

Motor constraints on vocal development in a songbird

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Abstract. The development and evolution of bird songs may be influenced by the mechanisms that underlie sound production, although the nature of this influence is not well understood. Here it is shown experimentally that vocal development in songbirds can be affected by physical limits on how birds are able to sing. Young swamp sparrows, *Melospiza georgiana*, were presented with conspecific song models modified such that rates of syllable repetition were increased above normal rates. Imitations of these songs were inaccurate in ways that indicated motor constraints on vocal performance and that did not indicate perceptual or memory-based constraints. Some song imitations were deficient in trill tempo and/or syllable composition, and others were produced with a species-atypical 'broken' syntax, in which pauses were interspersed within songs. These results illustrate how the development and evolution of trill structure can be limited by motor constraints on vocal production, and also identify a possible mechanism for the evolution of a novel form of song syntax.

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Although young songbirds generally learn their songs through imitation (Kroodsma 1982; Slater 1989), song development can still be a highly restricted process. For example, birds tend to copy conspecific and not heterospecific songs (Konishi 1978; Marler & Peters 1989), may not imitate songs heard before or after a 'sensitive phase' for song acquisition (Marler & Peters 1987), and may eliminate memorized song models from their vocal repertoires during song ontogeny (Marler & Peters 1982; Marler 1991). Such restrictions are thought to occur primarily as a result of selectivity in the mechanisms by which young birds memorize, store and access song representations during song ontogeny (Slater 1989). Much recent work has been directed towards understanding how song model selection is influenced by perceptual predispositions (e.g. Nelson & Marler 1993) and social interactions (e.g. Baptista & Petrinovitch 1984; West & King 1988; Beecher et al. 1994).

By contrast, song development is thought not to be restricted by limits on how birds are able to produce sound (Marler 1976, 1984; Konishi 1985). Once a songbird has memorized a song

model (during the 'memorization' phase of song learning; Slater 1989), it is thought that the subsequent reproduction of that model (during the 'motor' phase of song learning; Slater 1989) will not normally be impeded by limits on vocal performance. Evidence for this conclusion is that birds are sometimes able to produce good copies of heterospecific songs (e.g. Baptista & Petrinovitch 1984) and that the morphology of the vocal apparatus within oscine families is highly uniform (Ames 1971). Both lines of evidence suggest that the vocal physiology of related species within the Passeriformes is functionally equivalent, so that, for example, the tendency of birds to learn conspecific rather than heterospecific songs cannot be attributed to production-based constraints. Marler (1976, 1984) and Konishi (1985) acknowledged that the mechanics of sound production might limit song learning in other ways, for example, with respect to how variants of conspecific song are learned, although data in support of this point have been lacking.

Song production is of course constrained in an absolute sense: birds of a given size are physically unable to produce sounds beyond particular frequency ranges, durations and repetition rates (e.g. Ryan & Brenowitz 1985; Nowicki et al. 1992). It is not clear, however, how such constraints might

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affect vocal development. Presumably motor constraints normally play little role in vocal development, because birds usually accurately imitate song models that conspecifics were able to produce. That is, if adult birds are able to produce a particular song, there is no reason to suspect that young birds would be physically unable to produce accurate copies of that song. Over evolutionary time, however, song may undergo selection for structural changes (Slater 1989), for example in response to mating preferences (e.g. Ryan & Keddy-Hector 1992; Vallet & Kreutzer 1995) or in response to competition for a limited 'acoustic space' (e.g. Nelson & Marler 1990). Under such selection pressures, motor constraints on vocal development could presumably limit the degree and/or direction of song evolution.

Here I tested the hypothesis that performance limits on song production can restrict vocal development, using swamp sparrows, *Melospiza georgiana*, as experimental subjects. Swamp sparrow songs are characterized by two levels of organization; notes are arranged into syllables, and syllables are repeated to produce trills (Marler & Peters 1977; Fig. 1a, c, e). Trills are produced not only by wild birds, but also by swamp sparrows trained with model songs organized in a heterospecific syntax (with trills and 'note clusters'; Marler & Peters 1977) and by birds reared in acoustic isolation, without access to song models (Marler & Sherman 1985). The tendency for swamp sparrows to produce songs with a trilled syntax implies the presence of a central motor program for this attribute (Marler 1984), although features such as trill rate (the rate of syllable repetition within songs), note structure and syllable structure are clearly influenced by learning (Marler & Peters 1977; Marler 1984).

