

## S26-2 Bilateral motor skills in domestic canary song

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**Abstract** Songbirds may exhibit varying degrees of lateral syringeal dominance during song production. In the canary (*Serinus canaria*), the contributions that each side of the syrinx make to song can vary according to strain and individual abilities. Common domesticated, border and wild strains all sing complex syllables which appear to be produced by both sides of the syrinx. Using copulation solicitation displays (CSD) as the index of female preference in domestic canaries, we demonstrate that some complex syllables sung repetitively (“A” phrases, at  $\geq 16/s$ ) have clear behavioral significance during inter-sexual encounters. Moreover, male receivers may discriminate among conspecific song phrases; and “A” phrases are also used in intra-sexual communication. No strong syringeal lateral dominance was found when airflows, air sac pressures and sound production in the left and right bronchi were monitored in domestic males singing with both sides of the syrinx and vocal tract intact. We also confirm that “A” phrases of wide bandwidth (roughly 4 kHz) and sung at high repetition rates involve bilateral sound production. Unilateral bronchial plugs and nerve cuts reduced syllable complexity drastically, regardless of which side remained intact. Taken together, these data demonstrate that bilateral sound production is commonly used in the domestic canary, increasing phonetic and temporal complexity, two acoustic features of song that are important in inter- and intra- sexual communication.

**Key words** Bird song, Syrinx, Domestic canary, Neural lateralization, Vocalization

### 1 Introduction

In songbirds, the duplex structure of the tracheo-bronchial syrinx controls sound production independently on each side, thereby significantly increasing the flexibility of vocal production and the potential complexity of song. In some species, both sides of the syrinx contribute about equally to most of the song components. Conversely, Wasserschläger canaries exhibit a clear unilateral left dominance (Nottebohm and Nottebohm, 1976; Hartley and Suthers, 1990). Even though motor programs are sent to each side of the syrinx, the right side often remains silent in this strain (Suthers and Goller, 1997).

Other domestic, border and wild strains of canaries (*Serinus canaria*) frequently sing complex syllables that appear to be produced by both sides of the syrinx. Using the copulation solicitation display (CSD) as an index of female preference, we showed that at least some of the complex syllables, the “A” or so-called “sexy” phrases sung at high repetition rates ( $\geq 16/s$ ), had a clear behavioral significance during social encounters, especially for attracting domestic and Wasserschläger females (Vallet and Kreutzer, 1995; Vallet et al., 1997, 1998; Leitner et al., 2001). Recent experiments demonstrate that domestic females, whether raised in the aviary or acoustic isolation, prefer supernormal computer-edited phrases that maximize both the syllable rate and the frequency bandwidth of complex syllables (Draganoiu et al., 2002). Moreover, we found that male re-

ceivers may discriminate among conspecific song phrases, and that “A” phrases are used for intra-sexual communication as well (Parisot et al., 2002). Taken together, these data are consistent with the hypothesis that special complex syllable types might be a reliable index of male quality.

To assess the contribution made by each side of the syrinx to different types of syllables, and to study the motor constraints involved in producing simple and complex syllables in domestic canaries, we (1) examined the vocal ability of birds forced to sing on one side of the syrinx, and (2) monitored physiological correlates of phonation in birds singing with an intact vocal system (Suthers et al., 2001).

### 2 Materials and methods

To compare the properties of song produced on each side of the syrinx, the song repertoires of 8 adult male domestic canaries (*Serinus canaria*) were recorded before and after one side of the syrinx was surgically disabled by occluding one bronchus. Birds were anesthetized with chloropent (4.0  $\mu\text{l/g}$ , i.m.). The syrinx was exposed through a midline ventral incision in the interclavicular air sac and dental impression medium (Kerr, Light bodied permalastic) was injected into one primary bronchus a few rings below the syrinx and held in place by a droplet of tissue adhesive (Vet Bond). Four birds were injected in the left bronchus and the other four in the right. This bronchial plug abolished phonation in the ipsilateral side of the syrinx by pre-

venting air from flowing through it. The interclavicular air sac was then closed and the birds allowed to recover.

