RESEARCH ARTICLE

Bilateral coordination and the motor basis of female preference for sexual signals in canary song

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SUMMARY

The preference of female songbirds for particular traits in the songs of courting males has received considerable attention, but the relationship of preferred traits to male quality is poorly understood. Female domestic canaries (*Serinus canaria*, Linnaeus) preferentially solicit copulation with males that sing special high repetition rate, wide-band, multi-note syllables, called 'sexy' or A-syllables. Syllables are separated by minibreaths but each note is produced by pulsatile expiration, allowing high repetition rates and long duration phrases. The wide bandwidth is achieved by including two notes produced sequentially on opposite sides of the syrinx, in which the left and right sides are specialized for low or high frequencies, respectively. The emphasis of low frequencies is facilitated by a positive relationship between syllable repetition rate and the bandwidth of the fundamental frequency of notes sung by the left syrinx, such that bandwidth increases with increasing syllable repetition rate. The temporal offset between notes prevents cheating by unilaterally singing a note on the left side with a low fundamental frequency and prominent higher harmonics. The syringeal and respiratory motor patterns by which sexy syllables are produced support the hypothesis that these syllables provide a sensitive vocal–auditory indicator of a male's performance limit for the rapid, precisely coordinated interhemispheric switching, which is essential for many sensory and motor processes involving specialized contributions from each cerebral hemisphere.

Key words: hemispheric specialization, A-syllable, honest signal, minibreath, syringeal lateralization, female preference.

Received 1 March 2012; Accepted 14 May 2012

INTRODUCTION

Birds sing, at least in part, to attract a mate and to defend their territory against other males (Catchpole and Slater, 1995). Exactly how song contributes toward achieving these goals remains controversial, despite its relevance to vocal communication and the evolution of song diversity. In some species, females prefer males who exhibit particular song traits such as a large repertoire (but see Byers and Kroodsma, 2009), those who spend the most time singing, or those who sing a local dialect (reviewed by Gil and Gahr, 2002; Grether, 2010; Nowicki and Searcy, 2004; Podos et al., 2004; Podos et al., 2009; Riebel, 2009; Sakata and Vehrencamp, 2012; Vehrencamp, 2000). Models of adaptive sexual selection assume these traits convey information about the sender's genotypic or phenotypic quality, which females can use in selecting a mate. In order to prevent inferior males from exaggerating their fitness, the song trait must incur a cost or reflect a performance limit that ensures its honesty (e.g. Zahavi, 1975). Different song traits have different kinds of costs, but in many cases the cost or its relationship to male quality is unclear (Nowicki et al., 2002).

There is evidence that at least some aspects of birdsong are limited by physical or physiological constraints on vocal performance. Podos (Podos, 1997) pointed out that there appears to be a trade-off between producing high syllable repetition rates and maintaining a wide syllable bandwidth, implying it is difficult to do both. A plot of syllable repetition rate against syllable bandwidth gives a triangular distribution in which the upper boundary is considered to represent a performance limit. Female swamp sparrows, *Melospiza georgiana*, prefer males whose trilled songs approach a performance limit determined by the upper bound regression of a plot of trill rate against syllable bandwidth (Ballentine et al., 2004). Respiratory constraints limit the repetition rate at which air can be replaced between syllables (Suthers and Goller, 1997). Other lines of evidence include limitations in the ability to copy tutor songs in which syllable repetition rate has been increased (Podos, 1996) and in the finding that when a vocal mimic copies heterospecific song it uses the motor pattern of the tutor species (Zollinger and Suthers, 2004).

In some species, females are sexually responsive to a special syllable type. Examples include a buzz-like element in the song of water pipits, *Anthus spinoletta*, that predicts their pairing success (Rehsteiner et al., 1998), and the preference of female dusky warblers, *Phylloscopus fuscatus*, for males that maintain a certain sound level during song syllables (Forstmeier et al., 2002). In this study we focused on the sexy syllables of domestic canaries. At present, domestic canaries are unique in possessing a well-defined sexual song trait in which both the acoustic basis of female preference and the motor basis of syllable production have been extensively studied.

Vallet and colleagues (Vallet and Kreutzer, 1995; Vallet et al., 1998) showed that certain canary phrases containing syllables composed of two notes with a wide bandwidth of about 4 kHz, extending to low frequencies, and a high syllable repetition rate
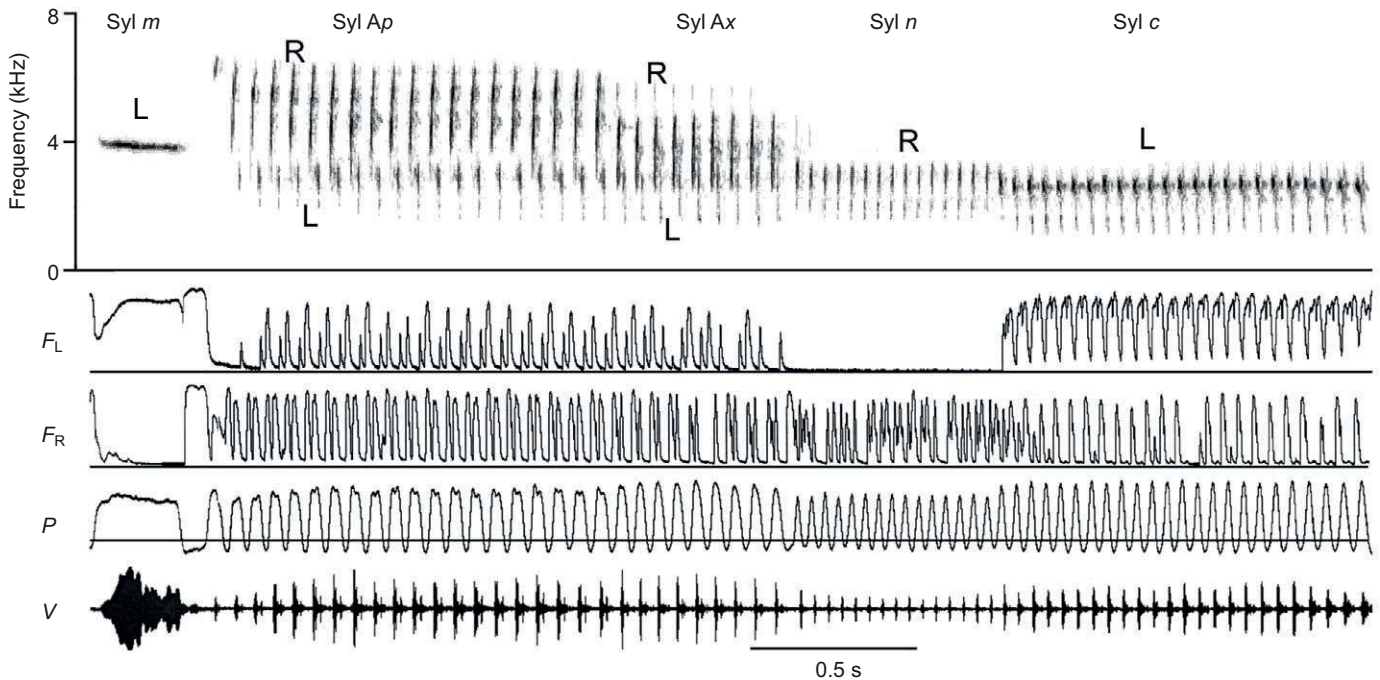
Fig. 1. Portion of a canary song showing phrases of five different syllables. Songs vary in length and in the number of syllable types they contain. Depending on the individual male, some songs may contain phrases of sexy A-syllables. Sometimes a bird sang successive phrases of different types of A-syllable, often in a sequence with other high repetition rate non-sexy syllables. In this figure, two minibreath A-phrases composed of syllables A*p* and A*x* are preceded by a phrase of nearly constant frequency *m*-syllables sung at a low repetition rate and followed by unilaterally produced frequency modulated (FM) syllables *n* and *c*. Although the repetition rate of syllables *n* and *c* is comparable to that of the sexy syllables, they consist of a single note and their bandwidth is considerably less than that of the preceding A-syllables. Syllable *n* is sung on the right side with the left side of the syrinx closed during the entire phrase. F_R, airflow through the right bronchus; F_L, airflow through the left bronchus; P, pressure in the cranial thoracic air sac; V, time waveform of song. Horizontal lines indicate zero flow and ambient (zero) pressure. As both inspiratory and expiratory airflow cools the heated thermistor bead, both inspiratory and expiratory airflow produce an upward deflection of the airflow signal. The direction of airflow depends on whether the subsyringeal air sac pressure is less than (inspiration) or greater than (expiration) the external ambient pressure. Phonation during song by these canaries was always accompanied by expiratory airflow. L and R in the spectrogram indicate notes produced on the left or right side of the syrinx, respectively. Syllable type (Syl; each syllable type is identified by a lowercase letter, which is preceded by 'A' if the syllable is A-type) is indicated at the top of the figure.

