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KINEMATICS OF BIRDSONG: FUNCTIONAL CORRELATION OF CRANIAL MOVEMENTS AND ACOUSTIC FEATURES IN SPARROWS

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Summary

The movements of the head and beak of songbirds may play a functional role in vocal production by influencing the acoustic properties of songs. We investigated this possibility by synchronously measuring the acoustic frequency and amplitude and the kinematics (beak gape and head angle) of singing behavior in the white-throated sparrow (*Zonotrichia albicollis*) and the swamp sparrow (*Melospiza georgiana*). These birds are closely related emberizine sparrows, but their songs differ radically in frequency and amplitude structure. We found that the acoustic frequencies of notes in a song have a consistent, positive correlation with beak gape in both species. Beak gape increased significantly with increasing frequency during the first two notes in *Z. albicollis* song, with a mean frequency for note 1 of 3kHz corresponding to a gape of 0.4cm (a 15˚ gape angle) and a mean frequency for note 2 of 4kHz corresponding to a gape of 0.7cm (a 30˚ gape angle). The relationship between gape and frequency for the upswept third note in *Z. albicollis* also was significant. In *M. georgiana*, low frequencies of 3kHz corresponded to beak gapes of 0.2–0.3 cm (a 10–15˚ beak angle), whereas frequencies of 7–8kHz were associated with flaring of the beak to over 1cm (a beak angle greater than 50˚). Beak gape and song amplitude are poorly correlated in both species. We conclude that cranial kinematics, particularly beak movements, influence the resonance properties of the vocal tract by varying its physical dimensions and thus play an active role in the production of birdsong.

Introduction

The beautiful and intricate patterns of sound that birds produce are often accompanied by complex motions of the head, throat and beak. The consistency of these movements during birdsong suggests that cranial motions may have a functional role in sound production. The mechanisms that birds use to produce sound, however, remain relatively

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unexplored (for reviews, see Gaunt, 1987; Nowicki and Marler, 1988; Brackenbury, 1989). Most models of avian sound production (e.g. Greenewalt, 1968; Gaunt and Wells, 1973) have proposed that the acoustic characteristics of song are determined entirely by the nature of the vibration of membranes in the bird's vocal source, the syrinx. More recently, evidence from birds singing in a helium atmosphere (Nowicki, 1987) demonstrated that the resonance properties of the vocal tract, including the trachea and oral cavity, may influence the sound that is produced during song. In this paper, we analyze the cranial kinematics and acoustic features of two species of sparrow to determine whether the cranial movements of singing birds, by modifying the physical configuration of the vocal tract, may have functional consequences for avian sound production.

In songbirds (suborder Passeri, or 'oscine' birds) the syrinx is located in the thoracic cavity at the junction of the primary bronchi and the trachea (King, 1989). Airflow from the lungs is thought to induce membranes on the anterior-most medial walls of the bronchi to vibrate and thus to act as an acoustic source (Greenewalt, 1968; Stein, 1968). Several pairs of intrinsic syringeal muscles cause modified bronchial rings to rotate, changing the tension and configuration of the syringeal membranes and, in this way, modulating the acoustic characteristics of the sound produced (Miskimen, 1951). Because there are two membranes, one located in the lumen of each bronchus, and the syringeal musculature and innervation are bilaterally distinct, it has been argued that the two syringeal sides are capable of producing sound independently (Borror and Reese, 1956; Greenewalt, 1968; Nottebohm, 1971). The 'two-voice theory' was recently confirmed by Suthers (1990) in an experiment using implanted sensors to monitor airflow and sound production simultaneously in both bronchi of a singing bird.

The functional role of vocal tract elements other than the syrinx in avian sound production is less clear. Until recently, it was widely assumed that the vocal tract and its associated acoustic properties play little or no role in song production (Greenewalt, 1968; Gaunt, 1987; Brackenbury, 1989). Instead, the acoustic attributes of birdsong were thought to be generated and modulated entirely by syringeal action. This view arose in part as a consequence of the two-voice theory. It was argued that a bird's vocal tract could not be acting as an acoustic resonator because a single resonator could not support two harmonically unrelated sounds, as are often produced by the two sides of the syrinx (Greenewalt, 1968). Furthermore, analyses of the relationship between acoustic frequency and amplitude in the songs of several species failed to reveal evidence for resonances and anti-resonances predicted from models of the vocal tract acting as a tube of a given length (Greenewalt, 1968). Both arguments, however, rest on questionable assumptions. The first presumes that vocal resonances are acoustically coupled to the source, in the manner of a musical wind instrument, an assumption that is certainly not valid for human speech production (Lieberman, 1977) and is unlikely to be valid for the production of birdsong (Nowicki and Marler, 1988). The second argument assumes that the acoustic properties of the vocal tract remain static during song, a point that is debatable given the extreme motions of the head, beak and neck made by singing birds.

Direct evidence demonstrating that vocal tract resonances influence song production was obtained by recording several species of oscine birds singing in a helium-enriched atmosphere (Nowicki, 1987). The effect of replacing the nitrogen in normal air with helium is to increase the speed of sound by about 70% and thus to shift acoustic resonances to higher frequencies. If acoustic resonances play a role in avian sound production, then song should be affected in helium. Nowicki (1987) observed a conspicuous effect that included the appearance of harmonic overtones in sounds normally appearing as pure-tone whistles and a shifted emphasis to higher-frequency components in broad-band sounds, such as is observed in helium speech (Holywell and Harvey, 1964). These observations are consistent with the hypothesis that the bird's vocal tract acts as an acoustic filter or otherwise influences the relative amplitudes of overtones produced (Nowicki and Marler, 1988). Thus, we predict that the acoustic properties of the vocal tract are actively modified during song to coordinate with syringeal activity, much as the acoustic properties of the human vocal tract are modified during speech in coordination with laryngeal activity (Lieberman, 1977).

How might a songbird modify the configuration of its vocal tract in order to change its acoustic properties? If, as a first approximation, the vocal tract is modeled as a tube open at one end, there are three simple ways its acoustic resonances could be altered (Nowicki and Marler, 1988). (1) The tube could be physically lengthened or shortened, lowering or raising its fundamental resonance frequency, respectively. Songbirds could conceivably vary tracheal length through the action of the tracheolateralis muscles that run laterally on either side of the trachea (McLelland, 1989). (2) The open end of the tube could be partially occluded, increasing the effective tube length and lowering the resonance frequency. The glottis is well positioned at the anterior-most end of the trachea to perform this task. (3) Finally, the open end of the tube could be flared, shortening the effective tube length and raising the resonance frequency. By opening or closing its beak, a bird may increase or decrease the 'flare' at the end of its vocal tract. Beak gape might also influence vocal tract resonances by acting to occlude the open end of the tube. The potential of these physical changes to modulate vocal tract resonances implicates the morphology and biomechanics of the tracheal skeleton, throat musculature, larynx, beak and head as functional systems that may be involved in song production.

In this study we analyzed the kinematics of head motion during song to test the hypothesis that beak gape and head motion are functionally correlated with acoustic frequency and amplitude. Because either increasing flare or decreasing occlusion would shorten the effective tube length of the bird's vocal tract, we predict that beak gape will correlate positively with acoustic frequency if dynamic changes in vocal tract shape play a functional role in song production. We studied two closely related species of emberizine sparrows, the white-throated sparrow (*Zonotrichia albicollis*) and the swamp sparrow (*Melospiza georgiana*). The songs of these two species differ radically in their frequency and amplitude structure through time, providing a useful contrast for interpreting the functional significance of kinematic and acoustic relationships.

Materials and methods

Subjects, song descriptions and sample sizes

Five male white-throated sparrows (*Zonotrichia albicollis* Gmelin) and five male