I manipulated songs that had been recorded from wild swamp sparrows (e.g. Fig. 1a, c, e) so that trill rates were increased above normal rates (e.g. Fig. 1b, d, f). These manipulated songs, which were designed to mimic one possible direction for evolutionary change in swamp sparrow songs (Fig. 2), were then presented as training songs to a group of young swamp sparrows. I hypothesized that young birds might be able to memorize and access these training songs as normal, but be unable to reproduce these songs as normal due to physical limits on vocal performance (including performance limits on vocal tract: Nowicki et al. 1992; Westneat et al. 1993;

syringeal: Gaunt 1987; and/or respiratory motor patterns: e.g. Brackenbury 1978; Hartley 1990) during song production. To demonstrate a role for motor constraints, two criteria need to be met: (1) deficiencies in vocal imitation need to occur in directions consistent with a hypothesis of motor constraints, and (2) deficiencies caused by motor constraints need to be discernible from deficiencies caused by other sources of constraint, such as those invoked by perceptual selectivity.

METHODS

Seven male swamp sparrows served as the experimental group. Birds three to eight days old, from four nests, were collected in the field from a population near Linesville, Pennsylvania. Birds were hand-reared (e.g. Marler & Peters 1988) and housed in individual cages inside two walk-in acoustic isolation chambers. An additional 12 males from the same population, hand-reared and subsequently housed in individual acoustic isolation chambers, served as a control group.

I constructed training models for the experimental group as follows: From each of seven wild songs (Fig. 1a, c, e; four others not shown), I digitized a single syllable at 25 kpt/s (Data Translation 2128G A/D board), using a high-pass filter to remove low frequency noise (Krohn-Hite 3500, 1 kHz corner frequency, 24 dB/octave) and a low-pass filter to prevent aliasing (Stanford Research Systems SR640, 10 kHz corner frequency, 115 dB/octave). Inter-note intervals were modified using SIGNAL sound analysis software (Beeman 1992). Within each syllable, all inter-note intervals were shortened by a single ratio. Identical copies of manipulated syllables were then concatenated, by that same ratio, to produce song models with faster trill rates. For example, the two inter-note intervals and inter-syllable intervals for the song in Fig. 1a were all reduced by the same ratio to create a training song with a trill rate 56% above normal (Fig. 1b). For the seven manipulated training songs, trill rates were increased between 26% and 92% above wild rates, which represents an increase of approximately two standard deviations above normal population trill rates (Fig. 2). Amplitude variation within manipulated songs was adjusted to match levels of amplitude variation within wild songs, and song durations were varied between 1.8 and 2.2 s, the

