

Lateralization and Motor Stereotypy of Song Production in the Brown-Headed Cowbird

Susan E. Allan^{1,*} and Roderick A. Suthers²

^{1,2}Medical Sciences Program, ^{1,2}Center for the Integrative Study of Animal Behavior, ²Program in Neural Science, ²Department of Biology, Indiana University, Bloomington, Indiana 47405

SUMMARY

Song production in adult brown-headed cowbirds (*Molothrus ater ater*) is lateralized, with a slight right syringeal dominance. The left side of the syrinx produces low-frequency (200–2000 Hz) notes within the introductory note clusters, while the right side produces the higher-frequency (1500–6000 Hz) introductory notes, the interphrase unit (10–12 kHz), and the final high-frequency whistle (5–13 kHz). Cross-correlation analyses reveal that individual cowbirds produce each of their four to seven song types with a distinct stereotyped motor pattern—as judged by the patterns of syringeal airflow and subsyringeal pressure. The acoustic differences

across song types are reflected in the differences in the bronchial airflow and air sac pressure patterns associated with song production. These motor differences are particularly striking within the second and third introductory note clusters where there is a rapid switching back and forth between the two sides of the syrinx in the production of notes. These motor skills may be especially important in producing behaviorally effective song.

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INTRODUCTION

The songbird's vocal apparatus, the syrinx, is composed of two separate sound sources. In most species that have been studied, these sound sources act independently (see Nowicki and Capranica, 1986, for exception), and yet there is unilateral dominance in the production of song (Nottebohm, 1971; Lemon, 1973; Seller, 1979; Williams et al., 1992). Canaries (*Serinus canaria*), for example, are left-side dominant, producing up to 90% of their song on the left side of the syrinx (Nottebohm and Nottebohm, 1976). Zebra finches (*Taeniopygia guttata*) are the only species known to show right-side dominance (Williams et al., 1992). Gray catbirds (*Dumetella carolinensis*) and brown

thrashers (*Toxostoma rufum*), on the other hand, produce sound either unilaterally or bilaterally with neither side being dominant (Suthers, 1990; Suthers et al., 1994).

The degree of syringeal lateralization and dominance can be directly examined by measuring bronchial airflow and air sac pressure during song production (Suthers, 1990; Suthers et al., 1994). Sound is produced as expiratory air is forced out through the syrinx and across the medial tympaniform membranes. Measurements of syringeal airflow and pressure provide an index to activity of respiratory and syringeal muscles which, by regulating pressure and flow, control the spectral and temporal properties of the vocalization (see Gaunt, 1987; Brackenbury, 1989, for review of the mechanisms of song production). Thus, through the measurements of bronchial airflow and air sac pressure, it is possible to deduce the motor action of syringeal and respiratory muscles and provide a quantifiable measure of the motor correlates of song production.

The stereotyped songs and limited repertoire of

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* To whom correspondence should be addressed (Medical Sciences Program).

brown-headed cowbirds provide the opportunity to examine the consistency of motor correlates across repetitions of a song type, within an individual, and potentially, across individuals. Individual cowbirds produce four to seven easily defined song types. Some song types may be shared by individuals living within a social group, however, each male also typically has a number of distinct song types within his repertoire (West and King, 1986). Despite the variation of song types across individuals, all song types of the brown-headed cowbird (*Molothrus ater ater*) consist of two phrases, the first of which contains alternating notes of low (200–2000 Hz) and high (2000–6000 Hz) frequencies and the second of which is a high-frequency whistle (6–12 kHz). The first phrase can be further divided into note clusters separated by brief intervals of silence. Following the last introductory note cluster, and prior to the final whistle, there is typically a brief high-frequency note, termed the *interphrase unit* (IPU, see West et al., 1979 and King and West, 1983 for more detailed descriptions of the acoustic characteristics of cowbird songs).

The goal of the current experiments is to investigate the motor control of the two sides of the syrinx in the production of song in adult brown-headed cowbirds. In the course of their extensive work on cowbird behaviors, West and King (e.g., West et al., 1979; King and West, 1983; King et al., 1986) have identified several features of male cowbird song, including the timing and relative frequencies of what they have termed *low-* and *high-voiced* notes within the introductory note clusters, which appear to have special importance in eliciting copulatory postures from females. By examining the motor correlates associated with these behaviorally important aspects of song, it may be possible to gain insight into the functional significance of unilateral syringeal dominance and/or syringeal lateralization in song production.

METHODS

Adult brown-headed cowbirds were wild-caught in Bloomington, Indiana during April 1992. Birds were individually housed in small cages, in visual and auditory contact with other male and female cowbirds, on a light/dark cycle simulating natural conditions. Experiments were conducted on five males from May to August 1992.

At least 100 songs from each bird were tape-recorded (Marantz cassette recorder, PMD 221) prior to surgery.

Since a cowbird typically sings all of its song types regularly, this insured that a number of exemplars of each song type were recorded. During preoperative recordings, the bird was also allowed to become accustomed to wearing an elastic belt around its thorax with a fastener (Velcro) positioned in the middle of its back.