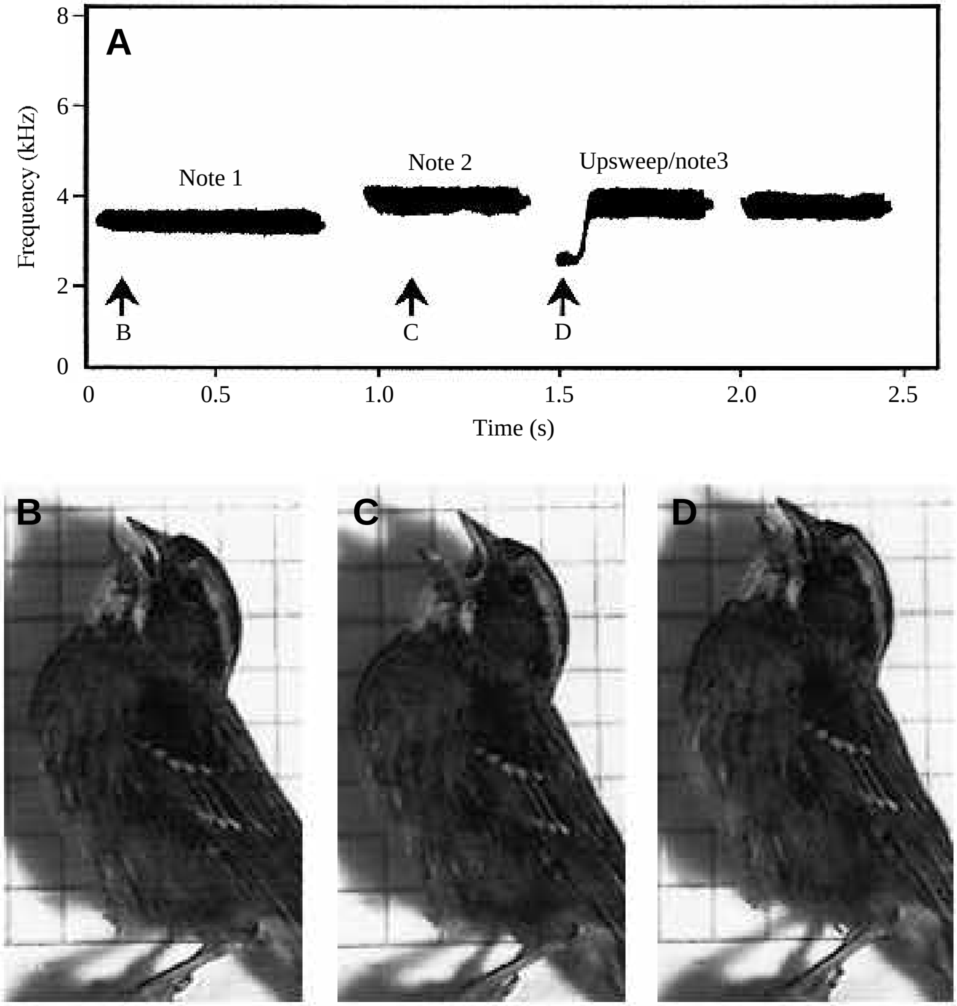

Fig. 1. Sonagram and associated video images of a white-throated sparrow song. The sonagram (A) shows the changes in frequency over time of the pure-tonal notes of the song. The first image (B) shows the partially closed beak associated with note 1, sung at a low frequency. The second image (C) illustrates the more flared beak position and more posterior head angle associated with note 2, which is sung at a higher frequency. The third image (D) corresponds to the lowest frequency at the beginning of the upsweep portion of note 3. The arrows in A mark the points in time from which video fields in B, C and D were taken.

swamp sparrows (*Melospiza georgiana* Lathan) were caught near Durham, NC, and maintained in captivity for up to 12 months. White-throated sparrows (WTS) typically sing a single song type. Swamp sparrows (SWS) may sing several different song types (Marler and Pickert, 1984). We obtained kinematic and audio data from five independent repetitions of all song types sung by each individual. Thus, 25 songs (5 individuals, 5 songs each) were analyzed for WTS, and 55 songs (5 individuals, 11 songtypes) were analyzed for SWS.

WTS songs usually consist of 4–10 pure-tone notes, each lasting up to 800ms (Fig. 1A). For the songs in our sample, the first two notes (‘note 1’ and ‘note 2’) were constant-frequency notes, the second sung at a higher frequency than the first. The third note began with a pronounced frequency modulation (‘upsweep’), starting at a lower frequency than note 1 and ending at the same frequency as note 2, and then remained constant at this higher frequency. One bird did not sing the upsweep portion of note 3, but instead sang only the constant high-frequency portion of this note. Following the first three notes, the birds added a variable number (1–7) of constant-frequency notes at the same frequency as the second and third notes. We present data from the first two notes of WTS song (N=25 for each) and the upsweep portion of the third note (N=20) because these notes encompass the majority of variability in acoustic and kinematic behavior in the WTS songs in our sample.

SWS songs consist of a series of repeated syllables. Each syllable is composed of several short notes (20–40ms), most of which are rapid, pure-tonal frequency sweeps (Fig. 2A). All SWS notes can be classified into six note types on the basis of duration and frequency variation and these types are universal for the species (Marler and Pickert, 1984; Clark *et al.* 1987). Different song types are produced by combining the same six note types in different orders. We used an established method of note type identification (Marler and Pickert, 1984; Clark *et al.* 1987) to classify SWS note types. We present data from note types II, V and VI, chosen because of their prevalence in our sample and their relatively long duration. Note type II was sung by four birds in a total of nine song types, with five replicates for each song type (N=45 total). Likewise, seven song types sung by four birds included note type V (N=35) and six song types sung by four birds included note type VI (N=30).

Kinematic recording and analysis

Singing birds were videotaped in cages (21.5cm wide×23cm high×23cm deep) with Plexiglas fronts. A single perch was oriented such that birds would sing in profile, at a right angle to the camera. A 1-cm^2 grid was placed immediately behind the perch for measurement calibration. Birds were videotaped using a Panasonic S-VHS AG-450 camera at 60 fields per second with a shutter speed of 1/1000s. Video images were transferred from S-VHS format to U-Matic SP format using a JVC HR-56600U recorder and a Sony U-Matic SP VO-9600 recorder. A time base corrector (Digital Processing Systems Inc., TBC/Framestore DPS-275) was used to maintain image alignment during transfer between formats. Time code images were overlaid at 1/60s using a Horita TH 162550 time code generator.

Video fields were examined by overlaying the computer image onto each video image and marking selected points with an on-screen cursor. Video tapes were played on a Sony BVU-920 U-Matic SP video cassette player with dynamic tracking, time base corrected, and interfaced with a Commodore Amiga 3000 computer and Commodore A2300 genlock board. The coordinates of the following four points were collected from each video field analyzed (Fig. 3): (*a*) the tip of the lower bill, (*b*) the tip of the upper bill, (*c*) the point at which the upper and lower bills meet, and (*d*) the back of the eye. Three kinematic variables were calculated from these coordinate data: (1) gape distance (Fig. 3:

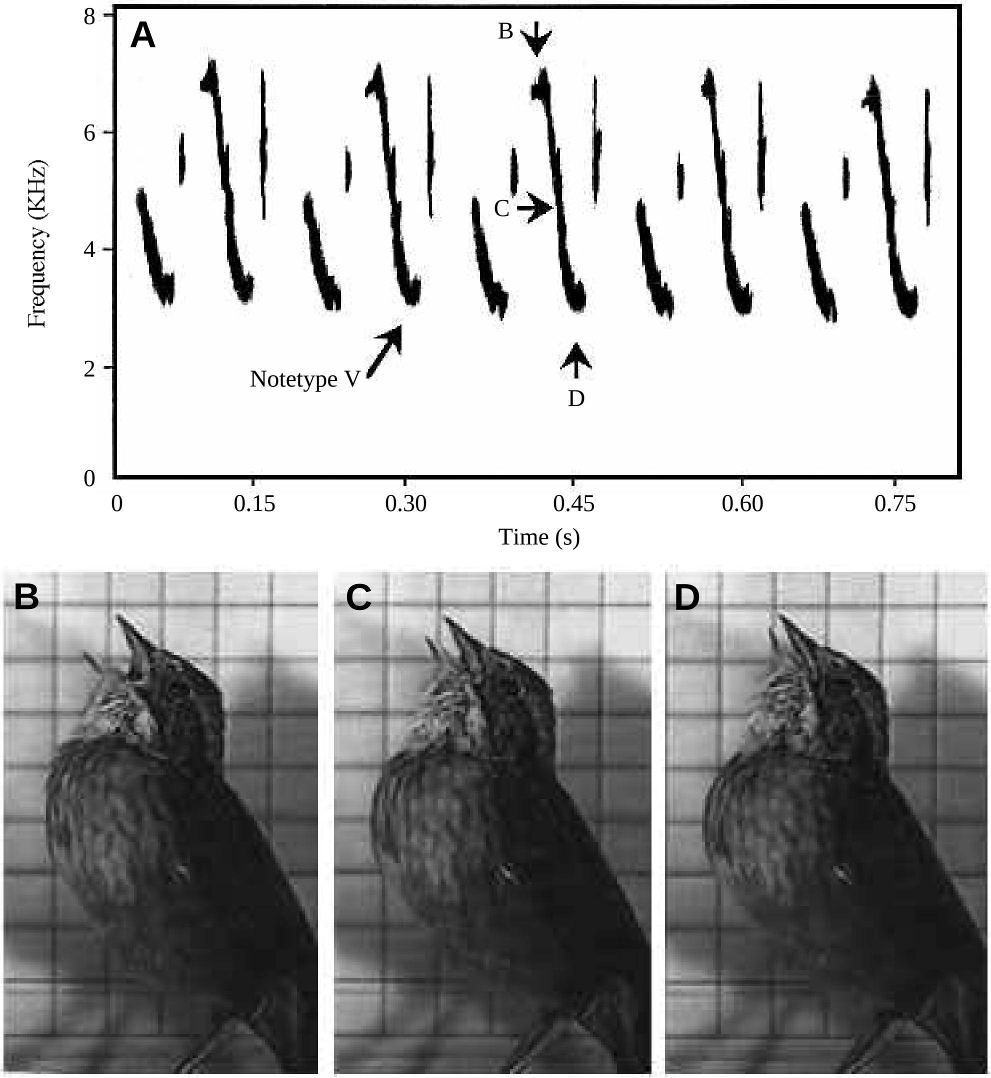

Fig. 2. Sonagram and associated video images of a swamp sparrow song. The sonagram (A) illustrates five repetitions of a four-note syllable, each note being a rapid frequency sweep. The first video image (B) shows the wide beak gape associated with the high frequency at the start of a note type V. The second and third images (C and D) illustrate the progressive closure of the beak as the note sweeps down to a lower frequency. The arrows in A identify the type V note in the repeating syllable and mark the points in time from which video fields in B, C and D were taken.

distance *a*–*b*), (2) gape angle (Fig. 3: angle *acb*) and (3) head angle (Fig. 3: angle between line *bd* and horizontal line *e*). Video analysis of each song involved digitizing 150–250 video fields, for a combined total of over 13000 video fields analyzed.