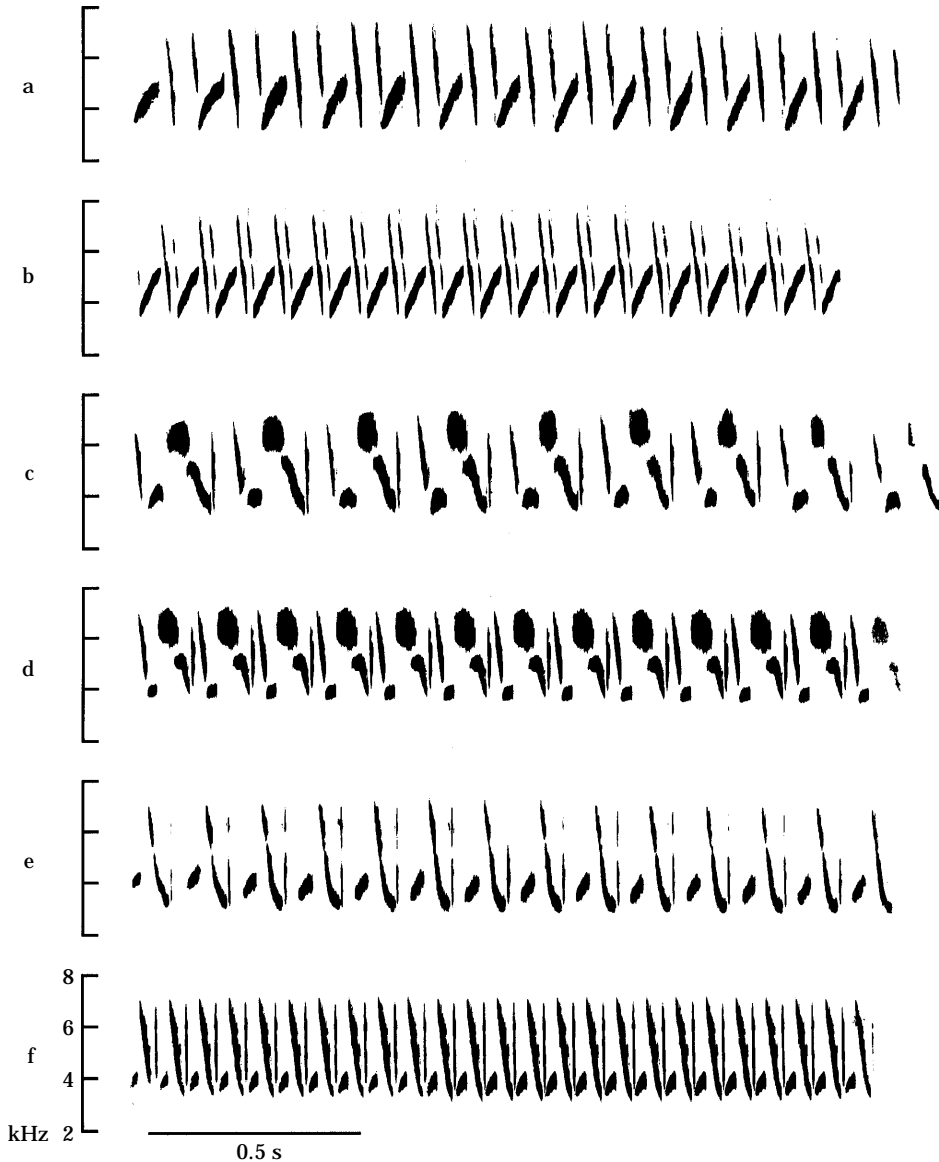


Figure 1. (a, c, e) Sonograms of advertisement songs from wild swamp sparrows. Notes (represented as continuous spectrogram traces) are arranged in syllables, which are repeated to comprise trills. (b, d, f) Manipulated versions of songs a, c and e that were used for training. Spectrograms produced on a Kay Elemetric Digital Sona-graph (Model 7800), 300-Hz filter bandwidth.

approximate range of song durations found within wild songs.

Training songs were presented to birds between 15 and 106 days of age, during the sensitive phase for song acquisition in the laboratory for this species (Marler & Peters 1988). Each day, birds

heard 48 repetitions of each training song. The seven experimental birds were trained with the set of seven manipulated songs, with all birds hearing all songs. The 12 control birds were trained with a set of seven songs at their natural speeds. Two song types presented to experimental birds were

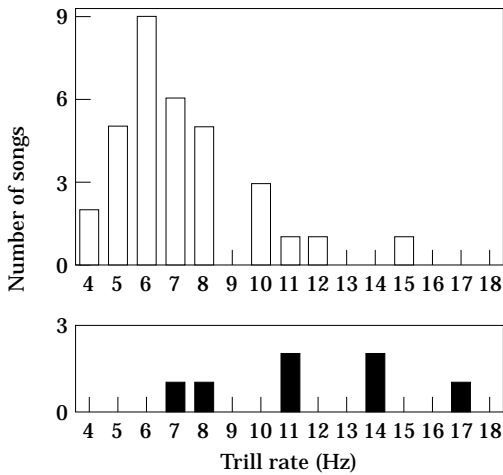


Figure 2. Frequency distribution of 'trill rates', the rates at which syllables are repeated within trills, for a population of wild birds in New York (open bars, mean \pm SD = 7.63 ± 2.34 Hz, $N=33$ trill types from 19 birds) and for manipulated model songs in this study (filled bars, 11.97 ± 3.63 Hz, $N=7$ trill types).

manipulated versions of songs presented to control birds.