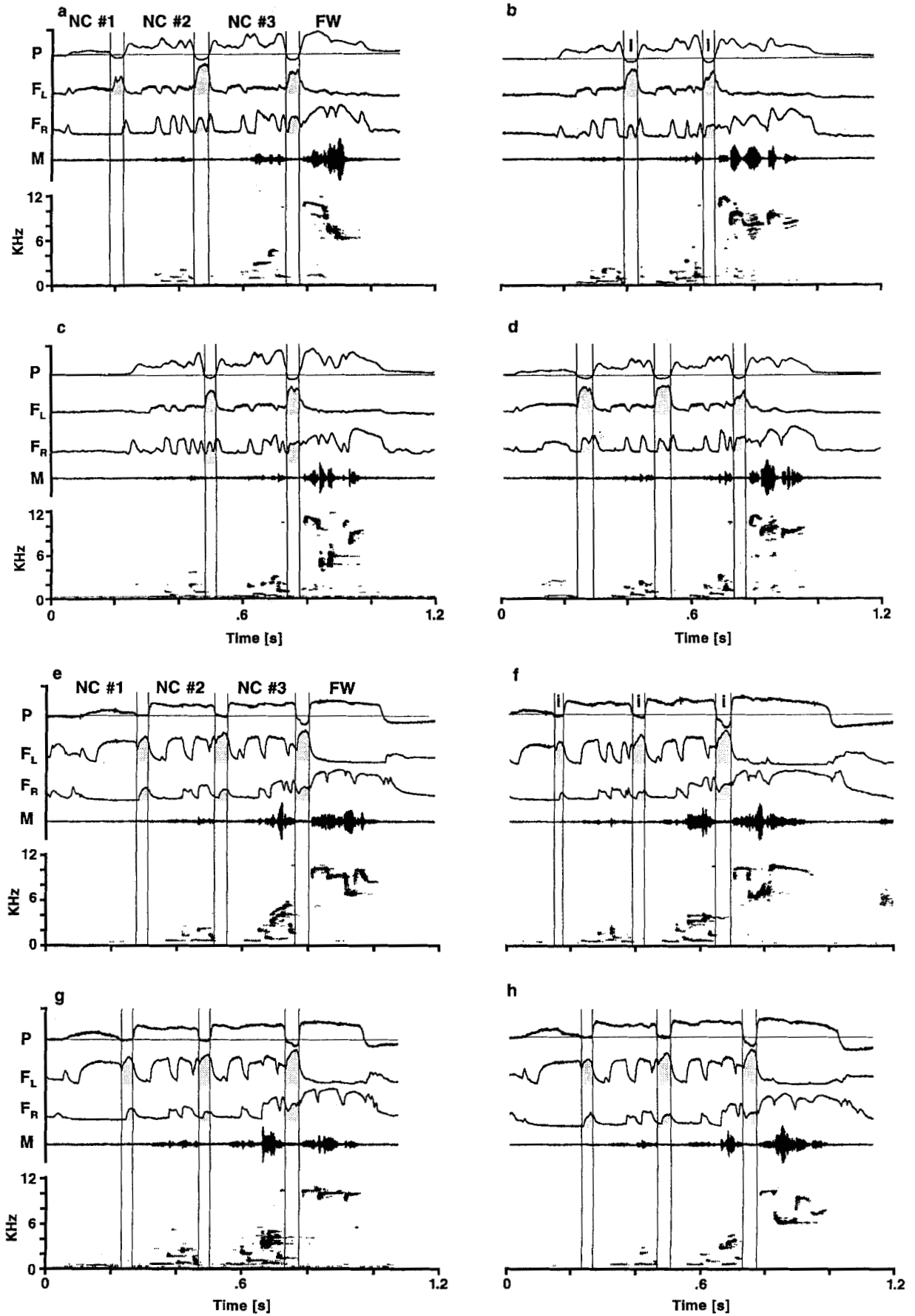
Procedure for Implanting Airflow and Pressure Transducers

Surgery was accomplished in two steps. First, the bird was anesthetized with isoflurane, and a silicone rubber cannula (Dow Corning, Silastic tubing 602-205) was inserted into one of the cranial thoracic air sacs.

The second step, taken after the bird had begun singing again in 1 or 2 days, consisted of implanting a micro-bead thermistor (Thermometrics BB05JA202, 0.13 mm diameter) into each primary bronchus to measure the rate of airflow through each side of the syrinx. Initially, atropine sulfate (8 μ l, s.c.) was administered to reduce airway secretions, and then the cowbird was anesthetized with chloropent (3 μ l/g, i.m., initial dose plus supplements as needed; the recipe for chloropent, which contains alcohol, propylene glycol, sodium pentobarbital, and chloral hydrate, can be obtained from Fort Dodge Laboratories, Fort Dodge, IA). An incision was made in the skin between the two clavicles ventral to the interclavicular air sac. The air sac was opened to expose the syrinx and bronchi. Each primary bronchus was reached by gently moving the syrinx to one side. A small hole was made in the ventral wall of the bronchus, four or five bronchial rings from the syrinx. The thermistor bead was inserted into the hole, positioned near the center of the lumen, and held in place with a microdrop of tissue adhesive on the outside of the bronchus (see Suthers, 1990). A pair of insulated wires (Cooner Wire, CZ1103) led from each thermistor through the incision in the air sac (which was closed with a suture and tissue adhesive) and then under the skin to the fastener on the back. Care was taken to provide enough slack in the wires so that they did not interfere with movement of the bronchi or syrinx. The distal ends of the wires were soldered to connectors on a backpack which was secured to the elastic belt. The air sac cannula was attached to a miniature temperature-compensated piezoresistive pressure transducer (Fujikura, model FPM-02PG) contained on the backpack. Wires from the backpack exited through the top of the cage and were connected to signal-conditioning and recording equipment. A lever arm with counterbalancing weights above the cage maintained a slight tension on the leads from the bird to prevent them from becoming tangled and permitted the cowbird to move freely within its cage.

Recording

Cowbirds resumed singing within a week after surgery. Initially, the high-frequency whistle was omitted, but full song was present 1–3 days after singing began. In order to



stimulate song, a female cowbird was placed in a separate cage immediately in front of the experimental male. A visual display, during which the male puffs up his chest and spreads his wings while directing his song to the intended recipient, normally accompanies a cowbird song (Bent, 1965). All cowbirds that were tested produced the display pre- and postoperatively and directed their songs towards the female. The experimental bird also maintained auditory and visual contact with other adult male cowbirds. Vocalizations were recorded with a microphone (Realistic model 33-985F) placed directly in front of the cage (15–30 cm from the bird).

The amount of current needed to maintain the heated thermistors at a constant temperature, using a feedback circuit (Hector Engineering) to compensate for the cooling effect of the airflow, provided a measure of the rate of airflow on each side of the syrinx. Direction of airflow could be deduced from the air sac pressure: expiration and inspiration being associated with positive and negative air sac pressure, respectively.

