

Ontogeny of vocal tract movements during song production in song sparrows

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Abstract. When adult songbirds sing, movements of the beak and other elements of the vocal tract are closely coordinated with the activity of the syrinx. The physical configuration of the vocal tract affects the tonal quality of sounds originating at the syrinx, and coordination between vocal tract movements and syringeal activity is thought to be necessary for the production of pure-tonal song. The ontogeny of this coordination in laboratory-reared song sparrows, *Melospiza melodia*, was examined. Developmental changes were quantified in (1) the acoustic structure of song notes, as measured by spectrogram cross-correlation, (2) the magnitude of beak movements during song, (3) the correlation between beak movements and acoustic frequency, and (4) the tonal quality of song. Each variable changed significantly over the course of song development, but at different rates. Note acoustic structure achieved adult-like form midway through song development, but increased use and coordination of beak movements were not observed until later stages of development. The late development of coordinated beak movements appears to correspond with the development of tonal quality. This finding suggests that the coordination of vocal tract movements with syringeal activity is delayed in ontogeny.

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Vocal learning in songbirds is characterized by a protracted period of motor development, during which time the songs of young birds progress from a babble-like rudimentary form ('subsong') to a highly stereotyped adult form ('crystallized song'; Thorpe 1961; Marler & Peters 1982a, b). Many authors have speculated that this progression reflects a need for young birds to practise and refine their ability to produce memorized songs (e.g. Konishi 1965; Konishi & Nottebohm 1969; Nottebohm 1970; Marler 1976). This interpretation is supported by the observation that species that do not imitate external models, such as flycatchers, do not proceed through a protracted phase of motor development (Kroodsma 1982, 1984, 1985; Kroodsma & Konishi 1991).

The syrinx is the primary sound-producing organ in birds, and refinement of its motor activity is presumably one important outcome of the gradual process of song development (Konishi

1985). The syrinx does not act alone in song production, however. Its activity must be coordinated with that of other motor systems, such as the respiratory muscles responsible for producing the patterns of airflow that underlie vocal production (Hartley 1990; Suthers et al. 1994) and muscles controlling vocal tract motions associated with song (Nowicki & Marler 1988; Westneat et al. 1993). The involvement of such motor components in vocal production suggests that establishing coordination between non-syringeal motor activity and the activity of the syrinx might be another important feature of gradual song development. To test this idea, we studied the development of vocal tract movements associated with song production in the song sparrow, *Melospiza melodia*.

Vocal tract movements in adult sparrows correlate precisely with timing and frequency characteristics of song (Westneat et al. 1993). Specifically, the degree to which the beak is open (beak 'gape') is highly correlated with the acoustic frequency of the sound being produced, such that the beak is opened more widely when higher frequency sounds are produced, and vice versa.

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Beak gape is, by contrast, only minimally correlated with sound amplitude during song production in adult birds (Westneat et al. 1993). Nowicki and his colleagues proposed that beak movements, along with other motions of the vocal tract, influence the tonal quality of song by dynamically modifying the vocal tract's resonance properties (Nowicki 1987; Nowicki & Marler 1988; Westneat et al. 1993).

In this study, we documented the ontogeny of vocal tract motions during song by measuring developmental changes in four variables associated with song production. First, using spectrogram cross-correlations (Clark et al. 1987), we quantified developmental changes in the acoustic structure of song. Such changes are likely to be due to developing control of syringeal motor activity (Clark et al. 1987). Second, using kinematic analysis, we quantified changes in the magnitude of beak movements during song as a measure of developing vocal tract motor activity. Third, we documented changes in the correlation between beak gape and acoustic frequency, as a measure of the coordination between the syrinx and the vocal tract. Finally, we quantified changes in the tonal quality of song, an acoustic feature thought to be affected by coordinated activity of the syrinx and the vocal tract (Nowicki & Marler 1988).