The following spring, songs produced by experimental and control birds were recorded using Marantz PMD 221 audio recorders. I determined each bird's song repertoire by visual examination of spectrograms (Kay Elemetric Digital Sona-graph, Model 7800). Each bird was recorded until its song repertoire was determined to be fully crystallized (Marler et al. 1988). Swamp sparrows generally crystallize between two and five song types each (Marler & Peters 1988), with little obvious structural variation between renditions of a given type.

I compared song types to song models, and identified cases of copying. Two researchers (S. Peters and J. Podos) independently rated each song type as either 'no copy', 'poor copy', 'fair copy' or 'good copy' (Marler & Peters 1988). This rating was based on an assessment of similarity between song types and putative song models, with respect to note structure and the sequence of notes within syllables. Song types that were fair or good copies were considered in further analyses. Other song types were excluded from analysis because of difficulties in assigning song types to song models with confidence, a step necessary for the analyses below. There was no discrepancy

between the two researchers in distinguishing fair or good copies from others.

I digitized five typical renditions of each crystallized song type at 25 kpt/s, as above. Values from all analyses below were averaged across the five renditions of each song type. I assessed the accuracy of note copying, on a note type by note type basis (note types were determined separately for each bird), using pair-wise spectrogram cross-correlation analysis (Clark et al. 1987; Nowicki & Nelson 1990). This technique determines the similarities between note copies and note models in terms of note duration, absolute frequency and modulations in frequency and amplitude within notes. Low similarity scores indicate that model and copy notes differ in their fine structure (inaccurate copy), and high similarity scores indicate that copy and model notes share a similar fine structure (accurate copy).

I measured timing characteristics of song copies from oscillograms. I used an on-screen cursor to measure the rates at which successive syllables were produced within each song. Accuracy of these measurements reflected the resolution of oscillograms (approximately ± 2 ms). Based on rate measurements, I calculated two variables for each song: 'trill rate', and 'trill rate deceleration'. Trill rate was calculated as the average rate of syllable repetition across the entire song. Trill rate deceleration was calculated as the difference in trill rate between the first two syllables in a song and the last two syllables in a song, which reflects the extent to which trill production slows during the course of a song.

RESULTS

In the control group, 7 of 12 birds produced a total of 12 fair or good copies of song models, as determined by visual examination of note structure. The accuracy of note copying by control birds, as determined by spectrogram cross-correlation scores, was on average \pm SD 0.665 ± 0.205 ($N=41$ note type comparisons). Song copies produced by control birds were accurate with respect to syllable structure and temporal features (Table I, first column). Trill rates of song copies in the control condition did not differ statistically from the trill rates of the song models from which they were copied (paired t -test, $t=0.907$, $df=11$, $P=0.384$).

Table I. Features of learned songs

	Training condition		
	Control	Experimental	
Trill syntax <i>N</i> (birds, song types)	Normal (7, 12)	Normal (5, 8)	'Broken' (3, 5)
Trill rate reduction*	3.3% (\pm 9.1)	20.5% (\pm 21.1)	3.7% (\pm 5.9)
Note omissions†	0	0 to 2	0
Trill rate deceleration‡	3.2% (\pm 1.6)	5.6% (\pm 7.3)	4.3% (\pm 3.7)

*Mean (\pm SD) percentage by which trill rates of song copies were slower compared to trill rates of their song models.

†Range of number of note types omitted per syllable from copies of model songs (not including omissions of note type 1 (Marler & Pickert 1984), which occurs often in laboratory rearing of this species).

