

Role of syringeal vibrations in bird vocalizations

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The sound-generating mechanism in the bird syrinx has been the subject of debate. Recent endoscopic imaging of the syrinx during phonation provided evidence for vibrations of membranes and labia, but could not provide quantitative analysis of the vibrations. We have now recorded vibrations in the intact syrinx directly with an optic vibration detector together with the emitted sound during brain stimulation-induced phonation in anaesthetized pigeons, cockatiels, and a hill myna. The phonating syrinx was also filmed through an endoscope inserted into the trachea. In these species vibrations were always present during phonation, and their frequency and amplitude characteristics were highly similar to those of the emitted sound, including nonlinear acoustic phenomena. This was also true for tonal vocalizations, suggesting that a vibratory mechanism can account for all vocalizations presented in the study. In some vocalizations we found differences in the shape of the waveform between vibrations and the emitted sound, probably reflecting variations in oscillatory behaviour of syringeal structures. This study therefore provides the first direct evidence for a vibratory sound-generating mechanism (i.e. lateral tympaniform membranes or labia acting as pneumatic valves) and does not support pure aerodynamic models. Furthermore, the data emphasize a potentially high degree of acoustic complexity.

Keywords: sound generation; vocal mechanism; syrinx vibrations; pigeon; cockatiel; hill myna

1. INTRODUCTION

The most widely accepted model of sound production in the vocal organ of birds, the syrinx, proposes that sound is generated by vibrations of syringeal structures (e.g. Brackenbury 1979; Casey & Gaunt 1985; Fletcher 1988, 1989; Gaunt & Wells 1973; Greenewalt 1968; Suthers 1990). A partial constriction of the syringeal lumen leads to higher velocity airflow, generating a suction force, which in combination with opposing viscoelastic forces triggers the presumed sound-generating membranes into vibration. Models based on this physical mechanism, however, have difficulty in explaining the generation of tonal sounds, which characterizes many bird vocalizations (e.g. Fletcher 1989).

Arising from this theoretical problem, alternative models of sound generation have been proposed. It was suggested that production of pure tones is possible if the syrinx operates like a hole-tone whistle. This whistle hypothesis was initially proposed to account for tonal vocalizations in doves and parrots (Gaunt 1983; Gaunt *et al.* 1982; Nottebohm 1976) and then also extended to songbirds (Casey & Gaunt 1985). A hole-tone whistle mechanism requires that syringeal structures form a rigid boundary and sound will be generated by self-sustained vortex formation rostrad to that constriction (Chanaud 1970; Wilson *et al.* 1971).

Endoscopic analysis of the pigeon and songbird syringes showed that during phonation flexible structures are adducted into the middle of the bronchial or tracheal lumen, at least partially making contact, much like the human vocal folds during speech (Goller & Larsen 1997*a,b*). The adducted structures are the medial and lateral labia (ML and LL) in songbirds and the lateral tympaniform membranes (LTM) in pigeons, but not, as suggested in earlier models, the thin medial tympaniform membranes (MTM) (e.g. Brackenbury 1989; Casey & Gaunt 1985; Greenewalt 1968). The endoscopic images revealed vibrations of the labia and LTM that coincided with sound production.

The phonatory configuration and the presence of vibrations strongly suggest that sound is generated by a vibration-based mechanism and not by a mechanism similar to the hole-tone whistle. However, the low temporal resolution of the endoscopic imaging system did not allow quantitative analysis of these vibrations. Consequently, a direct comparison of frequency and amplitude of the observed syringeal vibrations with those of the emitted sound is needed to test the vibration hypothesis, i.e. that the vibrating structures act as pneumatic valves.

In the present study, we present, to our knowledge, the first direct measurements of syringeal vibrations during brain stimulation-induced phonation in the intact syrinx and correlate them with parameters of emitted sound in pigeons (Columbiformes), cockatiels (Psittaciformes) and a songbird (Passeriformes). In all three groups of birds, these measurements in combination with endoscopic images of the phonating syrinx provide strong direct support for the vibration hypothesis.