Birds with unilateral bronchial plugs began to sing several days after surgery. Their post-plug song was recorded for several days to obtain a post-plug repertoire. After the full repertoire was recorded, the tracheosyringeal branch of the hypoglossal nerve on the plugged side was sectioned to paralyze the ipsilateral syringeal muscles. This was accomplished by anesthetizing the birds and making an incision in the neck over the trachea, midway between the glottis and syrinx. A section of the tracheosyringeal nerve about 3 mm long was removed on the side with the bronchial plug, which was not disturbed. The incision was then closed; and the birds often began to sing within a day or two after surgery.

Song was recorded with a Marantz PMD 20 cassette recorder and condenser microphone (LEM Industries, model EMU 4535). Birds were exposed to long day periods (16L8D) in individual cages in an aviary in visual and auditory contact with other canaries. The song repertoire of each individual was recorded before the bronchial plug (intact or control), after the bronchial plug but before the ipsilateral nerve cut (post-plug), and after the ipsilateral nerve was cut (post-cut). Prior to and after both surgical treatments, song was recorded for at least two 15 min recording sessions each day for about one week. More than 80 songs, each at least 0.7 s in duration, were recorded from each individual. Recorded songs were digitized at a sample rate of 22 kHz (16 bits) using SoundEdit 16 version 2 software (Macromedia). Minimum and maximum frequencies, the duration and syllable repetition rates were measured with cursors for each syllable type from the spectrograms. Syllable types were identified by visual inspection of the spectrograms.

In three canaries, the syrinx was exposed under anesthesia and a microbead thermistor (Thermometrics, Edison NJ, BB05JA202N) was placed in the lumen of each primary bronchus. The interclavicular air sac was sealed, and the thermistor leads attached to a small connector on a backpack. A silastic cannula was inserted into the cranial thoracic air sac and connected to a piezoresistive pressure transducer (Fujikura, model FPM-02PG) on the birds' backs. When they recovered from anesthesia, the birds were returned to cages. Signals from the thermistors indicating the rate of airflow through each side of the syrinx, and signals from the pressure transducer indicating subsyringeal pressure in the cranial thoracic air sac, were routed on fine wires from the backpacks through the top of the cage to signal conditioning and recording instruments. A feedback circuit maintained the thermistors at a constant temperature of about 60°C. The current needed to maintain this temperature provided a nonlinear measure of the rate of airflow. By monitoring the rate of airflow through each side of the syrinx and the driving respiratory pressure during song, we aimed to determine the sides of the syrinx used to produce each note.

## 3 Results

### 3.1 Repertoire size

Intact birds prior to bronchial plugging had a mean repertoire of  $32.4 \pm 6.9$  syllable types. Silencing one or other side of the syrinx with a bronchial plug caused only a slight drop in the size of the repertoire. The mean repertoire size of right-plugged birds was  $28.5 \pm 3.1$  syllables, and left-plugged birds  $25.7 \pm 6.1$  syllables. Most post-plug syllables were different from those in the intact, control repertoire: only 4 or 5 syllables in post right plug repertoires were present as well in the intact repertoire. Of the four birds plugged on the left side, three did not retain any syllables from the intact repertoire, and the fourth only 1.

Paralyzing one side of the syrinx by removing a section of the tracheosyringeal nerve ipsilateral to the bronchial plug had little further effect on mean repertoire size ( $31.8 \pm 10.2$ , right cut;  $27.5 \pm 9.8$ , left cut). Repertoires increased a little in some individuals and decreased in others, regardless of which side of the syrinx was disabled. Moreover, only a minority of the post-cut repertoires included syllables present in either post-plug or intact repertoires, again irrespective of the side disabled.