In order to record flow oscillations associated with the sound generated in each bronchus, a parallel output from each thermistor was high-pass filtered (at 200 Hz, Krohn-hite, model 3700) to attenuate the respiratory signal and further amplified (Princeton Applied Research, model 113) to extract the near-field bronchial sound picked up by the thermistors (oscillations in airflow due presumably to the vibration of the MTMs). The time constant of the microbead thermistor effectively limited its response to frequencies below about 3 or 4 kHz. When the frequencies exceeded the thermistor's response time, as in the case of the final whistle, the acoustic contribution from each side of the syrinx was inferred from the timing of bronchial airflow.

Bronchial airflow through each side of the syrinx and air sac pressure were recorded on separate FM channels of an instrumentation tape recorder (Racal, model 4DS) that has a flat response from DC to 2.5 kHz. Vocalizations and sound in each bronchus were recorded on separate direct channels having a flat response from 100 Hz to 18 kHz. These six variables were divided between two similar 4-channel recorders on which vocalizations and air sac pressure were duplicated and later used to synchronize the two tapes during analysis.

Analysis

Taped data were reproduced at half speed through anti-alias filters (TTE Inc, series J87, 60 dB attenuation/one-

third octave below 8 kHz) and digitized (Data Translation, DT-2821-G) at a sample rate of 20 kHz/channel (=40 kHz real time) on a 486 PC using **Signal software (Engineering Design, version 2.2)**.

Songs were classified into types by four independent observers who were given pre- and postoperative spectrograms (minimum $n = 50$) from each male, to visually group into song types by overlaying and subjectively matching them. The song types were distinctive enough that all observers arrived at the same classification.

Cross-correlation analyses (Signal software) were performed to quantify the degree of matching of spectrograms and their corresponding motor correlates (air sac pressure and bronchial airflow) across songs. For an extensive comparison of songs within and across individuals and song types, four distinct song types from each of two males (LBR and LGDG, Fig. 1) were selected for analysis, based on the number and high quality of the recordings of each song type in the birds' repertoires. Due to the length of the cowbird's song and in order to separately analyze portions of it, the song was segmented (≈ 300 ms) into its introductory note clusters and the final whistle. When a song type contained only two introductory note clusters [e.g., Fig. 1(b,c)], instead of three, the period of quiet respiration prior to the onset of the song was used to represent the first note cluster. This allowed us to normalize the number of note clusters, while keeping the syntax of the rest of the song intact.

Cross-correlation coefficients were calculated for all possible pairs of spectrograms, resulting in a $32 \cdot 32$ matrix (four exemplars of 8 song types = 32). Half of the matrix was redundant (1a versus 2a = 2a versus 1a; where the number and letter indicates song type and exemplar, respectively), and the self comparisons (1a versus 1a) were dropped, leaving 496 comparisons: 48 matching song type pairs and 448 nonmatching song type pairs. Since the songs were segmented into introductory note clusters and the final whistle, we had four cross-correlation matrixes for the spectrogram comparisons. In addition, we correlated the corresponding pressure, left bronchial flow and right bronchial flow for each of the spectrogram comparisons, resulting in 12 more cross-correlation matrixes. The complexity of the cross-correlation analysis and the necessity for high-quality recordings on all channels in order to obtain accurate correlations prevented us from running this extensive set of cross comparisons on all birds. However, smaller series of cross correlations compared the spectrogram and

Figure 1 Spectrograms of four song types for each of two adult cowbirds LBR (a–d) and LGDG (e–h) are displayed with their corresponding motor correlates. The songs can be broken into two or three introductory note clusters (NC) and a final whistle (FW), separated by Inspiration (I). P = cranial thoracic air sac pressure; F_R = airflow through the right bronchus; F_L = airflow through the left bronchus, M = vocalization recorded by microphone. Horizontal line on the pressure waveform indicates the zero line. Shaded areas under flow waveforms are inspiratory flow which is accompanied by a negative pressure. All other flow is expiratory (positive pressure).

Table 1 Number of Pre- and Postoperative Song Types¹

Bird ID	Preop (<i>n</i>)	Postop (<i>n</i>)
LGDG	5 (100)	5 (100)
LBR	5 (100)	4 (100)
YOR	5 (100)	5 (75)
RWR	4 (100)	3 (50)
PRS	7 (100)	2 (35)

Abbreviation: *n* = number of songs examined.

¹ All postoperative song types were also present in preoperative song.

corresponding motor correlate for each birds' own song types.

RESULTS

Each bird tested had a distinct repertoire of song types, with no song sharing between individuals. All birds, except PRS, produced the majority of their song types postoperatively, and all of these closely matched its preoperative counterpart (Table 1). PRS produced only two of seven preop song types postoperatively and these lacked the final whistle. Data were obtained from this male only during the initial days of singing after surgery since the thermistor leads broke before the bird sang its full song. The limited data collected from this bird are consistent with the findings we report in this article, but are not included in the quantitative analyses due to the lack of full postop song.

Similarities in Motor Patterns of Cowbird Songs

The song of the brown-headed cowbird is composed of two or three introductory note clusters followed by a high-frequency final whistle. The overall similarities of the bronchial airflow and air sac pressure patterns associated with song are similar within and across individuals (Fig. 1).

The pressure waveform of all cowbird song is divisible into three or four expirations, separated by 40–60 ms of inspiration. There is a tendency for expiratory pressure to increase with each successive note cluster and the final whistle. The first note cluster is not always present [e.g., Fig. 1(b,c)], but when it is, the pressure level is markedly reduced

relative to subsequent note clusters or the final whistle. This basic pressure pattern provides obvious inspiratory breaks at which to segment the song for the purpose of describing the motor correlates of song production.

The first two or three expiratory cycles correspond to the production of the introductory note clusters, which in the literature have been grouped together as phrase one (e.g., West et al., 1979). In our analysis, we include the high-frequency note (IPU) at the end of the last note cluster as part of that cluster, since it falls within the same expiratory phrase (see Fig. 1).

The lateralization of airflow, and therefore of sound production, through the right and left bronchi is also similar across song types, both within and across individuals. Left flow occurs during the first introductory note cluster, while the right flow is only occasionally present. The second and third note clusters consist of an alternation between, and some overlap of, left and right flow. The final whistle is produced only on the right side of the syrinx, with the left side being closed, allowing no airflow through the left bronchus.