By comparing the developmental trajectories of these four variables, we assess how vocal tract movements and their coordination with the syrinx develop, and we address the significance of gradual motor development of song in oscine birds. Furthermore, to the extent that developmental changes in different motor systems emerge independently during ontogeny, we also provide insight into their respective contributions to song production in adults.

METHODS

Subjects

Six male song sparrows were collected 3–6 days after hatching, between 5 and 22 May 1992, from a population in Durham, North Carolina. Birds were hand-reared in groups until about 10 days post-hatch, after which they were housed in individual sound-attenuation chambers and exposed to recorded songs of wild adult males. Model songs (16 song types) were presented to birds for

1 h each morning and afternoon from 15 to 105 days post-hatch, corresponding to the sensitive phase for song acquisition in the laboratory for this species (Marler & Peters 1987). For the duration of training, birds were maintained on a 14:10 h light:dark cycle (light onset 0700 hours). After training birds were maintained on a seasonally variable photoperiod cycle.

Recordings

Bi-weekly video-recordings were made of each bird from about 250 days post-hatch (January 1993), when subsong begins, to about 400 days post-hatch (May 1993), when song typically crystallizes. Additional video-recordings were made in July and September 1993. Each video-recording session consisted of 1 h of continuous filming, beginning approximately 30 min after lights on in the morning. Recordings were made using a Panasonic SVHS AG-450 camera (60-Hz sample rate) with a shutter speed of 1/500 s. The camera was positioned 1–2 m from a glass window located on the front of the bird's isolation chamber. Simultaneous sound recordings were made using a Realistic 33-1070B Omnidirectional Dynamic microphone and a Sony TC-D5M audio recorder, with synchronization signals added to both the video and audio recordings (Westneat et al. 1993). We made additional audio recordings (without video) so that each bird was sampled for 1 h weekly throughout song development. We adjusted audio recording levels during the course of the study to maximize the quality of recordings. As in other studies (e.g. Marler et al. 1988), we found a general increase in the amplitude of songs during development. Otherwise, recording and calibration procedures were as described in Westneat et al. (1993).

Song Sample

We determined each bird's adult song repertoire from visual examination of spectrograms made from audio recordings (Marler & Peters 1988; Podos et al. 1992), and selected one to three song types from each bird's repertoire for analysis. Song types were selected if a bird sang at least two examples of the song type during each of at least three video-recording sessions. From each of these song types, we identified a segment of repeated notes (one 'trill'; Mulligan 1966) for



Figure 1. Examples of a song segment produced by one individual at sub-plastic (SP), early plastic (EP), late plastic (LP) and crystallized (C) stages of development, arranged from least to most developed. Bracketed portions indicate the particular group of notes analysed for this case. Spectrograms produced by Kay DSP Sona-Graph model 5500, 300-Hz resolution.

developmental analysis (Fig. 1). We selected particular exemplars of these segments for analysis based upon the quality of video-recordings, including whether the bird was within the field of the camera, in profile and in focus.

The developmental stage of each exemplar was determined as described in Marler & Peters

(1982a, b). Briefly, we assigned exemplars to stages by assessing the presence or absence of unstructured subsong elements and the relative stereotypy of note morphology, including the consistency of note frequency and duration. We assigned each exemplar to one of five developmental stages, from least to most developed:

Table 1. Number of song exemplars included in four developmental analyses of 11 song type segments

