# Physical mechanisms and muscle activities generating complex sounds in birdsong

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# Contents

# A  Abstract

The goal of our proposed research is to understand the mechanisms involved in the generation of complex sounds present in birdsong, and unveil the role of the peripheral system in this process. This proposal utilizes observations on starlings, zebra finches and cowbirds, as their vocalizations present evidence of nontrivial acoustic features. Electromyographic data on these birds will allow us to study the degree to which neural instructions can account for the generation of the complex sounds. We plan to concentrate on describing the acoustic effects of feedback pressure into labial vibration and describing the acoustic effects of the interaction between sound sources.

# B  Personnel

- Franz Goller, PhD, Principal Investigator (100% effort) will oversee the operation of the project, and perform the experimental work on muscle activity and dynamical behavior of the syrinx in singing birds.

- Associate Research Scientist, Bernardo Gabiel Mindlin (100% effort) will be involved in the construction of mathematical models for the syrinx, exploring their dynamical behavior, and comparing with the experimental data.

- Postgraduate Research Scientist (to be named) (100% effort) will be involved in the analysis of the data and the modeling.

- Graduate Student (To be named) (100% effort) will be involved in the modeling, analysis of the data and perform experiments in the Goller Lab.

# A   Specific Aims

Much of the study of the behaviour that enhances the survival and reproduction of an animal is studied in terms of neurons and neural circuits. Behavior also involves strong interactions between nervous systems, body, and environment. A peripheral system imposes constraints on neural control, and also provides opportunities for the emergence of interesting behavior (Chiel *et al.* 1997). A wonderful example of this rich interplay is birdsong, where neural instructions drive a highly nonlinear physical system, the syrinx, capable of generating from simple whistles to most complex sounds (Suthers *et al.* 2002) (Fee et al. 1998). By complex sounds we denote irregular vocalizations (Herzel et al. 1995), mostly perceived as rough sounds. They can be found not only in birdsong but also in newborn cries (Mende *et al.* 1990), some vocalizations of infants (1), and humans with different voice-disorders (Herzel et al. 1995).

The goal of our proposed research is to understand the mechanisms involved in the generation of complex sounds present in birdsong, and unveil the role of the peripheral system in this process. This proposal utilizes observations on starlings, zebra finches and cowbirds, as their vocalizations present evidence of nontrivial acoustic features. A large body of electromyographic data on these birds allows us to study the degree to which neural instructions can account for the generation of the complex sounds.

This proposal is a continuation of an interaction begun in 2000, in which models of the avian vocal organ were developed and validated with electromyographic data. This synthetic approach to the problem complements traditional studies of the avian peripheral vocal system, allowing one to highlight what part of the complex sounds constituting some elements of birdsong are the result of complex orders by the nervous system, and which are the result of non-trivial physical effects (Fee et al. 1998) (Goller 1998). The results obtained by the models allows the design of new specific experiments and permits the integration of disparate observations.

The main goal of this study is to unveil the mechanisms responsible for nontrivial acoustic signatures as subharmonicity in the sound pressure time series. This study will be performed in the framework of the interaction between experimentally measured electrical muscular activity and the physical apparatus this activity ultimately drives. The proposal includes two specific aims:

**1. Describing the acoustic effects of feedback pressure into labial vibration**

The existence of subharmonic behaviour associated with the dynamics of the avian vocal organ was reported and interpreted in the framework of complex vibrational modes of syringeal labia (Fee et al. 1998). This mechanism of creating subharmonic signature in the acoustic signal depends on the structure of the vibrating source, and is independent of the interaction between sound source and vocal tract. Recent models show that subharmonicity can arise as the result of high pressure feedback on the vibrating labia, if the inertance of the tract is high. In order to find if this new mechanism of complexity plays a role in the generation of complex sound, experimental measurements of song and beak movement will be performed in zebra finches. The spectral patterns will be studied as fast beak movements take place, looking for dynamical signatures of high impedances.

**2. Describing the acoustic effects of the interaction between sound sources**

The syrinx of oscine birds has two parts, each of which can be controlled, to some degree, independently by the bird (see Fig.1) (Goller *et al.* 1995). Beyond this independence, the resulting sounds when two sources are active can show evidence of nonlinear coupling between them. The complexity of the physics involved requires an analysis beyond the cross modulation of the two signals. In order to determine whether this kind of vocalization is in fact the result of the physics or the consequence of complex motor controls, simultaneous measures of the dual air flows, electromyographic signals and sound must be performed. We plan to carry out a simultaneous study: experimentally on starlings and zebra finches and theoretically on mathematical models of two sources acousticially coupled to each other.

