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Motor mechanisms of a vocal mimic: implications for birdsong production

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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. 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 that they have been exposed to the strongest selective pressure to maximize their performance.

Keywords: motor lateralization; motor constraints; vocal mimicry; mockingbird

1. 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; Suthers 1990, 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 two or three 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 (figure 1*a*). The final whistle is always produced on the right side and includes very high frequencies (Allan & 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 *ca.* 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 programmes have evolved to operate within the limitations of respiratory, as well as syringeal, motor performance. Female preference for longer songs (Eens *et al.* 1993; Kempenaers *et al.* 1997) or faster syllable repetition rates (Vallet *et al.* 1998; Drăgănoiu *et al.* 2002) places 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 & 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 the performance levels 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 & Okanoya 1996; Suthers & Goller 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 *et al.* (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 to be 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

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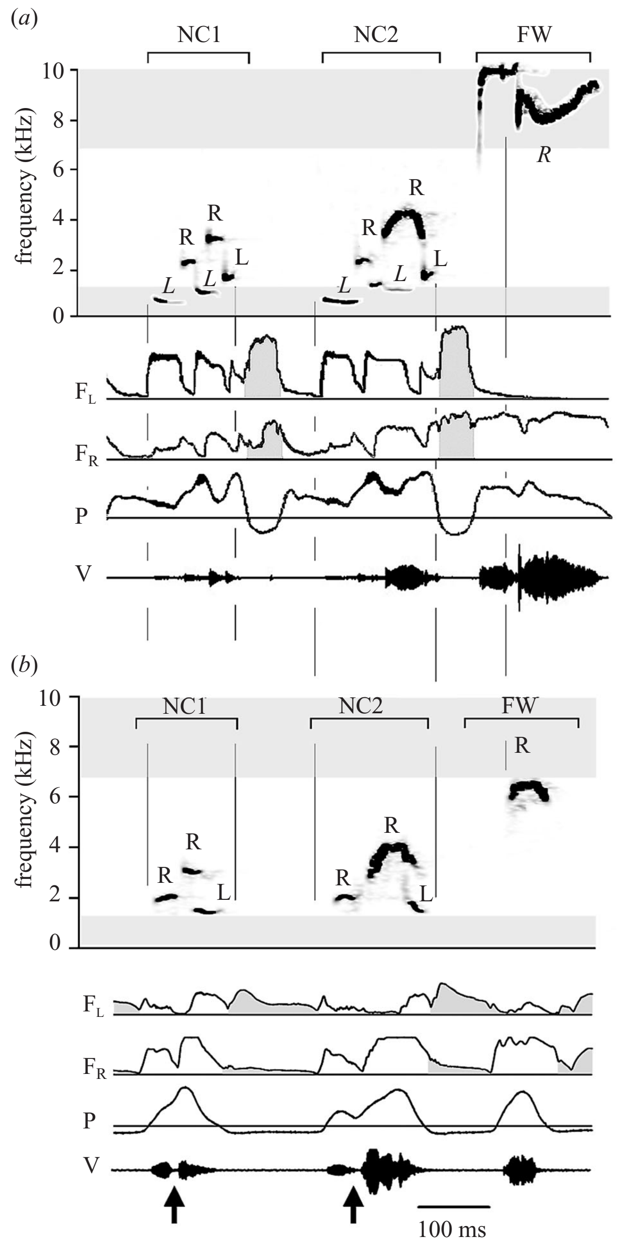

Figure 1. (*a*) Tutor song of the brown-headed cowbird YYY. Spectrogram (top panel) shows two note clusters (NC1 and NC2) in which notes were sung on alternate sides of the syrinx beginning with the first (lowest) note on the left (L) followed by a note on the right (R). Final whistle (FW) produced on 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 the spectrogram indicate frequencies outside the vocal range of mockingbird 123. Note that the lowest frequency notes in NC1 and NC2 as well FW were outside this mockingbird's range. (*b*) The mockingbird 123 copy of (*a*). Omission of notes in NC1 and NC2 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 the syrinx as the cowbird. The mockingbirds increased the duration of the remaining notes, thus maintaining the duration of the tutor note clusters. Duration of tutor NC1 and NC2 was 109 ms and 151 ms, respectively, before note deletion. The portions of NC1 and NC2 copied by the mockingbird were sung in 81 ms and 109 ms by the cowbird but expanded to 92 ± 11 ms (mean ± s.d.) and 147 ± 16 ms, respectively, by the mockingbird. F_L and F_R, rate of airflow through left and right sides of syrinx (airflow associated with positive pressure is expiratory; shaded flow (corresponds to negative pressure) is inspiratory); P, pressure in cranial thoracic air sac; V, oscillograph of vocalizations. Horizontal lines indicate zero airflow and ambient pressure.

