Beyond harmonic sounds in a simple model for birdsong production

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In this work we present an analysis of the dynamics displayed by a simple bidimensional model of labial oscillations during birdsong production. We show that the same model capable of generating tonal sounds can present, for a wide range of parameters, solutions which are spectrally rich. The role of physiologically sensible parameters is discussed in each oscillatory regime, allowing us to interpret previously reported data. © 2008 American Institute of Physics.

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Birdsong has become an animal model system for the study of learned vocalizations with remarkable parallels to human vocal development and sound production mechanisms. For this reason much of the research in this field focuses on the neural basis for motor control and learning. Yet, behavior emerges from the interaction between the central nervous system and its peripheral target organs. In this work we show that the most widely studied songbird, i.e., the Zebra finch, can benefit from nontrivial dynamical properties of its vocal organ to achieve distinctive acoustic features in its song. This work illustrates the need to address simultaneously questions on central motor control and peripheral mechanisms in order to unveil how complex behavior might be achieved.

I. INTRODUCTION

Songbirds are known as an animal model for learning: they require the exposition to a tutor and practicing in order to achieve the proper conspecific songs.1 For this reason, most of the research in birdsong production focuses on the neural circuitry necessary for its production and acquisition. Yet, behavior emerges from the interaction between a nervous system, a peripheral one, and the environment. Interestingly enough, the avian vocal organ, called the syrinx, presents strong fingerprints of nonlinearities and therefore, the way in which simple physiological instructions will be transduced into sound is not obvious.

In the last years, a number of models have been proposed in order to integrate the large body of experimental work2,3 with the expected basic mechanical processes involved in birdsong production.4–6 In this way, a picture starts to emerge in which the roles of different muscles used by a singing bird are unveiled.

The basic mechanism of birdsong production resembles the generation of voiced sounds by humans: the expiratory airflow can drive sustained oscillations of the membranes (vocal folds in humans and labia in birds).7,8 Therefore, the models of birdsong production aim at unveiling the main mechanisms and effects responsible for the dynamics of this valve. These models are implemented mathematically, and the synthetic sounds generated by them are compared with the data. They are realistic enough to be taken as an acceptable tutoring sound by juveniles in controlled experiments.9 Nonlinearities in these models can arise as nonlinear restitution forces, dissipative forces that enter during collision between labia, or the dependence of the interlabial pressure with the labial dynamics. If the internal structure of the oscillating labia which modulate the airflow is taken into account, the dimensionality of the models is large enough to display chaotic solutions.7,10

Low dimensional models, on the other hand, have been used to synthesize tonal sounds like the ones produced by Canaries (Serinus canaria) or Northern cardinals (Cardinalis cardinalis).

Yet, some birds, such as the Zebra finch (Taeniopygia guttata) produce spectrally rich sounds. In Fig. 1(a), a representative song of a Zebra finch is displayed.11 Some syllables are nearly tonal (the fundamental frequency is dominant), while in others, the energy is distributed among several super-harmonics of the fundamental frequency. Recently it was shown that the later sounds have a pulse tone register, and each acoustic pulse is related to a rapid opening of the labia followed by a long closure of the valve to the airflow.12

A recent work explored the existence of a relationship between the fundamental frequency and the richness of the spectrum of the syllables in the Zebra finch song. It was found that over a wide range of fundamental frequencies, the higher the value of the fundamental frequency, the poorer its spectral content.13 By plotting the spectral content index, a number describing the centroid of the spectrum of an acoustic signal14 as a function of its fundamental frequency, it was found that for several birds, and all the syllables within their repertoires with a well-defined fundamental frequency, the data were clustered around a simple curve. This suggests the existence of a common mechanism behind the generation of acoustically different sounds.