exceeding 15 syllables s^{-1}, were particularly effective in eliciting copulation solicitation displays (CSDs) from female canaries. Syllables with these characteristics were termed A-syllables (Vallet and Kreutzer, 1995). Subsequent experiments have shown that each of these acoustic features – increased repetition rate and increased bandwidth (Draganoiu et al., 2002), two-note syllable complexity (Pasteau et al., 2004) and the inclusion of low frequencies (Pasteau et al., 2007) – increased female preference as judged by the number of CSDs they elicit.

Suthers and colleagues described the motor dynamics of song production in domestic canaries, but did not include A-syllables (Suthers et al., 2004). The domestic common canary is an outbred strain that has not been subjected to strong artificial selection for either a particular song or appearance. Like other canary strains, its songs consist of variable sequences of different syllables, repeated to form phrases (Fig. 1). The number of different phrases and the sequence in which they are sung varies from song to song. Many domestic canaries, e.g. subordinate males and those with small song repertoires, rarely if ever sing A-syllables. A-syllables may thus also provide females with information on a male's social status and repertoire size. Unlike the highly lateralized, song-bred waterslager strain (Hartley and Suthers, 1990; Nottebohm and Nottebohm, 1976; Suthers, 1997), which has been the focus of most research on the neurobiology of canary song, domestic canary song is not strongly lateralized (Suthers et al., 2004). Sound

production is frequently switched from one side of the syrinx to the other between syllable types or notes within a syllable so that each side of the syrinx makes an important contribution to the total song repertoire of this strain. As in other songbirds studied, the two sides of the syrinx cover different, though overlapping, frequency ranges. In domestic canaries, fundamental frequencies below about 2.6 kHz are usually produced on the left side and frequencies above about 3.5 kHz are produced on the right side of the syrinx (Suthers et al., 2004).

An evaluation of the hypothesis that female preference for particular syllables has evolved because they are difficult to produce requires an understanding of the mechanisms required to produce such syllables as well as the specific properties of the syllable that are preferred by the female. The availability of extensive behavioral data documenting how changes in specific acoustic properties of the A-syllable and temporal patterns affect female preference makes this an ideal syllable and species in which to examine the underlying motor mechanisms. Song requires the precise control and coordination of multiple simultaneous and sequential motor patterns involving respiration, the separate sides of the bipartite syrinx, and the supra syringeal vocal tract. Errors or variation at any one of these levels could degrade the vocal signal. Here, we examined the respiratory and syringeal motor demands for producing sexy canary syllables with particular attention to production constraints that might limit the performance of these sexual signals.

MATERIALS AND METHODS

The male domestic canaries (*Serinus canaria*, Linnaeus) used in these experiments were reared in aviaries with other conspecifics at the University of Paris Ouest, Nanterre La Défense, France. Prior to an experiment birds were brought into breeding condition by moving them from short to long day (16h:8h L:D) photoperiods.

Most of the common domesticated male canaries reared in aviaries rarely, or in some cases never, sing sexy phrases. We recorded 10 different birds (more than 80 songs per bird) and selected 3 of them that frequently produced A-type phrases, either in social conditions or spontaneously. We identified sexy, A-syllables according to the criteria established in behavioral playback experiments (Vallet et al., 1998; Vallet and Kreutzer, 1995; Vallet et al., 1997; Draganoiu et al., 2002; Leitner et al., 2001); namely, that syllable repetition rate exceeds 15 syllables s^{-1} and that syllables consist of broad band frequency modulation that is not a simple continuous sweep but contains two notes and extends to low frequencies below about 2 kHz.

The surgical procedures are described in more detail elsewhere (Suthers et al., 2004). Prior to surgery the bird was anesthetized with chloropent (3.8–4.0 µl g^{-1}, i.m.; Fort Dodge Laboratories, Madison, NJ, USA). The rate of airflow through each side of the syrinx was measured by implanting a microbead thermistor (BB07PA302N, Thermometrics, Edison, NJ, USA) in each primary bronchus, several semi-rings below the syrinx. A pair of fine wires from each thermistor exited the interclavicular air sac through the mid-ventral incision, which was then carefully sealed. The wires were routed subcutaneously to micro-connectors on a backpack. A feedback circuit heated the thermistors to a constant temperature and the current required to maintain this temperature provided a non-linear measure of the rate of airflow. The heated thermistors were cooled by both inspiratory and expiratory airflow so flow in either direction produces an upward deflection of the airflow signal.