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2. MATERIALS AND METHODS

Seven male domestic pigeons (*Columba livia*), four male cockatiels (*Nymphicus hollandicus*), and a hill myna (*Gracula religiosa*) were acquired from a local vendor. The experiments were performed at the Biomedical Laboratory, Odense University Hospital, with permission from the Danish Animal Experimentation Inspectorate. All experiments were acute. Birds were anaesthetized by intramuscular injections of a Rompun–ketamine mixture (initial dose 20 mg kg⁻¹ xylazine hydrochloride and 40 mg kg⁻¹ ketamine hydrochloride; supplements were given as needed to keep them deeply anaesthetized for 3–4 h) and overdosed with pentobarbital at the end of experiments.

Anaesthetized birds were placed in a stereotaxic apparatus (KopfTM type 900). Phonation was induced by stimulating a vocal centre through a monopolar tungsten electrode with the indifferent electrode connected to the scalp (DISATM stimulator type 14E11, pulse duration 1 ms, train duration 1000 ms, pulse repetition rate 100 Hz, stimulus intensity 50–100 μ A). In cockatiels we stimulated the central nucleus of the anterior archistriatum (AAc), which projects directly to the tracheosyringeal motor nucleus (Striedter 1994). Hill myna vocalizations were elicited by stimulation of the high vocal centre (HVC). In pigeons we aimed at stimulating the dorsomedial nucleus of the intercollicular complex but needed relatively high stimulus amplitudes (about 100 μ A) indicating that the electrode tip only reached the vicinity of the nucleus (J. M. Wild, personal communication).

The rostral end of the trachea was exposed and an angiofibrescope was inserted through a small opening and guided close to the syrinx. The angiofibrescope, the video and sound recording, and the data processing were similar to those described in detail in Goller & Larsen (1997b). Neither the fibrescope nor the optic double fibre (see below) affected breathing as no 'forced' respiration was observed (tracheal diameters: about 6 mm in pigeons, and 2.1 mm in both cockatiels and the hill myna; angioscope outer diameter: 1.4 mm; double fibre outer diameter: 1.5 mm).

The microphone of a precision sound level meter (Brüel & KjaerTM type 2235; frequency response 5–13 000 Hz in linear mode) was placed 4–6 cm from the tracheal opening ensuring recorded sound levels of 60–75 dB. Recordings were A-filtered (500–10 000 Hz) to attenuate ambient noise (noise level about 50 dB(A)) with the exception of pigeon vocalizations, which were recorded in linear mode.

Syringeal vibrations were measured with a custom-built vibration detector emitting and detecting laser light through an optic double fibre, which could be placed in the trachea without obstructing airflow. The optic fibre terminated without a lens system producing a spot of light with a diameter varying from 10 mm at a distance of 20 mm to 3 mm at a distance of 3 mm. Prior to insertion of the optic fibre we used the endoscope to determine the distance from insertion site to syrinx such that the fibre tip was placed between 2 and 5 mm from the vibrating structures. The large spot diameter made it possible to register average vibratory activity of the structures reflecting the emitted light. Because of the vicinity of the tip to the LTM and labia obstructing the tracheal lumen, they were the most likely sources of reflected light but the set-up did not allow us to distinguish between radial and axial movement components. A phototransistor coupled to the receiving fibre produced a current proportional to the intensity of reflected light (amplification 20 000–200 000). Output voltage was proportional to vibration amplitude but depended on distance from fibre tip to vibrating

object. Although in single recordings this distance was kept constant, it could not be measured exactly, and signals are therefore presented in relative amplitudes. The frequency response of the vibration detector was determined by measuring its response to calibrated vibrations of a minishaker (Brüel & KjaerTM type 4810). A high-pass filter limited the frequency response by 12 dB octave⁻¹ below 100 Hz, while the amplitude was reduced by 8 dB octave⁻¹ above 1000 Hz. Signals from the sound level meter and vibration detector were recorded on a multi-channel DAT recorder (TEACTM type RD-135T, sample rate 48.0 kHz).

3. RESULTS

(a) *Endoscopic observations*

In pigeons, brain stimulation elicited a series of sound pulses. For each sound pulse the LTM were adducted into the tracheal lumen and returned to their abducted respiratory position between pulses. Syringeal action during the production of a single sound pulse is exemplified in figure 1a. In the resting position the bronchial septum and the bronchial lumina are clearly visible. Sound production is initiated by almost full adduction of the LTM. At the same time the dorsal wall starts to bulge into the lumen, probably because of increased pressurization. During phonation the ballooning LTM folds are bulging rostrally into the tracheal lumen and forming a narrow, irregular slot. The LTM and the dorsal wall return to their original respiratory position at the end of the sound pulse.

