New perspectives on the physics of birdsong

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In this work, we revisit the path that has been travelled during the last few years towards the modelling of the avian vocal organ, the *syrinx*, using numerical and theoretical techniques from bifurcation theory as analysing tools and present experimental support for the models. This fruitful perspective allowed the retracing of many acoustic features of syllables to intrinsic properties of the syrinx, thereby relocating the bird phonatory organ from the role of a mere vocal instrument of the nervous system to a central source of complex acoustical behaviour.

Keywords: birdsong; syrinx; dynamical models

1. Introduction

Vocal learning ability, accurate mimicry, song repertoires of extraordinary richness and acoustic versatility are some of the most seductive and intriguing aspects of the field of birdsong.

When confronted with the analysis of these phenomena, one might be tempted to think that such complex behaviours are to be associated with extremely complex, sophisticated neural control. This is a reasonable yet delicate hypothesis to make, the main objection being that the role of the peripheric anatomy could be considered mostly as a passive one. In the particular case of songbirds, articulation between the neural code and the actual song is exerted by the avian vocal organ. This organ, the *syrinx*, is a versatile organ that can display extremely rich dynamics when driven at different regimes. It is located at the junction of the primary bronchi and the trachea, where free moveable connective tissue membranes, the *labia*, are set in oscillatory motion through an energy exchange from the airstream propelled from the air sacs. Finally, the pressure perturbation attained at the level of the syrinx travels through the trachea and beak before leaving the bird as we hear it.

Birdsongs are constituted by sequences of stereotyped acoustic elements called syllables. These song units can be characterized by the shape of their fundamental frequency and their spectral content; in this work, we explore the acoustical effects that can be directly retraced to anatomical and physiological properties of the syrinx. In order to do so, we travel the path from descriptive to operational models of sound production in songbirds, translating sound features to physiological-related parameters of the model.

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One contribution of 14 to a Theme Issue ‘Topics on non-equilibrium statistical mechanics and nonlinear physics’.

This work is organized as follows. In §2, we present a brief glossary of birdsong, describing the basic anatomical elements involved in sound production, along with an acoustical description of the songs. These elements will be dealt with in §3, where we present a dynamical model for the syrinx and the physically relevant parameters driving it. In this section, we also present experimental support for the model and electronic applications. In §4, we go from descriptive to operational models of the syrinx, relating the physical parameters to physiological ones, and accounting for the acoustical features of song that are inherent to the nature of the vocal organ. In §5, we introduce other sources of acoustical complexity: the interaction between vocal tract and syrinx, and the coupling of the two sound sources in the oscine syrinx. The conclusions and future directions of this research line are discussed in the last section.

2. Elements of birdsong

Songbirds can be divided in two classes; roughly one half of the known species are vocal learners, i.e. they need tutors to incorporate their songs. For these birds, learning through imitation is essential for normal communication. Of special interest in this group is the suborder Oscines, equipped with a neural vocal architecture in which two neural pathways can be distinguished: a motor pathway and a pathway involved in song learning (Amador *et al.* 2008).

The suborder Suboscines presents many neural and anatomical differences with respect to the oscines. For instance, they are believed to be vocal non-learners and this difference is manifested in a central motor control of song that appears to be quite different in these two groups of birds. In fact, in some suboscine species, the forebrain set of vocal nuclei is entirely absent (Farries 2004).

Since oscines are capable of vocal learning, they have been largely studied, not only at the level of their neural organization but also at the physiological level. The oscine *tracheobronchial* syrinx is a double, bilateral structure located at the junction of the bronchi and the trachea as schematized in figure 1.