The direction of airflow was determined from the respiratory pressure, which was measured simultaneously *via* a Silastic cannula (i.d. 1.02 mm, o.d. 2.16 mm, length 55 mm; Dow Corning, Midland, MI, USA) inserted into a cranial thoracic air sac and connected to a miniature piezoresistive pressure transducer (model FPM-02PG, Fujikura Servoflo, Lexington, MA, USA) mounted on the backpack. Bilateral connections, *via* the interclavicular air sac, between air sacs on each side of the body ensure that the left and right primary bronchi are subjected to a similar subsyringeal pressure.

After surgery the bird was able to move about freely in its home cage while data on respiratory pressure and airflow through each side of the syrinx were transmitted on flexible wires that extended from the backpack through the top of the cage to signal conditioning and recording instruments. Song was recorded by a condenser microphone (model AT835b, Audio Technica, Stow, OH, USA) positioned about 0.5 m in front of the bird. During the following days, directed song, airflow through each primary bronchus and air sac pressure were recorded concurrently on separate channels of DAT tape using a data recorder (model RD135T, bandwidth DC–10 kHz per channel, TEAC America, Montebello, CA, USA).

After the experiment, the taped data were reproduced at half speed and converted into 'Signal' (Engineering Design, Berkeley, CA, USA) files with an equivalent real-time digitization rate of 40 kHz (Board 2821-G, Data Translation, Marlboro, MA, USA) per channel. Sound spectrograms were computed using a fast Fourier transform (FFT) length of 512 points with a Hanning window, giving a frequency resolution of 86 Hz and time resolution of 11.6 ms, unless otherwise indicated. Syllable fundamental bandwidth and frequency range were determined at 30 dB below the peak amplitude of power spectra.

RESULTS

Seven of the 59 syllable types sung by the 3 canaries in this study met previously established criteria (Vallet et al., 1998; Vallet et al., 1997; Leitner et al., 2001; Draganoiu et al., 2002) for 'sexy' A-type syllables. Each of the syllable types was identified by a lowercase letter, which was preceded by a capital 'A' if the syllable was a sexy syllable. Although it was not possible to conduct behavioral tests with these males to assess the potency of these syllables in eliciting sexual displays from receptive females, two of them – syllable A*p* and the trill – were shown in other experiments to be highly effective in eliciting CSDs. Syllable A*p* (Fig. 2A) is very similar to syllable A7 in a previous study (Vallet et al., 1998), which the authors showed to be highly effective in eliciting CSDs. The pulsatile trill in Fig. 3 is similar to domestic, border and wild canary A-phrases observed to evoke strong responses from females (Leitner et al., 2001; Vallet et al., 1997).

Respiratory dynamics: minibreaths

Examination of the respiratory dynamics that accompany A-syllable production indicates that they depend on precise coordination of very fast syringeal and respiratory motor patterns. Six types of A-syllable combined both minibreath and pulsatile respiratory patterns (e.g. Figs 1, 2). Minibreaths (Calder, 1970; Hartley and Suthers, 1989) are small inspirations between syllables that maintain the respiratory air supply during song by replacing, after each syllable, the air that was exhaled to produce it. Minibreaths may permit the bird to sing long songs without running out of air, but the time required for each minibreath limits syllable repetition rate (Suthers et al., 1999). These six A-syllable types had a mean syllable repetition rate of 17.8±1.9 syllables s^{-1}, fundamental bandwidths of 4.3±0.7 kHz and a minimum frequency of 1.34±0.20 kHz.

Three minibreath sexy syllables (A*x*, A*p* and A*z*) are shown in Fig. 2. In each of these syllables the first note is a steep upward sweeping frequency modulation (FM) produced by the right side of the syrinx while the left side is closed, as indicated by the absence of airflow through that side despite a positive subsyringeal (air sac) pressure. In syllables A*x* and A*z* the first note terminates at its peak frequency by closure of the right side of the syrinx. The left side of the syrinx then opens to complete the syllable with a steeply downward sweeping FM note. In syllable A*p* the first note does not end until slightly after its frequency has peaked and begun to decline. Syllable A*x* is transformed into syllable A*p* by an upward shift in the frequency range of the initial upward sweeping FM note generated in the right syrinx (Fig. 2A). This upward shift reduces frequency overlap between the two sides of the syrinx and increases the syllable bandwidth from about 4 kHz for A*x* to about 5 kHz for A*p*. Syllables A*x* and A*p* are terminated as air sac pressure becomes negative and both sides of the syrinx open for the bilateral inspiratory minibreath at the end of the second note. During the transition from A*x* to A*p* (between the 6th and 7th syllables in Fig. 2A), the left side of the syrinx remains closed, resulting in a unilateral minibreath through the right side. Similar unilateral minibreaths through the right side of the syrinx are present between the A*z* syllables that form the first phrase in Fig. 2B. A possible advantage of unilateral minibreaths may be that the bird does not have to abduct the left side for inhalation, but can instead maintain the adducted labia closer to the phonatory configuration in preparation for producing the next note.