During quiet respiration the syringeal configuration of anaesthetized cockatiels differed markedly from that of pigeons. The LTM were partially adducted into the tracheal lumen forming a significant constriction along their dorsoventral axis (figure 1b). Very little, if any, movement of the LTM could be observed during either respiratory phase. In response to brain stimulation, however, the syrinx typically moved rostrally during the build up of subsyringeal pressure and a further adduction of the LTM formed a narrow slot. Audible sound was produced only when the LTM clearly vibrated along part of this slot. The low temporal resolution of the video equipment did not make it possible to determine whether the LTM fully closed the lumen during each vibration cycle. Finally, the syringeal configuration of the hill myna during quiet respiration and sound production closely resembled that reported earlier for other songbirds (Goller & Larsen 1997b).

(b) *Comparison of emitted sound with syringeal vibration*

Pigeon cooing bouts (figure 2a) elicited by brain stimulation consisted of a series of typically three sound pulses each with a duration of about 70 ms (mean \pm s.d. = 70 \pm 30 ms, n = 186). An initial high amplitude cycle followed by one to two cycles of lower amplitude and a build up to constant high amplitude characterized the single sound pulse. The dominant frequency was typically 220 Hz (range 200–460 Hz) with some broad-band smearing at the beginning and end of each sound pulse (figure 2b).

We never observed phonation without simultaneous membrane vibration, whereas the opposite sometimes was