	Song type segment ID											Totals
	1	2	3	4	5	6	7	8	9	10	11	
Bird ID	1	1	2	2	3	4	5	5	6	6	6	
Note structure												
SP	—	—	6	7	—	—	—	—	—	—	—	13
EP	3	—	4	3	3	6	3	6	—	—	—	28
MP	3	—	—	3	3	—	—	—	—	—	—	9
LP	—	—	2	3	—	6	6	6	—	—	—	23
C	2	—	4	6	3	6	4	6	—	—	—	31
												104
Maximum beak gape												
SP	—	2	3	3	—	—	—	—	—	—	1	9
EP	3	3	2	1	3	3	2	3	5	4	1	30
MP	3	—	—	1	3	—	—	—	—	—	1	8
LP	—	—	—	1	1	3	3	3	4	—	—	15
C	2	3	2	2	3	3	2	3	—	3	2	25
												87
Gape-frequency correlation												
SP	—	2	3	3	—	—	—	—	—	—	1	9
EP	3	3	2	1	3	3	2	3	4	4	1	29
MP	3	—	—	1	3	—	—	—	—	—	1	8
LP	—	—	1	1	1	3	3	3	4	—	—	16
C	3	3	2	2	3	3	2	3	—	3	2	26
												88
Tonal quality												
SP	—	—	6	9	—	—	—	—	—	—	—	15
EP	3	—	4	3	3	6	3	3	—	—	—	25
MP	3	—	—	3	3	—	—	—	—	—	—	9
LP	—	—	2	3	—	6	6	3	—	—	—	20
C	2	—	4	6	3	6	4	3	—	—	—	28
												97

Statistical outliers, as determined by analysis of ANOVA residuals, were excluded from further analysis and are not shown here. SP: Sub-plastic song; EP: early plastic song; MP: mid-plastic song; LP: late plastic song; C: crystallized song.

sub-plastic song (SP), early plastic song (EP), mid-plastic song (MP), late plastic song (LP) and crystallized song (C) (Fig. 1). We pooled data from each analysis described below according to the assignment of exemplars to developmental stages (Table 1). Pooling exemplars by stage was preferable to pooling according to date because birds may develop song at different rates (Marler et al. 1988).

We performed the analysis of four acoustic and motor variables, described below, on the same sets of exemplars. Sample sizes in these analyses varied for three reasons: (1) we excluded different outliers from each sample, based on separate residual analyses (see below), (2) the acoustic recordings of four of the 11 song type segments (see Table 1)

were of relatively poor quality, precluding the possibility of conducting note structure and tonal quality analyses on this set of the sample, and (3) in some song type segments, we analysed multiple note types separately for the acoustic variables, but as a group for the two motor variables.

Analysis of Stereotypic Note Structure

To quantify changes in developing note structure, we compared notes from each of the five developmental stages to crystallized (C) renditions of the same note, using pair-wise two-dimensional cross-correlations of digital spectrograms. This method calculates the overall similarity of a pair of notes to each other, in terms of note duration,

absolute frequency, and changes in frequency and amplitude (see Clark et al. 1987, for a description of this technique; see Nowicki & Nelson 1990, for an example of its application). Low similarity, indicated by a cross-correlation score near zero, suggests that the two notes being compared vary widely in their fine structure. High similarity, indicated by cross-correlation scores approaching 1.0, suggests that a pair of notes shares a very similar fine structure.

All unique note types were identified for each song segment. Of these, we selected a subsample of note types from different song types for analysis based on the quality of a sufficient number of recordings (Table I). For each note type analysed, we calculated cross-correlation matrices between five renditions of the note averaged from crystallized song (C) and three renditions of the note averaged from each earlier developmental stage.

Analysis of Beak Movements

Kinematic (time-motion) profiles of beak movements during each exemplar of a song segment were measured following the methods described in Westneat et al. (1993). In brief, video-recordings of exemplars were copied on to U-Matic SP videotape, using a Panasonic AG-1960 SVHS videocassette recorder, a Sony VO-9600 U-Matic SP videocassette recorder, and a time base corrector (Digital Processing Systems, TBC/Framestore DPS-275). Individual video fields (at 16.67-ms intervals) were labelled sequentially using a Horita TG-50 time code generator, and video fields were displayed on an Amiga 2000 computer with a Commodore A2300 genlock board, using a Sony BVU-920 U-Matic SP videocassette player.

Using VidiTrack System software (Crenshaw 1992), data points were selected with an on-screen cursor, stored as *X*, *Y*-coordinates, and converted to metric units by a calibration program. We obtained coordinates for the following three points from each video field: (1) the tip of the upper bill, (2) the tip of the lower bill, and (3) a stationary reference point. For each exemplar, coordinate points were taken three times and averaged prior to calibration to minimize error associated with the process of point selection. We calculated beak gape (the distance between upper and lower bill tips) from these coordinates and plotted it as a function of time, providing a gape

profile for each analysed song segment. We determined widest beak gapes achieved during each exemplar by inspection of these kinematic profiles.