‡Mean (\pm SD) per cent change in trill rate between the first two and last two syllables in a song. Trill rates and trill rate decelerations for broken trills were determined from within multi-syllable segments.

In the experimental group, 6 of 7 birds produced a total of 13 fair or good imitations of training songs, with respect to note structure. Spectrogram cross-correlation scores averaged 0.673 ± 0.195 ($N=35$ note type comparisons), which did not differ statistically from cross-correlation scores of control birds ($t=0.255$, $df=34$, $P=0.800$). The syllable structure and/or temporal organization of these song copies, however, was highly inaccurate relative to the models from which they were copied. Inaccuracies in song type copies occurred in one of two ways. First, for 8 of the 13 song imitations, songs were reproduced with one or more of the following deficiencies: (1) reduced trill rates (compare Fig. 3a with Fig. 1b), (2) reduced numbers of notes contained within syllables (compare Fig. 3b with Fig. 1d) and (3) high values of trill rate deceleration. For these eight song copies, trill rates were significantly reduced compared to the trill rates of their particular song models (paired t-test, $t=2.648$, $df=7$, $P=0.033$). Table I (compare first and second columns) summarizes the differences in copying accuracy between these songs and song copies in the control group.

Second, for the remaining 5 of 13 song imitations in the experimental group, songs were produced with a 'broken' syntax (Fig. 3c-e), with pauses interspersed among multi-syllable segments. This form of song organization differs radically from previously documented forms of swamp sparrow song (e.g. Marler & Peters 1977; Marler & Sherman 1985; Nowicki et al. 1991).

Within multi-syllable segments of broken trills, I detected no differences between song copies and song models. That is, all three song features listed in Table I were copied with a degree of accuracy similar to that shown by control birds (Table I, compare first and third columns). As with control song copies, trill rates of song copies with broken syntax did not differ statistically from trill rates of their training songs (paired t-test, $t=1.506$, $df=4$, $P=0.207$). Further, cross-correlation scores for broken trills (average \pm SD cross correlation score= 0.614 ± 0.250 ; $N=10$) did not differ statistically from those of normal trills produced by experimental birds (0.696 ± 0.168 , $N=25$; $t=0.280$, $df=9$, $P=0.786$).

The syntax with which song copies were produced (normal or broken) corresponded to the degree by which song models were digitally manipulated above their wild rates (Table II). Eight of nine song types copied from the five least manipulated songs (Table II, trill rates increased by 56% or less) were produced with normal syntax, albeit with substantial deficiencies in other features. Four of four song types copied from the two most highly manipulated songs (Table II; trill rates increased by 87% or more) were produced with broken syntax.

By contrast, the type of syntax produced did not correspond to the absolute trill rates of manipulated song models (Table II). That is, song models with the fastest trill rates were not necessarily copied with broken syntax.

