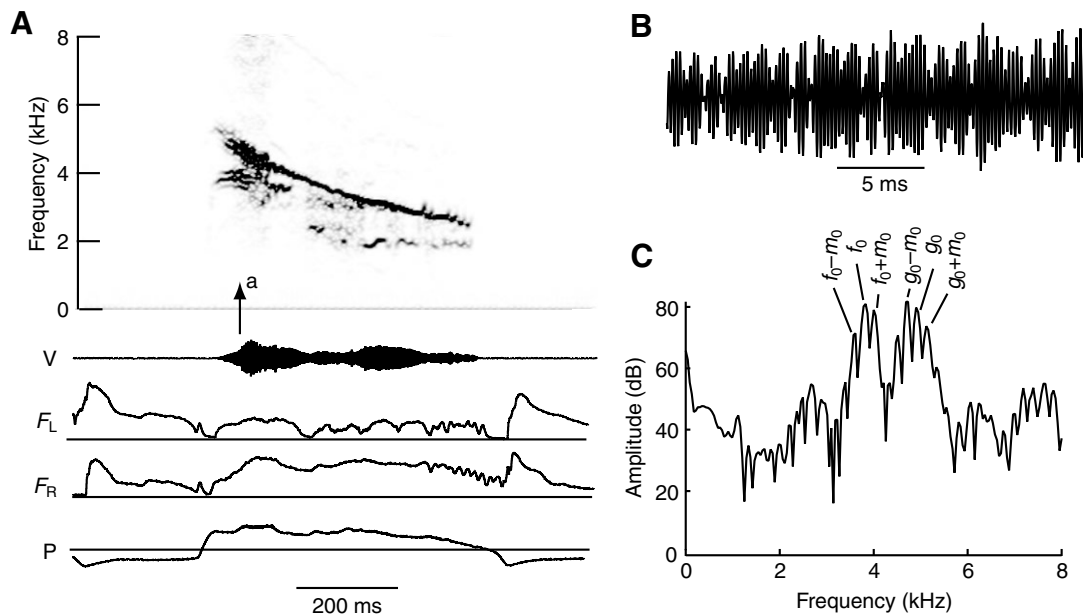


Fig. 8. (A) Dual biphonation (two-voice phenomenon with biphonation in both voices). The sound at the arrow consists of two fundamental frequencies (f_0 and g_0), both simultaneously modulated by a third frequency (m_0). Although f_0 and g_0 are modulated in opposite patterns in the frequency domain (one downsweeping and the other upsweeping in frequency), the rate of amplitude modulation frequency m_0 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. 3.

Fig. 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 contribution 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,B) and their absence in the flow rate on the left side (F_L in Fig. 9A,B) 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 airflow 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 from the bronchial flow signals.

DISCUSSION

Nonlinear phenomena vs two-voice complexity

Excised syrinx experiments predict that the tracheobronchial syrinx should spontaneously produce NLP in vocalizing songbirds (Fee et al., 1998), and NLP have been identified in the natural vocalizations of intact birds with only a single sound source (e.g. a tracheal syrinx), such as parrots and doves (Beckers et al., 2003; Fletcher, 2000; Lavenex, 1999). But in songbirds, the presence of the 'two voices' makes it difficult to identify some kinds of NLP on the basis of vocalizations alone. By recording the 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. This represents only about one-sixth of the sounds

containing apparent biphonation, chaos, frequency jumps 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 primarily on their 'two voices' for the rich diversity of complex sounds in their repertoires. Two-voice complexity may be easier to control than NLP and the availability of two sound sources might reduce the need for birds to rely on NLP, which are potentially less predictable, to increase vocal diversity. Nonetheless, our analysis of the peripheral vocal and respiratory dynamics associated with NLP provides insights into how songbirds might exploit the properties of each of its two sound sources, alone or in combination, to produce or avoid complex sounds. For example, a songbird might produce biphonation simultaneously with both 'voices' resulting in sounds with up to four unrelated frequencies, such as those described by Thorpe (Thorpe, 1961).