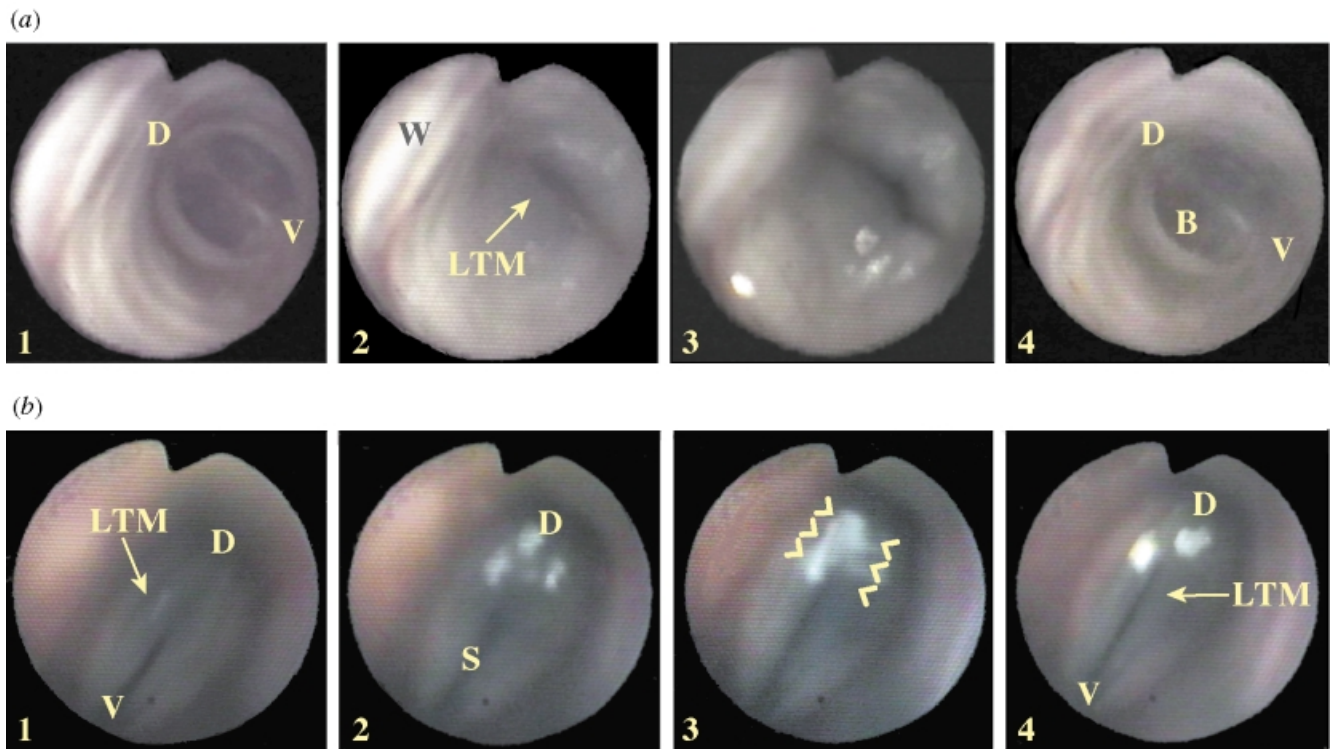


Figure 1. Internal top views of the phonating syrinx. (a) Production of a single sound pulse in the pigeon syrinx. Frames 1 and 4 show the syrinx in the quiet resting position. The bronchial septum is faintly seen between the bronchial lumina beneath the line defined by D and V. Frames 2 and 3 show that the rostrad ballooning LTM form an irregular slot during sound generation. (b) Initiation of a single sound pulse in the cockatiel syrinx. The LTM are partially adducted in the quiet respiratory position of anaesthetized birds (frame 1). In response to brain stimulation the syrinx often moves rostrally (frames 2–4). This is indicated by the increasing size of the syringeal structures because of decreasing distance to the endoscope lens and the increased brightness of light reflections. The slot partially closes (yellow arrowheads), and vibrations are observed when audible sound is produced. B, bronchial lumen; D, dorsal; S, slot; V, ventral; W, dorsal wall.

true. Syringeal vibration signals were very similar to the emitted sound signals in envelope, frequency, and temporal parameters (figure 2). The envelope variation of the single sound pulses described above was more pronounced in the vibration recordings. Power spectra indicate the high similarity in frequency between the two signals (figure 2*b*) and also show the tonal character of the vocalizations (i.e. f_1 is approximately 20 dB below f_0). Visual inspection of the video sequences at very low sound frequencies suggested radial vibration amplitudes between 0.5 and 1.0 mm, whereas calibration of the voltage output of the laser system indicated smaller vibration amplitudes (0.01–0.1 mm). However, exact calibration for *in situ* recordings is difficult for a number of reasons (e.g. exact distance to vibrating structures cannot be determined, mucus covering the fibre tip, unknown reflective properties of LTM, etc.).

For all cockatiel phonations elicited by brain stimulation we found high correlation between sound and vibration signals. A stimulation train to the AAc always generated a single sound pulse (figure 3*a*, duration 367 ± 175 ms, $n = 72$) with a short rise-time (15 ± 7 ms) and longer fall-time (33 ± 14 ms) but intensity and envelope varied from pulse to pulse. Low intensity sound pulses typically had a shorter duration and more tonal character (f_1 20–30 dB below f_0 , $n = 14$) than the very loud calls with complicated spectral energy distribution and amplitude changes (compare figure 3*c* and 3*b*).

The envelope of the vibration waveform recorded at the syrinx (figure 3*a*) reflected that of the sound pulse in duration but had nearly equal rise- and fall-times (16 ± 14 ms and 16 ± 7 ms, respectively). Sometimes low-frequency vibrations were observed right before the onset ($n = 36$ out of 72 observations) or after the cessation of audible sound ($n = 9$). These signals might result from the AC-coupling of the vibration recorder and indicate the overall repositioning of the syrinx during pressurization and relaxation. In vocalizations of low to moderate intensity the energy distribution across the harmonic spectrum of LTM vibrations was very similar to that of the emitted sound (figure 3*a,b*). They typically had a fundamental of 2.2 kHz (2.2 ± 0.2 kHz) and harmonics visible up to about 8 kHz. In the intense vocalizations nonlinear phenomena such as subharmonics (e.g. first 200 ms of figure 3*a,b*) and rapid frequency transitions were present in both the sound and vibration signals.

On a small time-scale there was a cycle-by-cycle concordance between sound and vibration signals but the shape of individual cycles differed (figure 3*c,d*). Large amplitude modulations (50–100%) in the sound envelope ($n = 11$) coincided with the occurrence of a rapid transition in oscillation frequency and an irregular low frequency wave superimposed on the ongoing oscillations in the vibration trace (figure 3*d*). The mechanical origin of this low frequency wave is unknown.

