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Neuromuscular control of vocalizations in birdsong: A model

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We present a dynamical model of the processes involved in birdsong production, relating qualitatively its parameters with biological ones. In this way, we intend to unify the activity patterns of the muscles controlling the vocal organ with the resulting vocalization. With relatively simple paths in the parameter space of our model, we reproduce experimental recordings of the Chingolo sparrow (*Zonotrichia capensis*).

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I. INTRODUCTION

Songbirds (or oscines) account for about 4000 out of roughly 9000 bird species known to exist [1]. For these species, learning through imitation has been found to play an important role in their complex vocal communication. It has been suggested that there may be common principles of learning and memory underlying human speech and the songs of birds (for a review, see [2] and references therein). For this reason, many experimental approaches are focused on understanding how song perception and production are represented in the brain. Experimental approaches to this question range from studies of spatial maps of gene expression correlated with song production and perception [3,4], functional analysis of lesions [5], electrophysiology of vocal control nuclei [6], and the detailed behavioral analysis of song ontogeny [7].

The scope of studies reflects the great range of neural structures known to be involved in some aspect of song learning [8]. This diverse neural activity is ultimately related to song output through the control of breath, and muscular tension in a set of six or seven muscles controlling the avian vocal organ, known as the syrinx. This organ plays a role similar to that of the larynx—it converts the energy of expiratory airflow to sound.

In recent years, Goller and Suthers have examined in detail pressure, airflow, and electromyographic activity in this organ [9]. Goller's recent videography has demonstrated the extent to which the underlying mechanism of sound production is shared between the human larynx and the syrinx. Similar to the larynx, the syrinx is located at the junction of the bronchi and trachea, and holds labia which are set in motion by expiratory airflow. These labia can be actively pulled against each other (adduction), and their tensions can be changed by muscles surrounding cartilaginous rings.

In this paper, we present a dynamical model of the processes involved in song production, at the level of the syrinx. This paper is based on the observed motor patterns of the syrinx described in the literature. Through the model we seek to unify an understanding of how the activity patterns of the muscles controlling the avian vocal organ relate to the resulting vocalization. A first step within this program was reported in [10]. There it was shown that the starts, stops, and pauses between birdsong syllables, as well as variation in pitch and timbre are inherent in the mechanics of the syrinx and can often be expressed through smooth and simple variations in the frequency and relative phase of two driving parameters. The first parameter considered in this paper was the bronchial pressure, and the second parameter was associated with the concerted activity of one or more syringeal muscles which change the elastic properties of the labia.

The model we present here includes as an addition the activity of muscles involved in the gating of airflow which involve the active opening and closing of the labia. The incorporation of the active gating mechanism allows for a closer relationship between the parameters of the model and the physiological measures described in the literature. Furthermore, this modification extends the variety of bird vocalizations that can be accounted for by simple periodic oscillations of air pressure, and labial stiffness.

The work is organized as follows. In Sec. II, we present a brief summary of the neuromuscular control of birdsong. A simple model for the motion of the labia is introduced in Sec. III. Section IV illustrates how a path in parameter space can be built to fit a syllable within a song, and Sec. V contains the analysis of an example (the Chingolo sparrow). Section VI contains our conclusions.

II. NEUROMUSCULAR CONTROL OF BIRDSONG

Birdsongs are usually relatively long and complex vocalizations, constructed by repetitions and alternations of simpler sounds known as syllables. In Fig. 1(a), we show the pressure fluctuations and the sonogram of a particularly simple song produced by a rufous-collared sparrow, or *Chingolo* sparrow (*Zonotrichia capensis*). A sonogram is just a plot of sound frequency in hertz as a function of time in seconds, and constitutes the standard way to represent a song. The individual markings on this sonogram are the syllables.

The sound-producing organ in birds is the syrinx. Like the larynx in humans, the syrinx contains labia which vibrate when air from the lungs is forced over them [1]. The modulation of air flow, induced by the moving labia, is responsible for the pressure fluctuations which generate the sound waves that (after being filtered by the vocal tract) constitute the song. In contrast to this basic similarity an important difference exists between the human vocal organ and the syrinx: the later is located at the junction of the two bronchi. Therefore, there are two potential sources of sound, one in each bronchus, providing birds with the possibility of generating