We found unilateral biphonation of two types in mockingbird song: as two harmonically unrelated fundamental frequencies, each independently modulated (Fig. 6), and as one f_0 modulated by a second, lower frequency, appearing as sidebands parallel to the f_0 in a narrowband spectrogram (Fig. 7). It is important to note that 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 and 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. $2g_0 - f_0$, $2f_0 - g_0$) (Giovanni et al., 1999; Herzel et al., 1995; Mergell and Herzel, 1997; Neubauer et al., 2001). In such cases, the two vocal folds oscillate at slightly different frequencies, each producing a separate sound pressure wave

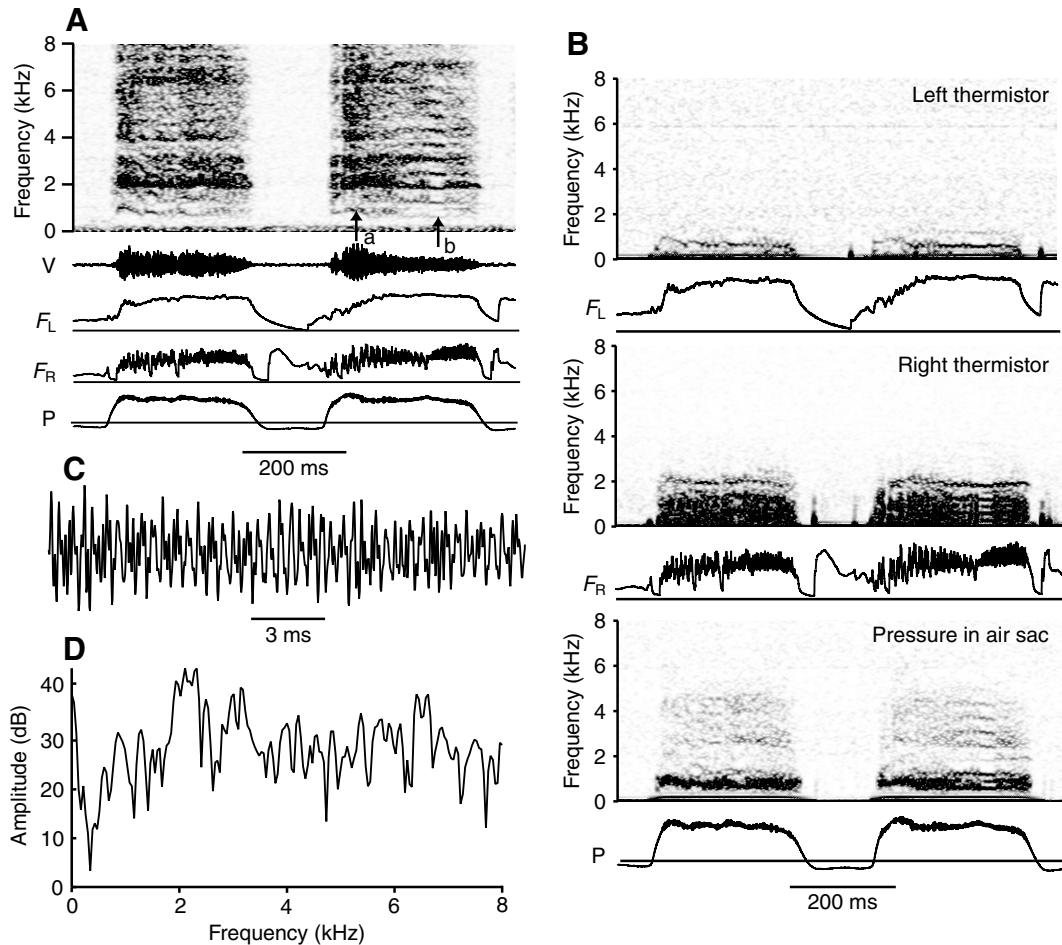


Fig. 9. Unequal contribution of right and left sides to bilaterally produced chaos. Chaotic sounds often contained harmonic windows, or brief moments of periodic oscillation, such as that seen around arrow b. Mockingbird 'loud hew' calls (A) were always produced with flow through both sides of the syrinx for the entire duration of the call. In most cases (56 of 67 calls) one side alone appeared 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 is shown by examination of sound recorded inside the right and left bronchi 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 airflow in the right side (F_R) shows an aperiodic, rapid modulation, which are not present in the flow on the left (F_L). Other abbreviations as in Fig. 3.

that is close to the 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. 1B), or the interaction of two higher tones, which are close in fundamental frequency (Fig. 1A). In either case, neither unilateral biphonation nor dual (two-voice) biphonation, together with their syringeal motor correlates, has been previously described in intact songbirds.