Analysis of the Correlation between Beak Gape and Acoustic Frequency

The correlation between beak gape and acoustic frequency was determined for each exemplar of a song segment. Audio recordings of exemplars were high-pass filtered to remove low-frequency noise (Krohn-Hite 3500, 900 Hz corner frequency, 24 dB/octave), low-pass filtered to prevent aliasing (Stanford Research Systems SR640, 10 kHz corner frequency, 115 dB/octave), and digitized at 25 kpt/s (Data Translation 2128G A/D board). Peak frequencies were calculated using discrete Fourier transforms of 64 pts (2.84 ms, 352 Hz resolution), at intervals of 16.67 ms, using SIGNAL sound analysis software (Beeman 1992). Because frequency was plotted as a function of time at 16.67-ms intervals (corresponding to the SVHS video-camera's sample rate), resulting frequency profiles for each song segment contained discrete frequency measurements whose timing corresponded precisely to the timing of video kinematic data points. To assess statistically the relationship between beak gape and acoustic frequency, for each exemplar, frequency was plotted as a function of gape at each corresponding 16.67-ms interval, and a least-squares regression was calculated for these two variables (as in Westneat et al. 1993). Error estimates for the calculation of the two motor variables are described in Westneat et al. (1993).

Analysis of Tonal Quality

Tonal quality refers to the relative distribution of acoustic energy across a signal's fundamental frequency and overtones (Marler 1969; Benade 1976; Roederer 1979). In pure-tonal sounds, such as those characteristic of 'whistled' birdsong, acoustic energy is concentrated in the fundamental frequency, with relatively little energy present in higher overtones.

To measure tonal quality, notes were digitized at 40 kpt/s (high-pass filter at 900 Hz, low-pass filter at 25 kHz) and single amplitude spectra were calculated across the duration of each note (32 kpt DFT, smoothed to 100-Hz frequency resolution;

Beeman 1992). We measured relative amplitudes (dB) of the fundamental frequency and the second harmonic of each note using an on-screen cursor and calculated the difference between them. Highly pure-tonal notes have little energy in their second harmonic and thus are characterized by larger amplitude differences. This variable, as with our measure of stereotypy in note structure, makes use of relative rather than absolute measures of amplitude, and thus should not be influenced by developmental changes in the absolute amplitude of songs.

Statistical Analysis

Developmental changes in each of the four variables (spectrogram cross-correlation scores, maximum beak gape, beak gape/acoustic frequency correlations, and tonal quality) were tested for significance using analyses of variance and post-hoc Tukey tests. Residuals were examined to test assumptions of the ANOVA and to identify outliers (Sokal & Rohlf 1981; Wilkinson 1989).

RESULTS

Note Structure

Spectrogram cross-correlation comparisons of developing song and crystallized song revealed that notes' structural similarities to crystallized notes increased throughout the course of development (Fig. 2a; $F_{4,99}=49.965$, $P<0.001$). Post-hoc testing showed significant increases between sub-plastic and early plastic song ($P<0.05$) and between early plastic song and mid-plastic song ($P<0.01$). Overall, changes tended to be greater between early stages than between later stages.