Audio recording and analysis

As they were videotaped, birds' songs were simultaneously recorded onto one channel

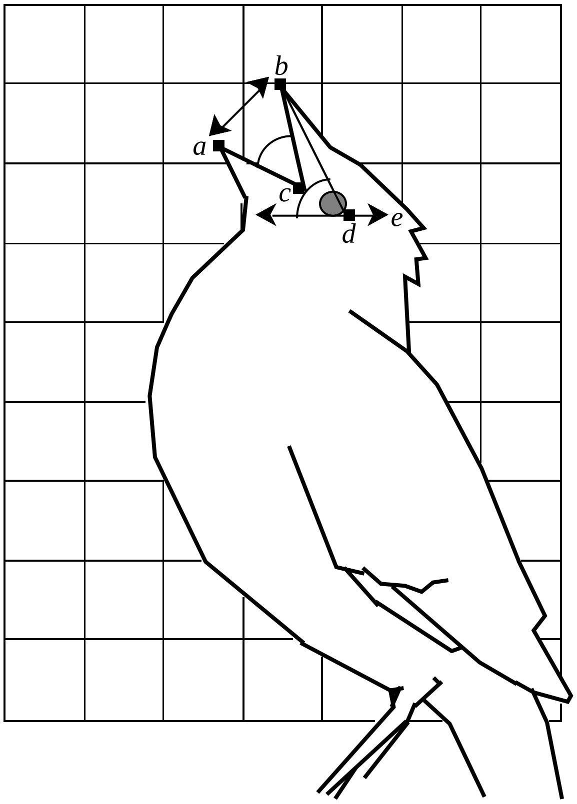

Fig. 3. Diagram of coordinates digitized from the video images of singing birds. Kinematic variables of interest are beak gape (line *ab*), gape angle (angle *acb*) and head angle (angle between line *bd* and the horizontal line *e*).

of a stereo tape recorder (Realistic 33-1070 microphone, Sony TC-D5M cassette recorder). The audio recording system had a frequency response of 40Hz–17kHz, ±3dB, with a signal-to-noise ratio of 58dB at peak level. To synchronize the video and audio records, a square-wave generator (Krohn-Hite 1200A) was used to record an electronic click every 500ms on the other channel of the audio tape. The square wave simultaneously powered a light-emitting diode (LED) placed in the frame of the video camera, turning it on, then off, every 500ms. The simultaneous electronic record on the audio track and on the video tape was used to align the two data sets in time.

Audio recordings of songs were digitized at 22.5×10^3 points s^{-1} (Data Translation 2821-F A/D board) using ‘SIGNAL’ digital signal processing software (Engineering Design) on an Intel 486-based microprocessor (Dolch Computer Systems), and stored on disk for analysis. Before digitizing, song recordings were high-pass filtered at 900Hz (Krohn-Hite model 3500, 24dB per octave), to suppress low-frequency background noise, and low-pass filtered at 10kHz (Stanford Research Systems model 640, 115dB per octave), to prevent aliasing.

Using the synchronizing click that immediately preceded the onset of a song as a starting reference, frequency and amplitude information were sampled from the audio data every 1/60s. A macro written in the SIGNAL programming language automatically calculated appropriate sample times and recalibrated synchronization with every 500ms reference click. A digital spectrogram of the song was calculated and displayed with appropriate sample times marked, and an on-screen cursor was used to measure the center frequency of each time point in the song that corresponded to a video frame.

Because of the different frequency modulation rates observed in WTS and SWS songs, different analysis parameters were used for each species. A 256 point discrete Fourier transform (DFT) was used for WTS songs (frequency resolution 88Hz, time resolution 11.4ms) and a 64 point DFT was used for SWS songs (frequency resolution 352Hz, time resolution 2.8ms). At each sample point, the root mean square amplitude was calculated automatically from the original time domain data. Additionally, the onset and offset times of each separate note (relative to the 1/60s sample time points) were measured from the digital spectrogram. The maximum amplitude in a signal was normalized to 0dB with other amplitudes reported as negative dB relative to this reference.

Data presentation and statistics

Our main goal was to test the hypothesis that acoustic features of the sound produced were predictable from cranial kinematics. To this end, we calculated regressions between kinematic and acoustic measurements taken from song notes with time-varying acoustic characteristics (i.e. the WTS upsweep and all SWS notes) or between notes with different acoustic characteristics (i.e. WTS notes 1 *versus* note 2). Least-squares regression was used even though both variables contained error, because our hypothesis is that kinematic variables (beak gape and head angle) predict acoustic variables (frequency and amplitude). A significance level of 0.01 was used as the criterion for a significant regression line, because the degrees of freedom were inflated by retaining multiple measures through time within the same notes.

Our second goal was to describe the covariation of kinematics and acoustics at each of the different levels at which variation might occur: between different songs of the same type, different note types, different song types, individuals and species. Analyses of variance (ANOVAs) on the slopes of regressions were used to test for differences within and between groups. Data sets were found to satisfy conditions of normality prior to statistical tests. All statistics were performed using SYSTAT 5.1 (Wilkinson, 1991).

White-throated sparrow

Using mean data from notes 1 and 2 and the constant-frequency portion of the third note in each WTS song, a multivariate analysis of variance (MANOVA) and separate univariate ANOVAs were performed on the frequency, amplitude, gape and head angle variables, with note type (three levels) and individual (five levels) as the main effects (N=75). This analysis allowed us to estimate the variability in acoustic and kinematic variables between the different note types and between different individuals producing the same note type.

Regression equations were obtained for four pairs of variables for each WTS song (five songs by five individuals): (1) frequency (dependent variable) by gape (independent variable), (2) amplitude (dependent) by gape (independent), (3) frequency (dependent) by head angle (independent) and (4) amplitude (dependent) by head angle (independent). The four regression equations were produced from two data sets from each song: the combined data of notes 1 and 2 and the upsweep portion of the third note.

Swamp sparrow

Because SWS notes are short in duration, the 60Hz video sample rate often captured only one or at most a few points within a single note. We used the repetitive nature of syllables within SWS songs to construct a picture of the kinematics of each note by ‘overlaying’ all the syllables in a song, using the onset time of the first note in each syllable to align the data. Thus, our view of the structure of SWS note types and song types is a composite one, averaged across all the repeated syllables in a song. Notes of very short duration (e.g. type I notes of 12ms or less; Marler and Pickert, 1984) were not represented accurately owing to the time base error in synchronization of audio and video, and thus are not included in our analysis.

We present data from SWS note types II, V and VI. To test the hypotheses that song frequency and amplitude are dependent upon kinematics, we calculated least-squares regression equations for note types II, V or VI in each SWS song in which they occurred. As with the WTS data, regressions describing kinematic/acoustic relationships were performed for each note type.

Levels of variation in kinematic/acoustic relationships

We tested for species differences, note type differences within species, and song type or individual differences within note type. To achieve this, the slopes of significant regressions between acoustics and kinematics were used in an overall nested ANOVA. Slopes of regression lines were used instead of the pooled data for a note type because combining the data sets artificially inflates the degrees of freedom due to multiple measures of variables through time within notes. In this analysis, the main effect was a comparison of the mean frequency/gape slope between species. Note types were nested within species, so that variances among the three SWS note types, and between WTS notes 1 and 2 and the WTS upsweep, were tested. Within note type was nested the effect of song type for the SWS and individual for the WTS.

Error estimates

The S-VHS video images had 525 lines vertical and 400 lines horizontal resolution. Error due to camera parallax was less than 0.01cm (standard deviation, N=5). Experimentor error in selecting screen coordinates for kinematic points ranged from a standard deviation (N=3) of 0pixels (0cm) for the tip of the bill to 1.2pixels (0.02cm) for the rear of the eye. Experimentor error in selecting screen coordinates for frequency and time measurements was much smaller than the theoretical resolution of the DFT analysis (above). Error was also associated with the synchronization of audio and video data. Detection of the synchronizing signal was accurate to within 0.02ms for the audio data, but to within 16.7ms for the video data. The timing of the square-wave signal from the audio track was used in synchronization, allowing us to reduce that error to about 8ms.

However, a conservative estimate of the error in synchronization of the audio and video tracks is one video field (16.7ms).

Results

Our results reveal consistent and significant positive correlations between acoustic frequency and beak gape for both sparrow species. Frequency and head angle were not consistently correlated in the time-varying frequency sweeps of SWS note types or the WTS upsweep, but were significantly correlated between WTS notes 1 and 2. Consistent correlations between acoustic amplitude and beak gape were observed only for the WTS upsweep note, and no consistent relationships were observed between amplitude and head angle.

Acoustic and kinematic patterns during song

Repetition of the same song type by the same bird appeared to be stereotypic in acoustic and kinematic pattern, and there were striking acoustic differences between the songs of the two sparrow species (Figs 1 and 2, Table 1). The duration of individual notes was an order of magnitude longer in WTS song than in SWS song. The frequency mean and range were greater for SWS notes than for WTS notes. The amplitudes of WTS notes varied, with that for note 2 being greater than that for note 1 and the upsweep. The SWS note types were of approximately equal amplitudes.

Kinematic analysis revealed a high degree of stereotypy in the motions associated with song production as well as pronounced species differences between WTS and SWS (Table 1). WTS produced their songs with modest body movements, whereas the SWS seemed to erupt into song with rapid head, beak and body movements. Interestingly, the maxima of kinematic variables were strikingly similar for the two species. Both WTS and SWS opened the beak to a maximum gape of over 1cm in all notes, corresponding to a beak angle of approximately 50˚ (Table 1). The beak was held open during the WTS notes, and the bird remained largely stationary, although beak gape occasionally dropped to near zero between notes and to a lesser degree during amplitude drops within a note (e.g. Fig. 4). In contrast to the WTS, the beak movements of the SWS was a blur in real time as the rapid series of frequency sweeps was produced. In spite of the rapidity of these movements, it was clear from video analysis that rapid opening and closing of the beak tracked the patterns of sound produced (Fig. 5).