Syllable A*z* is followed by syllable *v*, which is a single downward sweeping FM note composed of a fundamental with its second harmonic (Fig. 2B). A minibreath with unilateral left flow occurs during the transition from syllable A*z* to syllable *v* and again before
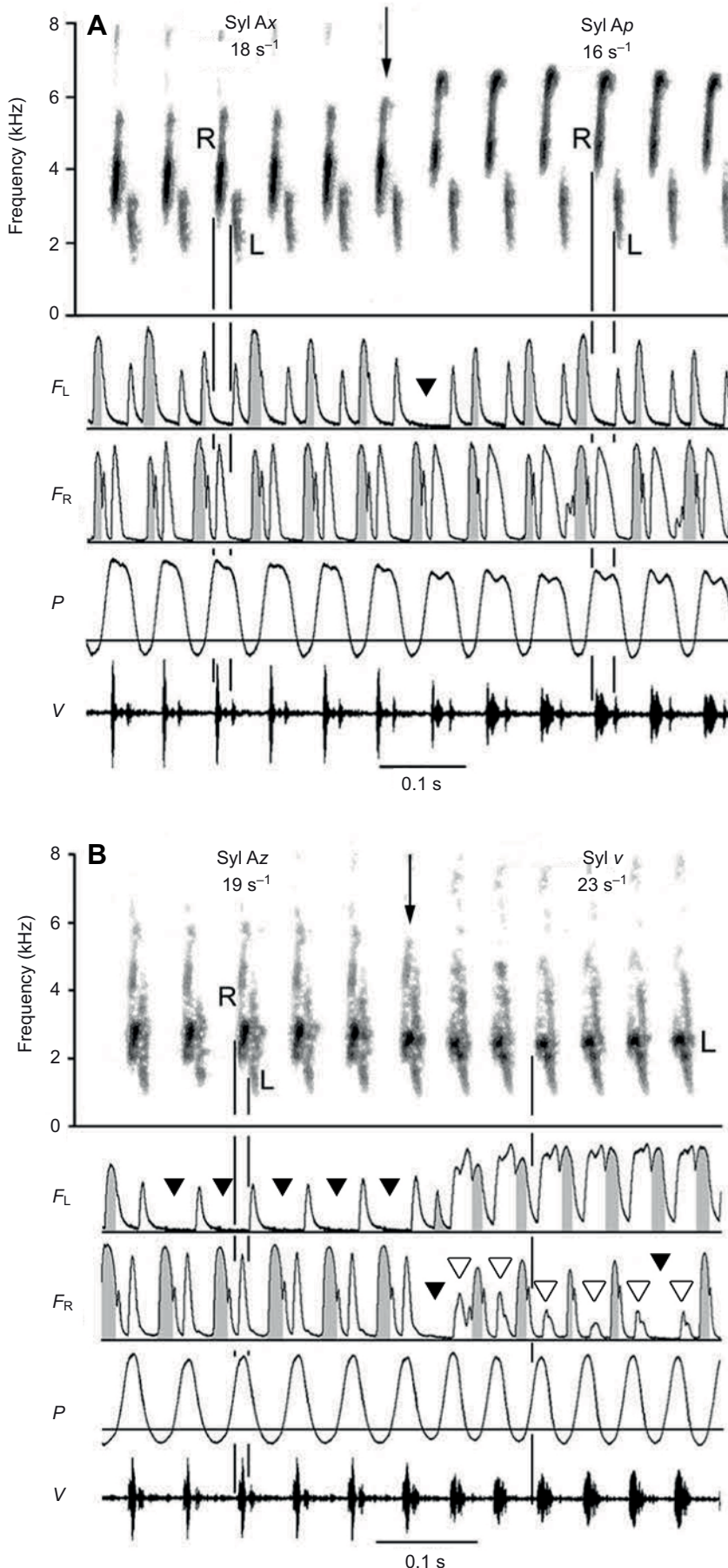
Fig. 2. Examples of complex syllables sung at high repetition rates. Inspiratory airflow is shaded. (A) The end and beginning of successive phrases containing sexy syllables A*x* and A*p*, respectively. The first note of both syllable types is produced on the right side of the syrinx and consists of an upward frequency sweep. In syllable A*p* the frequency range of this note is shifted upward, minimizing frequency overlap that is present between notes in syllable A*x*. The first note in syllable A*p* also acquires a small downward 'hook' at the top, suggesting tension on the right labia has peaked and is beginning to decrease. The first note is followed immediately, without an intervening minibreath, by a downward sweeping note from the left half of the syrinx. This note is the same in the two syllable types so that, in this example, syllable type is determined by the motor program to the right syrinx and a slight change in the frequency of the respiratory motor program. A minibreath after each syllable replaces the air exhaled to produce both notes. (B) End of a sexy syllable A*z* phrase and beginning of a phrase with syllable *v*. The first note of syllable A*z* is from the right side of the syrinx and is followed immediately by a note from the left side, which remains closed during the subsequent minibreaths between syllables. Syllable *v* is produced mainly or entirely on the left side. It does not contain two notes and is not a sexy syllable. Repetition rate is indicated at the top of the figure. Open triangles indicate irregular, low amplitude expiratory airflow through the right side of the syrinx, which may contribute a low amplitude sound at about 2.5 kHz simultaneously with the high amplitude sound generated by the high flow rate through the left side of the syrinx. Note that the time constant of the thermistor in the left bronchus does not allow the signal to return to zero between expiration and inspiration. Arrows indicate transitional syllables. Solid triangles indicate the side of the syrinx that is closed during inspiration, resulting in a unilateral minibreath. See legend of Fig. 1 for other symbols.
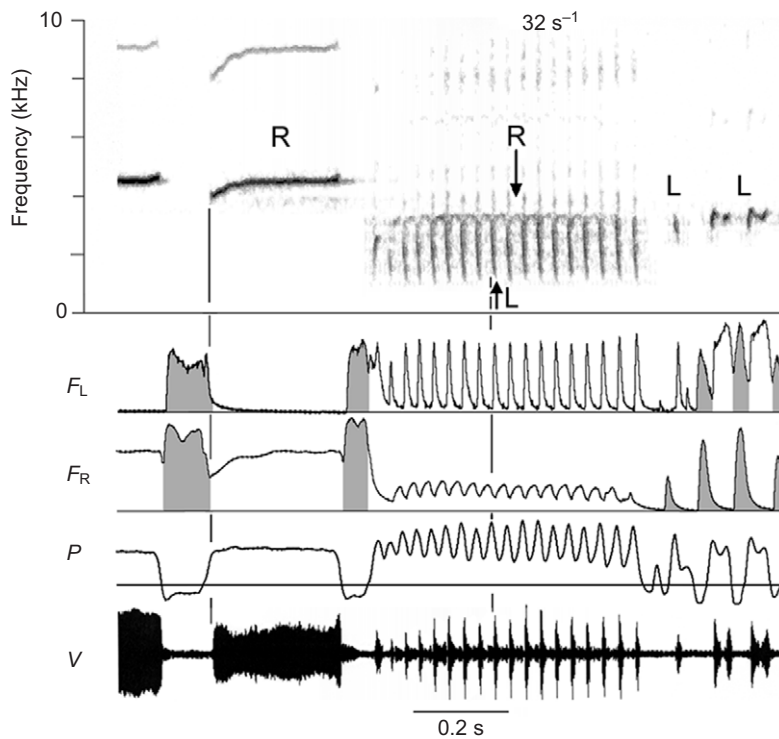
Fig. 3. A pulsatile trill that includes a contribution from each side of the syrinx. Air sac pressure remains positive during the trill. The left syrinx opens and closes at a repetition rate of $32\,s^{-1}$ to produce a series of brief FM sweeps with most of their energy between about 1 and 3.3 kHz. The right syrinx opens out of phase with the left to generate more nearly tonal sounds at about 3.3 kHz between each FM note. Trill follows a phrase of slow tonal notes creating a striking temporal and spectral contrast.

the last v syllable. Each v syllable is unilaterally produced by a stereotyped pattern of expiratory airflow through the left side of the syrinx. This expiratory airflow is in contrast to the reduced, variable flow rate due to leakage of expiratory air through the right side of the syrinx. Spectral analysis of the amplified thermistor output for airflow oscillation at the frequency of the fundamental also failed to detect evidence of sound in the right bronchus. If any sound is produced on the right side it is very low amplitude and simultaneous with that from the left side. Syllable v therefore consists of a single note and does not qualify as a sexy syllable.