Magnitude of Beak Movement

The average maximum beak gape observed during song increased significantly over the course of development (Fig. 2b; $F_{4,181}=66.553$, $P<0.001$). During sub-plastic song, birds sang with their beaks virtually closed, unless they were simultaneously feeding or preening. From early plastic song through mid-plastic song, detectable beak movements occurred in just over half of the song segments analysed (22 of 38 exemplars), and

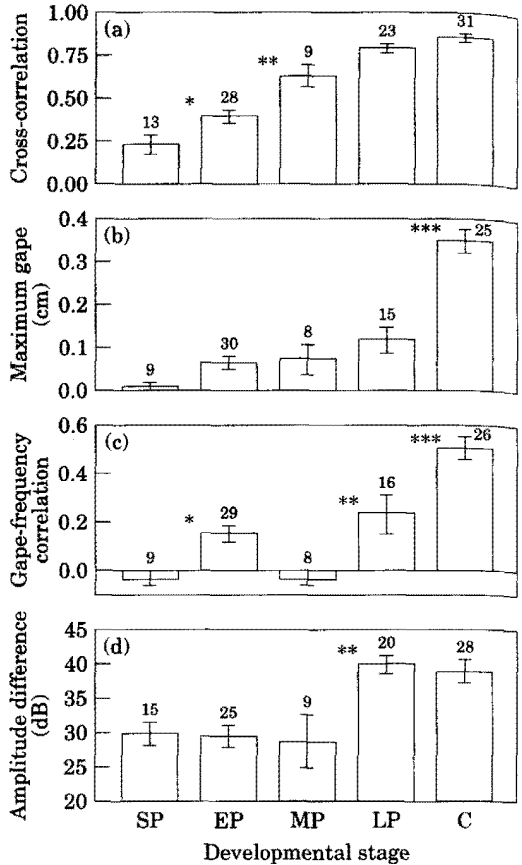


Figure 2. Means (\pm SE) for four variables describing developmental changes in song acoustic characteristics and motor performance, with stages of development arranged from the least to the most developed: SP: sub-plastic song; EP: early plastic song; MP: mid-plastic song; LP: late plastic song; C: crystallized song. (a) Spectrogram cross-correlation scores, (b) maximum width of beak gape during song, (c) correlation between acoustic frequency and beak gape, and (d) note tonal quality, measured as the amplitude difference (dB) between fundamental frequencies and second harmonics. * $P<0.05$; ** $P<0.01$; *** $P<0.001$ (post-hoc Tukey tests). Sample sizes are shown above bars.

when movements did occur, they were slight (maximum gape exceeded 0.3 cm only once). Birds usually opened and closed their beaks when singing late plastic song (12 of 15 exemplars), but average maximum gape measurements remained low (exceeding 0.3 cm only two times). The only statistically significant increase in average maximum beak gape occurred between late plastic and

crystallized song ($P < 0.001$). Birds opened and closed their beaks in all of the crystallized song segments analysed, and maximum beak gapes regularly exceeded 0.3 cm (17 of 25 exemplars), and on three occasions exceeded 0.5 cm.

Correlation between Beak Gape and Acoustic Frequency

Correlations between beak gape and acoustic frequency varied significantly across developmental stages (Fig. 2c; $F_{4,184} = 34.089$, $P < 0.001$). The percentage of analysed song segments yielding statistically significant correlations ($P < 0.01$) generally increased over the course of development (SP, 11%; EP, 36%; MP, 0%; LP, 50%; C, 84%). Wider beak gapes did not significantly correspond to higher acoustic frequencies within sub-plastic and mid-plastic stages. The correlation between frequency and gape increased significantly between sub-plastic and early plastic stages ($P < 0.05$), although the biological significance of this increase must be interpreted with caution because the absolute magnitude of beak motions is so low during these stages. The correlation also showed highly significant increases between mid-plastic and late plastic song ($P < 0.01$) and between late plastic and crystallized song ($P < 0.001$).

Tonal Quality

Tonal quality showed significant heterogeneity as a function of developmental stage (Fig. 2d; $F_{4,92} = 8.608$, $P < 0.001$). Throughout the first three developmental stages (SP, EP, MP), amplitude differences between notes' fundamentals and second harmonics were consistently near 30 dB. Differences significantly increased between mid-plastic and late plastic song ($P < 0.01$), and remained at about 40 dB during crystallized song.