The WTS tilted the head back when singing with the beak pointing upwards at a maximum angle of 60–80˚ to the horizontal (Table 1). Head angle often changed abruptly during or between notes (Fig. 4). The head of the SWS tilted back to a maximum of about 70–90˚ to the horizontal during song. Unlike the WTS, SWS head angle varied continuously, with minima at the start and end of a song and a maximum somewhere in the middle (Fig. 5).

Kinematic correlates of acoustic features

The degree to which cranial kinematics correlated with aspects of sound production in the two species is apparent in the primary data (Figs 2–5). For the WTS, an increase in frequency between notes 1 and 2 or in the frequency upsweep note (Fig. 4A) clearly

Table 1. *Summary of acoustic features and descriptive kinematics of birdsong production in white-throated sparrows (WTS) and swamp sparrows (SWS)*

	Mean	S.D.	Minimum	Maximum	Range
Note duration (ms)					
WTS note 1 (*N*=25)	837.8	99.0	636.5	947.3	310.8
WTS note 2 (*N*=25)	521.0	137.8	266.9	709.3	442.4
WTS upsweep (*N*=20)	120.9	22.2	83.4	150.1	66.7
SWS note type II (*N*=650)	23.1	14.4	9.0	66.0	57.0
SWS note type V (*N*=627)	36.5	11.9	18.8	66.0	47.2
SWS note type VI (*N*=558)	18.4	2.7	10.6	25.3	14.7
Note frequency (Hz)					
WTS note 1	3312	493	2602	4204	1602
WTS note 2	3944	597	3299	5284	1985
WTS upsweep	3130	546	1905	4030	2125
SWS note type II	4696	734	3080	6109	3029
SWS note type V	4481	1183	3010	7711	4701
SWS note type VI	5331	873	3637	7677	4040
Note amplitude (dB)					
WTS note 1	−9.1	6.4	−26.4	0.0*	26.4
WTS note 2	−5.5	5.8	−26.4	0.0	26.4
WTS upsweep	−12.3	8.9	−26.4	0.0	26.4
SWS note type II	−9.0	6.7	−30.4	0.0	30.4
SWS note type V	−7.5	6.7	−31.2	0.0	31.2
SWS note type VI	−8.7	6.5	−33.9	0.0	33.9
Beak gape (cm)					
WTS note 1	0.4	0.3	0.0	1.1	1.1
WTS note 2	0.7	0.2	0.1	1.2	1.1
WTS upsweep	0.5	0.3	0.1	1.1	1.0
SWS note type II	0.8	0.1	0.3	1.1	0.8
SWS note type V	0.7	0.2	0.2	1.1	0.9
SWS note type VI	0.8	0.2	0.3	1.1	0.8
Beak gape angle (degrees)					
WTS note 1	16.6	11.0	0.0	47.4	47.4
WTS note 2	29.5	10.5	5.4	54.5	49.1
WTS upsweep	23.2	12.1	0.0	47.2	47.2
SWS note type II	35.8	6.6	11.4	51.7	40.3
SWS note type V	29.5	9.2	7.8	51.3	43.5
SWS note type VI	35.7	7.1	13.4	50.8	37.4
Head angle (degrees)					
WTS note 1	36.5	10.5	1.5	60.8	59.4
WTS note 2	51.7	10.4	22.9	82.2	59.3
WTS upsweep	50.5	9.8	35.6	74.8	39.1
SWS note type II	42.9	15.1	3.0	85.4	82.4
SWS note type V	55.3	13.2	0.7	87.6	86.8
SWS note type VI	40.7	16.5	4.7	72.8	68.1

*Maximum amplitude is 0dB by definition (see Materials and methods).

Mean values are more relevant for constant frequency WTS notes 1 and 2, whereas ranges are more relevant for frequency sweeps of WTS and SWS.

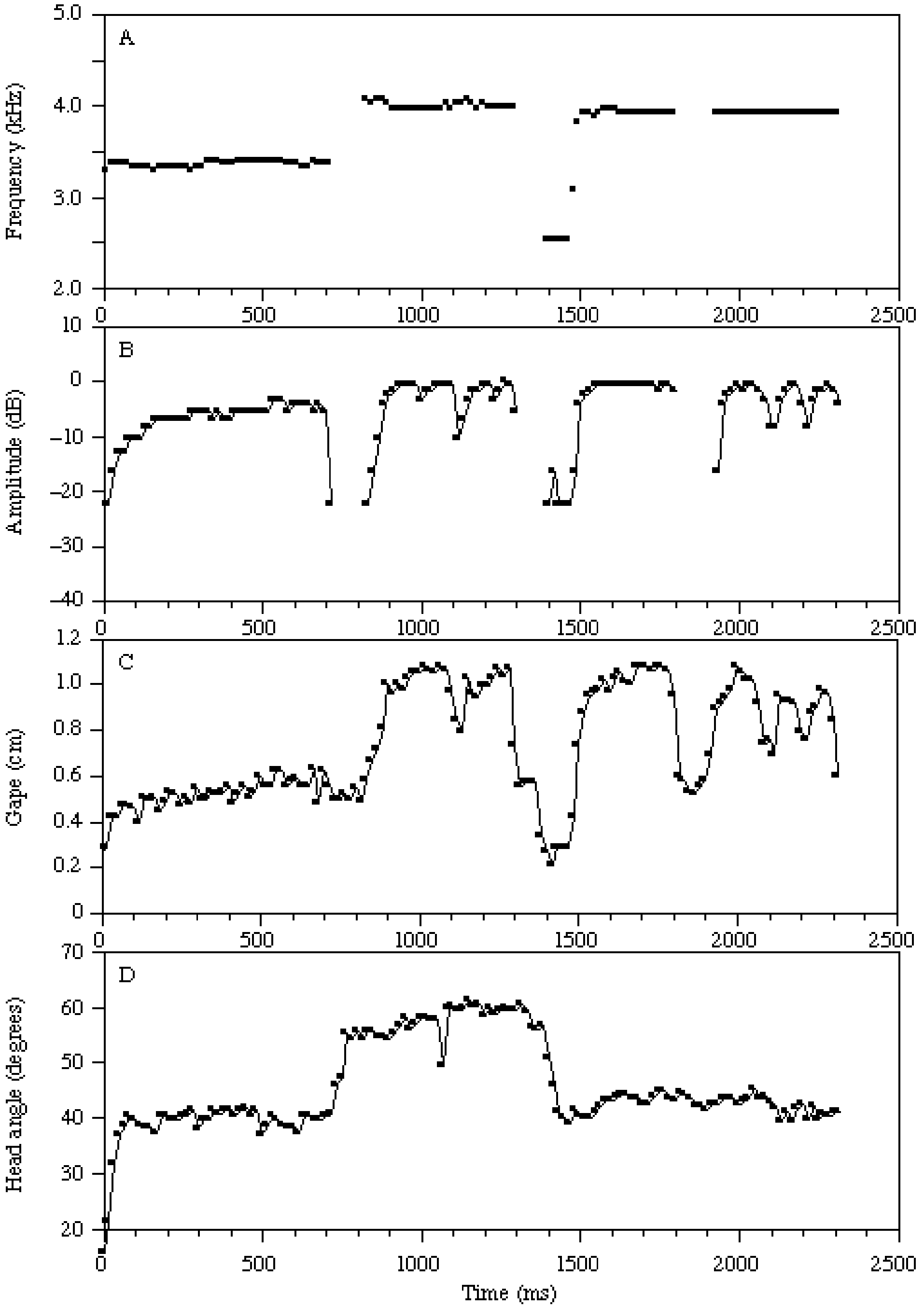

Fig. 4. Profile of acoustic and kinematic variables of a single white-throated sparrow song. Data points are sampled every video field or 16.7ms. (A) Frequency of notes; (B) amplitude of notes; (C) gape distance of beak; and (D) head angle.