# B   B. Background and Significance

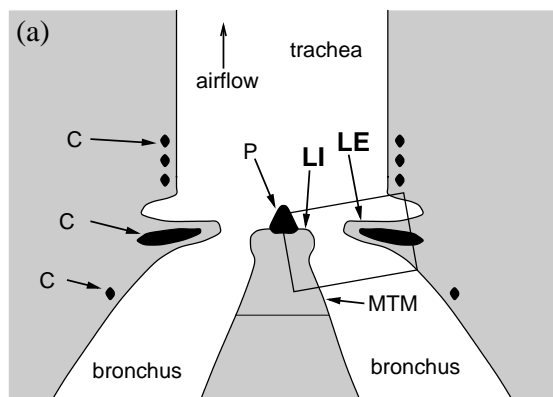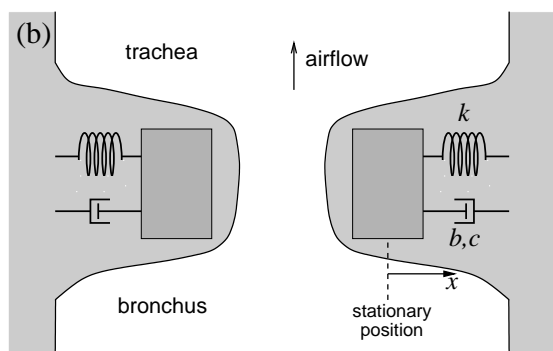**B1 Complex physics and simple instructions**

Figure A.0.1: Schematic of the ventral view of a songbird syrinx

Until recently, it was assumed that the central nervous system directly controls the complex features of song (Konishi 1994). To advance beyond this, it was necessary to formulate adecquate physical models of the syrinx (Fee et al. 1998), in order to close the path that leads from the brain to the sound. These models were formulated after a long research effort which investigated the motor activity of various muscles involved in the control of the syrinx (Goller *et al.* 1996a) (Goller *et al.* 1996b), its anatomy, and the nature of the sources of sound (Goller *et al.* 1997). Once formulated, it was possible to find an example of complexity in sound pressure as a result of the nonlinear nature of the syrinx (Fee et al. 1998). These results are of interest for those interested in evolutionary and ecological aspects of vocal behavior in birds, since the acoustic signatures of the complex nonlinear effects add to the acoustic complexity of the song and, therefore, might be perceptually significant. In any case, complexity of the signal can no longer be associated with a precise neural control, but peripheral contributions have to be taken into account (Goller 1998).

## B2 Neural description of song production

What is now described as the vocal control pathway for song production can be traced back to the seminal work of Fernando Nottebohm (Nottebohm *et al.* 1976) who described the projections from the high vocal center (HVc) to the robust nucleus of the archistratum (RA), and finally to the tracheosyringeal motor nucleus (nXIIts) in the Canary (*serinus canaria*). This nucleus contains neurons which control the activity of syringeal muscles. Of comparable importance for vocal production is the control of abdominal and intercostal expiratory muscles that determine precise inspiratory and expiratory patterns (Wild *et al.* 1997). Recent recordings from the premotor circuits HVc and RA in singing birds show how a population of neurons form an explicit representation of time in a motor sequence (Hahnloser *et al.* 2002). This work suggests that the architecture of connectivity between HVc and RA determines important acoustic features, although a complete mapping of the central neural activity onto peripheral motor action requires to correlate activity in the central motor pathway with both activity of syringeal muscles and respiratory pressure (Suthers *et al.* 2002) (Gardner *et al.* 2001),

(Laje *et al.* 2002 a) (Laje *et al.* 2002 b). In fact, a contribution of recently proposed theoretical models of the avian vocal organ is that the appropriate mapping from central neural activity onto peripheral motor action is through the study of correlations with specific control parameters instead of with acoustic properties of the vocalizations.

**B3 Muscle activity controling the syrinx**   Between the brain activity and the song, there is a peripheral system which consists of a complex physical apparatus, the syrinx, controlled by a set of muscles. A long term research program provided us with a detailed picture of the role of the different syringeal muscles in gating the airflow and sound production in singing bird (Goller *et al.* 1996a) (Goller *et al.* 1996b).

Each sound generator is controlled by a set of six syringeal muscles. In spontaneously singing brown thrashers (*Toxostoma rufum*) the role of different muscles was investigated with electromyographic techniques combined with simultaneous monitoring of airflow and air sac pressure (Goller *et al.* 1996a). The amplitude of EMG of the ventral syringeal muscle (vS) was highly correlated with the fundamental frequency of the vocalization. Based on this strong correlation and consistent with anatomical considerations this muscle is believed to control the tension of the oscillating labia. Activity of the ventral and dorsal tracheobronchialis muscles was correlated with syringeal abduction (opening of airways) and adduction (closing of airways), respectively. The lateral part of the dorsal syringeal muscle also acts as an adductor of the lateral labium. The medial portion of the dorsal syringeal muscle most likely effects adduction of the medial labium (Goller et al. 2002), although no electromyographic data have been recorded from this muscle during spontaneous song. All this coordinated muscle activity control a nonlinear physical apparatus, and in order to integrate the full process, from brain to sound, it is required to understand its response to the muscular instruction that drive it.