HVC stimulation in the hill myna always produced concurrent syringeal vibration and sound signals of

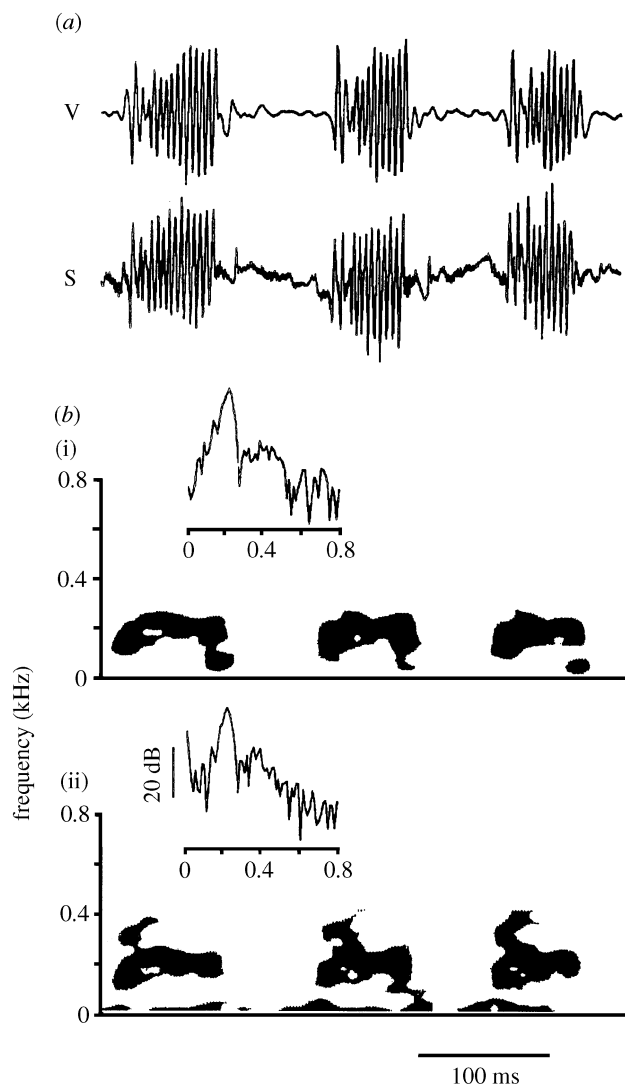


Figure 2. Brain stimulation-induced coo sequence in pigeons. (a) Waveforms of vibration (V) and sound (S) signals. (b) Spectrograms of (i) the vibration and (ii) sound signals in (a). The upturned U-shape was characteristic for these spectra. Insets are power spectra of the vibration and sound signals for the first syllable.

100–250 ms duration. We observed three types of sound: sparse harmonic sounds (38%), dense harmonic sounds (16%), and a combination of the two (46%).

Compared with those of pigeons and cockatiels the myna vibration traces had a low signal-to-noise ratio and vibration amplitudes during tone production were always relatively small (figure 4a). This probably reflects the much smaller vibrating labial surface areas of the myna. Nevertheless, vibration spectrograms exhibited a distribution of fundamentals and harmonics very similar to those of the sound spectrograms. Characteristically, large low-frequency vibrations preceded and succeeded vibration pulses but not sound pulses. These vibrations may arise from the syringeal reconfiguration for phonation, i.e. rostral movement of the syrinx and labial adduction in preparation for sound production followed by a caudal movement and labial abduction after the cessation of phonation.

In expanded waveforms of sounds with sparse harmonic character (not illustrated) there was a clear 1:1

relationship between fundamental vibration and sound amplitude, in spite of the noisy vibration trace. The broad-band dense harmonic sounds (figure 4b) consisted of trains of impulse sounds (figure 4c). The vibration signal exhibited the same periodicity as the sound, but consisted of square wave-like fluctuations phase-coupled with the impulses of the emitted sound.

4. DISCUSSION

The endoscopic evidence shows that the phonatory position of the syrinx is similar in all three groups of birds investigated here. Flexible structures, LTM in pigeons and cockatiels, and ML and LL in the myna, are adducted into the syringeal airways and form a narrow slot. Vocalizations following brain stimulation in pigeons validate the results of an earlier endoscopic analysis of air-induced phonation (Goller & Larsen 1997a). Also the observed phonatory position in the myna is very similar to the observations made using brain stimulation in other songbirds (Goller & Larsen 1997b).