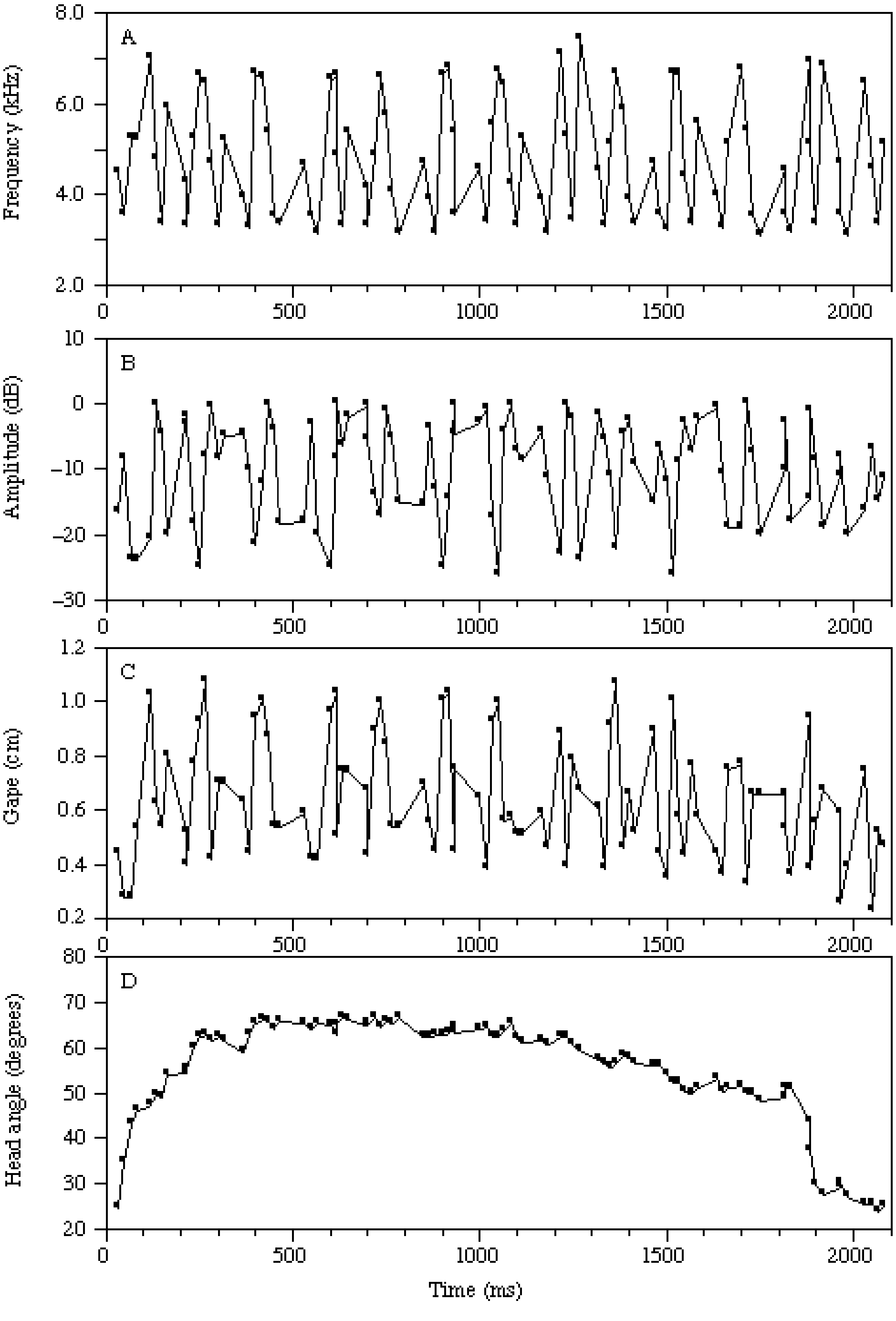

Fig. 5. Profile of acoustic and kinematic variables of a single swamp sparrow song. Data points are sampled every video field or 16.7ms. (A) Frequency of notes; (B) amplitude of notes; (C) gape distance of beak; and (D) head angle.

corresponded to an increase in gape (Fig. 4C). Head angle in the WTS (Fig. 4D) also increased during the transition from production of the low-frequency note 1 to the higher-frequency note 2. For the SWS, frequency maxima (Fig. 5A) corresponded closely with peaks in gape (Fig. 5C). Maxima and minima in amplitude (Fig. 5B) were offset from gape and frequency, and head angle (Fig. 5D) appeared to be uncorrelated with sound production other than increasing at the beginning and decreasing at the end of the song. The strong relationship between song frequency attributes and beak gape in SWS is most clear when kinematic data for all the syllables in a song are overlaid to gain a picture of the average syllable (Fig. 6). Frequency upsweeps such as note type II (Fig. 6A) were correlated with increasing beak gape, whereas frequency downsweeps such as note type V (Fig. 6B) and note type VI (Fig. 6A) were associated with decreasing beak gape.

We used ANOVAs to test two hypotheses: (1) the kinematic and acoustic variables of WTS note 1 (a low-frequency note) are different from those of the higher-frequency notes 2 and 3, and (2) WTS individuals differ significantly in the kinematics and acoustics of their songs. A highly significant effect of both note type and individual was found for all variables by both the univariate ANOVA and the MANOVA, supporting the two hypotheses above. *Post-hoc* comparisons showed that note 1 was significantly different from both note 2 and note 3 in all variables, but that note 2 and the constant portion of note 3 were not significantly different.

To test whether relationships between kinematic and acoustic variables were significant, separate regression analyses were performed on data from each of the frequency sweep notes from both species and on the combined data from WTS notes 1 and 2. In these tests, frequency and amplitude (dependent variables) were regressed against beak gape (Table 2) and head angle (Table 3) as the independent variables. Beak gape angle was not analyzed because it had the same pattern as beak gape. Increased beak gape was significantly associated with increased frequency between the first two notes of WTS song in all cases but one (WTS 4), with an average frequency for note 1 of about 3300Hz corresponding to a gape of about 0.4cm (a 15˚ angle) and an average frequency for note 2 of about 3950Hz corresponding to a gape of about 0.7cm, a 30˚ angle (Table 1). The regression between beak gape and frequency for the upsweep of the third note also was significant in every case. There was no consistent relationship between gape and amplitude for notes 1 and 2 in WTS song. Amplitude was significantly correlated with gape, however, during the WTS upsweep in all four cases (Table 2).

The transition from note 1 to note 2 in WTS song was accompanied by an increase in head angle, which was a significant predictor of note 1 and 2 frequencies in the regression analysis for four out of five birds (Table 3). Head angle did not similarly correlate with frequency in the upsweep, however, and it often returned to the lower angle for the constant-frequency portion of the third and subsequent notes, even though the acoustic frequencies of these notes were the same as for note 2 (e.g. Fig. 4D). Finally, there was no consistent relationship between head angle and amplitude in WTS song.

Beak gape also was a strong predictor of acoustic frequency for all three SWS note types (Table 2), despite the rapidity of frequency changes in these notes compared with WTS notes (e.g. Fig. 6). Low frequencies of about 3kHz corresponded to beak gapes of 0.2–0.3 cm (10–15˚ angle), whereas higher frequencies in the range of 7–8kHz were

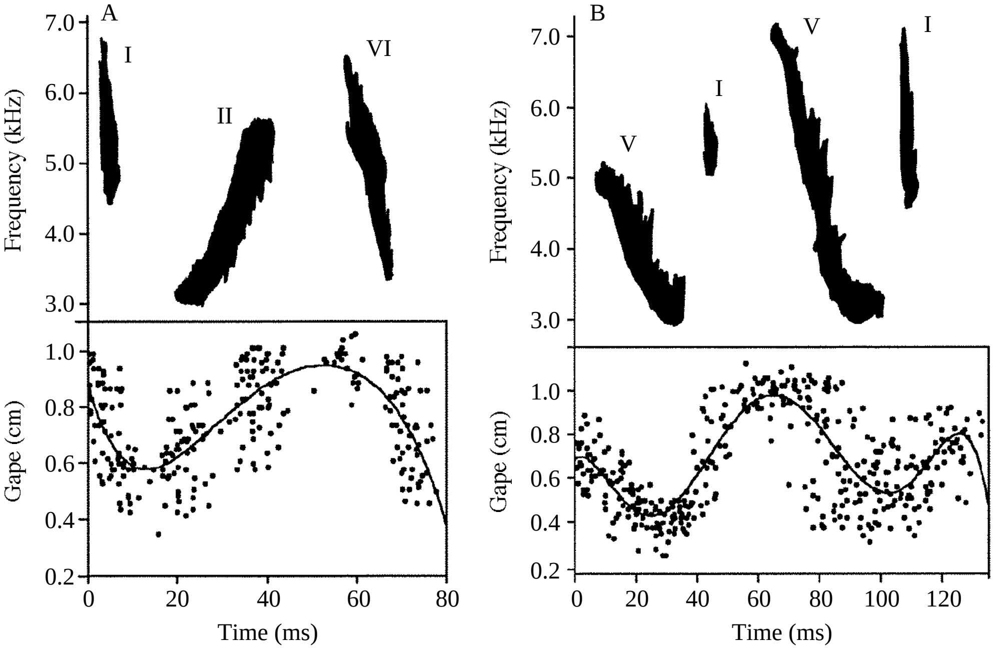

Fig. 6. Summary plots of ‘averaged’ swamp sparrow songs illustrating the relationship between acoustic frequency and beak gape for two song types. (A) Sonagram of one syllable of a song containg note types I–II–VI. The plot of gape distance over time includes the summed data from 15 consecutive repetitions of the syllable from a single song. Note the increase in gape during the note type II upsweep and the decrease in gape during the note types I and VI downsweeps. (B) Sonagram of one syllable of a song containing note types V–I–V–I. The plot of gape distance over time includes the summed data from 15 consecutive repetitions of the syllable from a single song. Note the decrease in gape associated with decreasing frequency in both type V notes.

associated with flaring of the beak to a distance of over 1cm, or over 50° (Table 1). Only three cases in the SWS data set failed to show significant association between gape and frequency (two type IIs and one type V, Table 2). The relationship between beak gape and amplitude in SWS note types was inconsistent. Although nine out of 22 total cases showed a significant regression, four of these had positive slopes while five had negative slopes. Head angle was not a good predictor of either frequency or amplitude in SWS notes (Table 3). Six cases out of 22 showed a significant relationship between head angle and amplitude, but three of these had a positive slope while the other three had a negative slope.

Pooling data across all WTS notes, there is a strong correlation between frequency and beak gape (Fig. 7A, r^2=0.71) and no correlation between amplitude and gape (Fig. 7B, r^2=0.03) for WTS notes 1 *versus* 2. The pooled data for the WTS upsweep reveal a strong correlation between frequency and gape (Fig. 7C, r^2=0.79) and a weaker correlation between amplitude and gape (Fig. 7D, r^2=0.51). The results for SWS note types II, V and VI, pooled across all songs in which that note occurred, showed strong positive correlations between frequency and gape, but the correlation between amplitude and gape was not significant for any of the three notes (Fig. 8).