Despite the similarity in the basic respiratory pattern and in the contribution of the two sides to the production of notes, important differences in the motor correlates across song types are still apparent. Song types (within and between individuals) differ in the number of introductory note clusters, the timing and frequency of the notes within the note clusters and the frequency pattern of the final whistle. These differences in the acoustic output are reflected in the fine structure of the motor correlates.

Lateral Asymmetry in Sound Frequency

There is a striking asymmetry in the frequency range of notes produced by each side of the syrinx (Fig. 2). The left side of the syrinx generates the low-frequency (<2000 Hz) introductory notes. The right side of the cowbird syrinx produces high-frequency introductory notes (1–6 kHz), the IPU (10–12 kHz), and the final high-frequency whistle (6–12 kHz). Furthermore, notes produced on the left side are typically constant frequency with only slight frequency modulation, while the notes and final whistle produced on the right side of the syrinx typically have pronounced frequency modulation (Fig. 3).

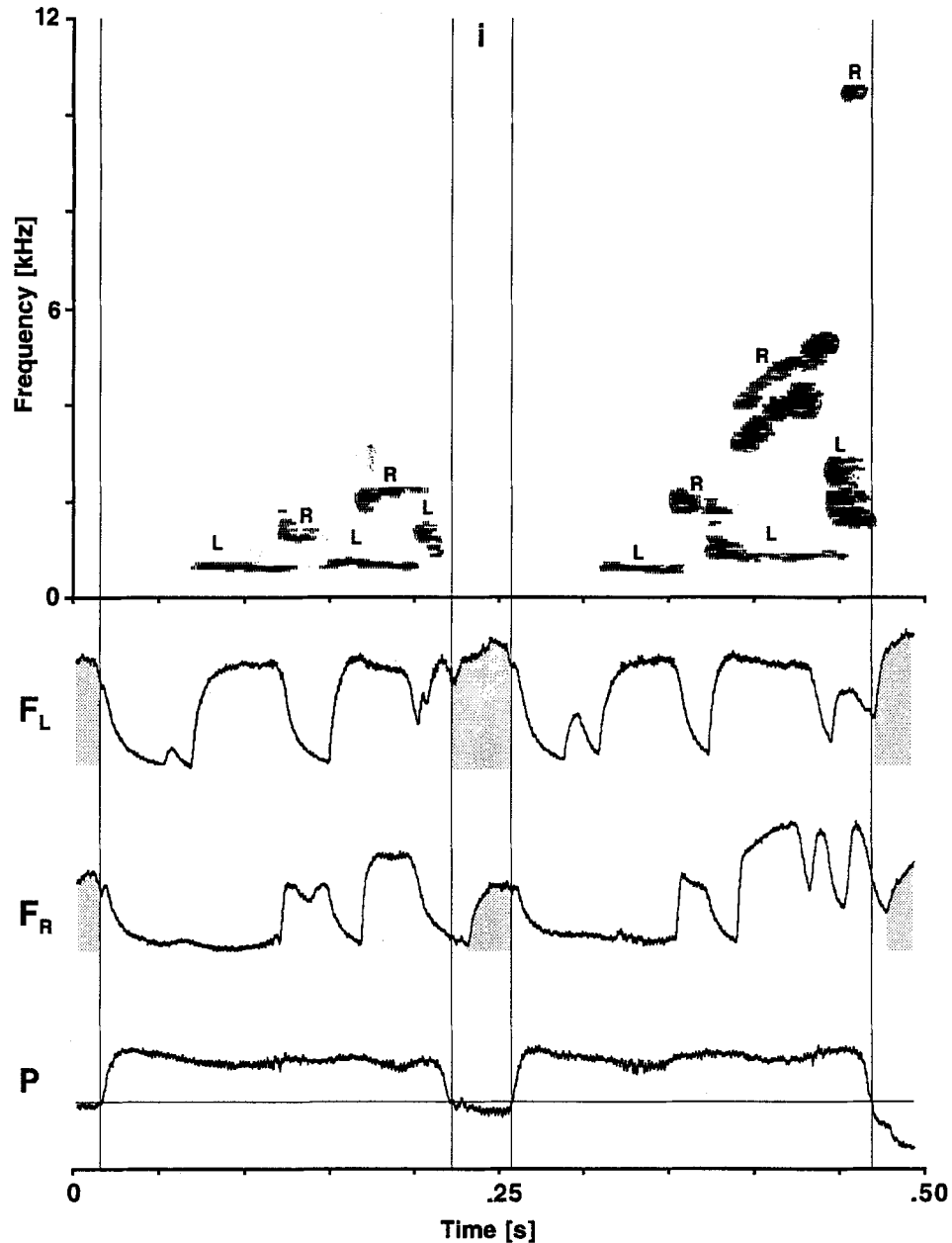


Figure 2 Expanded view of introductory note clusters [song type from Fig. 1(e)] showing asymmetries between the two sides of the syrinx. L = notes produced on the left side of the syrinx; R = notes produced on the right side of the syrinx. Left side notes are lower in frequency and relatively constant frequency compared to the higher and more modulated frequencies of the right side notes. Inspiratory (shaded areas) and expiratory airflow is delayed on the right side relative to the onset flow on the left side.

Bilateral Differences in Respiratory Pattern

There are some consistent differences between the respiratory pattern through each side of the syrinx. In all songs of each bird, inspiratory airflow always begins on the left side of the syrinx about 5–15 ms

before it is initiated on the right side. Left-side inspirations have a duration of about 35–50 ms, whereas inspirations on the right side have a duration of 15–40 ms, though they are sometimes intermittent and often appear to have a relatively lower flow rate than that on the left.