Beyond high frequency sounds (almost tonal), and spectrally rich harmonic stacks (with fundamental frequencies ranging from 500 to 800 Hz), the Zebra finch song includes noisy notes, for which the computation of a fundamental frequency is not trivial. It was shown that many of those syllables involve the use of the two acoustically independent sound sources that songbirds have.15 In these cases, the left
and right sides produce acoustically independent sounds with different modulation patterns,\(^1^5\) giving rise to very complex sounds. These syllables are left aside of our study, which focuses in the question of how a single sound source can generate both tonal sounds and harmonically rich sounds with a well defined fundamental frequency. Recently, the harmonic-to-noise ratio\(^1^6\) was used to quantify animal sounds which are a mixture of regular components and noisy ones. In the problem of the dog barking, for example, the regular part is likely to be associated with the oscillation of the vocal folds, while the noisy ones are likely to be either due to chaotic motion of the vocal fold tissue\(^1^7\) or turbulence of the air. In the Zebra finch, these effects might play a role, as well as the acoustical effects emerging from the interaction between the sounds generated by the two independent vocal sources. More work is needed to unveil the processes involved in Zebra finch noisy notes.

From a dynamical point of view, low dimensional models can present periodic oscillations which are spectrally very rich. The aim of this work is to revisit a simple (low dimensional) model for birdsong production, focusing on the search of spectrally rich oscillations. We describe the global bifurcations that give rise to such solutions, and inspect under what conditions they can occur. Bifurcation diagrams in terms of physiological relevant parameters are described, and the acoustic features of the sounds associated with those solutions are discussed.

This work is organized as follows. Section II presents the model. Bifurcation diagrams are discussed in Sec. III. The sounds which can be generated by the described dynamics are presented in Sec. IV. The last section contains our discussion and conclusions.

II. THE MODEL

One of the first low dimensional models for the dynamics of a membrane in an airflow was proposed by Titze\(^7\) and further studied by others.\(^1^8\) According to this model, the motion of the oscillating tissues is represented as a surface wave propagating in the direction of the airflow. This wave is modeled in terms of two basic modes: a lateral displacement of the tissues, and a flapping like oscillation responsible for an out of phase oscillation of the top and bottom parts of the membranes (see Fig. 2).

The simplest assumption for the existence of self-sustained oscillations is that through a particular phase difference between these modes the system is capable to gain energy in each cycle. The obvious way to accomplish this is to have a convergent profile when the labia move away from each other, and a divergent when they approach. Instead of this configuration, having a less divergent profile when opening than when closing, provides the same effect with not such a dramatic change in the orientation of the profiles [see Fig. 2(b)]. This configuration of profiles allows to have a higher interlabial pressure when the labia are moving apart. In this way, this nonuniform force acting on the membranes allows a net gain of energy in each cycle. The whole movement can be visualized as an upward propagating wave on the membrane.

In order to describe this motion, one can call \(a_1\) (\(a_2\)) the half separation between the lower (upper) edges of the labia [see Fig. 2(a)]. Under the hypothesis of a mucosal wave motion on a membrane, these half separations can be written in terms of the midpoint position of a membrane \((x)\) and its velocity \((v)\). If the time that takes the wave to propagate half the vertical size of the labia is \(\tau\), the half separations between the edges of the membranes will satisfy

\[
 a_1 = a_{01} + x + \tau v, \\
 a_2 = a_{02} + x - \tau v, 
\]

where \(a_{01}\) and \(a_{02}\) are the half separations at the rest (nonoscillating) state. Computing the average pressure between the labia,\(^7\) one obtains

\[
\]
where $p_{\text{sub}}$ stands for the sublabial pressure. Now it is possible to go beyond the kinetics of the labia to the dynamics. The equations of motion for the variable $x$ is derived taking into account dissipation, elastic restitution, nonlinear dissipation, and read

$$
\frac{dx}{dt} = y, \quad (4)
$$

$$
\frac{dy}{dt} = \left( \frac{1}{a_0} \right) \left( -k(x)x - \beta(y)y - cx^2y + f_0 + a_{\text{lab}} p_{\text{sub}} \left( \frac{\Delta a + 2\tau y}{a_{01} + x + \tau y} \right) \right). \quad (5)
$$