Table 2. *Results of regression analyses of frequency (dependent variable) against beak gape (independent variable) and amplitude (dependent variable) against beak gape (independent variable) for notes 1 and 2 and the frequency upsweep of the third note in white-throated sparrows (WTS) and note types II, V and VI in swamp sparrows (SWS)*

	Frequency × gape				Amplitude × gape			
Bird	Slope	*y*-intercept	r^2	*F*-ratio	Slope	*y*-intercept	r^2	*F*-ratio
WTS note 1–2								
WTS 1	1563.9	2665.4	0.85	44.1*	13.9	−17.2	0.54	9.5*
WTS 2	1624.9	2502.3	0.99	933.5*	1.3	−3.6	0.10	0.9
WTS 3	1773.7	2696.0	0.94	115.6*	−12.9	−3.1	0.29	3.2
WTS 4	651.7	4052.7	0.04	0.3	−4.2	−4.5	0.03	0.2
WTS 5	1268.3	2799.4	0.98	388.9*	16.7	−19.2	0.87	51.4*
WTS upsweep								
WTS 1	1356.7	2599.4	0.73	69.1*	15.1	−15.9	0.27	9.8*
WTS 2	2056.2	1946.0	0.89	252.8*	37.1	−31.6	0.66	65.3*
WTS 3	2581.9	2018.9	0.76	113.0*	30.0	−25.5	0.46	30.4*
WTS 5	1823.9	2087.4	0.86	266.9*	22.5	−26.9	0.63	75.3*
SWS type II								
SW1 type II	5677.7	−242.2	0.61	385.0*	39.1	−42.3	0.21	66.8*
SW2 type II(a)	1408.9	3035.2	0.44	158.1*	−1.3	−9.0	0.00	0.3
SW2 type II(b)	−14.1	5431.4	0.00	0.0	−11.1	−8.9	0.13	7.8*
SW2 type II(c)	192.1	3151.8	0.21	17.4*	0.5	−20.1	0.00	0.0
SW3 type II(a)	−132.0	6397.9	0.00	0.5	10.2	−17.3	0.02	1.9
SW3 type II(b)	2507.2	3431.9	0.41	133.9*	16.8	−19.6	0.11	25.2*
SW3 type II(c)	1336.0	3418.6	0.14	13.8*	6.3	−13.4	0.02	1.6
SW4 type II(a)	2439.3	2745.2	0.14	14.7*	−10.1	4.1	0.04	3.6
SW4 type II(b)	811.3	4639.9	0.15	34.5*	14.6	−21.7	0.07	15.4*
SWS type V								
SW1 type V	4574.5	630.4	0.40	90.2*	−19.6	7.5	0.04	6.3*
SW3 type V	1422.0	2910.5	0.45	150.3*	4.6	−8.4	0.03	6.5*
SW4 type V	−3.4	3930.1	0.00	0.0	−0.8	−10.7	0.00	0.1
SW5 type V(a)	3145.9	2198.1	0.56	183.9*	−1.9	−6.7	0.00	0.3
SW5 type V(b)	4767.7	1426.4	0.61	342.8*	−11.8	−0.4	0.12	31.1*
SW5 type V(c)	4470.1	1950.5	0.49	251.1*	−4.5	−4.0	0.02	4.8
SW5 type V(d)	4889.6	1172.5	0.53	265.1*	−6.3	−2.5	0.04	9.3*
SWS type VI								
SW1 type VI	5744.5	97.5	0.35	37.1*	7.3	−16.3	0.01	0.4
SW2 type VI(a)	3729.0	2256.0	0.54	140.6*	−7.5	−3.7	0.03	4.1
SW2 type VI(b)	2090.5	3615.1	0.41	75.4*	0.0	−8.3	0.00	0.0
SW3 type VI	3701.0	2968.0	0.42	81.6*	−6.4	−5.8	0.03	3.3
SW4 type VI(a)	5711.2	560.1	0.44	86.7*	−13.6	4.5	0.07	9.0*
SW4 type VI(b)	5698.7	468.0	0.47	156.9*	−0.7	−6.7	0.00	0.0

For SWS songs, types (a), (b) and (c) indicate the same note type from different song types.
Each regression was performed on data from five pooled songs (**P*<0.01).

Table 3. *Results of regression analyses of frequency (dependent variable) against head angle (independent variable) and amplitude (dependent variable) against head angle (independent variable) for notes 1 and 2 and the frequency upsweep of the third note in white-throated sparrows (WTS) and note types II, V and VI in swamp sparrows (SWS)*

	Frequency × head angle				Amplitude × head angle			
Bird	Slope	*y*-intercept	r^2	*F*-ratio	Slope	*y*-intercept	r^2	*F*-ratio
WTS note 1–2								
WTS 1	28.99	2182.0	0.28	3.14	0.53	−33.02	0.75	23.91*
WTS 2	25.09	1857.1	0.58	11.25*	0.01	−3.77	0.03	0.22
WTS 3	21.64	2361.2	0.77	26.22*	−0.24	2.91	0.54	9.55*
WTS 4	38.50	3305.8	0.46	6.76*	0.06	−10.06	0.02	0.15
WTS 5	15.84	2954.9	0.40	5.31*	0.18	−16.19	0.26	2.82
WTS upsweep								
WTS 1	14.53	2734.9	0.12	3.63	0.07	−9.63	0.01	0.21
WTS 2	16.73	1873.2	0.02	0.83	0.26	−30.45	0.01	0.47
WTS 3	−7.29	3306.8	0.01	0.41	0.06	−17.03	0.00	0.11
WTS 5	0.66	3180.5	0.00	0.00	0.09	−16.98	0.00	0.11
SWS type II								
SW1 type II	3.88	4444.2	0.00	0.61	0.12	−14.87	0.02	4.58
SW2 type II(a)	−3.76	4274.7	0.01	2.29	−0.19	−0.21	0.10	23.29*
SW2 type II(b)	7.19	4990.8	0.20	12.84*	−0.03	−14.37	0.00	0.05
SW2 type II(c)	3.34	3071.7	0.05	3.49	−0.33	0.21	0.10	7.34*
SW3 type II(a)	5.31	6065.8	0.09	8.10*	0.14	−15.67	0.04	3.55
SW3 type II(b)	−2.71	5492.4	0.00	0.86	0.11	−11.83	0.05	9.53*
SW3 type II(c)	7.15	4082.2	0.04	3.93	0.06	−11.71	0.02	1.88
SW4 type II(a)	5.96	4601.5	0.00	0.22	0.23	−9.89	0.06	5.31
SW4 type II(b)	3.75	5259.2	0.01	1.10	0.29	−15.70	0.05	10.46*
SWS type V								
SW1 type V	0.97	4521.7	0.00	0.06	0.00	−9.30	0.00	0.00
SW3 type V	−2.11	3913.8	0.00	0.72	0.07	−8.30	0.03	5.14
SW4 type V	1.58	3888.2	0.01	1.45	0.06	−12.56	0.00	0.55
SW5 type V(a)	2.33	3670.9	0.00	0.35	0.03	−9.55	0.00	0.60
SW5 type V(b)	3.15	4778.9	0.00	0.14	0.01	−8.49	0.00	0.05
SW5 type V(c)	7.26	4350.0	0.00	0.82	0.04	−8.79	0.00	0.75
SW5 type V(d)	0.67	4555.1	0.00	0.01	0.09	−12.49	0.03	6.06*
SWS type VI								
SW1 type VI	14.08	4242.3	0.02	1.08	0.20	−20.19	0.03	2.42
SW2 type VI(a)	7.37	4841.9	0.01	0.91	−0.21	1.41	0.09	11.85*
SW2 type VI(b)	9.37	4505.3	0.01	0.42	0.02	−9.26	0.00	0.02
SW3 type VI	12.08	5036.4	0.02	2.02	0.03	−9.12	0.00	0.24
SW4 type VI(a)	−9.42	5940.9	0.00	0.23	0.14	−11.20	0.01	1.61
SW4 type VI(b)	−1.32	5337.1	0.00	0.02	0.08	−9.20	0.01	0.88

For SWS songs, types (a), (b) and (c) indicate the same note type from different song types.
Each regression was performed on data from five pooled songs (*$P<0.01$).