### 3.2 Effect of surgery on frequency range

Surgical treatment reduced the range of sound frequencies according to the side of syrinx disabled. In intact birds, maximum frequencies of repertoire syllables ranged between about 2 100 and 7 800 Hz. In birds with the right syrinx disabled so that vocalizations originated only on the left side, whatever the treatment, the upper portion of frequency distribution above 5 800 Hz was lost. Distribution of minimum sound frequency, however, changed little. Silencing the left side of the syrinx had the opposite effect. Neither bronchial plug nor nerve cut altered maximum frequencies much but greatly reduced the number of syllables with minimum frequencies below about 1 700 Hz.

In the light of lateral differences in frequency range, it is not surprising that disabling one side of the syrinx reduced the fundamental bandwidth of the syllables. In intact repertoires, 27 % of the syllables had a bandwidth greater than 3 500 Hz, but after unilateral bronchial plugging, this dropped to 9% and remained at this value after ipsilateral nerve cutting as well.

### 3.3 Syringeal contributions to song

Analysis of the patterns of airflow through each side of bilaterally intact syringes during spontaneous song indicates that each side of the syrinx produces some of the syllables in the repertoire. Neither side of the domestic canary syrinx dominates song production consistently. In some multi-note syllables, birds switch sound production from one side to the other between notes. Both sides of the syrinx rarely if ever produce sound simultaneously. The canary controls which side of the syrinx generates sound by

using syringeal muscles to close the labial valve at the cranial end of one bronchus, thereby preventing airflow through that side of the syrinx and silencing it.

## 4 Discussion

We have shown that unilateral bronchial plugs and nerve cuts to the syringes of male domestic canaries has little effect on the number of song syllables, but that the composition of the repertoire is very different. We do not know if the new syllables that appear after surgical intervention are the result of disrupted or incomplete motor patterns of intact syllables. The frequency range of syllables depends on which side of the syrinx is intact. Silencing the right side causes the loss of high frequencies and silencing the left side loses low frequencies. This indicates that each side of the syrinx in canaries is specialized to cover different though overlapping ranges of frequencies.

Post-plug and post-nerve cut syllables were generally simpler in their structure. Although a few two-note syllables were produced by lesioned birds, they lacked the bandwidth characteristic of “sexy” syllables most effective in eliciting CSD’s from receptive females. Overall, syllable complexity was drastically reduced in most of the birds, regardless of which side remained intact. In post-operative birds, high frequency sounds (6.0–9.0 kHz) were produced exclusively by the right side of the syrinx. However, either side appeared to contribute to syllables within the frequency band of 0.5 to 6.0 kHz. In this frequency domain, both left and right nerve-cut canaries reorganized their syllable repertoire.

Studying airflow and air sac pressure in males singing with both sides of their syringes and vocal tract intact, we demonstrated that domestic canaries, unlike conspecific *Wasserschläger* males, show no strong syringeal lateral dominance. We also confirm that “A” phrases with a wide bandwidth (roughly 4 kHz), and sung at high repetition rates, are produced by sequential contributions from both sides of the syrinx. Once again, the vocal register of the right side was found to extend to higher frequencies than that of the left.

By using both sides of the syrinx in song production, domestic canaries can increase the phonetic and temporal complexity of their songs. Previous work shows that these two acoustic features are important in inter-sexual and in-

tra-sexual communication (Vallet and Kreutzer, 1995; Vallet et al., 1997, 1998; Leitner et al., 2001; Parisot et al., 2002). In domestic canaries, certain sequential contributions from both sides of the syrinx may be needed to produce complex syllables with a large bandwidth. This is certainly an important additional cue used by females during inter-sexual communication (Draganoiu et al., 2002). “Sexy” phrases of complex syllables sung at a high repetition rate are only common in the songs of certain individual males. Their production may demand excellent motor skills that indicate something about the fitness of the singer and/or his hormonal, reproductive state (e.g., Leitner et al., 2001).

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