**B4 Vocal models and nonlinearities**

The avian vocal organ of songbirds is composed of modified cartilages and specialized muscles that are located at the junction between primary bronchi and trachea. Small masses of connective tissue, the medial and lateral labia are located at the cranial end of the bronchus ((Goller *et al.* 1997), (Suthers *et al.* 2002). The oscillatory regime displayed by the labia is determined by the airflow and labial tension. This, is controlled by ipsilateral members of several pairs of muscles, which are innervated by the ipsilateral tracheosyringeal branch of the hypoglossal nerve. A model was recently proposed which related its parameters with biological ones (Laje *et al.* 2002 a). Recent work (Mindlin *et al.* 2003) shows that the model, whenever driven by experimental electromyographic data, is able to properly reproduce the songs uttered during the experimental session. This model, as well as previous ones (Fee et al. 1998), are simplified versions of models proposed to generate voiced sounds by humans (Titze 1988). Yet, much of the literature of voice production limited the interest in nonlinearities to the fact that glottal pulses were harmonically rich (Titze *et al.* 1994). In part, this is understandable since neither rich modal structure nor acoustic feedback (Laje *et al.* 2001) seem to play a relevant role in human vocalizations. The models predict that scaling down the problem to the size of the avian vocal organs, feedback induced subharmonicity is likely to occur. This is due to the fact that wide beaks increase the inertance of the tract and its coupling to the sound sources, driving the dynamical system to regions where subharmonic solutions of the oscillating labia are found (Laje *et al.* 2001). **B5 Lateralization of bird song**

The most convincing example of functional lateralization of the brain in animals is singing behaviour in songbirds (Nottebohm 1970) (Suthers *et al.* 1990), with asymmetries ranging from unilateral vocalizations to almost equal contributions from each syringeal side. This diversity constrasts with the absence of laterality in morphology and and activity of higher central song nuclei (McCasland 1987). A key element to solve this puzzle is the observation that of all muscles relevant to song production in brown thrashers (*Toxostoma rufum*), only the activity of those involved in gating regulating airflow is lateralized (Goller *et al.* 1995). This simplicity at the level of the neural control does not mean that the produced sounds are simple. In particular, when the two sound sources at the syrinx are active, rather complex sound can be produced (Nowicki *et al.* 1986).

The coexistence of simple instructions and non trivial vocalizations can be understood if we take

into account that the physical apparatus involves is highly nonlinear, and therefore some subtle physical mechanisms enter the picture. Such mechanisms allow an increase spectral and temporal complexity of sound used in vocal communication. In fact, the dependence of sound frequency on the gating parameters for given labial tension values predicted by recent nonlinear models (Laje *et al.* 2002 a) allows us to expect that the onset of regimes with equal contributions from each syringeal side will have a complex dynamics. In fact, equal tensions with different gating strengths precludes slightly different frequencies at each sound source, and therefore the potential for highly nontrivial dynamics as coupling between sources becomes significant. The experimental and theoretical study of this mechanism permits us to explore the degree of complexity which the mechanics allows to add to the song with lateralization of a single neural instruction.

### B6 Search for basic mechanisms

Between the brain instructions and the song a physical apparatus, the syrinx, adds temporal and acoustic complexity. In the control of this physical apparatus several driving parameters converge: tension of the oscillating labia, airflow that sets the labia into motion, and finally a supravocal system. The nonlinear nature of the avian vocal organ receiving these complex signals anticipates nontrivial effects which we plan to address both experimentally and theoretically. The approach through mathematical models of the physical mechanisms of the syrinx will be an important complement to the more traditional approach towards the study of motor control of birdsong. This kind of interaction has recently suggested that investigating temporal relationships between control parameters might be more profitable than directly correlating neural instructions with acoustic outputs (Suthers *et al.* 2002). Along that line, we plan to integrate models ((Gardner *et al.* 2001), (Laje *et al.* 2002 a), (Laje *et al.* 2002 b)) and empirical work ((Goller *et al.* 1995), (Goller *et al.* 1996a), (Goller *et al.* 1996b), (Goller *et al.* 1999)), driving theoretical models with experimentally recorded data, in order to inspect the degree to which complex sounds can emerge out of simple driving instructions.