Located into the syrinx, the labia are analogous to the vocal folds that are anchored to the larynx in the human phonatory system: they act as valves that are set in motion by the airflow passing through them. These oscillatory valves are composed of connective tissue and are surrounded by a family of muscles. There are evidences that the *tracheobronchialis ventralis* (*vTB*) and *tracheolateralis* muscles actively control the separation of the labia, while the *siringealis dorsalis* (*dS*) and the *dorsal tracheobronchial* (*dTB*) close the air passage through the labia. This group is therefore correlated with the adjusting of oscillatory conditions of the labia (Goller & Suthers 1996). On the other hand, the *siringealis ventralis* (*vS*) muscle is correlated with the frequency of the vocalizations and is believed to control the stiffness of the labia by adjusting the distance between the supporting cartilaginous rings. Two other types of syrinx have been reported: the *tracheal* syrinx, with a single sound source, and the *bronchial* syrinx, in which the two sound sources are asymmetrically located in each bronchus. Throughout this work, we deal mainly with tracheobronchial syringes, which have been extensively studied in oscines, it remaining largely unknown whether vocal muscles contribute to frequency control in suboscines. Despite the differences among these groups, the physical mechanisms that lead to sound production

Figure 1. (a) Sketch of a ventral section of the tracheobronchial syrinx (adapted from Laje *et al.* 2002) and (b) the main muscles governing it (adapted from Gardner *et al.* 2001) along with (c) the constituents of the physical model of the syrinx.

are general for all birds. Once the oscillations at the syrinx are reached, the air perturbation travels upwards through the tract formed by the trachea and the beak. This passage through a confined region affects the final acoustic signal. Most importantly, a *filtering* effect takes place. From a physical point of view, the problem is that of a tube excited by a sound source at one end and opened at the other. The processing of the acoustic signal can be described as follows: the sound waves travel back and forth in the tube, bouncing at the ends and interfering with themselves. The interference enhances the so-called resonant frequencies f_n (for an open-end tube of length L , $f_n = (2n - 1)c/4L$) and depresses others. The global result is a modulation of the original sound spectrum. All these physiological processes are therefore articulated to produce the sounds that ultimately configure the songs. We next analyse the elements of the song structure.

From an acoustical point of view, birdsongs are complex, organized acoustic compositions. The conventional song unit is the *syllable*, the smallest repetitive sound gesture. Syllables are easily recognized in the standard representation of birdsong, the sonogram, in which the time evolution of the sound frequency is displayed in a colour code associated with the power intensity. In this work (figures 2–5), darker shades of grey correspond to higher spectral intensities.

Figure 2. (a,b) Two sonograms of a recorded song of a chingolo sparrow and the numerical simulation using syrinx equation (3.4) together with equation (3.5) for the tract. (c) The ellipses correspond to the excursions in parameter space (p_0, k) leading to each syllable. The phonation is prevented whenever $f_0 > 0$ (dotted line) and to allow phonation when the muscle is inactive ($f_0 = 0$). The numbering corresponds to the successive syllables, the last one (number 4) repeated seven times. This figure is adapted from Laje *et al.* (2002), where parameter values are specified.

In figures 2–4, we show sonograms from oscine birds: a chingolo sparrow (*Zonotrichia capensis*), a cardinal (*Cardinalis cardinalis*) and a zebra finch (*Taeniopygia guttata*), respectively. In figure 5, a very stereotyped song from the suboscine great kiskadee (*Pitangus sulfuratus*) is displayed.

As readily seen from the figures, the different song programmes can be the result of quite complicated combinations of syllabic repertoires (for some species such as brown thrashers, repertoires can have thousands of syllables), sometimes organized out of nearly fixed blocks of syllables called *motifs*. From pressure studies, it is known that songs are not completed with a single breath at the beginning but instead very short falls of pressure below atmospheric pressure occur between syllables that enable the bird to execute very long song sequences (Hartley 1990). These *minibreaths* are observable in the pressure time traces of figures 3 and 5.