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 from that of its tutor. If, however, 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 & 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 (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 not only copied 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.

2. METHODS

(a) *Rearing and tutoring of birds*

Mockingbirds that were 2–5 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 the northern cardinal, the brown-headed cowbird, the Wasserslager canary and the eastern towhee (*Pipilo erythrophthalmus*) 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

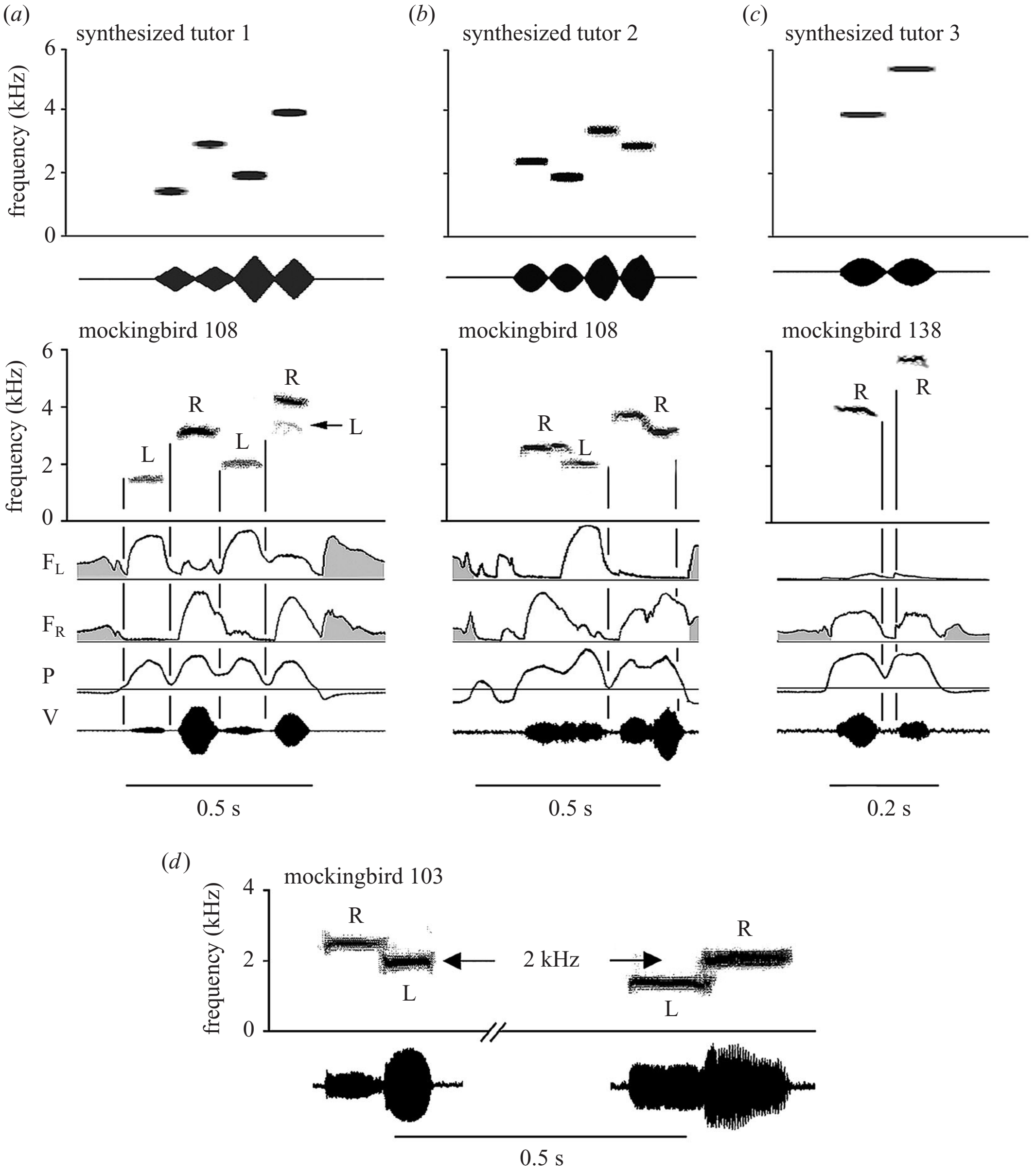

Figure 2. Mockingbird copies of synthetic cowbird-like note clusters. (*a*) When mockingbirds sang successive notes in the cluster on alternating sides of the syrinx, like a cowbird, they reproduced the immediate onset, stepwise frequency changes present in the tutor song. When both notes were outside 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 owing 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 was adjusted for the second tone. In this case the spectral contrast of the tutor sound was preserved, but the temporal pattern was 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 dependent. In these examples, mockingbird 103 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. For other abbreviations, see figure 1.

and towhee songs; group 2, synthetic sounds; and 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 *ca.* 2 h a day between the age of 10 days and six months and then every other day until 12 months old. Each tutor file was *ca.* 50 s 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 five to eight 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.

(b) *Surgery and recording of vocal mechanisms*

Pre-operative song was recorded for one to two weeks from adult birds (older than 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 $\mu l\ g^{-1}$ body weight, and a silastic cannula (Dow Corning Corp., internal diameter 1.02 mm, external diameter 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, which 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 30–50 cm in front of the cage. All procedures were approved by the Institutional Animal Care and Use Committee of Indiana University, Bloomington.

Surgery was conducted on 16 males. Bilateral bronchial airflow and respiratory pressure were recorded from five male birds during song, consisting of one bird in group 1, two birds in group 2 and two birds in group 3. Unilateral airflow and pressure were recorded from an additional four birds, consisting of one bird in group 1, two birds in group 2 and one bird in group 3. The fine wires routed under the skin from both thermistors to the backpack broke before the remaining seven birds sang. Pre- and post-operative songs from each bird were compared by visual inspection of spectrograms, and no differences were observed.