# C   C. Preliminary studies

This proposal is a continuation of a collaboration begun in 2000, in which recently proposed models of the syrinx were developed and validated with electromyographic data of the muscles that control it. This is an example of the productive results of our interdisciplinary effort.

Between the actual song and its complex representation at the level of the brain (central motor control) stands the avian vocal organ. A continuous research effort has been carried out to investigate the motor activity of various muscles and their role in controlling the vocal organ (Goller *et al.* 1996a). The avian vocal organ, the syrinx, is located at the junction of the primary bronchi and trachea. Freely moveable connective tissue masses, labia, are set in vibratory motion by expiratory airflow. Their position in the airstream can be actively controlled by syringeal muscles (gating muscles). Similarly, action by syringeal muscles is thought to allow control of the tension of the vibrating labia. The electromyographic activity of the muscles involved in these processes has been recorded for some species together with the vocal behavior. Recently, a dynamical model of the processes involved in birdsong production was presented (Gardner *et al.* 2001) (Laje *et al.* 2002 a). The parameters are, in principle, the time varying forces produced by vocal muscles. In our preliminary work, we measured electromyographs (EMGs) from muscles and chose magnitudes for these functions that come the closest to replicating the bird songs.

### C1 Experimental validation of physical models for birdsong

In this proposal, we integrate two lines of research: (1) the experimental studies leading to unveiling the role of different syringeal muscles in song production (Goller *et al.* 1996a), (Goller *et al.* 1996b) and (2) theoretical modeling of the avian vocal organ (Gardner *et al.* 2001), (Laje *et al.* 2002 a). The purpose of this integration is to study mechanisms in which the physics of the vocal organ contribute to non trivial acoustic features of the vocalizations. A first step in this program was taken in a collaboration between the authors of this proposal, as is being presented in (Mindlin *et al.* 2003). The aim of that

study was to validate the interpretation of the model parameters in biological terms.

The model analyzed in our preliminary analysis assumed the validity of the source-filter approximation, i.e. the possibility of understanding the dynamics of the labia independently of the acoustic feedback produced by the passive tract. It describes the behaviour of the labia when airflow passes between them. In previous work it was shown that driving the model with simple functions of time representing vocal muscles and bronchial pressure, the outcoming airflow generates sound that resembles bird songs. In our preliminary studies, we drived the model with functions whose time dependence comes from recordings of muscle activities and airsac pressure. We simultaneously recorded the birds' songs, compared them with synthetic songs, and found that the model produces recognizable songs. In figure 2 we show the sonograms of recorded fragments of songs (a, b), and the sonograms of synthetic songs (c, d) generated when the model was driven with the smoothed envelopes of the activities recorded during the vocalizations.
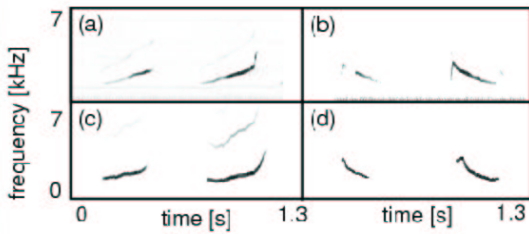


Figure C.0.2: Synthetic song, and song produced when our model is forced by the data.The sonograms of recorded fragments of songs (a, b) and the sonograms of synthetic songs (c, d) generated when the model was driven with linear functions of the smoothed envelopes of the activities recorded during the vocalizations.

The model used to create this synthetic song is a simple dynamical system for the departure of the midpoint of a labium from the prephonatory position, $x$ (Gardner *et al.* 2001), (Laje *et al.* 2002 b), (Laje *et al.* 2002 a), which is treated as a point mass subjected to several forces (see Fig. 1):

$$\frac{dx}{dt} = y(t) \tag{C.0.1}$$

$$\frac{dy}{dt} = -\epsilon x(t) - Cx(t)^2 y(t) + By(t) - D_0, \tag{C.0.2}$$

where $\epsilon$ stands for the restitution constant of the labium, $B$ is the total dissipation constant (constituted by both the negative dissipation induced by the interlabial pressure as discussed above, and the positive linear dissipation of the system), and $D_0$ measures a constant force (which displaces the equilibrium of the system). Large values of $D_0$ represent active adduction, since it prevents oscillations by placing the membranes at their minimum distance. It is then related to the activity of the $dTB$ or lateral part of the $dS$ muscle (see Figure 1). The details of the mechanics are not completely known, but the $dTB$ presumably rotates the bronchial ring pushing the inner labium into the lumen. The activity of the $vS$ muscle is positively correlated with the frequency of the vocalization. Therefore, in the model it is associated to the parameter $\epsilon$. It is likely that the longitudinal tension of the labia, caused by contraction of the $vS$ muscle, alters their elasticity. Therefore, it is natural to associate it with the restitution constant in the model.