The onset of expiratory bursts associated with

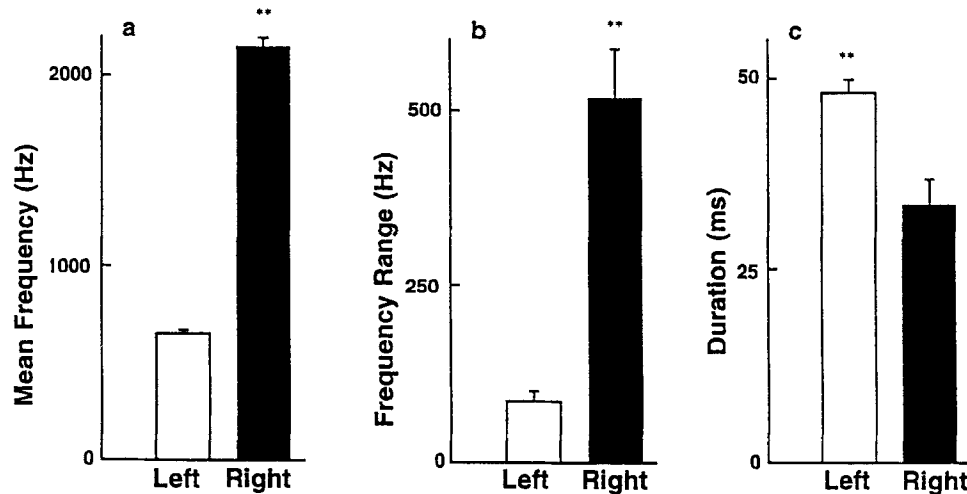


Figure 3 Characteristics of introductory notes produced on the left side (open bars) and on the right side of the syrinx (filled bars). (a) Average mean frequency of notes. (b) Average frequency range of notes (maximum frequency—minimum frequency for a given note). (c) Average duration of notes. ** $p < 0.01$.

phonation during a song also begins earlier on the left than on the right in all song types. Furthermore, the left side always produces the initial note in the second and third note clusters. This is followed by a right side note, usually with substantial overlap of production.

Stereotypy of Motor Patterns

The acoustic or phonetic structure of cowbird song is very similar for each song type produced by an individual bird. Each song type is produced with a distinctive, stereotyped motor pattern—as judged by the patterns of syringeal airflow and subsyringeal pressure—which is almost identical for each repetition of a given song type (Fig. 4). This is true even when these repetitions are separated by many intervening songs of different types.

In order to quantify their acoustic and motor similarity, four representations of each of four song types from each of two males were tested for the strength of correlation between their spectrogram and the motor correlates accompanying their production (Table 2). Songs classified subjectively as being of the same type have the highest spectrogram cross-correlation coefficients, supporting the subjective classification. As expected, nonmatching song types within and between the males have lower spectrogram cross-correlation coefficients than matched song types. In addition, the motor correlates for matched song types have significantly higher cross-correlation values than any of

the nonmatched pairs of song types [Fig. 5(a)]. This relationship holds for the pressure and bronchial flow patterns separately (Table 2).

A high correlation between the flow patterns from the right side of the syrinx for two matched or unmatched songs is accompanied by a similar correlation between the corresponding flows from the left side of the syrinx. This relationship is particularly striking in the case of matching song types [Fig. 5(b)]. Furthermore, two song types that have poorly correlated left airflow patterns also have poorly correlated right flow patterns. The tight correspondence between how closely correlated the left flows of two song types and the right flows of two song types are, indicates that motor action on both sides of the syrinx is important in determining the song type.

We also analyzed each note cluster and the final whistle separately to determine the relative contribution of each component to the motor separation between song types (based on the cross-correlation coefficients). Figure 6 shows a representative example of this analysis, comparing the flow patterns of one song type to all other song types analyzed. Differences in the motor correlates between song types for the first note cluster and the final whistle are not pronounced. These two components of the song are typically produced unilaterally and with little variation in the fine detail of the airflow pattern. In contrast, the second and third note clusters are produced by distinctively different patterns of airflow in different song types. There is a rapid