Respiratory dynamics: pulsatile expiration

The 7th A-syllable phrase was produced by a series of pulsatile expirations during a sustained expiratory effort. During pulsatile expirations the bird maintains a positive expiratory pressure and phonation is produced by syringeal muscles that control the release of brief puffs of air. This A-syllable (Fig. 3) had a bandwidth of only 2.37 kHz, which swept down to a minimum at 1.09 kHz but through the use of pulsatile expiration it achieved an exceptionally high repetition rate of 32 syllables s^{-1}. Each steep FM sweep is produced by a brief expiration through the left syrinx. Between each of these FM notes, the right syrinx generates a nearly constant frequency note centered at ~3 kHz. The bandwidth of this syllable is only about 2.4 kHz, although it extends down to 1 kHz. The absence of minibreaths permits a higher syllable repetition rate (32 *versus* ≤25 syllables s^{-1} with minibreaths), which may compensate for the relatively narrow bandwidth, but places an upper limit on phrase duration as respiratory volume is depleted with each syllable. Except for its shorter duration, this trill is similar to sexy phrases of domestic, border and wild canaries that have been observed to be particularly effective in eliciting CSDs (Leitner et al., 2001; Vallet et al., 1997).

Relationship between trill rate and frequency bandwidth

The relationship between syllable repetition rate and bandwidth is shown in Fig. 4 for all syllable types and also according to the side(s) of the syrinx that produced the syllable. Because of the limited sample size and variation, the upper bound has not been calculated but it appears the A-syllables must be close to this line. The linear regression is significant only for the syllables produced on the left side of the syrinx (Fig. 4C). It is interesting that these syllables, unlike those of other songbirds (Podos, 1997), have a positive relationship between trill rate and frequency bandwidth. Female preference for wide bandwidths (Draganoiu et al., 2002) and low frequencies (Pasteau et al., 2007), which are generated on the left side of the syrinx, might provide a selective pressure for wider bandwidth at higher trill rates typical of A-syllables. Fig. 5 provides a visual summary of the relationship between A-syllables and other syllables sung by our three birds.

Unilateral two-note syllables

Some birds sang two-note syllables at repetition rates exceeding 15 syllables s^{-1} after one side of their syrinx was silenced by a bronchial plug and section of the ipsilateral tracheosyringeal nerve (Suthers et al., 2004). Experiments on domestic canaries with one side of their syrinx disabled confirm the importance of bilateral phonation to increased bandwidth. Normal intact domestic canaries never sang unilateral two-note syllables at sexy syllable repetition rates, but after the right side of the syrinx was silenced with a bronchial plug and denervated by sectioning the ipsilateral tracheosyringeal nerve (Suthers et al., 2004), some birds invented new two-note syllables which they sang unilaterally on their intact left side. These syllables differed in important ways from A-syllables. (1) Their fundamental bandwidth was narrower (left side 2.1±0.5 kHz, N=11; right side 3.1 kHz, N=1) than that of most A-syllables (4.1±1.0 kHz, N=7). (2) Unilaterally disabled birds usually had shorter inter-note intervals (<4 ms) than intact birds (3.4–12.0 ms). The shorter interval of disabled birds might be due to the unilateral as opposed to bilateral nature of the motor response. (3) The morphology of most unilateral two-note syllables was simple and the note structure was poorly differentiated compared with A-
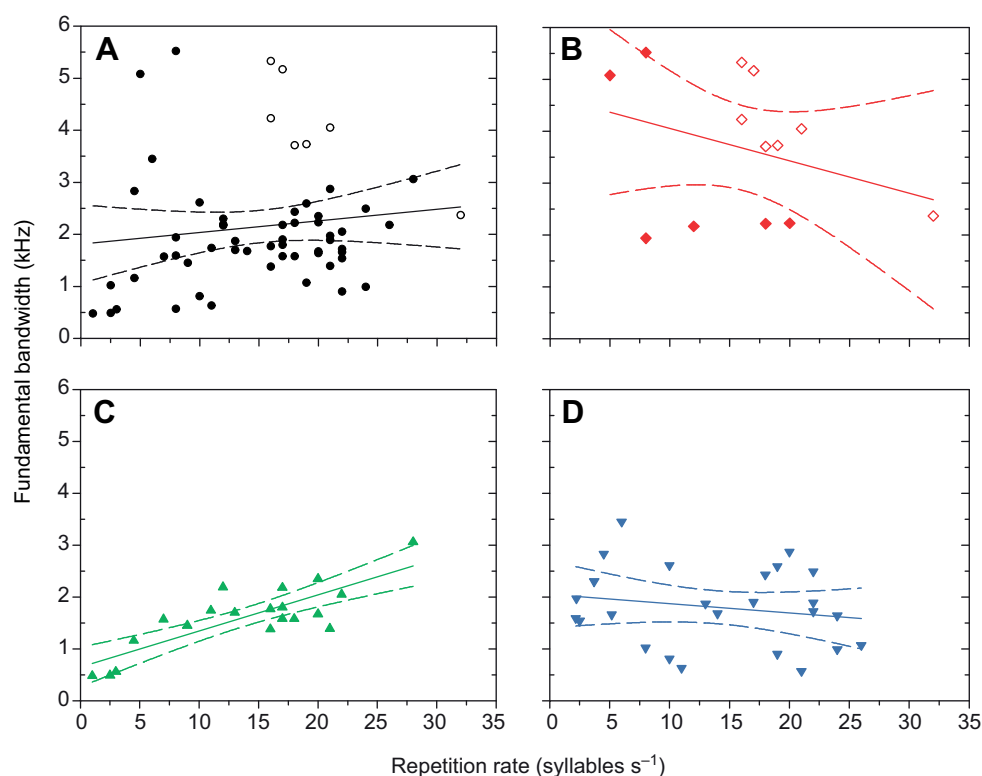
Fig. 4. Relationship between syllable repetition rate and bandwidth. (A) All syllable types sung by the three birds. R^2=0.017, P=0.321, N=59. (B) Bilaterally produced syllables with components from each side of the syrinx. R^2=0.103, P=0.284, N=25. (C) Syllables produced on the left side of the syrinx. R^2=0.662, P<0.001, N=20. (D) Syllables produced on the right side of the syrinx. R^2=0.035, P=0.370, N=25. The open symbols in A and B are A-syllables. Dashed lines indicate the 95% confidence interval.

syllables. (4) Post-operative unilateral two-note syllables were generally at a low intensity with a poor signal-to-noise ratio compared with syllables from intact birds (Figs 6, 7). Birds in which the left side of the syrinx was disabled never sang two-note syllables at repetition rates exceeding 15 syllables s^{-1} (Suthers et al., 2004).

These effects of peripheral denervation are consistent with those reported previously (Halle et al., 2003) following a unilateral lesion in the song control nucleus HVC (used as a proper name) in male domestic canaries. After a lesion in either the left or right HVC, the number of single note syllables recovered to about 40% that of the pre-operative repertoire, but the new repertoire contained very few two-note syllables (four syllables for 6 birds), none of which were sexy syllables, as all had repetition rates <12 syllables s^{-1}.