Figure 3. Experimental support for the sound production model (equations (3.4) and (3.5)) fed with physiological instructions (a) of air sac pressure, vS and dTB muscle activities. The smoothed time traces of the solid curve with squares, solid curve and dotted curve are associated with parameters p_0 , k and f_0 , respectively. (b,c) Sonograms of the recorded and resulting synthetic syllables. Adapted from Mindlin *et al.* (2003).

A spectroscopic analysis of the syllables reveals many possible fundamental frequency traces: constant, up-sweeps, down-sweeps, ‘n’-shaped and more complex curves. Frequency and duration ranges vary across the different bird species; for instance, the chingolo sparrow presents syllabic fundamental frequencies typically ranging from 2 to 7 kHz and durations from 10 to 300 ms (figure 3).

A first question then arises: what are the basic physical ingredients to construct a model for the generation of sounds in the syllabic ranges? We address this issue in the next section.

3. A descriptive model of the syrinx

One of the simplest models that captures the physical principle of energy transfer from the airflow to the tissue membranes was originally introduced by Titze (1988) for the vocal folds. This mechanism was recently observed using videography in the syrinx Larsen & Goller (1999), and is based upon the observation of surface waves travelling upwards through the folds during the oscillatory cycle, presenting a syrinx of convergent profile when the labia move away from each other and a syrinx of divergent profile in the closing semicycle (figure 1).

While presenting a convergent profile during the opening cycle, the interlabial pressure is closer to the bronchial pressure, while it approaches atmospheric pressure when presenting a divergent profile, in the closing cycle. This asymmetry of the syringeal pressure values in the complete cycle ensures an overall force in the direction of the velocity of the labia, transferring energy from the airstream to the moving tissue, eventually compensating its dissipative effects and allowing sustained oscillations.

The simplest way to describe the principle of self-oscillating dynamics of the labia is to consider the dynamics (per unit area) for the midpoint of the folds

$$M\ddot{x} = -Kx - B\dot{x} + P_s - F_0, \quad (3.1)$$

where M is the mass of the labium, K its stiffness and B a constant characterizing the dissipation of the tissue. P_s is the syrinx interlabial pressure and F_0 a constant force term that controls the stationary position of the labia. Dividing by the mass and rearranging the equation into an explicit two-dimensional form gives

$$\left. \begin{aligned} \dot{x} &= y, \\ \dot{y} &= -kx - (\beta_1 - p_0)y - f_0, \end{aligned} \right\} \quad (3.2)$$

where we use lower cases for the redimensioned parameters, and a first-order approximation for the average interlabial pressure $p_s = p_0 y$ (Titze 1988), making it proportional to the air sac pressure p_0 and ‘in phase’ with the velocity of the oscillating membrane. Even at first order, this system captures the basis of labial dynamics: when the energy transfer from the airstream p_0 compensates the dissipation β_1 , we have $\beta_1 - p_0 = 0$ and the system reduces to the harmonic oscillator, with solutions reproducing the appropriate syllable frequencies for realistic parameter values (Laje *et al.* 2002). On the other hand, whenever the dissipation takes over pressure ($\beta_1 > p_0$), the oscillations are damped, and the system returns eventually to rest.

A first correction to the system would be to avoid the divergence of solutions in the case $\beta_1 < p_0$. For this, we consider a nonlinear dissipation function,

$$\dot{x} = y, \quad (3.3)$$

$$\dot{y} = -kx - (\beta_1 + \beta_2 x^2 - p_0)y - f_0, \quad (3.4)$$

which accounts for the effect of collision of the labia for large-amplitude oscillations. This is a first-order nonlinear function that preserves the symmetry of the dissipation function, i.e. an odd function of the velocity and even function of the space.

From a dynamical point of view, this system is a slight variation of the van der Pol oscillator: at the point of instability, relaxation oscillations are born in a Hopf bifurcation with no spectral content and they become spectrally richer as they grow in amplitude.