Signals were analysed with Signal, v. 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 mean ± s.d. unless otherwise noted. Spectra for bandwidth measurements were generated in Igor Pro using 512-point fast Fourier transform 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 carried out in a similar manner, by generating a power spectrum of the whole syllable, and measuring the frequency bandwidth at –20 dB.

3. RESULTS

(a) *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 *ca.* 750 Hz or higher than *ca.* 7 kHz), mockingbirds either omitted these notes or substituted a note at a frequency within their vocal range (figure 1*b*), indicating that their frequency limitation is due to a production, as opposed to auditory, constraint. As in other songbirds (Suthers 1999), mockingbirds sang their lowest frequencies with the left syrinx and their 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 and 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. Because the first two left-side notes of the cowbird's note clusters (figure 1*a*) were below the frequency range of mockingbird 123, he omitted them and began his copy of each note cluster (figure 1*b*) with two notes on the right side of the syrinx. The two mockingbirds that sang cowbird songs ($n = 45$) always sang each of these notes on the same side as the cowbird tutor (figure 1*b*), 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 (figure 1*b*).

Figure 3. Mockingbird copies of extended FM sweeps. (*a*) and (*b*) When mockingbirds used a similar motor pattern to that of a cardinal to produce FM sweeps, their copy resembled the tutor's 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 programme to sing both downward (*b*) and upward (first sweep in (*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 continued sound production on the first side of the syrinx after starting phonation on the contralateral side, different frequencies from each side resulted in biphonation absent from the tutor song. (*d*) The more precisely a mockingbird switched sides mid-sweep, the more linear the resulting sweep was, while more temporal overlap in phonation from the two sides resulted 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 the result of 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 resembled the tutor's in spectral quality, but had a significantly reduced bandwidth compared with the tutor sweep (mean unilateral: 2.96 ± 0.715 kHz; mean bilateral: 4.7 ± 0.52 kHz ($t = 8.761$, d.f. $= 38$, $p < 0.001$, $n = 198$ sweeps)).