The first term corresponds to a nonlinear restitution force, where $k(x) = k_1 + k_2 x^2$. The second term accounts for dissipation, with $\beta(y) = \beta_1 + \beta_2 y^2$. The third term is also a nonlinear dissipation that becomes relevant as $x$ takes large values, corresponding to large departures from the rest position. In this way, this position dependent nonlinear dissipation serves to model collisions between labia or with containing walls, either one bounding their motions. The term $f_0$ accounts for a force that is independent of the labial dynamics, and serves to model active gating. Finally, the last term describes the force $f_{\text{lab}}$ acting on the labium due to the interlabial pressure: $f_{\text{lab}} = a_{\text{lab}} p_{\text{lab}}$. Where $\Delta a = a_{01} - a_{02}$. A slightly simplified version of this model (without nonlinear restitution) was used in Ref. 4 to synthesize canary song. In order to do so, the dynamics of $x$ is used to emulate the modulations of airflow that are responsible for the generation of sound waves. To achieve acoustically realistic sounds, these pressure fluctuations are further filtered emulating the action of a vocal tract. For the case of Zebra finches, this enhances frequencies of the sound source in the range of $3-6$ kHz.

The model was further studied by Lucero to investigate oscillation hysteresis. It is interesting to notice that the existence of nonlinear components in the restitution forces for labia was recently found to play an important role in the frequency control of song by a suboscine bird, and qualitatively increases the dynamical possibilities of the model. With its simplicity, this model allowed to identify parameters necessary to account for important acoustic features found in birdsong, such as the temporal evolution of the fundamental frequencies of different syllables. The pressure $p_{\text{sub}}$ was identified as the parameter responsible for the onset of the membrane oscillatory motion, and for several oscine birds, $k_1$ was found to be responsible for the tension of the oscillating labia, which contributes to the value of the fundamental frequency of the uttered sound.

### III. BIFURCATION DIAGRAMS

We start our analysis of the dynamics presented by this model with an inspection of its fixed points. They are characterized by $y = 0$, and the solutions of

$$
p_{\text{av}} = p_{\text{sub}} \left( 1 - \frac{a_2}{a_1} \right), \quad (3)
$$

- $(k_1 + k_2 x^2)x + f_0 + a_{\text{lab}} p_{\text{sub}} \frac{\Delta a}{a_{01} + x} = 0. \quad (6)$

In previous works, a fixed point losing its stability in a Hopf bifurcation was identified as the basic mechanism leading towards the periodic modulation of airflow, and therefore of sound production. Yet, the model presented here displays a richer set of solutions.

We analyze the bifurcation diagram of our system in terms of the parameters which were found to be relevant for song production. In Fig. 3 we display a region of the parameter space $(p_{\text{sub}}, k_1)$ for which three fixed points exist (shaded region). The other parameters were chosen within biologically sensible ones in such a way that $(-f_0 + k_1 a_{01}) = 0$ and $(p_{\text{sub}} \Delta a + f_0 a_{01}) = 0$, which guarantees a change in the number of solutions of Eq. (6) as $k_1$ and $p_{\text{sub}}$ are slightly changed (see the caption of Fig. 3). Outside this region, a unique fixed point exists. The edges of the cusp shaped region in the parameter space correspond to saddle-node bifurcations (dotted lines in Fig. 3), where a pair of fixed points collide in a unique one with zero linear eigenvalues.

As was mentioned above, the possibility of some of these fixed points undergoing oscillatory instabilities (Hopf bifurcations) was identified as a way to originate periodic motion of the labia, and therefore modulations of the airflow. Hence, it is sensible to perform a linear stability analysis in order to identify the region of the parameter space where these instabilities occur. Computing the eigenvalues of the Jacobian of the system described by Eqs. (4) and (5) we searched for the subset of parameters where the fixed points of our model would present complex eigenvalues with zero real parts, conditions that are necessary for Hopf bifurcations. The continuous curves in the region of $(p_{\text{sub}}, k_1)$ under
The existence of one-dimensional paths in parameter space where saddle-node (or saddle repulsor) bifurcations take place, and one-dimensional paths where Hopf bifurcations occur, preclude the possibility of rich dynamics when they meet. In Fig. 3 we display a region of the parameter space of our model where different dynamical regimes were found. The different insets display the solutions that we found in each of the regions with different dynamical behavior.