In order to validate the model we recorded these variables and use them to drive the model and compare synthetic and recorded songs. Electromyographic data were recorded using a procedure described in (Goller *et al.* 1996a). Briefly, we proceeded as follows. Air sac pressure was recorded with a flexible cannula inserted into the anterior thoracic air sac and connected to a piezoresistive pressure transducer. To record muscle activities, wire electrodes were implanted into syringeal muscles. The electrodes were prepared from insulated stainless steel wire and secured to the tissue with a microdrop of tissue adhesive. Before closing the air sac, all the wires were led out and routed to the back. Our preliminary analysis was conducted on 13 song elements with simultaneous recordings of $dTB$ activity,

$vS$ activity and $P$ (pressure). The data were taken from two cardinals (Cardinalis cardinalis), hereafter called bird 1 and bird 2.

EMGs were sampled at 40000 points per second. We took the absolute value and then replaced each point by the average of its 2000 neighbors. The rectified, smoothed envelope of the EMG provided a relative measure of muscle activity that could be used in the model to understand how muscles contribute to movements leading to the slowly evolving acoustic features of song syllables.

We then proceeded to integrate the model for the dynamics of the labia with the smoothed envelope of the activities of vS (K) and dTB (D) muscles, and the air sac pressure data (P). For simplicity, we assumed a linear relationship between the smoothed envelope of the EMG recordings and the tension of the respective muscles, as well as a linear relationship between the air sac pressure and the driving average interlabial pressure. Notice that the last relationship is predicted by the model (Laje *et al.* 2002 a), while the linear relationships between smoothed envelopes and tension is an hypothesis to be tested. For all the simulations, we used

$$\epsilon = \epsilon_{1,1} + \epsilon_{1,2}K \tag{C.0.3}$$
$$B = \beta_{1,1} + \beta_{1,2}P \tag{C.0.4}$$
$$D_0 = \delta_1 D, \tag{C.0.5}$$

a set of linear relationships that allow us to fit frequency ranges for the synthetic sounds generated by our model, when it was driven by $\epsilon$, $B$ and $D_0$. The fitting was performed for each bird, since the amplitude of an EMG may vary between individuals depending on the input impedance of electrodes. For each bird, a syllable was used to find the coefficients. The coefficients in Eq. (3) were adjusted so that the frequencies at the starts and ends of the synthetic syllable would be those of the recorded syllable. The coefficients of Eq. (4) were chosen such that the synthetic and recorded syllable would start and end at the same times. The coefficient in Eq. (5) is such that $D_0$ has the minimum value at which an oscillation of the model can be prevented, when $D$ reaches a local maximum, close to the start of the syllable (Laje *et al.* 2002 a). As an example, for one of the birds in our study, we found $\epsilon_{1,1} = 1.25 \times 10^8$ $(\frac{1}{s})$, $\epsilon_{1,2} = 7.5 \times 10^9$ $(\frac{1}{Volt\,s})$ , $\beta_{1,1} = -2 \times 10^3$ $(\frac{dyn\,s}{g\,cm})$, $\beta_{1,2} = 5.3 \times 10^4$ $(\frac{dyn\,s}{Volt\,g\,cm})$, $\delta_1 = 15 \times 10^6$ $(\frac{dyn}{Volt\,g})$. These coefficients then allows us to convert the measured activity into driving functions of our model, and generate synthetic songs as the ones displayed in Figure 2. The fit is performed with one syllable, and used for all the other utterances of the same bird.

The qualitative agreement indicates that the model captures the basic mechanisms, and that the biological interpretation of its parameters is meaningful.

## C2 Preeliminary data showing the limits of validity of the source filter model

The previous model could generate recognizable songs, but it can not account for complex acoustic features as the one displayed in the Zebra finch sonogram of Fig. 3. In this figure, subharmonics arise at certain times. These submultiple frequencies of the fundamental frequency affect the acoustic properties of the vocalization, and reveal interesting mechanisms at the level of the source of sound. The supra harmonics of a signal do affect the timbre, but not its period. Subharmonics, on the other hand, reveal that the nonlinearities are playing a substantial role.

Many mechanisms are compatible with the existence of subharmonics. The labia might be supporting non trivial modes of oscillations, or the acoustic feedback might be affecting the motion of the labia (Laje *et al.* 2001). In the latter, the separation between source and filter no longer holds. Feedback arises when the glottal system is coupled to the vocal tract, and pressure reverberations are allowed to return to the folds and perturb their dynamics. The modeling of this physical mechanism is less simple, since the equations for pressure in the vocal tract must be solved simultaneously with those describing the dynamics at the glottis. The source filter approximation assumed that the glottis output impedance is much larger than the vocal tract imput impedance. Therefore, it is natural to expect it to fall if the filter inertance increases. In the second inset of Fig. 3, we show a measurement that we performed on the beak aperture of the bird while singing the song of the first inset, by means of a Hall effect transducer. As expected, the spectrum displays signature of subharmonicity as the beak widens.