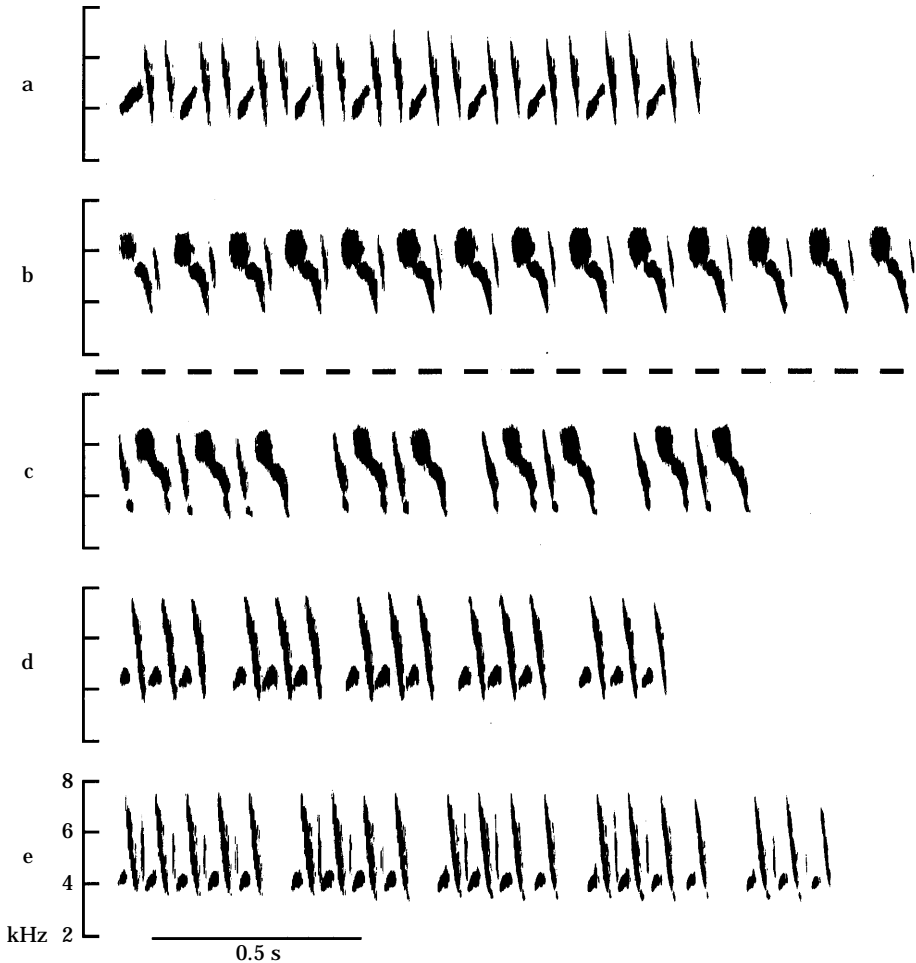


Figure 3. Typical imitations of manipulated training songs (Fig. 1b, d, f), from 5 different birds. (a, b) Trills with normal syntax. Song A has a syllable composition and magnitude of trill rate deceleration comparable to its model song, but a reduced trill rate. Song B is comparable to its model song in all temporal features, but is characterized by note omissions. (c, d, e) Trills with broken syntax. Pauses are interspersed among multi-syllable segments.

DISCUSSION

In general, inaccuracies in song copying may derive from constraints operating during either the memorization or motor phase of song learning (Marler 1976; Slater 1989). For 'age-limited' learners such as the swamp sparrow (Marler & Peters 1988), in which memorization and motor phases are clearly separated in time (Marler & Peters 1982, 1988), constraints on song selection should be expressed independently of constraints associated with the reproduction of memorized song models. To assess the role of motor con-

straints in this experiment, it was first necessary to demonstrate that song model memorization was not affected by the trill rate manipulation.

Note copying, as revealed by spectrogram cross-correlation scores, was as accurate in the experimental group as it was in the control group. Furthermore, the percentage of birds in the experimental group that produced fair or good copies of notes (6 of 7 birds) was comparable to, if not somewhat higher than, that found in the control group (7 of 12 birds), and also to a group of swamp sparrows from a previous study that were exposed to normal conspecific song models (12 of

Table II. Relation between model song features and imitated song features

Bird	Model song number						
	1 (26%, 8.2)	2 (49%, 17.4)	3 (51%, 14.3)	4 (56%, 11.1)	5 (56%, 7.2)	6 (87%, 11.2)	7 (92%, 14.4)
1					N _(b) †		
2				N*†	N†		B _(d)
3					B _(c)		B
4			N*				
5		N‡		N _(a) *	N‡		
6	N†‡					B	B _(e)

N indicates that song copies were produced with normal syntax, B with broken syntax. Model songs are arranged from left to right according to the degree to which trill rates were digitally increased (first value in parentheses). Trill rates (Hz) of model songs are indicated by the second value in parentheses. Lower case letters in parentheses refer to songs illustrated in Figure 3 (a=Fig. 3a, b=Fig. 3b, etc.). Note that broken-trill syntax occurred only in copies of the most highly manipulated song models.