We examined 140 mimicries by three 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 100–200 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. Mockingbirds sang successive tones with opposite sides of their syrinx, like the notes in a cowbird's note cluster, in 35% (49 syllables) of

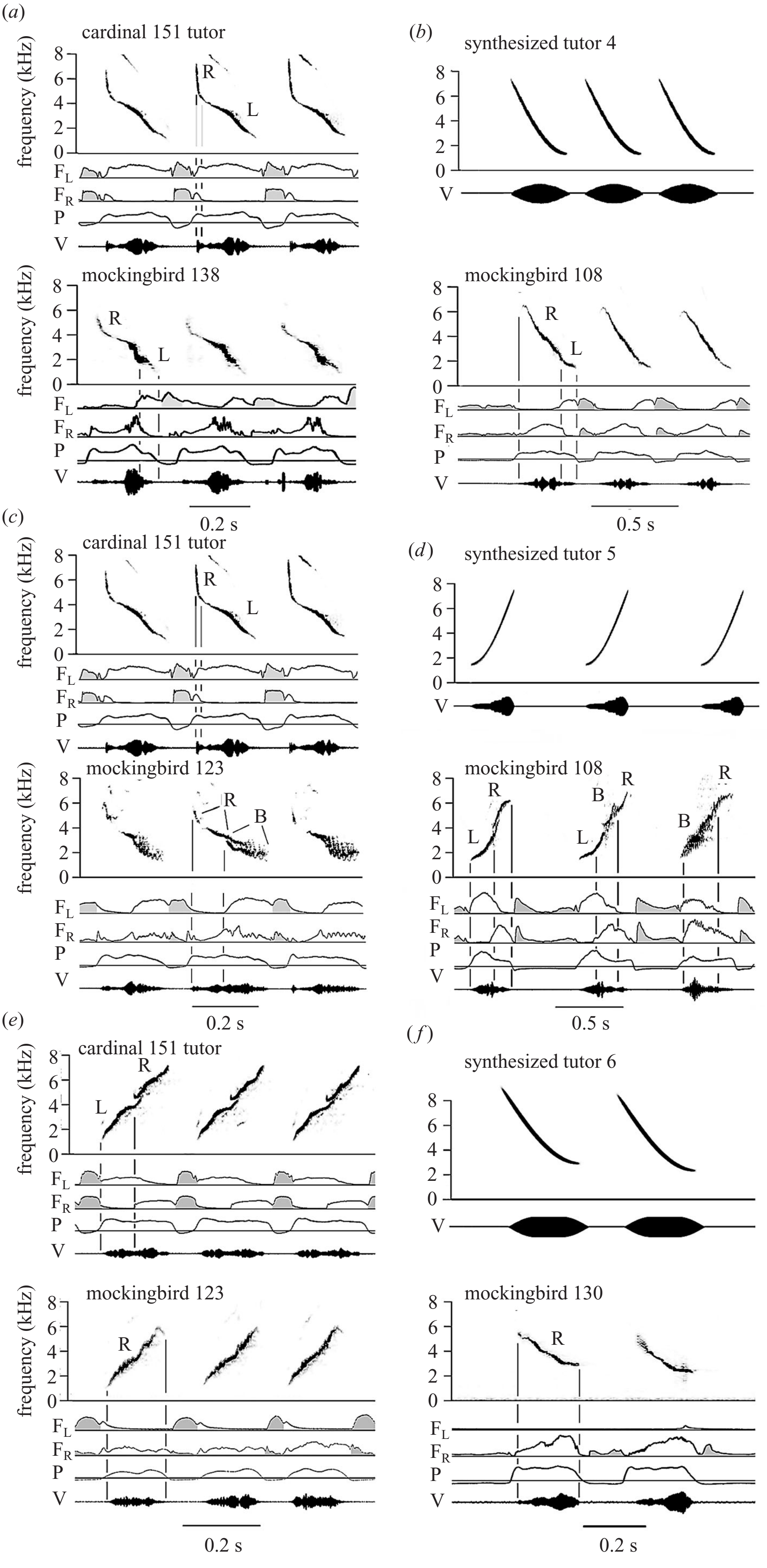

Figure 3. (*Caption opposite*.)