The appearence of subharmonics at the times in which beak aperture was maximal, is an indication that feedback is playing a major role in the generation of these complex acoustic features.
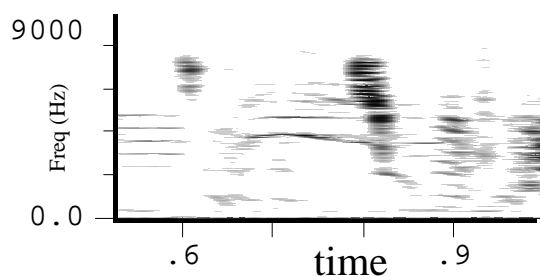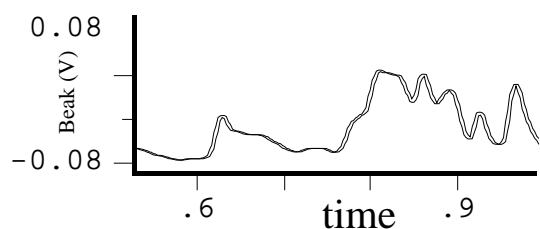


Figure C.0.3: Signatures of subharmonicity in the sonograms (a), beak aperture (b)

# D    D. Research Design and Methods

In this proposal, we work under the hypothesis that the physics of the avian vocal organ, a nonlinear device, is able to generate complex acoustic signals even when driven by simple motor instructions. In order to test this hypothesis, we will undertake two different approaches: experimental and modeling. Experimentally, we will measure the electrical activity in several muscles controling the syrinx as well as beak movements during singing. In terms of modeling, we will explore different mechanisms able to generate complex acoustic signals.

### D1 Mechanisms underlying the generation of subharmonic signatures in song
*How do birds generate complex sounds with subharmonic components using one sound source ?*

### Rationale and hypothesis

In the literature, a mechanism by which the avian vocal organ adds complexity to the song, was explored in the framework of the two mass model of the labia (Fee et al. 1998). Yet, even before exciting higher order modes in the oscillating tissue, it is possible to obtain subharmonic responses if acoustic feedback is considered (Laje *et al.* 2001). In our preliminary data, we found suggestive correlations between subharmonic signatures and beak aperture. Therefore, we suggest that a simple labial con-figuration in a strongly coupled source-filter situation can account for the appearence of subharmonic signatures in many songs.

To test this hypothesis, we will undertake two approaches: experimental, and theoretical. The experimental part of the work will be carried out in the Department of Biology, University of Utah. The analysis of the models consistent with our hypothesis will be carried out at the Institute for Nonlinear Science, University of California, San Diego.

### Experimental work
### Systems with feedback

The models developed so far in order to model the dynamics of the syrinx have assumed the validity of the source-filter separation. Our preliminary analysis indicate that for wide open beaks, signatures of subharmonicity are found. In order to address this issue, we will first work with a model that assumes two modes of oscillation for the labia (as in (Gardner *et al.* 2001), based on a model proposed by Titze

in (Titze 1988)) but without neglecting the effect of the feedback. In order to do so, we have to move outside the source-filter paradigm, and solve simultaneously the labial dynamics and the pressure waves in the tubes representing tract and beak. The system of equations ruling the motion of the midpoint of a labium $x(t)$ will then read:

$$m\frac{d^2x}{dt^2} + Kx + (B + Cx^2)\frac{dx}{dt} = P_l, \tag{D.0.6}$$

with

$$P_l = P_i + (P_s - P_i)\frac{(\delta x_0 + 2\tau x')}{(x_{01} + x + \tau x')} \tag{D.0.7}$$

where $P_l$ stands for the interlabial pressure, $P_s$ for the bronchial pressure, and $P_i$ the input pressure at the vocal tract. The parameters $x_{01}$, $\delta x_0$ and $\tau$ represent geometric features of the labial structure (Laje $et$ $al.$ 2001). According to our hypothesis, for situations in which the beak is wide open, the assumption that $P_i$ will be approximately that of the atmosphere is not valid. The complete problem, with boundary conditions, has to be addressed. Modeling the trachea and beak by means of tubes, we can write (Gardner $et$ $al.$ 2001):