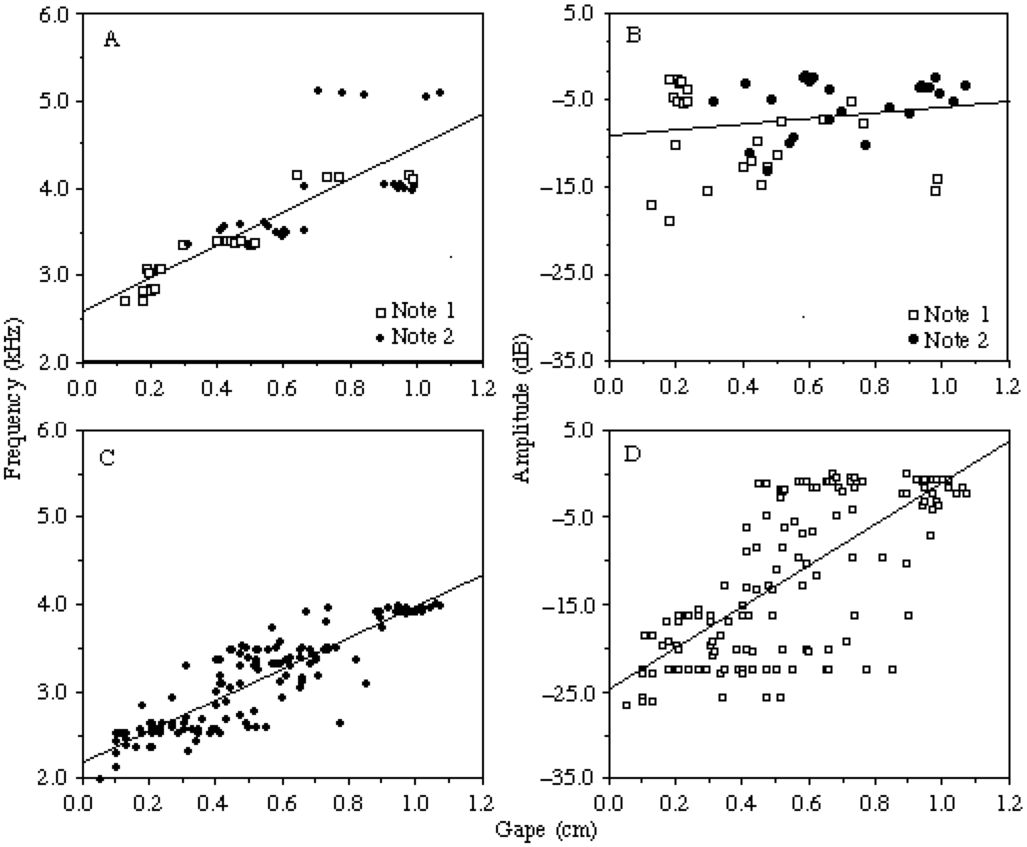

Fig. 7. Summary plots of beak gape as a predictor of frequency and amplitude in the white-throated sparrow. (A) The change in frequency from note 1 to note 2 is accurately predicted by the flaring of the beak, although there is overlap among different birds (y=1904x+2575, r^2=0.71, P<0.01). (B) Changes in beak gape during notes 1 and 2 are not closely associated with amplitude (y=3.0x−8.9, r^2=0.04, P=0.19). (C) The increase in frequency during the upsweep of note 3 is accurately predicted by the flaring of the beak (y=2184x+1807, r^2=0.79, P<0.001). (D) The upsweep note also shows a significant relationship between beak gape and amplitude (y=23.7x−24.7, r^2=0.51, P<0.001).

Levels of variation in kinematic/acoustic relationships

The set of significant regression slope data from the above analysis of gape and acoustic frequency was pooled in a nested ANOVA (Table 4) that tested for species differences and for effects due to note type within species and for song type or individual within note type. The WTS data were the slopes of the frequency/gape regression lines of notes 1 *versus* 2, and the upsweep; the SWS data set consisted of the slopes of the frequency/gape regressions of note types II, V and VI. There was a highly significant difference between species in the frequency/gape relationship, and a highly significant effect of note type (Table 4). *Post-ho*c comparisons of note types revealed that the regression slopes of each note type were different from all others, except that SWS type II was found not to be different from the WTS upsweep. A significant effect of song type

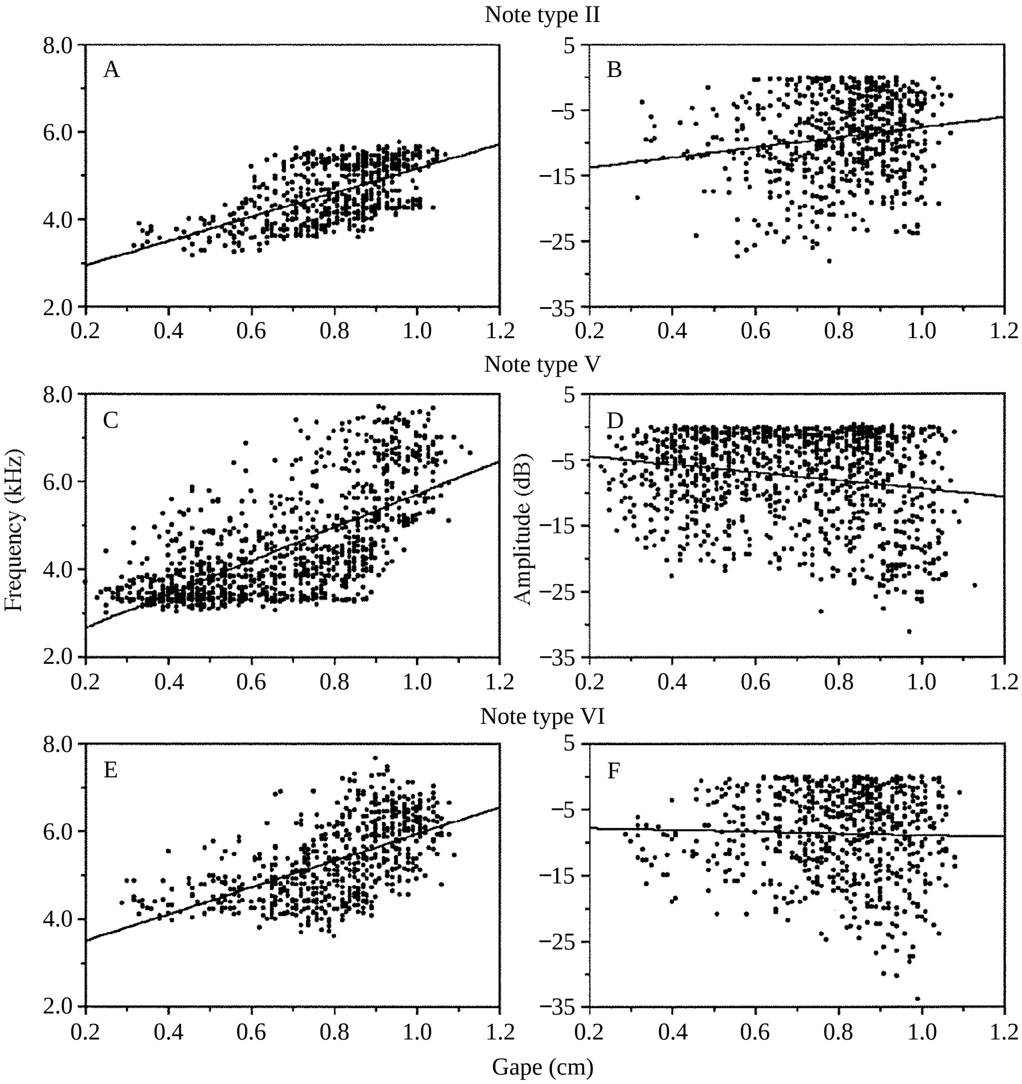

Fig. 8. Summary plots of beak gape as a predictor of frequency and amplitude in the swamp sparrow. (A) Gape/frequency in note type II (y=2759x+2392, r^2=0.36, P<0.001). (B) Gape/amplitude in note type II (y=7.7x−15.4, r^2=0.03, P=0.06). (C) Gape/frequency in note type V (y=3799x+1901, r^2=0.46, P<0.001). (D) Gape/amplitude in note type V (y=−6.14x−3.3, r^2=0.04, P=0.04). (E) Gape/frequency in note type VI (y=3039x+2894, r^2=0.32, P<0.001). (F) Gape/amplitude in note type VI (y=−1.3x−7.6, r^2=0.001, P=0.38).

was found for the SWS note types, but no significant effect of individual variation was found for the WTS.

Discussion

Kinematic analyses of head and beak motions associated with song in both white-throated sparrows and swamp sparrows strongly support the hypothesis that such motions

Table 4. *Results of a nested analysis of variance (ANOVA) on the slopes of the relationships between frequency and gape in the two sparrow species*

Factor	Frequency/gape
Nested ANOVA	
Species (d.f.=1, 110)	36.33*
Note type (d.f.=4, 110)	130.03*
Song type: SWS II (d.f.=6, 110)	37.91*
Song type: SWS V (d.f.=5, 110)	20.71*
Song type: SWS VI (d.f.=5, 110)	18.13*
Individual: WTS note 1-2 (d.f.=4, 110)	0.70
Individual: WTS unsweep (d.f.=3, 110)	2.10
Post-hoc comparisons	
SWS/ WTS note types (d.f.=1, 110)	221.56*
SWS II/SWS V (d.f.=1, 110)	147.76*
SWS II/SWS VI (d.f.=1, 110)	255.95*
SWS V/SWS VI (d.f.=1, 110)	14.93*
SWS II/WTS upsweep (d.f.=1, 110)	1.22
SWS V/WTS upsweep (d.f.=1, 110)	89.90*
SWS VI/WTS upsweep (d.f.=1, 110)	165.55*

Main effects were tested at the level of species (N=2) and note type (SWS N=3, WTS N=2).

Nested factors tested for significant differences between song types within each note type for the SWS and for differences between individuals for the WTS. Planned *post-hoc* comparisons tested for significant differences between note types.

Values in columns are F-ratios. (*P<0.01).

function in sound production in songbirds. Specifically, dynamic changes in beak gape are highly correlated with the acoustic frequency of the sound produced. Beak gape was a significant predictor of acoustic frequency in four out the five WTS note 1 to note 2 transitions, all four WTS upsweeps, and in 19 of the 22 SWS notes examined (Figs 7 and 8, Table 2). The three exceptional SWS notes that showed no significant frequency/gape correlation in fact prove the rule. All three of these cases were ‘buzzy’ mid-range notes with relatively little frequency variation, and thus would not be expected to show a strong correlation between gape and frequency.