In order to generate song, it is assumed then that the bird produces a set of basic gestures that are identified with the parameters of the model: the elasticity term k is associated with the activity of syringeal muscles controlling the stiffness of the labia (vS activity is shown to be correlated with the frequency of the vocalization and not with airflow gating; Goller & Suthers 1995), the parameter p_0 with the air sac pressure and f_0 with the active airflow gating controlled by muscles dS and vTB (Laje *et al.* 2002).

Right after being created at the syrinx, the sound wave of speed v travels through the bird's trachea and beak.

Approximating this vocal tract by a tube of length L characterized by an impedance with respect to atmospheric pressure, i.e. a reflection coefficient α , the sound wave at the tube entrance $a(t)$ can be calculated as the result of the reflections in the tube:

$$a(t) = p_{\text{in}}(t) - \alpha a\left(t - \frac{2L}{v}\right), \quad (3.5)$$

where p_{in} stands for the pressure fluctuations injected into the tract owing to the airflow modulations.

With the complete model for the vocal anatomy (equation (3.4) for the syrinx and equation (3.5) for the tract), a natural question arises: what kind of excursions in the parameter space should the bird have to coordinate in order to reproduce the different syllable types?

In order to answer this question, we first make the following remarks.

- (i) We note that the bifurcation diagram in parameter space (p_0, k) shows a critical value of pressure p_0 above which the self-oscillations are induced through a Hopf bifurcation (figure 2, shaded region). In this region, the fundamental frequency of the oscillations increases with tension k as indicated by the curves of iso-fundamental frequency (Gardner *et al.* 2001).
- (ii) The time scales associated with the duration and the fundamental frequency of the syllables are well separated, and therefore the time course of k will essentially trace the time course of the fundamental frequency.
- (iii) Since many birdsongs are constituted by repetitions of roughly similar elements followed by minibreaths, we assume that the paths in parameter space (p_0, k) should be cyclic across songs (Laje *et al.* 2002).

In this way, each syllable type can be expressed as follows:

$$p_0(t) = p_a + p_b \cos(\phi(t)), \quad (3.6)$$

$$k(t) = k_a + k_b \cos(\phi(t) + \phi_0), \quad (3.7)$$

Figure 4. (a) Sonogram from a song of zebra finch *Taeniopygia guttata* and (b) syllable classification scheme (f_{aff} , SCI). Adapted from Sitt *et al.* (2008).

i.e. as elliptic paths in parameter space (p_0, k) that depend on simple linear $\phi(t)$ functions. The onset and termination of phonation is controlled by f_0 , as phonation is prevented when a threshold is exceeded ($|f_0| > k\sqrt{(p_0 - \beta_1)/\beta_2}$).

Examples of the synthesized syllables are displayed in figure 2 for a chingolo sparrow song (Laje *et al.* 2002). Minibreaths between syllables are easily explained from this description: they correspond to the little portion of the excursion in parameter space occurring outside the oscillation region for negative pressure values.

This is a remarkable property of the proposed model: a two-dimensional dynamical system driven through elliptic trajectories in parameter space span all the repertoire of syllabic types (Mindlin & Laje 2005).

Beyond this appealing property, such a small number of variables and parameters needed to synthesize song from physiologically related instructions allow us to conceive applications for the proposed model. There is evidence that during the period of vocal learning, juvenile songbirds reconfigure their brains. Moreover, adult birds are subjected to active auditory feedback to maintain the quality and stability of their crystallized songs: in particular, recent experiments showed that deafening adult birds causes normal song degradation (Nordeen &

Figure 5. Typical great kiskadee (*Pitangus sulfuratus*) three-syllable song. (a) Simultaneous measurements of air sac pressure and song spectrogram and (b) the simulated song using (i) a linear restitution function, (ii) a first order nonlinear restitution function when the syrinx model is fed with (iii) the pressure time trace. Adapted from Amador *et al.* (2008).

Nordeen 1992; Leonardo & Konishi 1999). Therefore, it is of particular interest to design experiments to manipulate auditory feedback in real time, without interfering with either the motor or the auditory pathways.