$$P_i(t) = a(t) = I\frac{dU(x, x', t)}{dt} + b_b(t - \tau_1), \tag{D.0.8}$$

$$b_b(t) = r_{1,2}a(t - \tau_1) + t_{1,2}c_b(t - \tau_2), \tag{D.0.9}$$

$$b_f(t) = t_{1,2}a(t - \tau_1) + r_{1,2}c_b(t - \tau_2), \tag{D.0.10}$$

$$c_b(t) = \alpha b_f(t - \tau_2), \tag{D.0.11}$$

where $\alpha$ accounts for the reflection coefficient of the interface between the last tube and the atmosphere, $\tau_i$ the time the sound wave travels along the $i_t h$ tube, $r_i$ and $t_i$ the reflection and transmission coefficients of the $ith$ tube. $P_i(t)$ can be computed in terms of the dynamical variables describing the labia (Gardner $et$ $al.$ 2001) (Laje $et$ $al.$ 2001). The variable $a$ ($b_b$) stands for the forward (backward) wave in the first tube, $b_f$ ($c_b$) stands for the forward (backwards) wave in the second tube, which will model the beak, and $U$ stands for the airflow. This system displays complex dynamics, and subharmonicity is found for high impedances (Laje $et$ $al.$ 2001), even if one tube is used to model the tract.

We plan to study the bifurcations of this system as the parameters are varied, and also, as discussed in our preliminary analysis, study the solutions and sounds generated when the parameters are driven by the electromyographic and beak data recorded in our experiments. We plan to integrate numerically the differential equations with standard Runge Kutta techinques, and use software tools (dstools) to study the bifurcation skeleton of the system (Solari $et$ $al.$). Mode mode interactions will be used to study the system close to linear singularities, and particular attention will be payed to the generation of subharmonic such as the ones which could account for the structure seen in Fig. 3.

Once the dynamics for fixed parameters is understood, we will proceed as in our preliminary analysis, assuming that in order to generate a syllable, the parameters have to sweep a region of parameter space so that we move within and outside of the region of parameter space where oscillations take place. Since now the geometry of the tubes plays a significant role, in order to reproduce the experiments, not only we do consider $k$ as a function of time (envelope of vS activity), but also the reflection and transmision coefficients $r_{1,2}$ $t_{1,2}$ will be functions of time. To map beak activity to these tube parameters we write

$$r_{1,2} = \frac{A_1 - A_2}{A_1 + A_2}, \tag{D.0.12}$$

and $t_{1,2} = 1 - r_{1,2}$, where $A_i$ is the area of the $i^{th}$ tube. Then, we consider that $A_2$ is proportional to the measured beak aperture. With these functions of time (envelope of vS muscle activity and $A_2$ as

beak aperture), we plan to proceed to generate synthetic syllables, which will be compared spectrally to experimental recordings as in our preliminary analysis.

**Comparisons between models and experiments**

In our preliminary analysis, we generated synthetic songs after numerically solving the dynamical equations for the labia. Within the framwork of a model, we can compute the time derivative of the airflow once the labial dynamics is determined (Gardner *et al.* 2001). In this way, a numerical file emulating the sound pressure waveform can be created. That file can be converted into a standard sound format, and treated as a recorded file. In our preliminary studies, the Linux software package *snd* was used to process both synthetic and recorded *wav* files. In these studies the comparison between synthetic and natural sounds was of a qualitative nature. The sonograms (time course of the spectral properties of windowed data) were compared in a qualitative way, finding satisfactory that the initial and final frequencies of a synthetic and a recorded syllable would match.

In this proposal, we will advance into a a quantitative comparison between the synthetic and the natural sounds. We will continue working with sonograms for both cases, but we will compute cross correlations between them. As in our preliminary study, the parameters used to convert electrical activities into biologically relevant driving parameters for our model will be chosen to minimize the difference between synthetic and recorded sounds for one syllable, for a bird during a continuous recording session. After the parameters are chosen, we plan to study the statistical distribution of the correlations between the recorded sounds, and the synthetic ones for several syllables.

**D2. Subharmonicities in utterances that involve two sound sources.**

*What are the mechanisms by which two sources generate complex sounds?*

**Rationale and hypothesis** As described in Section B4, the instructions sent to the two sides of the bipartite avian vocal organ allow the bird to perform internal duets between the two sources of sound. There is evidence that this behavior can produce complexity beyond the simple superposition of sounds (Nowicki *et al.* 1986): the acoustic signals of one source can induce a change in the dynamics of the labia of the other sound source, as suggested by the data displayed in Figure 4.
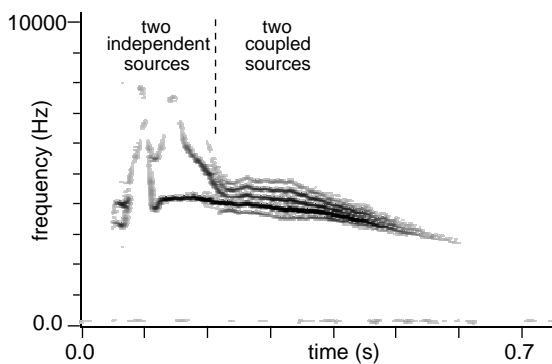