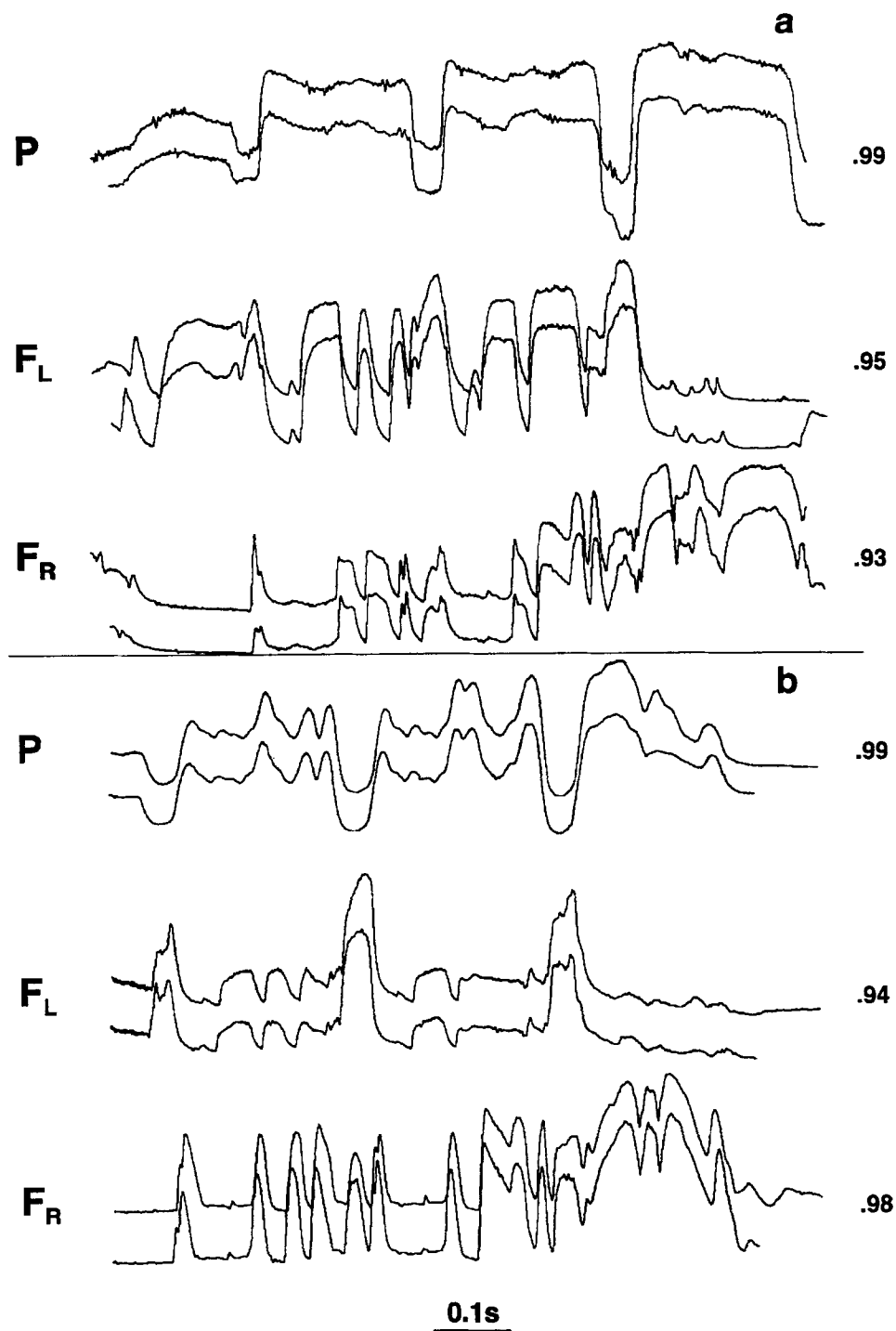


Figure 4 Examples of two renditions of a given song type, separated by a number of intervening songs, for (a) LGDG and (b) LBR. Note the near perfect match between the bronchial airflow (F_L, F_R) and air sac pressure (P) patterns for the two renditions of the same song type. Values to the right of each pair of lines indicates the cross-correlation coefficient.

Table 2 Average Cross-Correlation Coefficients for Four Song Types Sung by Male Cowbirds LGDG and LBR¹

	<i>N</i>	Pressure	Right Flow	Left Flow	Spectrogram
Matching ²	48	0.998 (0.005)	0.979 (0.008)	0.952 (0.018)	0.805 (0.044)
Nonmatching ³	448				
Between birds	256	0.947 (0.013)	0.686 (0.030)	0.681 (0.049)	0.227 (0.047)
Within birds	192	0.958 (0.006)	0.729 (0.020)	0.742 (0.027)	0.512 (0.061)

¹ Average cross-correlation coefficient (\pm S.D.).

² Matched songs were always by the same individual since no song types were shared. Cross-correlation coefficients are significantly higher (ANOVA- $p < 0.001$) for matched song types than nonmatched song types.

³ Nonmatching song types comparisons within birds have significantly higher cross coefficient ($p < 0.001$) than nonmatching song types between birds.

switching back and forth between the two sides of the syrinx during the production of the second and third introductory note clusters, which is not present during the rest of the song. Therefore, it is not surprising that the flow patterns of these two note clusters best distinguish the song types. These data further indicate that the motor differences between song types are not produced only on one side of the syrinx, since, as the correlation between the left flows weakens so does that between right flows.

DISCUSSION

Motor Stereotypy within Song Types

It is important to bear in mind that the method we have used to compare motor patterns of different songs includes the activity of those muscles that control syringeal resistance and respiratory muscles controlling air sac pressure. Any activity of syringeal muscles that does not affect syringeal resistance, for example, is not included in our assessment of the motor pattern. Even allowing for this limitation, however, the stereotypical nature of the motor pattern accompanying the production of each cowbird song type is striking. The overall bronchial airflow and air sac pressure patterns associated with each cowbird song type is similar within and across individuals.

Cowbirds utilize both sides of the syrinx during song production. The introductory notes are produced with either side independently or with both sides contributing, while the final whistle is produced only on the right side with the left side closed. The left side of the syrinx produces low, constant frequency notes within the introductory

note clusters. The right side of the syrinx produces high-frequency introductory notes as well as the high-frequency whistle at the end of each song, with marked frequency modulations. The pressure pattern for all song types is easily separated into distinct respiratory phrases, corresponding to the syllables of cowbird song.

Not only were the overall motor actions similar across individuals, there was a near perfect match between the airflow and pressure patterns across repetitions of a given song type within an individual. Suthers (1990) found that a note or syllable was represented with remarkably similar patterns for airflow and pressure for gray catbirds and brown thrashers. Catbirds and thrashers have large variable repertoires, making comparisons within a syllable type difficult. The stereotyped songs of cowbirds allowed us to examine similar song types, as well as numerous repetitions of the same song. The results from the mimic thrushes and the cowbirds suggest that specific, stereotyped motor patterns produce unique vocalizations and support the hypothesis that in cowbirds each song type is produced by a specific stereotyped motor pattern. Presumably, a specific combination of motor commands to the syringeal and respiratory muscles results in a unique set of airflow and pressure patterns for each song type. Unfortunately, no cowbirds in the current experiments shared song types, therefore, we could not determine if different individuals produce the same song types using identical motor programs.

Individual birds differ in the degree of motor similarity between their different song types. For example, both LBR and LGDG produce distinct song types, as identified by spectrogram matching and cross-correlation analyses. However, the mo-