In Zysman *et al.* (2005), a biomimetic device emulating the action of the avian vocal organ was constructed. This electronic circuit analogically integrates equation (3.4) for the dynamics of a syringeal labium which is equivalent to the acoustic pressure pattern executed by tonal birds, constituting a robust, low time-processing device suitable for carrying out online alterations of auditory feedback. Yet, these experiments require measuring physiological variables for long periods of time, keeping cannulae inserted in the air sacs or muscles wired for days after surgery, which is unlikely to be feasible.

A solution was explored by extracting the controlling parameters of the syrinx out of birdsongs in real time. For that, two transducers were built: one that reconstructs the air sac pressure from the sound signal in real time and the other for the tension of the vS muscle.

Tests were performed in which recorded vocalizations of cardinals were reconstructed in two steps: first, air sac pressure and tension of the labia were driving reconstructed using the transducers and, second, the reconstructed functions were fed to the electronic syrinx. Sonograms of both the real song and the reconstructed one present qualitatively the same features.

In this way, these devices open new perspectives for the experimental work in the field, making it possible to perform specific changes in biologically relevant parameters that can be made within very short response times (of approx. 10% of the syllabic duration).

So far, we successfully compared the synthetic sounds coming from the numerical integration of the descriptive model for the syrinx equation (3.4) and vocal tract equation (3.5) with experimental song recordings. Moreover, features like low-dimensionality and few driving parameters allowed the construction of biomimetic applications. Beyond all these suggestive features, the model can also be tested and validated when driven with experimental instructions from singing birds.

In Mindlin *et al.* (2003), simultaneous recordings of dTB and vS muscle activities along with air sac pressure were made from 13 samples of spontaneous songs from two cardinals (*Cardinalis cardinalis*). With this specific choice, i.e. one gating and one labium stiffness-related muscles, experimental signals were associated to the parameters of the model f_0 and k . The muscle activity was recorded through electromyographs (EMGs), measured by electrodes implanted into the syringeal muscles. EMG records consist of spiky signals that need to be smoothed and rectified (Mindlin *et al.* 2003) in order to obtain envelope curves that can be used as inputs for the model equation (3.4).

On the other hand, pressure–time traces were captured by a cannula inserted into the anterior thoracic air sac and connected to a piezoresistive pressure transducer. The details of the procedure can be found elsewhere (Goller & Suthers 1996). These time traces were associated with the parameter p_0 .

Linear relationships were assumed between smoothed vS and dS muscle activity and air sac pressure and the corresponding parameters of the model. After the scaling, the syrinx model was fed with the parameters in order to synthesize song.

Beyond the remarkable agreement between synthetic and experimental songs (as shown in figure 3), the model predicts that for upsweeps, the lower value of f_0 that prevents phonation at the beginning of the syllable is smaller than the value of f_0 at its end. This prediction of the model was observed for all the experimental data analysed.

4. Acoustic complexity and syrinx dynamics

So far, we analysed the implications of a descriptive model of the syrinx. Within this model, modulations of fundamental frequency could be mapped to simple trajectories in phase space for the driving parameters. For many bird species that produce nearly tonal syllables, like sparrows (figure 2) and cardinals (figure 3), this model holds. On the other hand, zebra finches produce a wide variety of syllables with variable spectral load (figure 4).

In order to investigate the nature of this variability, two quantities were defined from the spectral characterization of the syllables: the *average fundamental frequency* (f_{aff}) and the *mean spectral frequency* (f_{msf} ; Sitt *et al.* 2008). The f_{aff} is determined as the mean pulse rate for low-frequency sound segments and as the first peak in the fast Fourier transform for high-frequency sound segments and the f_{msf} as the ponderate sum of the frequency peaks f_i using the relative spectral

energies as weights

$$f_{\text{msf}} = \frac{\sum_i f_i \epsilon_i}{E}. \quad (4.1)$$

The *spectral content index* $\text{SCI} = f_{\text{msf}}/f_{\text{aff}}$ allows us to compare the spectral content of different syllables.