*Copied songs were at least 30% slower than the model songs from which they were copied.

†One or two note types of the model song were not copied (not including omissions of note type 1: Marler & Pickert 1984).

‡Trill rates within songs decelerated by at least 10%.

Birds 1–3 and 4–6 were reared separately.

15 birds; Marler & Peters 1988). These results suggest that birds in the experimental group were able to acquire, memorize and access note representations from manipulated song models as normal.

Note acquisition and reproduction might involve mechanisms or neural representations distinct from mechanisms of tempo and syntax acquisition and reproduction (Marler 1984; Güttinger 1985). Multi-syllable segments of broken trills (Fig. 3c–f) provide evidence for a lack of influence of perceptual or memory-based constraints on higher levels of song organization. Within multi-syllable segments, all attributes of model songs were reproduced with a degree of accuracy comparable to that found in the control group (Table I). Thus, even for copies of the most highly manipulated song models, deficiencies in vocal imitation could not be attributed to limits in birds' ability to perceive, store and access neural representations of song.

The likely alternative source of constraints to account for observed deficiencies in song copies is that of motor limits on vocal performance. Two attributes of song copies in the experimental group are consistent with this interpretation. First, copying errors suggested that birds encountered physical difficulties when producing trills. For example, imitations with normal syntax produced by experimental birds showed significant trill rate

reductions, but did not show trill rate augmentations (e.g. Fig. 3a). This is the expected result if birds' ability to sing is indeed constrained by vocal mechanics, i.e. by the ability to produce rapid breaths, syrinx musculature modulations, and/or vocal tract modulations during song production. Similarly, note omissions rather than note additions (Fig. 3b), within-trill decelerations rather than within-trill accelerations, and pauses within a normally continuous syntax (Fig. 3c–e) suggest performance limits on the mechanics of sound production. In other words, the song characteristics of imitations in the experimental group deviated in a one-tailed fashion, and the directions of these deviations were consistent with a hypothesis of motor constraints.

Second, song copies were produced according to one of two mutually exclusive modes of syntax, with a discrete transition specified between the two modes (Table II). For the eight song type imitations produced as normal trills ('N' in Table II), at least one of three characteristics of each song type was largely deficient relative to the model song from which it was copied. By contrast, the five song type imitations produced as broken trills ('B' in Table II) were produced with no such deficiencies, at least as measured within multi-syllable segments. Furthermore, broken-trill syntax occurred only in imitations of song models with trill rates increased 56% or more above that

song model's original rate. This set of outcomes suggests an analogy between song learning and the production of other kinds of behaviour patterns, such as terrestrial locomotion, in which discrete and threshold-dependent modes of behaviour indicate constraints on motor efficiency or competency (e.g. Alexander 1980, 1984).

Whether song copies were produced with broken syntax or normal syntax depended not upon the absolute trill rates of the song models from which they were copied, but rather on the extent to which trill rates of song models were increased above their original values (Table II). This result suggests that absolute trill rate alone in swamp sparrow songs is not a reliable indicator of how difficult a song is to produce, and also indicates that the development of broken-trill syntax is not caused by an absolute perceptual filter, with only those song models produced at particularly rapid speeds being restructured with a broken syntax.

These results offer insight into how motor constraints can impose selectivity on song learning, at least for the imitation of songs with modified trill rates. The idea that motor constraints could restrict song learning was anticipated by Marler (1976, 1984) and Konishi (1985), although specific details of how motor constraints would be expressed could not have been predicted.

Motor Constraints and Development

Effects of motor constraints on song learning probably emerge during the motor phase of song ontogeny (Slater 1989), in the context of a mismatch between neural representations of memorized song (what birds aim to produce) and motor limits of the vocal apparatus (what birds are able to produce). For most song copies in this study, this mismatch resulted in deficiencies in syllable structure and/or timing attributes. For copies of the most highly-manipulated songs, however, birds compensated to produce accurate copies of most song features. An outcome of this compensation was the reorganization of song into a syntax that is highly atypical for the species.