The relationship between beak gape and amplitude is inconsistent (Table 2, Figs 7 and 8). The only robust correlation we observed was for the frequency upsweep in WTS song (Fig. 7D). This association may be spurious, given that the increase in amplitude across the upsweep is coincident with a pronounced frequency change, but we cannot rule out the possibility that amplitude is partially determined by beak gape. We return to this point again below. There also is no clear relationship between head angle and the acoustic features of songs, with the exception of the frequency difference at the transition between notes 1 and 2 in WTS song (Table 3). Head angle did not correlate with frequency in the WTS upsweep, however, and it often returned to a lower angle for the third and subsequent notes even though the frequencies of these notes were the same as that of note 2 (e.g., Fig. 4D). This pattern suggests that head angle is less likely to be functionally involved in sound production, but may be related instead to a visual display function associated with song.

The strong correlation between beak gape and frequency suggests that gape is a functional determinant of the acoustic frequency properties of songs in the two species of sparrow we studied. Clark (1976) anticipated this result by proposing that phylogenetic differences in the head movements of passerine birds might correlate with broad differences in the acoustic quality of songs produced by different taxa. In a theoretical model of song production, Fletcher (1988) argued convincingly that vocal tract acoustic properties could account for observed amplitude distributions of broad-band harmonic bird sounds, illustrating his point with calls of the Australian raven (*Corvus mellori*). Recently, Hausberger *et al.* (1991) demonstrated a static relationship between maximum beak gape and the frequency of maximum amplitude in harmonic calls of the barnacle goose (*Branta leucopsis*, order Anseriformes). Our data show that *dynamic* changes in the frequency characteristics of pure-tonal bird songs are correlated with equally dynamic changes in beak gape. Furthermore, we find this relationship in two species with species-typical songs that differ markedly in the nature of their time-varying acoustic characteristics.

Source-filter models of songbird phonation

The correlation we observe between beak gape and acoustic frequency is consistent with the hypothesis that vocal tract resonances act as an acoustic bandpass filter (Nowicki, 1987), selectively attenuating frequencies that fall outside the filter's resonance passband in a manner similar to that proposed for the human vocal tract in the 'source-filter' model of speech production (Fant, 1960). This model suggests that the pure-tonal 'whistles' characteristics of many bird songs are generated as harmonic signals by the syringeal source, and those vocal tract resonances effectively filter out all but a single dominant frequency, such as the fundamental or the second harmonic. An alternative model, equally consistent with our data, suggests that vocal tract resonances directly influence the vibration characteristics of the syringeal membranes, by constraining them to vibrate in a more nearly sinusoidal fashion and thus suppressing the production of overtones at the source (Nowicki and Marler, 1988). The latter model is similar to one proposed for the human soprano singing voice (Rothenburg, 1981, 1987).

Neither of these functional models imply that vocal tract resonances directly determine the fundamental frequency of sound produced by the source, such as is the case for most musical wind instruments (Benade, 1976). In clarinets or trombones, for example, changes in the effective length of the resonance tube cause the instrument's acoustic source (i.e. the reed or lips) to change frequency by a proportional amount. The fact that pronounced frequency shifts are not observed when birds sing in helium/oxygen (which causes a 70% upward shift in resonance frequencies) rules out this possibility for birdsong production (Nowicki, 1987). Both models argue instead that the vocal tract influences the *relative amplitudes* of different frequencies produced at the source by attenuating or suppressing frequencies falling outside the passband of vocal tract resonances. In this sense, the vocal tract can be said to modify the tonal properties of the sound produced.

Available data do not allow us to choose between these two models of vocal tract function. Both models, however, imply that the major resonance frequency of the vocal tract should be centered squarely at the fundamental frequency (or the second harmonic) of the signal produced by the syringeal vocal source. More significantly, both models predict that vocal tract resonances must be actively modified during song in coordination with changes in the frequencies produced by the syrinx, to maintain the overlap between the two. Thus, the vocal tract filter can be thought of as ‘tracking’ frequency changes in the output of the syringeal source. Such tracking must involve dynamic changes in the configuration of the vocal tract. Our data demonstrate that variation in beak gape represents one important factor contributing to this process.

Changes in beak gape could modify the resonance frequency properties of a bird’s vocal tract in at least two ways. As the beak opens, the vocal tract may be effectively shortened as the distal portion of the tube formed by the trachea and the oral cavity is flared (Lieberman, 1977; Fletcher, 1988). ‘Lip-rounding’ in human speech, while not strictly an analogous process, provides an example of how changes in effective vocal tract length contribute directly to changes in acoustic resonance frequencies (Lieberman, 1977). Another effect of changing beak gape might be to change the impedance at the anterior end of the vocal tract, like occluding the open end of a simple tube. As the beak closes, the open end of the tube becomes more occluded, resulting in lower-frequency resonances. Both of these possible acoustic mechanisms predict that wider beak gapes should correspond to the production of higher-frequency sounds, as we observed.

The relationship between beak gape and frequency was significant in almost every case examined. The slopes of these regressions, however, differed significantly between the two species and among the specific notes compared (Table 4). Such differences are expected if differences in vocal tract anatomy (between the two species) or in the acoustic fine structure of the particular note produced (between and within species) requires consistently different patterns of beak motion. Thus, the significant differences between slopes of the gape/frequency regressions reinforce our conclusion that beak motion is functionally related to sound production.

These models of vocal tract function do not preclude a secondary correlation between beak gape and amplitude. If the source is producing a constant-frequency sound, for example, then we would predict a decrease in beak gape to result in a lower amplitude, as follows. With decreasing gape, the resonance frequency of the vocal tract lowers, moving away from the unchanging source frequency. The fundamental frequency of the source is attenuated because it is no longer centered in the vocal tract’s shifted resonance passband. Interestingly, an occasional brief decrease in amplitude (amplitude ‘drop-out’) of 8–10dB is commonly observed in the middle of WTS constant-frequency notes (e.g. Fig. 4B). These drop-outs are paralleled by brief decreases in beak gape (Fig. 4C), as predicted. Similarly, we would expect to observe changes in amplitude if the vocal tract’s resonance frequency were held constant while the vocal source changed frequency, because of the source frequency moving into or out of the fixed vocal tract resonances. Such a result is observed in experiments in which birds sing after their beaks have been temporally fixed at a constant gape distance (S. Nowicki, W. Hoese and N. Boetticher, unpublished data). In general, the consequence of a misalignment between the vocal source and vocal filter is a decrease in amplitude of frequencies falling outside the vocal tract’s resonance passband. Ordinarily, a bird is actively modifying its vocal tract resonances to maintain this alignment, resulting in the primary correlation we observe between beak gape and song frequency.

Vocal tract coordination in song production

Beak gape appears to be an important functional determinant of vocal tract acoustic properties, based on the data we have presented as well as theoretical analyses (Fletcher, 1988). We do not suggest, however, that the beak is the only morphological element capable of influencing the frequency response characteristics of the vocal tract. It is almost certain that dynamic changes involving other morphological structures play some role in production. Consider the larynx, for example. Most contemporary theories of avian phonation have de-emphasized or ignored the potential functional role of the larynx, because it does not act as a vocal source in birds as it does in most other air-breathing tetrapods (but see Nottebohm, 1975; White, 1968). A bird's glottis, however, is fully capable of opening and closing (McClelland, 1989), motions that prevent unwanted materials from entering the trachea during feeding and drinking (Heidweiller and Zweers, 1990). Given the position of the larynx at the anterior-most end of the trachea, this structure is also ideally located to provide a variable constriction that could modify impedances, as with beak opening and closing, and thus significantly modify vocal tract resonances (Nowicki and Marler, 1988). Research involving X-ray cinematography will be needed to evaluate further the functional role of the larynx in vocal production.

Dynamic changes in vocal tract morphology may have more profound functional consequences for song production than simply modifying the vocal tract's resonance frequency. Our present analysis is confined to 'whistled' songs that are characterized by an extremely narrow bandwidth at any one time. Songbirds are also capable of producing sounds that have significant energy across a wide bandwidth. These sounds may have a well-defined overtone structure, such as a series of harmonics, while in other cases they may be noisy, and some species switch rapidly between narrow-band and wide-band sounds in adjacent notes of the same song (Marler, 1969; Nowicki and Marler, 1988). Several investigators have argued that the songbird syrinx might operate in fundamentally different modes when producing such acoustically distinct sounds (Gaunt and Gaunt, 1985; Fletcher, 1988; Nowicki, 1989). Thus, extreme differences in bandwidth, such as those between whistled and harmonic song notes, may reflect different modes of vocal tract function. These different modes may correlate with modes of syringeal action or with changes in the degree of coupling between the syringeal sources and the vocal tract. Although we can only speculate on the specific mechanisms involved, it is likely that such transitions, if they occur, are also mediated by changes in the configuration of the bird's vocal tract.

Our evidence that the mechanics of the vocal tract modulate the acoustic content of birdsong has implications for research programs focused on the development and function of birdsong as a complex behavior. Considerable research on the neural circuits responsible for the production, perception and development of birdsong (Konishi, 1985; Nottebohm, 1991; Marler, 1991) has focused on the syrinx and the motor pathway leading to it *via* the hypoglossal nucleus of the brainstem (nerve XII) as the pathway for the control of song. Similarly, research on the functional morphology and evolution of song in birds (Brackenbury, 1989; Gaunt and Gaunt, 1985; King, 1989) has typically targeted syringeal morphology, leaving cranial structure as the province of feeding studies (Bock, 1964; Bühler, 1989; van Gennip and Berkhoudt, 1992; but see Nowicki *et al.* 1992). Our demonstration that changes in vocal tract configuration coordinate closely with syringeal activity suggests a new set of issues that must be addressed by neurobiologists and functional morphologists alike. Specifically, it is now necessary to explore the neuromuscular and musculoskeletal systems associated with control of the cranial region, and the neural mechanisms that are responsible for coordinating the vocal tract with the syrinx in birdsong production.

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