Then, for a large variety of songs of different birds, a graph was constructed with each syllable corresponding to a point in the $(f_{\text{aff}}, f_{\text{sci}})$ space (figure 4). Surprisingly, all the points cluster in a small region, strongly suggesting a functional relationship between fundamental frequency and spectral richness of the bird sounds.

In order to analyse the data, we consider the model described in equation (3.4) taking explicitly into account the surface profile of the syrinx observed during videoscropy. Taking straight lines to simplify the geometry of the membranes (figure 1), it is possible to relate the positions of the upper edge a and lower edge b of the labium in terms of a phenomenological constant τ as follows (Gardner *et al.* 2001):

$$\left. \begin{aligned} a &= a_0 + x + \tau \dot{x}, \\ b &= b_0 + x - \tau \dot{x}. \end{aligned} \right\} \quad (4.2)$$

Substituting these equations into an expression proposed by Titze (1988) for the average syringeal pressure $p_0 = p_s(1 - a/b)$ in terms of the air sac pressure p_s , the dynamics of the labium results

$$\dot{x} = y, \quad (4.3)$$

$$\dot{y} = -k(x)x - \beta(x, y)y + p_0 \frac{\Delta a + 2\tau y}{b_0 + x + \tau y} - f_0, \quad (4.4)$$

where $\Delta = a_0 - b_0$ is the syrinx profile difference at rest (figure 1).

Compatible with the symmetry of the restitution (odd spatial function) and the dissipation (odd velocity and even space functions), the first terms of their nonlinear expansions are: $k(x) = k_1 + k_2 x^2$ and $\beta(x, y) = \beta_1 + \beta_2 x^2 + \beta_3 y^2$.

The coefficients k_2 , β_2 and β_3 become relevant as the departure of the rest position and the velocity of the labia reach large values, i.e. for fast and large oscillations, and their actual values (used to synthesize song) are several orders of magnitude smaller than the coefficients of the linear terms k_1 and β_1 (Sitt *et al.* 2008).

From a dynamical point of view, a possible candidate bifurcation for the described spectral richness is a saddle node in a limit cycle (SNILC): oscillations start as a stable stationary point is annihilated by an unstable one. Right after the bifurcation takes place, the system spends much of its time in the region near the bifurcation (its period T is proportional to $(a_c - c)^{1/2}$, where a is the control parameter and a_c its value at the bifurcation). As the oscillations are born with finite amplitude and zero period (Sitt *et al.* 2008), they display a rich spectral content. In Sitt *et al.* (2008), it is shown that this bifurcation can be identified in system (4.4).

Remarkably, placing the parameters in the vicinity of the bifurcation and classifying the simulated sounds in the $\text{SCI} = f_{\text{msf}}/f_{\text{aff}}$ space as a function of the pressure p_0 , we obtained a curve that closely fits the experimental points (dotted

line in figure 4) for low-frequency syllables. This prediction of the model is consistent with experimental observations of no ventral syringeal muscle activity for low-frequency sounds (Vicario 1991).

Moreover, the model gives an insight for a possible biological mechanism responsible for the relationship between fundamental frequency and spectral load in high-frequency sounds (above 1.5 kHz): assuming a linear coupling between the ventral syringeal muscle activity f_0 and the pressure p_0 , the obtained theoretical curve fits closely the experimental data points (figure 4, solid line).

In this way, the dynamical signature revealed by the spectral content versus fundamental frequency in the zebra finch allows a simple biological explanation in terms of the model: a vocal organ ‘tuned’ in the vicinity of an SNILC bifurcation can produce a variety of spectrally rich sounds by the driving action of the air sac pressure or a simple combination of air sac pressure and dorsal muscles.