In region 1 of Fig. 3, a unique fixed point is found. Region 3 (inside the shaded region) presents three fixed points: in the transition from region 1 to region 3, a saddle-node bifurcation generates the two additional fixed points. The attractor generated in this bifurcation undergoes a Hopf bifurcation as we enter region 4. The separation between regions 4 and 5 is defined by an homoclinic bifurcation: the limit cycle of region 4 collides with the saddle fixed point. Region 7 is dynamically equivalent to region 3, just as region 6 is equivalent to region 4. Interesting enough, region 5 (separated from regions 4 and 6 by homoclinic bifurcation lines) presents a dynamically rich structure: the unstable manifold of the saddle is part of the stable manifold of the attractor. In this way, when we change the parameters in order to move from region 5 to region 2, a saddle node in a limit cycle bifurcation (SNILC) takes place.

It is interesting to discuss the degree of generality of the set of solutions found in the analysis here reported. Notice that whenever there are both a one-dimensional set of parameters where a saddle-node bifurcation and a Hopf bifurcation take place, it is generic that they meet. Whenever that occurs, any model can be reduced to a normal form whose dynamics take place, and one-dimensional paths where Hopf bifurcations occur, preclude the possibility of rich dynamics when they meet. In our model, the parameter \( p_{\text{sub}} \) was important to overcome dissipation and turning on the oscillations via the energy transfer to the labia, and \( k_1 \), correlated with the fundamental frequency of the vocalizations. The oscillations occur.

On the other hand, for other oscine birds, as the Northern cardinals and Brown thrashers (Toxostoma rufum), the activity of ventral syringeal muscles strongly correlates with the fundamental frequency of the vocalizations. It was suggested, and mathematical models were consistent with the interpretation, that these muscles change the restitution forces of the oscillating labia, and therefore the larger the activity of those muscles, the larger the frequency of the vocalizations. It is important to notice that the sounds produced by these birds are nearly tonal, so the model used to reproduce the data explored the Hopf bifurcation and not the SNILC. This two behaviors are contemplated in our model, as it is shown in Fig. 3, paths A and B.

As we mentioned before, the reason for choosing the parameters \( p_{\text{sub}} \) and \( k_1 \) in our inspection of the dynamical responses of the system is biased by previous works, where experimentally and theoretically it was shown that \( p_{\text{sub}} \) was important to overcome dissipation and turning on the oscillations via the energy transfer to the labia, and \( k_1 \), correlated with the fundamental frequency of the vocalizations. There are two other parameters that have an important effect in the solutions of our model. The term \( f_0 \) corresponds to a force independent of the labial dynamics, and it has been interpreted in terms of the action of active gating by oscine birds (controlled by dorsal syringeal muscles). Mathematically, this term avoids oscillations by moving the fixed point to regions of the space where dissipation is too high (either pushing the labia together, or contracting them towards the containing walls). In terms of our model, the increase of \( f_0 \) does in fact turn oscillations off. In Fig. 4 we show how the bifurcation diagram is translated to the right as \( f_0 \) is increased. In this way, if the system is in a region of the parameter space where it is oscillating (region 2 in Fig. 3), it is possible to increase \( f_0 \) until entering to the region 1 where no oscillations occur.
bifurcation, it is needed that the Hopf line touches the saddle-node line in such a way that the regions 2 and 5 are adjacent and the borderline separating these regions is a saddle-node bifurcation (as is shown in Fig. 3). For $\Delta a > 0$, only one fixed point exists, and the only qualitative change that is possible to find if the parameters are changed is a Hopf bifurcation giving rise to nearly tonal oscillations. In this way, the same model is capable of presenting the rich dynamics associated with spectrally rich sounds and tonal sounds.

**IV. PATHS IN PARAMETER SPACE**

In previous works, computational models were used to synthesize birdsong. Slow parameter changes in pressure were used to place the model in a region of the parameter space where oscillations would occur, and eventually to return the system to a region of nonoscillating solutions. The acoustic features of the sounds would depend on the values of the other parameters, which could also change slowly or remain fixed. Actually, some of these models were driven by experimentally recorded parameters (as the air sac pressure and activity of ventral syringeal muscles) and used to generate synthetic sound. In this section we explore the parameter space through different paths, in order to describe acoustically the sounds generated. Since new dynamical regimes exist, new acoustic features are expected.