The endoscopic images of the cockatiel syrinx represent, to our knowledge, the first direct visual observation of the vocal organ of a parrot during phonation. The tracheal airways are constricted by the LTM as they fold along their dorsoventral axis and protrude into the lumen. This observed phonatory position largely confirms a model based on morphological and physiological observations of several parrot species (Gaunt & Gaunt 1985), but is in contrast to another model based on the morphology of an Amazon parrot (*Amazona amazonica*) (Nottebohm 1976).

In all three species endoscopic images indicate that the adducted flexible structures vibrate during sound generation as was reported previously for three different songbirds (Goller & Larsen 1997b). This qualitative observation is now confirmed by the quantitative measurements of vibrations in the intact syrinx during brain-stimulated vocalizations. Frequency and amplitude characteristics of syringeal vibrations generally match those of the emitted sound. Syringeal vibrations without accompanying sound production are often observed in response to brain stimulation, whereas we never made the opposite observation. Together with the reasonably large radial vibrations amplitudes these observations provide the first direct evidence in support of the vibration hypothesis (the vibrating structures acting as pneumatic valves).

Most of the pigeon vocalizations and a few of the cockatiel calls elicited by brain stimulation qualify as tonal sounds when defined as having the levels of all upper partials at least 20 dB below the level of the fundamental (Greenewalt 1968, table 12). Even for these tonal sounds, smooth sinusoidal syringeal vibrations are observed and directly reflect the emitted sound (figure 3c), suggesting that also in this case vibratory motion modulating the airflow is the primary sound source. This observation suggests that the vibrating structures do not close the syringeal aperture during the vibration cycle, when producing tonal sounds, in contrast to the production of dense harmonic sounds (see below). Moreover, in cockatiels we see a continuum from high harmonic emphasis to tonal character without any indication of altered vibratory behaviour. Together these observations indicate that