these mimicries (figure 2*a*). 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, stepwise change between two frequencies with an inter-note interval of 10 ms or less. All three 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%; figure 2*b*) or separated by a silent interval (72%; figure 2*c*). 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 three 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) ($t = 1.67$, d.f. = 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 (figure 2*d*). Abrupt, transient frequency jumps produced by a single side were observed rarely in mockingbird song (0.1% of 3000 syllables from three birds) and probably reflect intrinsic nonlinear behaviour of the syrinx (Fee *et al.* 1998). This type of frequency jump was never used by birds mimicking a tutor sound.

(b) *Cardinal-like frequency modulated 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 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 four 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 (figure 3*a*; table 1). In 12–43% 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 (figure 3*c*; table 1). We measured the frequency bandwidth of a 25 ms portion of the sweep centred 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, $n = 21$, $p < 0.001$, d.f. = 3, one-way ANOVA and Tukey test) and also than sweeps in which the mockingbirds switched sides smoothly like a cardinal (715 ± 266 Hz, $n = 35$, $p < 0.001$, d.f. = 3). The mean duration of overlap was significantly greater ($p < 0.050$, $n = 54$, d.f. = 3) in mockingbirds that did not switch sides smoothly (e.g. figure 3*c*) than in those that did (e.g. figure 3*a*), or than in the cardinal tutors. Corresponding segments of mockingbird syllables with good switches between sides did not differ significantly from those of the cardinal tutors. Three out of the four mockingbirds occasionally attempted (5–29% of their sweeps) to sing cardinal sweeps using only a single side of the syrinx (figure 3*e*; 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 (figure 3*b*,*d*,*f*). Four birds used a coordinated mid-syllable right–left switch in 92–100% of their copies of synthesized tutor sweep four (figure 3*b*). When copying a synthesized upward sweeping FM, two of these birds always switched smoothly from left to right in mid sweep (e.g. first sweep in figure 3*d*). The other two birds switched smoothly in 83% or 70%, respectively, of all syllables analysed ($n = 55$), but in other cases sang all or part of the sweep with simultaneous airflow through both sides of the syrinx. These periods of bilateral phonation were significantly greater in both duration ($p < 0.001$, $n = 75$, d.f. = 3) and bandwidth ($p = 0.001$, d.f. = 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. figure 3*d*) was not significantly different than that of the synthesized tutors (659 Hz), indicating a very precise left–right switch. Unlike the cardinal tutors, who switched sides between 3.5 and 4.0 kHz, the mockingbirds in this study switched sides between *ca.* 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 (figure 3*e*,*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 with sweeps produced bilaterally (4.68 ± 0.52 kHz; $t = 8.761$, d.f. = 38, $p < 0.001$, $n = 198$ sweeps; four birds).

(c) *Canary-like long duration, high repetition rate trills*

Temporal, as well as spectral, aspects of song are subject to performance limits. Attempts by two 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} (figure 4*a*), neither bird copied the mini-breath respiratory pattern used by the canary (figure 4*c*), 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 (figure 4*d*). Within each note 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

Table 1. Contribution of left and right syrinx in mockingbirds copying the extended FM sweep of the cardinal.

	mockingbird				
production pattern	138	123	130	103	mean
good left–right switch[a]	52%	59%	59%	57%	57%
left–right overlap[b]	31%	36%	12%	43%	27%
unilateral sweep	17%	5%	29%	0%	11%
n	23	153	17	7	

[a] Overlap less than 15 ms.

[b] Overlap 15 ms or more.