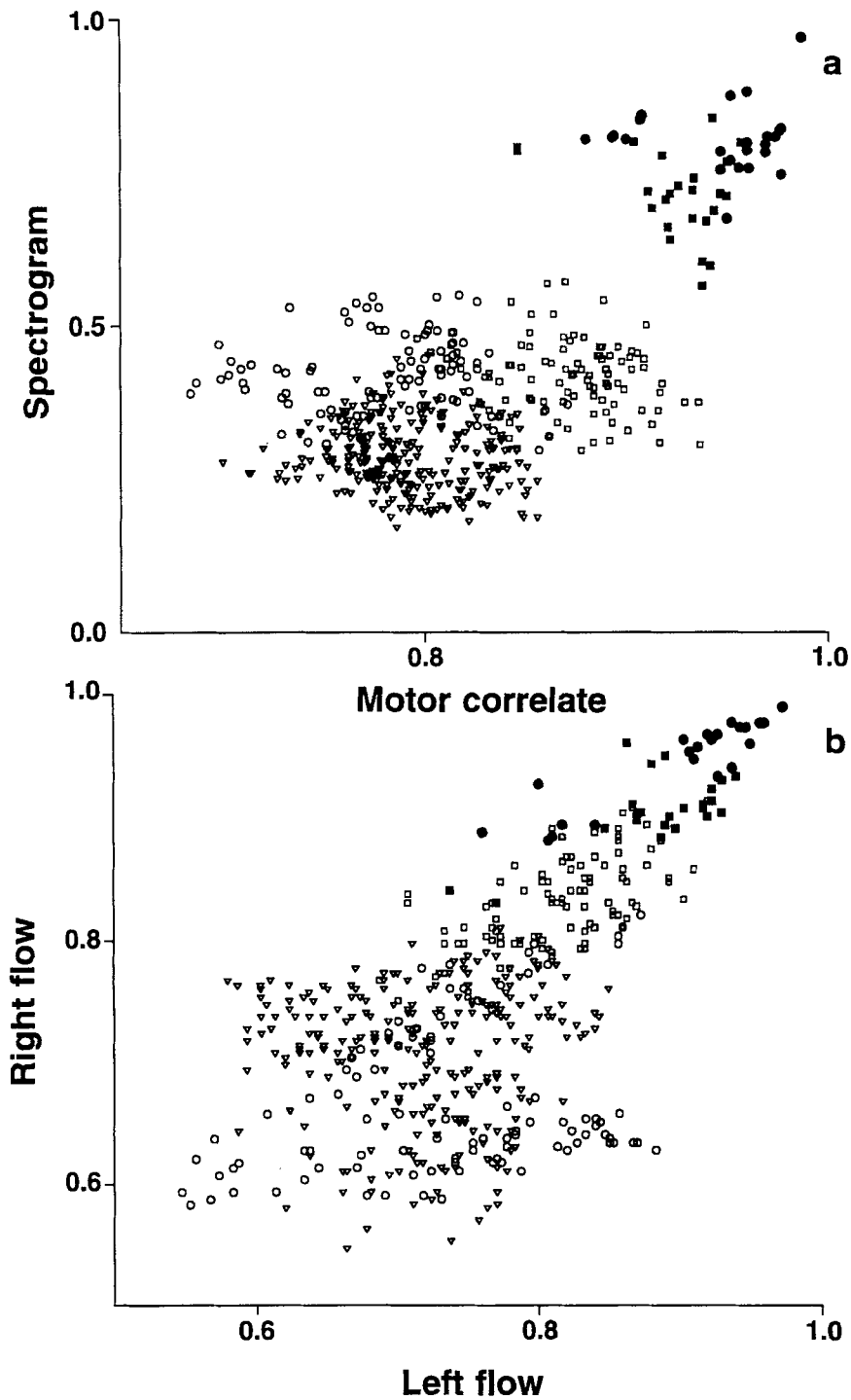


Figure 5 Cross-correlation analysis of four examples of each song type shown in Figure 1. (a) Correlation coefficients for each pair of spectrograms versus an average of the correlation coefficients for F_L/F_L , F_R/F_R , P/P for the same pair on songs. (b) Correlation coefficients for F_L/F_L versus F_R/F_R for each pair of songs. Filled symbols are matching song types. Open symbols are nonmatching song types. Circles represent within bird, LBR, comparisons. Squares represent within bird, LGDG, comparisons. Triangles represent between bird non-matching song type comparisons.