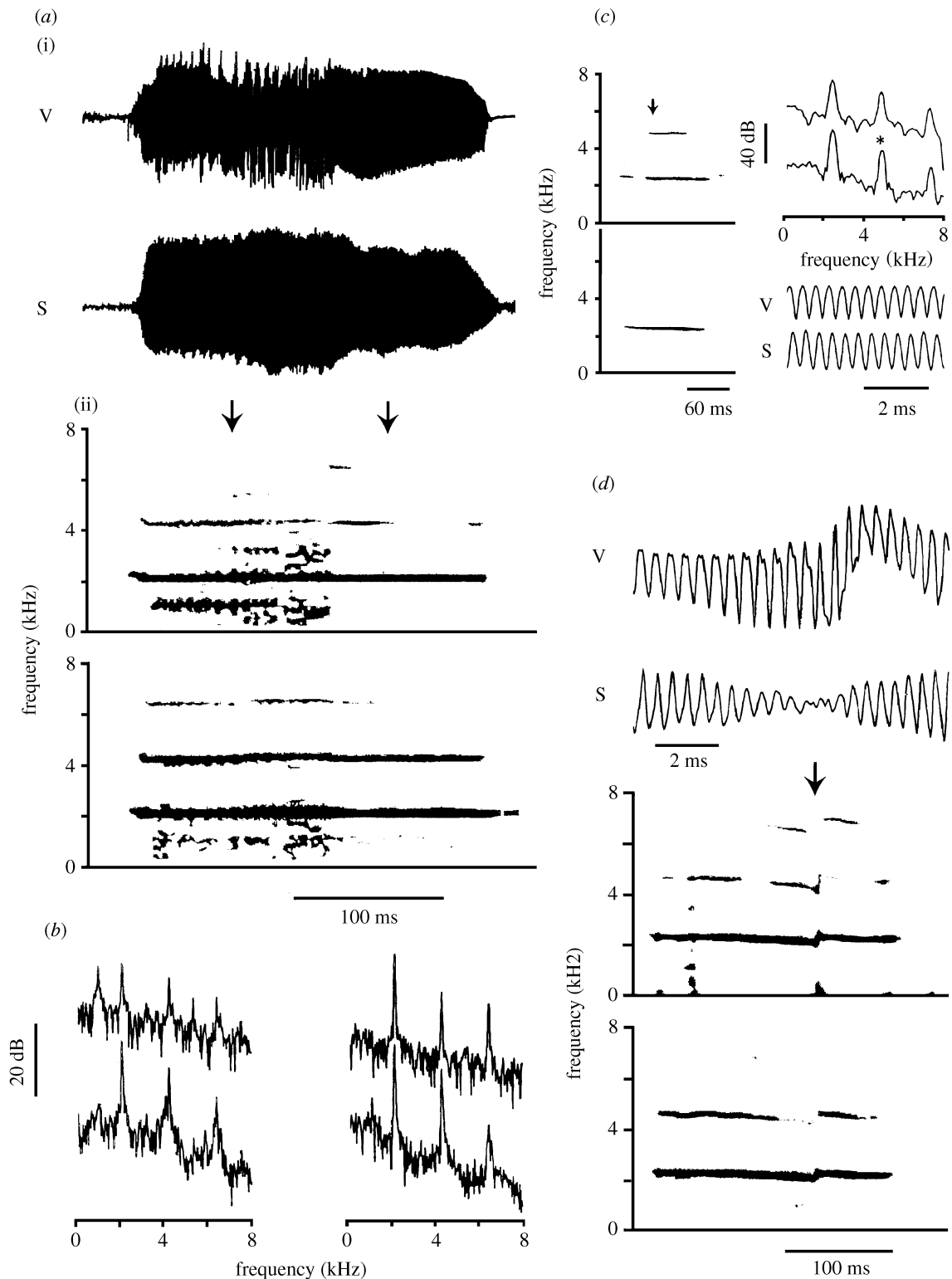


Figure 3. Brain stimulation-induced phonation in cockatiels. (a) Waveforms and spectrograms of vibration and sound signals of moderate intensity. (b) Power spectra of the vibration and sound signals calculated at the times indicated by arrows in (a). (c) Spectrograms of low intensity tonal sound (*, f_1 is 24 dB below f_0) and associated vibration, with expanded waveforms and power spectra at the time indicated with an arrow. (d) Fine structure of an intense sound with a complex spectrum showing the occurrence of a sudden frequency transition (aperiodic amplitude variation in S at lowest amplitude) and the associated amplitude changes in vibration and sound at the time indicated with an arrow in the spectrogram. Note the otherwise close relationship between cycles of sound and vibration. In each panel the upper trace is vibration (V) and the lower trace is sound (S).

a separate mechanism, such as the hole-tone whistle mechanism (Nottebohm 1976; Casey & Gaunt 1985), may not be needed to account for tonal vocalizations. Studies of vocalizations in a heliox atmosphere in doves (Ballintijn

& ten Cate 1998), budgerigars (Brittan-Powell *et al.* 1997) and songbirds (Nowicki 1987) support this interpretation. The difficulty of earlier theoretical models of the songbird syrinx in explaining the generation of tonal sounds