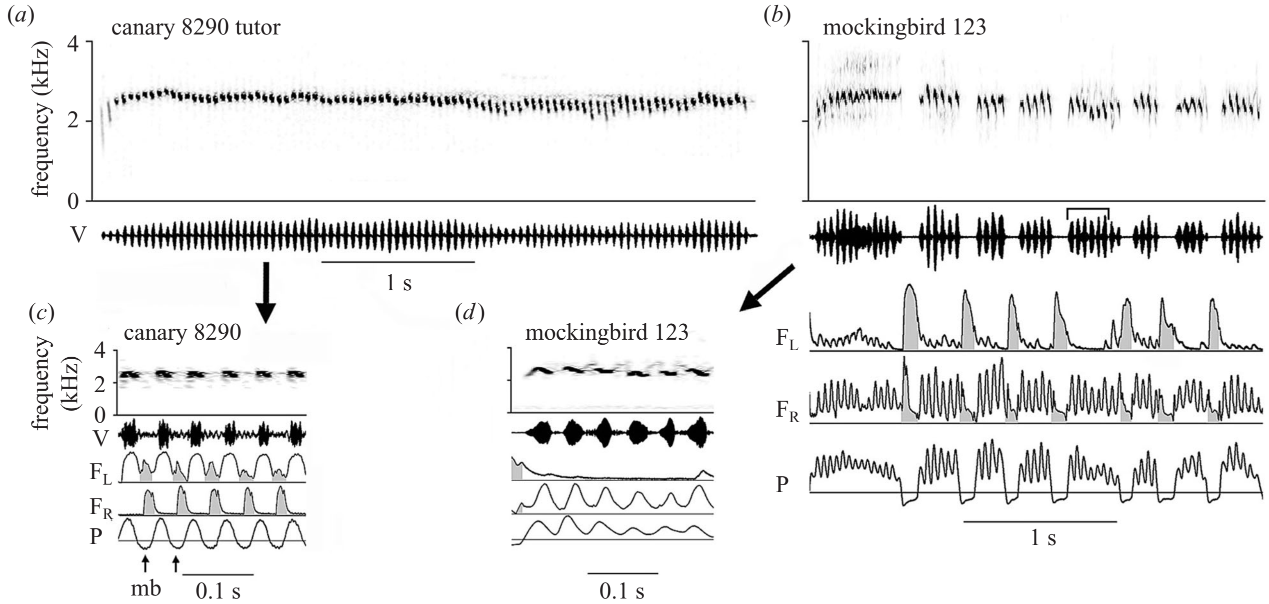

Figure 4. (*a*) Wasserslager canary tutor song. (*a*) and (*c*) The canary sings this uninterrupted trill for 4 s. He maintains this rapid repetition of syllables ($20\ s^{-1}$) by taking 'minibreaths' (mb) between each syllable (small arrows in *c*). (*b*) and (*d*) The much larger mockingbird cannot 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 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 s 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.

of trill segments sung by mockingbirds using this pulsatile respiratory pattern was 0.54 ± 0.18 s (range of 0.19 to 0.98 s), interrupted by breaths with a mean duration of 0.19 ± 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 (*ca.* $10\ s^{-1}$). When using minibreaths, mockingbirds in this study were able to sing uninterrupted trills with durations as long as 9.8 s (mean duration trill with minibreaths 3.6 ± 2.1 s, $n = 25$). The duration of uninterrupted trills produced by using a minibreath respiratory pattern was significantly longer than that of trill segments produced with the pulsatile respiratory strategy ($t = 2.002$, d.f. = 57, $p < 0.001$).

4. 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, however, 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 (West *et al.* 1979; King *et al.* 1981, 1986; King & 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 & 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 two octaves with no perceptible interruption of the sound. It is this extended bandwidth and smoothly coordinated midsweep 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; Drăgănoiu *et al.* 2002). The mockingbird's version of the high syllable repetition rate canary trill differed from the tutor's 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 the next by a silent interval for an inspiration.

The mockingbird's segmentation of canary trills is probably 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. $30\ \mathrm{s}^{-1}$ in *ca.* 18 g canaries; $16\ \mathrm{s}^{-1}$ in *ca.* 40 g cardinals; $10\ \mathrm{s}^{-1}$ in *ca.* 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 $20\ \mathrm{s}^{-1}$ (figure 4*a*). Instead the mimic was forced to resort to a pulsatile expiratory pattern so as 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 probably 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 into short bouts of syllables (Derrickson & 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 behavioural 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 no less than *ca.* $10\ \mathrm{s}^{-1}$. The mean length of a minibreath song bout was more than six times that of the pulsatile note clusters in the mockingbird's renditions of the canary trill (see § 3c). 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 such as 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) 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.

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