Production and control of nonlinear phenomena

We hypothesize that although production of NLP is a passive biomechanical process, birds may sometimes exert voluntary control over the conditions under which it occurs. However, in other cases NLP might be 'unintentional,' resulting from instabilities of the vocal system. The occurrence of NLP in mammalian vocalizations increases as sound level and frequency increase, suggesting it may be produced by driving the vocal system to its performance limit (Riede et al., 2007) and past threshold points that mark boundaries between stable vibratory modes.

In a zebra finch excised syrinx preparation, it was demonstrated that a linear increase in subsyringeal pressure results in bifurcations between different vibratory modes (Fee et al., 1998). The absence of a consistent relationship between the occurrence of NLP and a detectable increase in rates of bronchial air flow, subsyringeal air sac pressure, or f_0 in our mockingbirds may reflect the availability of respiratory, syringeal and upper vocal tract neuromuscular control in our live birds. Although we did not observe a consistent pattern in the direction or rate of bronchial airflow or in subsyringeal pressure associated with the occurrence of NLP, the fact that frequency jumps were significantly (but not always) correlated with increased variability in the rate of airflow is consistent with the hypothesis that at least some NLP reflects a failure in vocal motor control. Nonlinear theory suggests that even very small changes in control parameters such as subglottal pressure can result in production of NLP. There are many potential control parameters that we did not measure, such as syringeal resistance, the tension of the oscillating labia or the pressure and flow profiles across their surface.

Source–source and source–tract interactions

We found several cases of airflow through both sides of the syrinx generating three independent frequencies (f_0 , g_0 and m_0). Nowicki and Capranica (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 each case of bilateral biphonation the frequency of the amplitude modulation (m_0) was the same for both the left- and right-produced fundamentals supports their hypothesis of source–source coupling in the oscine syrinx.

Possible mechanisms of source–filter and source–source interactions were investigated recently using computational models (Laje and Mindlin, 2005; Laje et al., 2008), which demonstrate that such interactions could indeed produce the complex, multi-frequency sounds observed in birdsong. Laje and Mindlin's results are relevant to our observations, because they demonstrate how sounds, such as subharmonics, previously presumed to be NLP in intact songbirds such as zebra finches (e.g. Fee et al., 1998), could alternatively be the result of acoustic interactions between the two sides. In addition, Nelson (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 an as-yet-unidentified third independent modulator in the syrinx, but further evidence for the identity or existence of such a structure is lacking.

These simulations and models demonstrate that crosstalk between a fundamental frequency and resonance frequencies may affect the vibration of the source. The likelihood of an interaction of sound source and vocal tract filter increases if vocal tract impedance is adjusted to match the impedance of the source (Titze, 2008). A highly variable vocal tract system with complex motor patterns has been demonstrated in songbirds (Fletcher et al., 2006; Riede et al., 2006), and thus one may expect that songbirds, like humans, have a variety of vocal 'tools' at their disposal to avoid or minimize the occurrence of involuntary NLP during song.

Deterministic chaos in calls and song

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 may 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, chaotic vibratory modes are also presumably induced involuntarily at times. Broadband, aperiodic sounds were found within a small number of otherwise pure-tonal song elements. These erratic occurrences of chaos may be more akin to those described in the mammalian literature, which are often attributed to pathologies (Herzel et al., 1994; Mende et al., 1990), instabilities in the vocal system (Mergell et al., 2000), increasing or maximizing frequency or amplitude levels (Berry, 2001; Brown et al., 2003; Riede et al., 2007), or abrupt desynchronization of the vibrating labia (Neubauer et al., 2001). Instances of chaotic sounds within more tonal vocalizations were likely involuntary, as they rarely occurred more than once in the same syllable type from the same bird.

Possible communicative roles of nonlinear phenomena

Several communicative functions of NLP have been hypothesized. For instance, it has been suggested that increased vocal 'roughness' might 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; Fitch et al., 2002; Volodina et al., 2006; Wilden et al., 1998). Additionally, NLP may function to increase the auditory impact of calls (Owren, 2003; Owren and Rendall, 2001), and so could be useful both for attracting allies or mates, as well as for signalling status or physical condition. 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. The extent to which birds use nonlinear phenomena as salient features in vocal communication varies significantly between species. Species differences in the inclusion of NLP in their vocal signals may reflect the need, in part, to achieve an appropriate balance between syllable stereotypy and syllable diversity.

LIST OF ABBREVIATIONS

AM	amplitude modulation
f_0	fundamental frequency
F_L , F_R	air flow rate through left/right side
FM	frequency modulation
g_0	second independent frequency
m_0	modulating frequency
NLP	nonlinear phenomena

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