Another very illustrative example supporting the key role of nonlinearities in the syrinx comes from the order Suboscines, a group of birds that does not belong to the songbirds and whose general differences from oscines were presented in §2.

The particular case of the great kiskadee (*Pitangus sulfuratus*) presents a tracheosyringeal syrinx with two independently controlled sound generators, each of which consists of a pair of oscillating labia. Three pairs of muscles take control of the syrinx: the extrinsic muscles m. sternotrachealis and m. tracheolateralis and the intrinsic muscle m. obliquus lateralis.

The song of the great kiskadee consists of a nearly fixed sequence of three syllables that presents an interesting property: simultaneous recordings of air sac pressure and fundamental frequency look very alike (both time traces are shown in figure 5b).

This resemblance was quantified in Amador *et al.* (2008) and the analysis confirmed a highly significant linear correlation between fundamental frequency of the syllables and air sac pressure for this bird, suggesting a weak (if any) dependence of the song on the activity of the syringeal muscles.

To confirm the independency of the sound generation from the activity of syringeal muscles, experiments were performed comparing songs of normal birds and birds with both tracheosyringeal muscles transected. While equivalent experiments performed in songbirds reveal striking changes in song production and even complete loss of phonation (Daley & Goller 2004; Suthers & Zollinger 2004), the air sac pressure patterns and songs of the kiskadee remained remarkably unaffected by denervation (Amador *et al.* 2008).

How does the syrinx behave when controlled by the single variable representing air sac pressure p_0 ? In Amador *et al.* (2008), numerical integration of a set of equations for a flapping model was performed. Interestingly, a striking quantitative agreement between synthetic and natural songs was achieved when the restitution constant k was expanded to first-order nonlinear terms (consistent with its odd symmetry), $k = k_1 + k_2 x^3$, while the linear case performed poorly (figure 5b).

In this way, a very simple mechanism of transducing air sac pressure into frequency modulations is revealed: when the hypothesis of a linear restitution approximation is replaced by a first-order nonlinear one, the air sac pressure does not only account for the onset of oscillations but it also shifts the midpoint of the folds, transducing higher pressure into higher oscillation frequencies.

5. Other sources of acoustic complexity

In the previous section, we showed that much of the acoustic richness of birdsong emerges from the nonlinear nature of the syrinx. Nevertheless, the isolated sound source is not the only possible origin of rich acoustic behaviour in birds. In this section, we will briefly describe the acoustical effects that may take place when considering the feedback between the syrinx and the vocal tract, i.e. the *source-filter* interaction, and the *source-source* interaction, in the case of bilateral syringes.

Throughout this work, we treated the problem of sound generation in birds under the assumption of the source-filter hypothesis. According to this hypothesis, the source of sound and the filtering of the tract are acoustically uncoupled. This is the case for the voice during normal speech (Titze 1988).

In Laje & Mindlin (2005), a two-dimensional model for the syrinx (as the one of equation (4.4)) is used to explore the coupling effects with the vocal tract. The reason behind this choice is a compromise between realism and mathematical simplicity: a higher dimensional model of the syrinx would be capable of generating complex labial dynamics by itself, so we restrict ourselves to the simplest case to specifically study the coupling effects.

The coupling is taken into account by considering an expression for the interlabial pressure p_0 that explicitly depends on both the sublabial pressure p_s and input pressure at the vocal tract p_i . In Laje & Mindlin (2005), it is shown that p_i is a combination of both the pressure perturbations injected locally into the vocal tract by the sound source and the pressure resulting from the reflections at the end of the tract, $p_i(t) = s(t) - \gamma p_i(t - T)$, where $s(t) = \alpha(x - \tau y) + \beta(y - \tau \dot{y})$. Here, T is the time for the sound wave to propagate back and forth through the tract and γ is the reflection coefficient for the tract-atmosphere interface.