The mechanisms underpinning this compensation deserve further exploration. During song ontogeny, birds compare vocal output with stored representations of song (Konishi 1965; Konishi & Nottebohm 1969; Marler 1976). Perhaps, during this process, birds are able to assess the extent to

which song copies are deficient as imitations due to motor limitations, and to compensate as appropriate. That different birds developed songs with broken-trill syntax suggests that the form of compensation observed here was not simply a random form of sensorimotor improvisation (see Marler 1984). Further, the finding that individual birds were able to produce song types with both forms of syntax (Table II, birds 2 and 6) indicates that the process of compensation was specific to particular song types and not to an individual's song production system as a whole.

These outcomes in general demonstrate a previously undescribed level of plasticity in the sensorimotor phase of song development. They also provide support for the idea that phonological and syntactic song features are processed on different mechanistic levels, with deficiencies in one level not necessarily linked to deficiencies in the other. It is not clear why syntactic rather than phonological structure was compromised as an outcome of motor constraints, and not vice versa. Perhaps the mechanics of song production defines the degree to which phonological and syntactic levels of organization are able to respond to developmental perturbations. Regardless, these results parallel the finding that phonological and syntactic levels in swamp sparrows are distinct with respect to birds' selectivity in responsiveness to song models (Marler & Peters 1977; Marler 1984).

Motor Constraints and Evolution

The demonstration that motor constraints can limit song development bears upon recent discussions concerning the evolution of animal signals (Ryan 1990; Endler 1993). These discussions have focused on the roles of signal perception (Basolo 1990) and signal transmission (Endler 1992) in signal evolution, and also on experimental support in favour of these roles. By contrast, the role of production-based motor constraints on signal evolution is less well understood (Endler 1993). The evolutionary effects of motor constraints on acoustic signals are normally inferred using descriptive approaches, including (1) analyses of correlations between morphology and signal structure (Wallshläger 1980; Ryan & Brenowitz 1985; Ryan & Drewes 1990) and (2) analyses of time or energy dependency in signal use (Ryan 1986, 1988; Halliday 1987; Lambrechts

& Dhondt 1988; Eberhardt 1994). The approach taken in this paper introduces a novel, experimental means of assessing the role of motor constraints on signal evolution.

Consider the evolution of trill structure in swamp sparrows. The distribution of trill rates in wild swamp sparrows is fairly normal, with a maximum trill rate of about 15 Hz (Fig. 2). This distribution might have been shaped by a number of selective pressures, such as by those associated with acoustic adaptation (Wiley 1991) and those associated with competition for a niche in 'acoustic space' (Nelson & Marler 1990). Based upon a knowledge of vocal physiology, one might also infer a role for motor constraints (Nowicki et al. 1992), for example in limiting trill rate evolution. The present study was designed to test this inference, by training birds with songs beyond the natural trill rate distribution (Fig. 2). Limits on song learning, if shown, can translate into limits on song evolution because of the relationship between song development and song evolution (Slater 1989).

These results suggest that motor limits on song learning can indeed curtail the evolution of increased trill rates in swamp sparrows, either by causing songs to remain at slower speeds or by forcing songs to lose components of syllable structure and/or consistency of trill rates within songs. Thus, barring evolutionary changes in the mechanisms underlying sound production, selection for increased trill rates would be counteracted by the limiting effects of motor constraints. The present data also suggest that motor constraints could have a creative as well as a limiting effect, by causing song copies to be reconfigured into a broken syntax. From a functional perspective, broken trills might not serve as effective communication signals, given their species-atypical nature. This form of song organization could, however, enhance the communicative effectiveness of song, given that (1) swamp sparrows are able to perceive and process songs with fast trill rates, as demonstrated by their ability to learn song models in this study, (2) broken trills are structurally more complex than normal trills, and (3) broken trills are structurally novel compared to normal trills. If so, and if broken-trill syntax proves to be heritable, motor limits as demonstrated here could not only set a constraint on song evolution, but could also provide a mechanistic basis for an evolutionary novelty.

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