DISCUSSION
Motor correlates of A-syllables
The experiments we have described here provide the first direct information on the motor dynamics responsible for the production of A-syllables in the domestic canary. A-syllables are characterized by several acoustic properties that have been shown to be important in determining female preference. These include a syllable rate >15 syllables s^{-1}; two notes that are produced sequentially on opposite sides of the syrinx; a frequency bandwidth of about 4 kHz; and the inclusion of low frequencies.

Respiratory constraints on sexy syllable repetition rate
Respiratory requirements of song can exert important constraints on its tempo and duration. The notes within each sexy syllable are produced by pulsatile expiration and minibreaths are inserted between syllables (with the exception of the trill in Fig. 3). The combination of these two respiratory strategies permits high note repetition rates, as no minibreath is taken between notes. Phrase

duration is not limited by depletion of the respiratory volume, which is replaced after each syllable. The same respiratory technique is used to produce low repetition rate two-note syllables [e.g. fig. 7 in our previous publication (Suthers et al., 2004)].

If the receiver attends to note repetition rate, then two-note syllables can double the effective signal repetition rate that is otherwise possible using a minibreath respiratory pattern with single note syllables. It is interesting that the minimum syllable repetition rate required to qualify as a sexy syllable (~15 syllables s^{-1}) gives a note repetition rate (~30 s^{-1}) equal to the syllable rate at which phrase length in canaries begins to be limited by depletion of the respiratory air supply (Hartley and Suthers, 1989; Suthers et al., 2004). Above this syllable repetition rate, canaries must switch to pulsatile expiration in which air is not replaced between syllables, thus placing an upper limit on phrase duration. By producing two-note syllables separated by minibreaths, the bird is able to combine in a single phrase the high repetition rates of pulsatile expiration with the extended phrase duration made possible by minibreaths.

Syringeal constraints on sexy syllables
Achieving high syllable repetition rates requires precise coordination between the contraction of respiratory muscles, which provide the driving force that powers phonation, and that of syringeal muscles. Dorsal syringeal muscles control the labial valve at the cranial end of each bronchus, opening it to allow phonation during positive respiratory pressure. Ventral syringeal muscles control sound frequency by varying the tension on the vocal folds. Elemans and colleagues have shown that the syringeal muscles of European starlings (*Sturnus vulgaris*) and zebra finches (*Taeniopygia guttata*) have evolved superfast contractile kinetics (Elemans et al., 2008). They are active in phase with song modulations up to 200 Hz and can do mechanical work up to 250 Hz *in vitro*, clearly suggesting
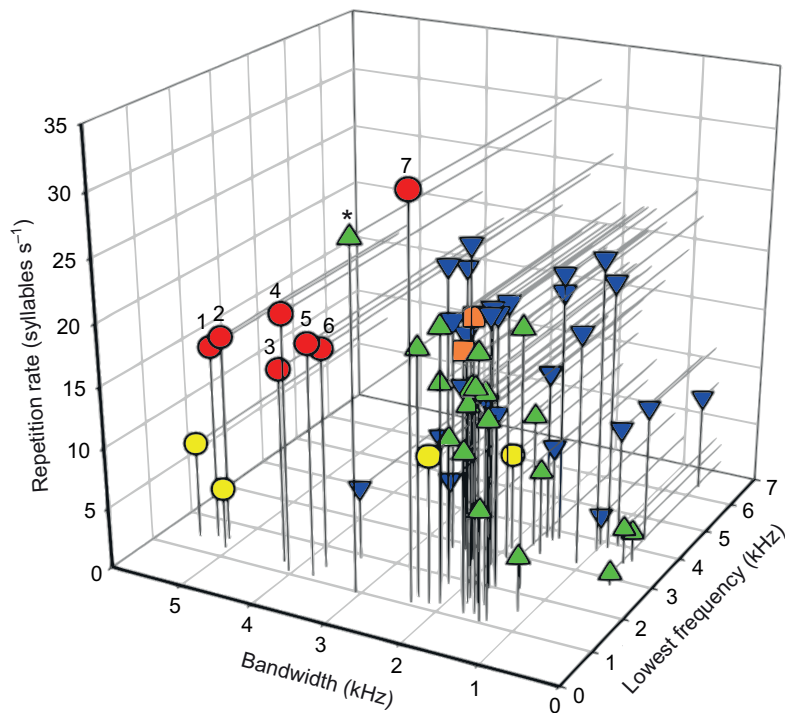
Fig. 5 Each syllable type recorded from 3 birds singing with their vocal system intact, plotted according to its fundamental bandwidth, repetition rate and lowest frequency. A-syllables (red circles), including all two-note syllables at repetition rates ≥15 syllables s^{-1}, stand out from the rest of the repertoire. A-syllable types 1–6 were separated by minibreaths; type 7 (see Fig. 3) was produced by pulsatile expiration but contained two notes. The remaining four two-note syllables (yellow circles) were sung at lower repetition rates and two had a relatively narrow bandwidth. Two syllables (orange squares) included flow through both sides of the syrinx but consisted of only one note. Syllables produced by the left syrinx alone (green triangles) generally had lower fundamental frequencies than syllables produced only by the right syrinx (inverted blue triangles). The high repetition rate left side syllable marked by an asterisk was produced by pulsatile expiration and had one note. Gray horizontal lines from the symbols to the grid at the back of the figure are provided to accurately indicate syllable repetition rates.

a strong selective pressure for rapid modulation of song and high trill repetition rates.

Bilateral phonation increases syllable bandwidth by taking advantage of the different frequency ranges of which each side of the syrinx is capable. By phonating sequentially on each side of the syrinx, instead of simultaneously as during two-voice syllables, domestic canaries may have evaded production constraints that could otherwise limit the difference between simultaneously generated left and right fundamental frequencies. In two-voice species, such as brown thrashers (*Toxostoma rufum*) and gray catbirds (*Dumetella carolinensis*), the difference between the left and right fundamental frequencies is usually substantially less than that between the fundamental of each side during unilateral phonation (Suthers et al., 1994). In the case of two-voice syllables the frequency difference between sides of the syrinx might be limited by the bandwidth of the resonance filter in the suprasyringeal vocal tract or there may be biomechanical or physical interactions between the left and right sides of the syrinx (Nowicki and Capranica, 1986; Riede et al., 2006) that restrict their ability to simultaneously oscillate at widely different frequencies. Sequential phonation in A-syllables also provides domestic canaries with an acoustic cue that could allow the receiver to discriminate bandwidth due to unilateral overtones from that due to bilateral phonation (see below).