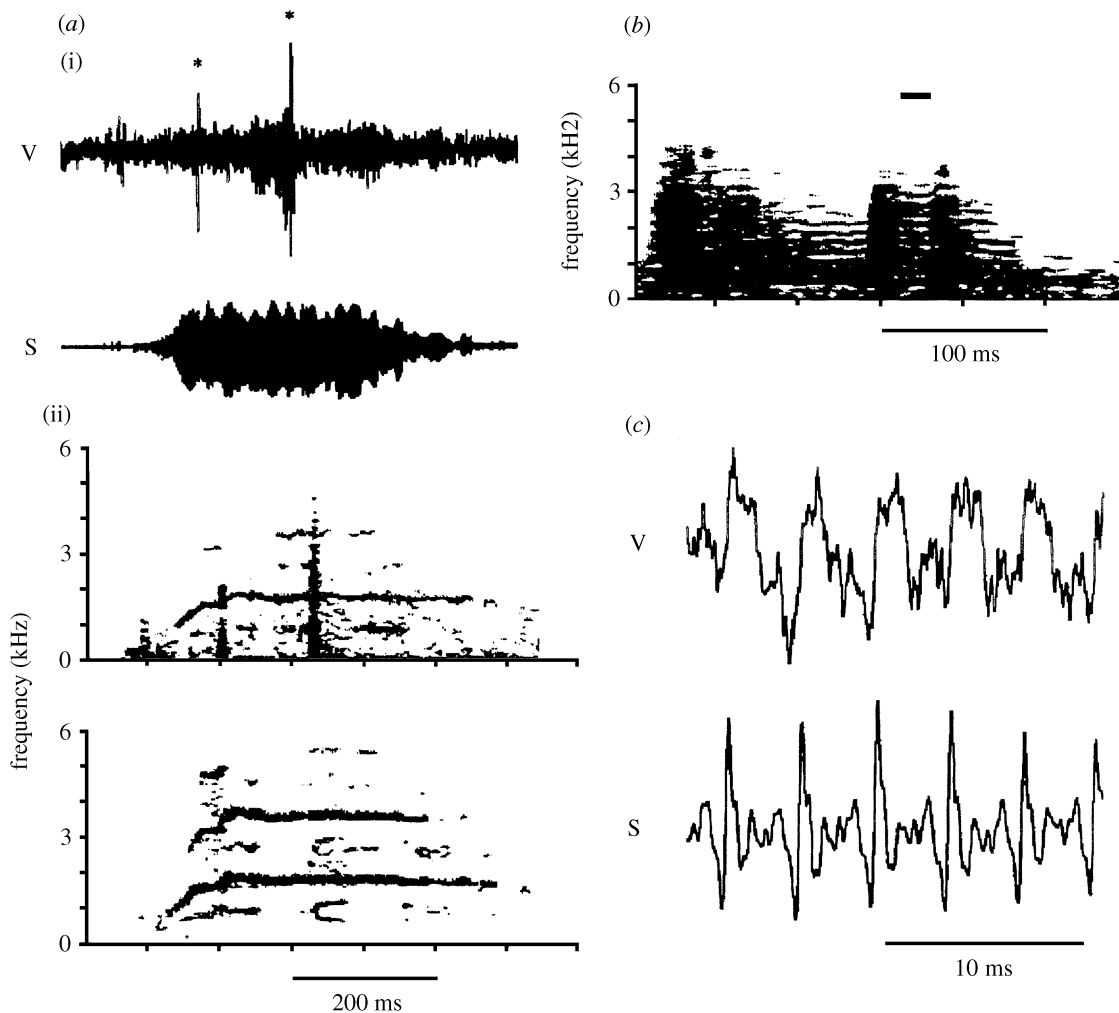


Figure 4. Brain stimulation-induced phonation in the hill myna. (a) A sound with sparse harmonic character indicates the close correspondence between vibration and sound recordings despite the noisy vibration signal. (b) A dense harmonic sound indicated as a spectrogram consists of (c) a train of impulse sounds, which are accompanied by simultaneous almost square wave-like fluctuations in the vibration trace. Horizontal bar in (b) indicates the segment illustrated in (c). Asterisks indicate fluctuations in the vibration trace, the mechanical origin of which is unknown. Upper traces: vibration (V); lower traces: sound (S).

(Fletcher 1988, 1989) may lie in the previous emphasis on the MTM, rather than the labia, as principal sound-generating structures (Fry 1998).

Although the principal sound-generating mechanism in the bird syrinx is based on vibration of syringeal structures acting as pneumatic valves, there is mounting evidence for a high complexity of vibrations and additional acoustic mechanisms, similar to observations on human vocal folds (Titze 1994). Nonlinear effects, such as period doubling and mode locking, have been identified in zebra finch song (Fee *et al.* 1998). In cockatiel vocalizations we frequently find subharmonics and rapid frequency transitions. Such phenomena may cause large amplitude modulation in natural vocalizations (e.g. Banta 1998). A different mode of vibratory behaviour is evident in the dense harmonic sounds of the myna, where syringeal vibrations differ significantly in shape from the sound signals. A theoretical mechanism proposed to account for the generation of similar sounds predicts that the vibratory structures, in the case of songbirds the ML and LL, close against each other once in each cycle of their motion (Fletcher 1988). Alternatively, the complex waveform of the vibration signals may result from combined

reflections of the laser signal from the left and right sound generators of the songbird syrinx. Vibratory behaviour of these independent sound sources may generate acoustic interactions similar to those observed in chickadee calls (Nowicki & Capranica 1986*a,b*). Although the exact mechanisms cannot be described at present, new interpretations, such as those discussed above, enable us to develop a deeper understanding of the vocal mechanisms of birds, emphasizing potential for complexity arising from multiple mechanisms rather than a dogmatic search for pure simplistic models.

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