DISCUSSION

Previous analyses of vocal development in birds have focused solely on changes in the acoustic characteristics of song (e.g. Marler & Peters 1982a, b; Clark et al. 1987). To our knowledge, ours is the first study that directly assesses the development of some aspect of motor performance associated with song production. Our data demonstrate that the motor actions underlying

song production emerge gradually during vocal development, as is the case for acoustic features of song. This finding, while not surprising, lends empirical support to the hypothesis that the protracted period of song development in songbirds reflects a period of motor 'practice'. Our data also reveal that various mechanisms underlying the production of song develop at different rates.

The similarity of developing notes to their crystallized forms, as measured by spectrogram cross-correlation, increased more dramatically in earlier than in later stages of development (Fig. 2a). This ontogenetic trajectory is similar to that described by Clark et al. (1987) for song note development in swamp sparrows, *M. georgiana*. In contrast, average maximum beak gape values remained low throughout early stages of development and significantly increased only later, in the transition from late plastic to crystallized song (Fig. 2b). The average correlation between beak gape and acoustic frequency fluctuated but remained low across the earliest developmental stages, as would be expected given that the birds moved their beaks little or not at all when singing during these stages. The gape-frequency correlation then significantly increased in the transitions from mid-plastic to late plastic song, and from late plastic to crystallized song (Fig. 2c). A change in the tonal quality of notes (a decrease in harmonic content) was also observed later, in the transition from mid-plastic to late plastic stages (Fig. 2d). These differing trajectories for different measures of song development suggest that the control and activity of multiple motor systems involved in song production develop independently and asynchronously.

Consider, for example, measures of song development during the mid-plastic stage. The time-varying frequency and amplitude characteristics of notes produced at this time were very adult-like, as evidenced by an average 62.9% cross-correlation similarity to their final crystallized versions (Fig. 2a). At the same stage, however, both average maximum beak gape values and average correlations between beak gape and acoustic frequency were far below the levels they later reached when song crystallized. Average maximum beak gape values remained consistently below 0.1 cm in mid-plastic song (Fig. 2b); in fact, measurable beak movements did not occur in half of the song segments analysed at this stage. We found no significant correlations between gape and acoustic frequency for those cases in which

beak motions did occur, and the mean correlation was close to zero (Fig. 2c). It is clear from these data, then, that song sparrows are able to produce notes that are almost adult-like in their acoustic fine structure, while still making minimal and uncoordinated beak movements, and before producing sounds with adult-like tonal quality.

In general, the frequency and amplitude modulations superimposed on a fundamental frequency in bird songs are most likely to be produced by variable patterns of airflow and changes in the tension of vibrating membranes in the syrinx (Greenewalt 1968; Gaunt 1987; Suthers et al. 1994; Gaunt & Nowicki, in press). These features of song, then, rely on activity of the syringeal musculature and its coordination with muscles associated with respiration. The supra-syringeal vocal tract (including the trachea, oral cavity and associated structures such as the beak) is also thought to play an essential role in song production, by modifying the tonal quality of sounds produced at the syrinx, in a fashion roughly analogous to the way in which the human vocal tract modifies sounds generated by the larynx (Nowicki & Marler 1988; Westneat et al. 1993; Gaunt & Nowicki, in press). For an adult bird to produce pure-tonal song according to this model, it must coordinate effectors that modify the physical dimensions of the vocal tract, such as muscles controlling the beak, with those governing the output of the syrinx. Acoustic resonances of the vocal tract are thought to be actively and rapidly modified to 'track' the frequency-modulated output of the syrinx. By contrast, vocal tract modulations do not appear to covary with sound amplitude consistently, as indicated by the data of Westneat et al. (1993). Our present data suggest that, in young birds, the processes of achieving an appropriate output from the syrinx and of coordinating syringeal output with vocal tract resonances proceed at different rates in the motor development of song.