Female preference for A-syllables depends on a suite of acoustic traits

If we are to understand the evolution of female preference for A-syllables we need to know the extent to which other acoustic features of A-syllables influence female preference. This has now been quantified in a series of behavioral experiments by observing female responses to the manipulation of a single acoustic parameter. These experiments have shown that female domestic canaries have a directional predisposition favoring an increase in the magnitude of each of the acoustic features that characterize A-syllables.

Thus, Draganoiu and colleagues showed that female canaries have a directional preference for wideband syllables (Draganoiu et al., 2002). The number of CSDs elicited by an A-syllable increased as the syllable's bandwidth was increased from 2 kHz to a normal 4 kHz and an exaggerated 6 kHz while syllable repetition rate was kept constant at 16 or 20 syllables s^{-1}.

Pasteau and colleagues investigated female preference for syllable complexity (Pasteau et al., 2004). They compared female responses to phrases composed of a single syllable type – upward sweeping, downward sweeping or constant frequency – sung at 32 syllables s^{-1}, to her responses to phrases of complex syllables produced by combining the simple syllables in a particular sequence to form diversified phrases of complex syllables in which the note repetition rate was still 32 s^{-1}. Female canaries preferred the complex syllables, regardless of the order in which the three kinds of simple note were arranged.

In another experiment, they tested the preferences of female canaries for low, normal or high pitched sounds (Pasteau et al., 2007). Controlling for bandwidth, they found that female canaries preferred sexy syllables at their normal frequency and those with a downward frequency shift of 1.5 kHz, compared with syllables shifted upward 1.5 kHz above their normal frequency. They also showed that the preference for low pitched and normal pitched sexy syllables is not affected by the frequency contrast between the pitch of the sexy phrase and that of the phrases that immediately precede and follow it.

Pasteau and colleagues performed a similar series of experiments to determine female preference for changes in the sound intensity level ('loudness') of sexy phrases (Pasteau et al., 2009a). When exposed to sexy phrases reproduced at approximately the 'normal' intensity recorded in the lab and at either twice or half the normal peak-to-peak intensity, females significantly preferred the loud and normal intensities. If the intensity of only the non-sexy adjacent phrases was increased, it did not consistently invoke an increase in female preference.
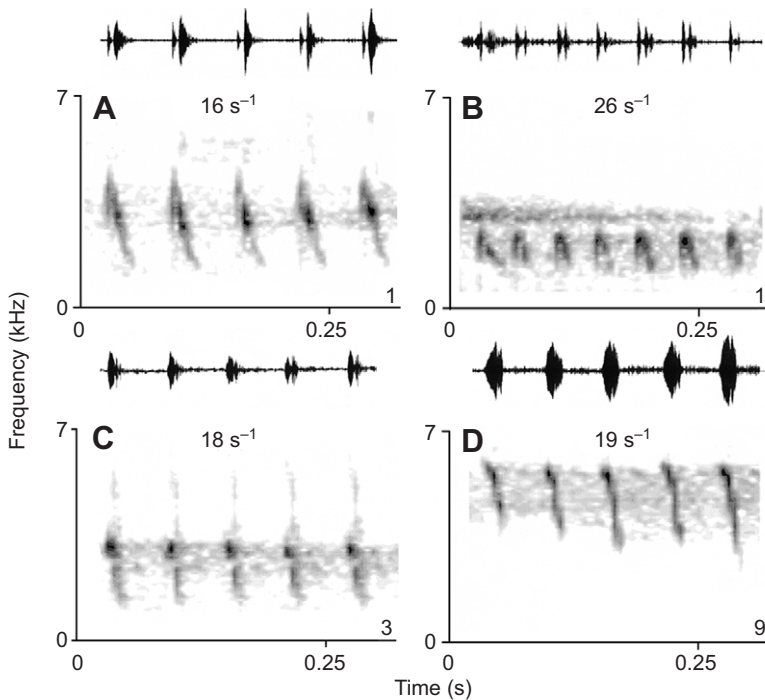
Fig. 6. Examples of complex syllables sung at rates of >15 syllables s⁻¹ by birds with one side of the syrinx disabled. The syllables in A–C were sung by birds that had their bronchus plugged and tracheosyringeal nerve cut on the right side. The syllable in D, sung by a bird with a bronchial plug and tracheosyringeal nerve cut on the left side, has some amplitude modulation but does not contain distinct notes. Horizontal band of noise just above syllables in B is environmental sound not produced by bird. Number in lower right corner identifies individual bird.

Finally, they tested the effect of the length of a phrase of sexy syllables on female preference (Pasteau et al., 2009b). They presented females with test songs that were identical except for the length of the sexy phrase, which was 1.0, 1.5 or 2.0 s. The female responses show a clear preference for long sexy phrases.

A question of obvious interest is whether the female preferences Pasteau and colleagues reported in the preceding experiments depended on or were affected by their auditory or sexual experience and social interactions with other canaries. In order to assess this possibility, in each of the above-described experiments, Pasteau and colleagues divided the female canaries into two groups. One group was raised in the presence of other juvenile and female canaries, but had never heard or seen male canaries older than about 30 days when subsong first begins. The other group was raised in an aviary with adult and juvenile birds of both sexes. This experimental design made it possible to determine whether the response to the parameter being tested depended on previous auditory or sexual experience or whether the preferences of naive females indicated a predisposition for the parameter being tested. In every case, the preferences of the adult females reared in an aviary were similar to those of females reared in acoustic isolation from males, indicating female preferences represent a predisposition that does not require prior auditory, sexual or social experience.

As female preference for each of the A-syllable traits tested is directional (Draganoiu et al., 2002; Gil and Gahr, 2002; Pa and Hickok, 2003; Pasteau et al., 2004; Pasteau et al., 2007; Pasteau et al., 2009a; Pasteau et al., 2009b; Vehrencamp, 2000), both models of receiver bias and of honest signaling through adaptive sexual selection should favor males who maximize the perceptually important properties of sexy phrases (Gil and Gahr, 2002; Rowe and Skelhorn, 2004; Vehrencamp, 2000)

Many complex behaviors depend on rapid interhemispheric coordination

The bipartite syrinx of Oscine songbirds is well suited to convey information on the sender's vocal performance limit, which often requires millisecond precision in interhemispheric coordination and is susceptible to disease and subtle environmental stresses. Adult swamp sparrows subjected to early nutritional stress during critical periods in song development produce less accurate copies of model songs than do control birds (Buchanan et al., 2003; Nowicki et al., 2000; Nowicki et al., 1998; Nowicki et al., 2002). Their song nuclei HVC and the robust nucleus of the arcopallium (RA), which has an important role in determining the timing and fine structure of notes and syllables and in coordinating respiration and phonation (Chi and Margoliash, 2001; Hahnloser et al., 2002; Sturdy et al., 2003) (reviewed by Suthers and Margoliash, 2002; Vu et al., 1994; Yu and Margoliash, 1996), are smaller than those of controls.