In Fig. 5 we illustrate our results. In panel (a), we show the sonogram of the synthetic song generated when the parameters are moved along the closed path A displayed in Fig. 3. This path consists of a cyclic movement of the parameter $P_{sub}$ [Fig. 5(c)] for a fixed value of $k_1$. The chosen value of $k_1$ guarantees that the oscillation starts in a SNILC bifurcation. As the system enters the region of the parameter space where the oscillations take place, sound is generated. As in Refs. 4, 5, and 8, the oscillations of the labia are used to generate an oscillating airflow which is finally used to synthesize sound. Notice the rich spectral content of the sound, indicated by many dark lines in the sonogram. In the inset of Fig. 5(a) we illustrate the generated time series data. Its shape is very different from a simple harmonic oscillation, which is also clear from its spectrum. It is illustrative to compare these results with the sound generated using the path labeled B in Fig. 3, where the only changed parameter is $k_1$ and the variation of $P_{sub}$ is the same of path A. In this case [Fig. 5(b)], the system undergoes a Hopf bifurcation, where a harmonically poor oscillation is born. The sonogram displays, for the same resolution, a smaller number of curves, the shape of the oscillations resembles simple harmonic ones (of growing amplitude as expected in a Hopf bifurcation as the parameters are increased), and finally the spectrum of a segment shows supra-harmonic peaks of small amplitude.

The synthetic sounds generated in Fig. 5 illustrate how the two different dynamical mechanisms for generating oscillations discussed in this work can account for the spectral features of the representative syllables described in Fig. 1. As in the syllable displayed in Fig. 1(b), the synthetic sounds originated in a Hopf bifurcation have almost all their energy in the fundamental frequency. The synthetic sounds originated at a SNILC [Fig. 5(b)], will have a rich spectral content. In the experimental data [Fig. 1(c)], beyond a rich spectrum we can observe the influence of the vocal tract which emphasizes the harmonics between 3 and 6 kHz (an effect not considered in our model).

Notice that in the sonogram of Fig. 5(b), there is still a small dependence of the fundamental frequency with the pressure. This is a consequence of the nonlinear term in the restitution force. As the pressure is increased, the fixed point moves away from its rest position. In this way, with a fixed value of $k_1$, we obtain modulations in the fundamental frequency of the sound trough modulations in the pressure. This
effect was already discussed in the framework of the sound production of a suboscine bird (the Great Kiskadee), which does not require an active control of ventral muscles to produce variations of the fundamental frequency of its vocalizations. In some oscine species, where wide excursions in fundamental frequency is an appealing characteristic of their vocalizations, it is likely that they require more than this small dependence of frequency with air sac pressure, and an active control through ventral syringeal muscles is to be expected.

The last characteristic of the song that we synthesize is the capability of uttering multiple syllables with the same pressure pulse. In Zebra finch it is observed that there are pressure pulses. In Zebra finch it is observed that there are

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V. CONCLUSIONS

In this work, we have studied the solutions of a simple model of birdsong production. The introduction of a nonlinear component of the restitution force allowed us to find a rich variety of dynamical regimes. Beyond the oscillations born in a Hopf bifurcation, which was already reported as a plausible mechanism for the onset of tonal sounds, we found a variety of different dynamical regimes. Their existence, in the model, depend on the prephonatory shape of the labial configuration. This prephonatory shape is not only the initial condition but defines an average convergent or divergent profile as the dynamics of \( x \) defines only a small departure from the rest position.

One of the most interesting scenarios found in the model was the existence of SNILC bifurcations, where a saddle fixed point whose unstable manifold is part of the stable manifold of an attractor, collides with it. Oscillations of zero frequency are born at the bifurcation. As the bifurcation parameter is slightly moved away into the region of parameter space where oscillations occur, the frequency increases. These oscillations are spectrally very rich, generating sounds with non tonal features. In this way, different spectral features of sound originate in the dynamics of the avian vocal organ.

The nonlinear nature of the avian vocal organ was already reported to have important consequences in the sound it produces, from subharmonic solutions to nontrivial transduction of pressure into frequency, among other effects. In this work we describe the dynamics behind the relationship between fundamental frequency and spectral content in some sounds (those originated at SNILC bifurcations).

In the study of birdsong, a large effort is made in order to understand the neural basis of the motor commands responsible for the different acoustic features of the song. Yet, behavior emerges from the interaction of a nervous system, a peripheral system, and environment. This study illustrates that many features might not require separate instructions, but are linked by the nature of the dynamical solutions of the peripheral system.