From the simulations of the complete model of interacting sources and tract, it is observed that complex periodic and aperiodic solutions appear, as well as period-doubling bifurcations. In the particular case of suppressing the tract coupling and considering only the two sources active, sound simulations display subharmonic content that is not present in the individual source spectra. The analysis developed in Laje & Mindlin (2005) allows us to make predictions that could be tested through specific experiments. The core idea is that coupling parameters $\alpha \propto \sqrt{\rho}$ and $\beta \propto \sqrt{\rho}$ can be modified through the atmospheric pressure ρ if, for instance, atmospheric nitrogen were replaced with the lighter helium.

Experiments of this type were performed in the past to test other hypotheses (Nowicki 1987). Results were either changes in the fundamental frequency of the oscillations or changes in the resonant frequencies of the vocal tract with little or no effect on the fundamental frequency. However, other effects could be expected from strong enough coupling effects: in particular, simulations of a single source with feedback show that as the pressure parameter p_s is decreased, subharmonic frequencies disappear in a period-halving bifurcation in normal air, while they are not present at all in a helium-like atmosphere. Interestingly, this effect would disappear if the dynamical origin was different: simulations of more complex syrinx models

such as the asymmetric two-mass model without vocal tract coupling are less sensitive to density changes in the atmosphere and consequently the subharmonic spectral content is present in either the normal or the heliox atmosphere.

6. Conclusions and future perspectives

In this work, we reviewed the main results in the mathematical modelling of the syrinx. The starting point was a sound production model capturing the physics of the oscillatory dynamics of the labia, driven by parameters that can be easily associated with physiological instructions. This model is capable of producing synthetic songs in the correct acoustical ranges, showing good qualitative agreement with experimental sound records for all the studied species. Moreover, driving the syrinx model with real physiological instructions recorded from the activity of muscles and air sac pressure during spontaneous singing allowed one to test specific predictions of the model and producing very similar real and synthetic songs.

An interesting feature of the model is its mathematical austerity: a condition that allows conceiving robust, self-standing biomimetic applications. As a particular case, in this work, we reviewed an analogic circuit that successfully mimics an electronic syrinx, adaptable to generate sound in real time upon physiological instructions, making it specially suitable for feedback auditory experiments.

Next we showed how the addition of first-order nonlinear terms to the basic model leads to the dynamical conditions accounting for the spectral richness displayed by non-tonal birds. Of special interest is the study of a bird belonging to the Suboscine suborder, a class of birds whose vocal mechanisms remain in other respects largely unknown.

Finally, alternative sources of acoustical complexity in birdsong were presented when the coupling effects of two sound sources and the acoustic coupling of the sound sources with the vocal tract were taken into account.

Merging mathematical modelling with complex biological behaviour accounts for just a few successful examples in the literature (Golubitsky *et al.* 1999). The analytic programme reviewed in this work demonstrates it to be a good vehicle to identify the different sources of complexity in birdsong and, interestingly, it also suggests what types of syringeal control could be expected from a vocal neural programme: one that exploits the nonlinear nature of its peripheric organs, in which slight changes in the neural instructions could promote rich and complex acoustic responses.

This programme opens a spectrum of future research lines, starting with the exploration of the dynamical regimes of a fully developed syrinx model, which is already an ongoing work (Amador & Mindlin 2008).

Another branch is the development of biomimetic technology devoted to artificially replace not only anatomical parts but also neural portions of biological systems and helping elucidate the neural song programme through acoustic feedback experiments. We arrive in this way at the theoretical motivation of this research, which is to unveil the path that goes from the syrinx to the brain (Abarbanel *et al.* 2004; Amador *et al.* 2005; Trevisan *et al.* 2006) and to build a

model of the vocal production and song generation and coding, a virtual brain and periphery revealing the very nature of the interactions between nervous system and anatomy.

This work was partially funded by the University of Buenos Aires, CONICET, ANPCyT and NIH (through grants R01 DC-06876 and R01 DC-04390).

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