A growing body of research indicates that the two cerebral hemispheres in vertebrates are often specialized to process different aspects of particular behaviors, thus placing a premium on interhemispheric coordination and integration when executing the complete behavior (Schmidt, 2008). The rapid switching of phonation between the left and right sides of the syrinx is a prominent feature of the songs of many birds as they take advantage of lateralized differences in frequency range, frequency modulation, etc. (Suthers et al., 1994).

Despite a left hemisphere dominance for human speech, it is now realized that both hemispheres contribute to speech production (Terao et al., 2001) and each hemisphere is specialized to process different aspects of speech (Friederici and Alter, 2004). Hemispheric specializations for song discrimination, involving different auditory processing in the forebrain of each hemisphere, have also been reported in songbirds (Cynx et al., 1992; George et al., 2005).

As pointed out by Schmidt, lateral specialization of the cerebral hemispheres is not limited to vocal behavior (Schmidt, 2008). Hemispheric lateralization of visual functions is well known (Gunturkun, 1997). Migratory birds can only sense the direction of the magnetic field for compass orientation with their right eye (Wiltschko et al., 2002). Lateralization of visual perceptual information and memory storage has been described for food-storing marsh tits (Parus palustris) (Clayton and Krebs, 1994). Even these
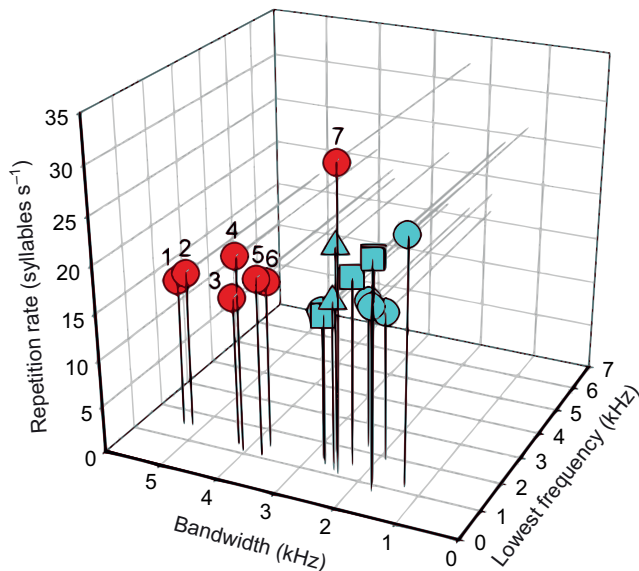
Fig. 7. The importance of using both sides of the syrinx to produce sexy syllables is illustrated by the properties of unilateral two-note syllables sung by domestic canaries after the right side of their syrinx was disabled by denervation and a bronchial plug [data from Suthers et al. (Suthers et al., 2004)]. After surgery, all pre-operative multinote syllables with repetition rates >13 syllables s^{-1} disappeared from the post-operative repertoire, but 3 of 4 birds with the left side of their syrinx intact added between two and five new, high repetition rate (>15 syllables s^{-1}) multinote syllables to their post-operative repertoires. These unilateral multinote syllables differed from sexy syllables in having a narrow bandwidth (2.1±0.5 kHz, N=11 post-operative left syllables versus 4.1±1.0 kHz, N=7 intact sexy syllables). They were also low intensity and had a simpler, more poorly differentiated note structure compared with sexy syllables. Birds with a bilaterally intact vocal system never sang high repetition rate, unilateral, two-note syllables. Different light blue symbol shapes represent different birds. Red circles are sexy syllables.

few examples are enough to indicate the wide range of behaviors and physiological processes that depend on rapid, reliable interhemispheric communication.

We suggest that A-syllables serve female canaries as a sensitive bioassay indicating the health of prospective mates. If she chooses a male who fails to sing A-phrases or is unable to achieve a high performance level she runs the risk of having a mate of poor genetic quality, or who is sick, old or a victim of early nutritional or developmental stress, or who is otherwise inferior. In humans, bimanual motor skills requiring the coordination of finger movements between hands in rapid antiphasic rhythms are one of the first motor skills to deteriorate with age (Gentner, 1988; Wishart et al., 2000) and age-related declines in out of phase bimanual control are accompanied by age-related declines in the size and integrity of the callosum.

Songbirds do not have a direct connection between the telencephalic nuclei of their song system. Neurophysiological experiments are beginning to elucidate some of the mechanisms involved in the coordination of songbird hemispheres during song, including a key role for song nucleus RA (Ashmore et al., 2008a; Ashmore et al., 2008b; Schmidt, 2003; Schmidt et al., 2004). Some neurophysiological evidence indicates that during song the dominance of the cerebral hemispheres rapidly switches back and forth from side to side many times per second. The function of this rapid interhemispheric switching is still unclear, but it is hypothesized that it increases the processing power of each

hemisphere while keeping the two sides synchronized (Schmidt, 2008; Wang et al., 2008).

A-syllables as honest indicators of bilateral competence

Behavioral experiments have shown that female canaries have a preference for exaggerated versions of each of the suite of traits that make up A-syllables, but the relationship of these individual traits to male fitness is not always clear. Exactly how is the increased bandwidth or high repetition rate in a male's song related to his fitness? What selective pressures might have led to the evolution of the particular constellation of features that contribute to female preference? Are the behaviorally important traits in A-syllables redundant or do each provide different information that when combined with the other traits give a more sensitive measure of fitness?

We hypothesize that the suite of traits that characterize A-syllables have evolved as a particularly sensitive and reliable vocal–auditory measure of the male's ability for rapid interhemispheric processing of sensory and motor information – a more sensitive and reliable measure of bilateral coordination than would be possible if relying on any single trait. The behaviorally important acoustic properties of sexy syllables are exactly those needed to enable the receiver to discriminate between bilaterally versus unilaterally produced syllables. The inclusion of low fundamental frequencies below 2 kHz indicates a contribution from the left side of the syrinx. The preference for a wide bandwidth increases the probability that both sides of the syrinx are contributing to the syllable. The possibility of 'cheating' by producing a low fundamental on the left side with strong overtones to attain a wide bandwidth is ruled out by the temporal offset between notes from the two sides of the syrinx, confirming that the high frequency note arises on the right side. The requirement for a high syllable repetition rate >15 syllables s^{-1} displays the sender's performance limit for interhemispheric coordination. Females who prefer these traits should have a higher probability of choosing a male with excellent bilateral coordination than females who choose based on only one or a few of the traits.

LIST OF ABBREVIATIONS

CSD	copulation solicitation display
F_L	airflow through left side of the syrinx
F_R	airflow through right side of the syrinx
FM	frequency modulation
P	respiratory pressure in cranial thoracic air sac
RA	robust nucleus of the arcopallium
V	vocalization

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