The relationship that we observed between beak movements and song tonal quality is not simple, however. The transition to late plastic song is marked by a significant change in tonal quality, towards the production of more highly pure-tonal sounds (Fig. 2d). Coinciding with this change is a significant increase in the average correlation between beak gape and acoustic frequency (Fig. 2c), consistent with the hypothesis that beak movements play a causal role in determining song

tonal quality (Nowicki & Marler 1988; Westneat et al. 1993). But the average magnitude of beak movements during late plastic song is still very low, and it does not significantly increase until the transition to crystallized song (Fig. 2b). A further highly significant increase in the gape-frequency correlation also occurs in the transition from late plastic to crystallized song (Fig. 2c). Contrary to our expectations, these two changes in measures of vocal tract motor function are not matched by a concomitant change in tonal quality, which remains unchanged between late plastic and crystallized song (Fig. 2d).

Two explanations could account for this apparent discrepancy. First, coordinated beak motions may not be particularly important for the production of pure-tonal sounds. This explanation seems unlikely, given the strength of evidence from adult birds concerning the use of the beak in song production. Westneat et al. (1993) found a strong positive correlation between beak gape widths and the acoustic frequencies of sound produced in two species, swamp sparrows and white-throated sparrows, *Zonotrichia albicollis*. Similar results have been obtained in song sparrows and canaries, *Serinus canarius* (J. Podos, unpublished data). This relationship is consistent with the idea that changes in beak gape physically alter the length of the vocal tract as well as the acoustic impedance of the open end of the tract, thus modifying acoustic resonances of the tract, with wider gapes corresponding to higher frequencies and vice versa (Nowicki & Marler 1988). These observational studies are further supported by an experiment in which white-throated sparrows and swamp sparrows with their beaks temporarily immobilized produced songs that were normal in all respects except for changes in tonal quality and frequency bandwidth consistent with the loss of the ability to change vocal tract resonance properties (S. Nowicki, W. Hoese & N. Boettcher, unpublished data).

A second, more likely possibility is that other elements of vocal tract motor function also contribute, along with beak motions, to the emergence of adult-like tonal quality. Nowicki & Marler (1988) suggested, for example, that the glottal constriction of a bird's larynx may strongly influence vocal tract resonance frequencies by changing the acoustic impedance of the anterior end of the trachea. Westneat et al. (1993) emphasized that the beak is unlikely to be the only

functional component of the vocal tract involved in vocal production; it is simply the most readily observed. Thus, the offset in developmental trajectories that we observed may reflect changes in the motor activity of other effectors, such as the glottis, and their coordination with syringeal output. If so, our data suggest that other aspects of vocal tract function may also be delayed in development as compared to syringeal function.

Further refinement of beak use and coordination (most noticeably, wider gaping and a large increase in average maximum gapes during song) may continue throughout a bird's life. Preliminary observations show that older (2–3 years) wild-caught song sparrows commonly achieve maximum gapes of more than 1 cm during song production (J. Podos, unpublished data), as do wild-caught white-throated sparrows and swamp sparrows (Westneat et al. 1993). In our sample, maximum gape values only approached 0.6 cm. This result suggests that even after crystallizing songs acoustically, adult birds may continue to develop and modify beak movements, possibly without a great deal of further refinement with respect to acoustic timing and frequency modulation. Increased gape width and beak use appearing late in development and into adulthood may have other effects, such as allowing birds to produce songs with greater absolute amplitudes or improved tonal quality. We believe that the analysis of song and associated motor systems beyond the first year of development will yield additional insight into the nature of singing behaviour, and in particular into the relationship between vocal tract function and song tonal quality.

The development of coordinated beak movements is an easily observable process that may illuminate how sensory feedback can play a role in song development. It is well documented that songbirds must be able to hear themselves sing in order to develop normal song: birds deafened after exposure to song models but before they begin motor development fail to produce pure-tonal songs with normal structure (Konishi 1965; Konishi & Nottebohm 1969; Marler 1976; Slater 1989). It is likely that birds perceive and assess the tonal properties of their developing song as they do timing and frequency characteristics, and learn to adjust their vocal tract movements in order to produce highly pure-tonal songs. If so, the analysis of developing beak motions provides a direct means by which the relationship between motor

development, acoustic development and feedback mechanisms can be explored.

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