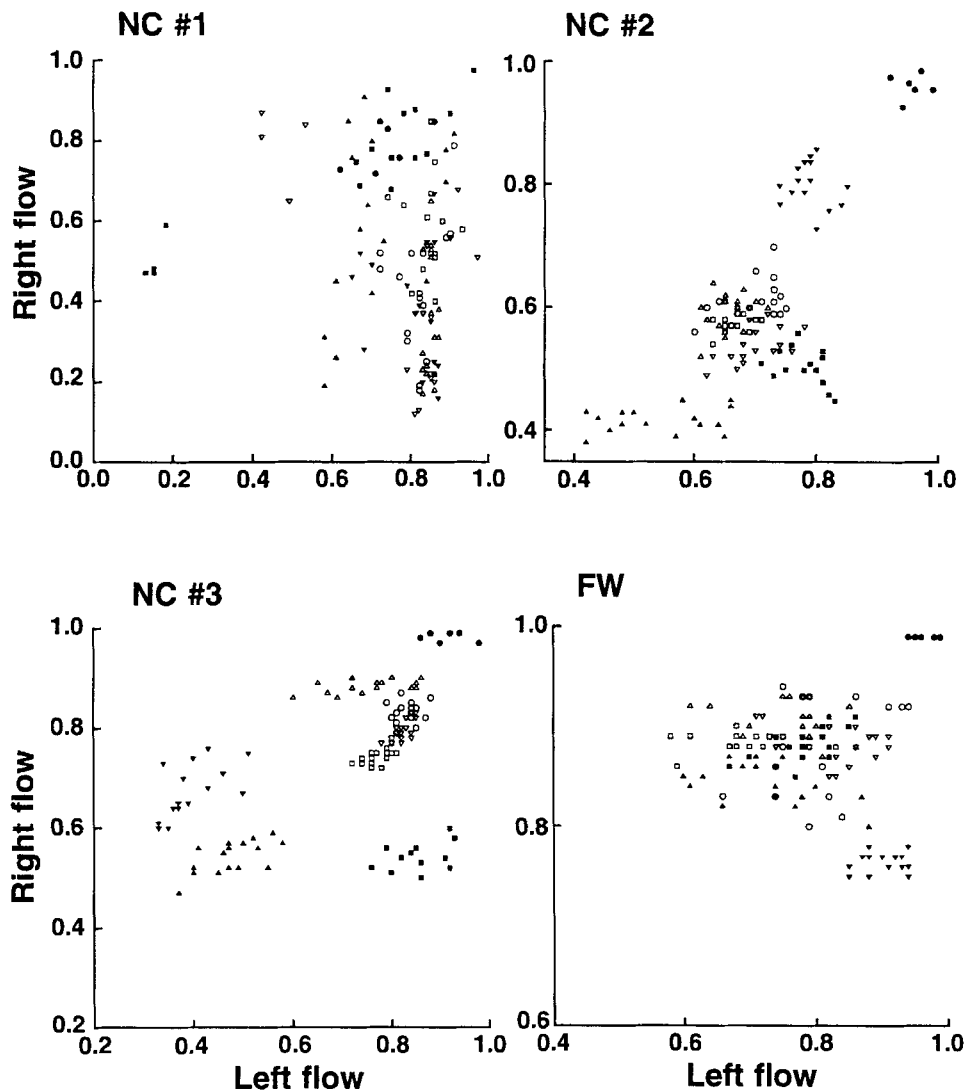


Figure 6 Correlation coefficients for F_L/F_L versus F_R/F_R for one song [Fig. 1(c)] type compared against all other song types, separated into the note clusters (NC) and the final whistle (FW). Filled symbols are within bird song type comparisons. Open symbols are across bird song type comparisons. Different symbols are used for each song type compared with song type 1c.

tor correlates for LGDG's nonmatching song types are more stereotyped (higher cross-correlation coefficients) than LBR's nonmatching song types, despite similarly low cross-correlation coefficients for the spectrogram comparisons (Fig. 5). This suggests that LGDG accomplished vocal diversity between song types with smaller or more subtle changes in motor pattern than does LBR. More cross-correlation analyses for more males are needed to determine the significance, if any, of the differences in the stereotyped nature of the motor correlates across song types within an individual.

Lateralization and Dominance

Cowbird song is lateralized in that introductory notes are produced on each side of the syrinx independently. Yet, cowbirds do not show unilateral dominance in the production of these notes. However, while both sides of the syrinx are responsible for the production of some introductory notes within the note clusters, the frequencies of the notes are higher, the frequency modulation is more pronounced, and there is more variation in the types of notes produced on the right side. Further-

more, there is a right syringeal dominance in the production of the final whistle. In contrast, most of the left side notes are relatively low, constant-frequency notes with little variation. These differences between the two sides suggest a dominance of the right side in the production of song.

It is not clear if the more complex phonology of right side notes, compared to those on the left, requires more precise motor control over the ipsilateral syringeal muscles. Modulations in frequency on the right tend to be tightly correlated with changes in the rate of expiratory airflow. The role of syringeal muscles in regulating changes in frequency is uncertain. Conceivably it may be as difficult to produce a constant frequency as it would be to generate frequency modulation. Although there are no obvious differences in the mass of muscles on each side of the cowbird syrinx, more subtle anatomical constraints, such as bilateral differences in the size or physical properties of the MTMs, may necessitate asymmetries in sound production, and limit the classes of notes either side of the syrinx can produce. Electromyographic studies are necessary for determining the contribution of the syringeal muscles to different classes of notes.

Williams et al. (1992) suggested that it is not the side of dominance per se that is critical, but instead the ability to functionally partition the two sides of the syrinx during song production. Williams and McKibben (1992) found a difference in the classes of syllables that zebra finches altered or dropped due to unilateral sectioning of the right tracheosyringeal nerve as compared to sectioning the left nerve, suggesting that the two sides of the syrinx are differentially responsible for the control of given classes of syllables. Furthermore, catbirds and thrashers, which show no syringeal dominance in syllable production, have a tendency to produce different classes of notes on the two sides of the syrinx (Suthers et al., 1994). The significance of this functional partitioning of acoustic output is unclear. Limiting the production of particular frequencies, or classes of notes to one side of the syrinx may enhance the bird's ability to produce a wide range of frequencies or more complex two-voiced syllables.

Behavioral Significance

The motor control of song has evolved under the selective pressures for vocal communication. It is therefore important to consider how behaviorally important aspects of cowbird song are represented

in its motor control. West and King (West et al., 1979; King et al., 1981, 1986; King and West, 1983) demonstrated that the introductory notes and IPU of the male cowbird's song are critical in determining a song's potency, that is, its ability to elicit a stereotyped copulatory posture from the female. Since the quality of the song is a major determinant of the breeding success and all song types of one male typically have the same degree of potency (West et al., 1981), it is possible that if the acoustic features determining potency are known, the underlying motor correlate may also be identified.

King and West (1983) tested the functional significance of the cowbird's two voices by examining the females' responsiveness to experimentally manipulated songs. They demonstrated that the presence of the low, constant-frequency notes within the introductory note clusters, considered the "low-voice," enhances the quality of a song, as perceived by females. They suggested that the timing and intensity of the low-voiced notes, relative to the high-voiced notes provide information to females on the songs' quality (cf. West et al., 1979; King et al., 1986).

Other acoustical differences within cowbird song, such as the number of introductory notes, the inclusion of the IPU prior to the onset of the whistle, and the relative amplitude of the IPU distinguish the high-quality songs preferred by the females from other song types (West et al., 1979; King et al., 1980; King and West, 1983; West and King, 1988).

Our findings support a left-right separation of the low and high voices, in that the low-constant frequency notes are produced on the left side and the high-frequency notes are produced on the right side of the syrinx. However, in addition to the low-constant frequency notes, the left side of the syrinx also produces the slightly higher frequency FM note at the end of each introductory note cluster (excluding the IPU), which King and West attribute to the high-voice. With this exception, the low and high voices, as defined by West and King, correspond to sounds produced on the left and right sides of the syrinx, respectively.

The majority of the acoustic features West and King have found to be behaviorally significant involve the relationship between the low- and high-frequency notes which are produced on different sides of the syrinx. The timing and relative frequencies of the two sides of the syrinx are thus important factors in mediating the female's preference, suggesting that the left-right alternation of

sound production is important in producing behaviorally effective cowbird song. Interestingly, it is during the second and third note clusters whose motor correlates best delineate the song types based on cross-correlation analyses, that the males are making rapid adjustments in the configuration of the two sides of the syrinx in order to produce a series of alternating notes. The ability of the male cowbird to coordinate the two sides of the syrinx to produce an acoustic feature preferred by females, such as a low-high note combination, may in some way reflect his overall fitness. If so, the female could potentially determine a male's fitness through the song types he produces.

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