Figure D.0.4: Fingerprints of source source interaction

We suggest that the acoustic coupling between the two sources of sound is responsible for the generation of complex sounds. The nonlinearities in the avian vocal organ provide the basic template to understand the process. We suggest that the nature of the physical apparatus not only anticipates that eventual sounds of different frequencies will mix nonlinearly; it also constrains the frequencies of the labial oscillations at their onset. In order to test this hypothesis, experimental and theoretical work will carried out. The experiments, electromyographic studies of the muscles driving the syrinx, will be performed by Goller. The analysis of the models, will be carried out by Mindlin working closely with the experiment.

**Experimental studies**

**Dynamical modeling of two sources interacting acoustically**

So far, the existence of frequencies that were the sum and the difference of the fundamental frequencies of the two sources, was explained in terms of a generic nonlinear interaction (Nowicki *et al.* 1986).

We plan to investigate the source of these acoustic signatures in terms of the precise mechanisms involved in the generation of a complex labial dynamics. This will allow us to link these signatures with specific biological parameters. We will begin our theoretical study of this phenomenon by studying the dynamics of two sources acoustically coupled (Gardner *et al.* 2001):

$$\frac{dx_1}{dt} = y_1 \tag{D.0.13}$$

$$\frac{dy_1}{dt} = -k_1 x_1 - \beta_1 y_1 - c x_1^2 y_1 + P_l \frac{a_0 + b_0 + 2\tau y_1}{x_1 + b_0 + \tau y_1} + d_1 \tag{D.0.14}$$

$$\frac{dx_2}{dt} = y_2 \tag{D.0.15}$$

$$\frac{dy_2}{dt} = -k_2 x_2 - \beta_2 y_2 - c x_2^2 y_2 + P_l \frac{a_0 + b_0 + 2\tau y_2}{x_2 + b_0 + \tau y_2} + d_2 \tag{D.0.16}$$

$$P_l = a(t) = \frac{dU(x_1, x_2, x_1', x_2')}{dt} + b(t - \tau_1), \tag{D.0.17}$$

$$b(t) = \alpha a(t - \tau_1), \tag{D.0.18}$$

Where $U$ stands for the airflow, $d_i$ for the activities of the dorsal muscles, and $x_i$ the deviation of the rest position of the labia in the different sources. $\alpha$ accounts for the reflection coefficient of the interface between the tube and the atmosphere, $\tau_1$ the time the sound wave travels along the tube. The variable $a$ ($b$) stands for the forward (backward) wave in the tube. Notice that now only one tube is used, in order to progressively study the effects due to acoustic interaction between the two sources without considering feedback effects due to wide beak aperture.

The same techniques described previously will be used to analyze this system. and use software tools (dstools) to study the bifurcation We will search for regimes in which labial complexity might arise, and inspect how it translates into acoustic features in the song.

Once the stationary regimes are understood, we will proceed as in our preliminary analysis, forcing the system of equations with the experimental measurements. Driving of this model with the experimental records of muscle activity and bronchial pressure will allow us to compare the data with the predictions associated with specific mechanisms. Our previous work (Laje *et al.* 2002 a) suggests that even with the same tension of the m. syringealis ventralis, two sources that turn their activity on at different times will start with slightly different frequencies, opening the path to non trivial nonlinear interactions between the sources. This will be tested in the model and the experiment.

### Db4. Comparisons between models and experiments

We plan to compare synthetic generated songs produced with our model with recorded ones. The comparison with be performed at the level of the sonograms, which resolve the spectral content of the utterances in time.

We also plan to compare the synthetic songs generated by driving the system with biological data to the song actually vocalized while the driving parameters were recorded, computing correlations between the sonograms of the synthetic and natural songs or all inspected syllables. In order to do so, the rectified, smoothed envelope of the EMG will provide a relative measure of muscle activity that can be used in the model to understand how muscles contribute to movements leading to the slowly evolving acoustic features of song syllables. As in our preliminary analysis, the envelopes of left and right $vS$ activities will force the labial tensions $k_1$ and $k_2$ in the model, and the envelopes of right and left $dS$ activities will force $d_1$ and $d_2$, after proper scaling.

The measurement of the activities of the $dS$ muscles and $vS$ muscles during utterances that involve two sources will be of particular interest: according to our models, even if both left and right vS activity receives the same neural instructions, if one of the sources begins to oscillate before the other, the two oscillations will start at slightly different frequencies. We will compare these values with the predictions of the model.

# E   E. Human Subjects

# F   F. Vertebrate Animals

# G   Literature Cited

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