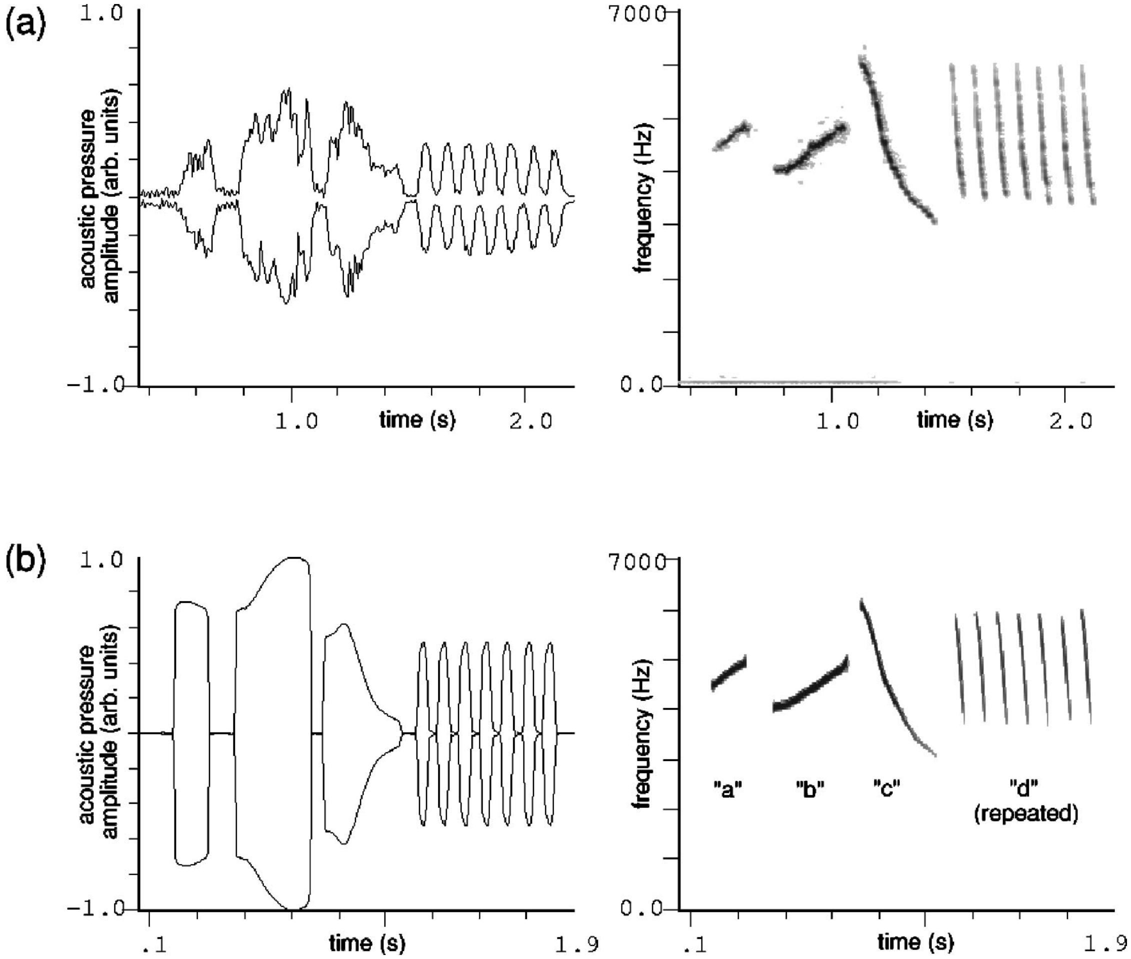

FIG. 1. (a) Waveform and sonogram of an actual Chingolo's song (*Zonotrichia capensis*). The spectrum is enhanced for all syllables around 4.5 kHz due to the first formant (resonance) of the Chingolo's vocal tract (length: ~ 1.9 cm). (b) Waveform and sonogram of a synthetic song, obtained by first integrating the equations for the model along the path shown in Fig. 7, and then filtering with a uniform, 1.9-cm-long vocal tract.

remarkably complex sounds. A schematic picture of the syrinx is displayed in Fig. 2(a).

The exact nature of the physics of sound production on each side of the syrinx has been the subject of some debate. The functional homology to the physics of laryngeal sound production has been suggested for some time [17,1], but recently Goller has given the clearest evidence that a flow-induced vibration of two soft tissue masses known as medial and lateral labia is the source of sound in the syrinx [11].

This observation differs from a variety of previous models for sound production in the syrinx. The first alternative model postulated that the pure tonal sounds of some songs could be explained if the syrinx operated like a hole-tone whistle, that is, sound production by vortex shedding through a fixed constriction in the syrinx [12]. Direct evidence against the hole-tone model evidence has come from Goller's endoscopic imaging. These studies established that labial oscillations were always present during phonation [13], and were in particular present even in pure-tone vocalizations.

The second alternative model of the physics of the vocalizations focused on the possible role of the medial tympaniform membrane—a thin membrane which is stretched across a void in the medial wall of the syrinx. When the syrinx is held in the phonating position, this membrane is stretched, and was seen to vibrate during some vocalizations. A model which focused on the movement of this membrane assumed that the boundary conditions of the membrane were those of a vibrating drum [14]. In order to produce vocalizations with natural spectral content, the pressure assumed to drive the tympaniform membrane was composed of a harmonically complex pressure waveform. This complicated expiration pattern does not correspond to the simple pressure traces measured by Goller and Suthers in a variety of vocalizations. In general, the difficulty of generating harmonically related overtones with a pinned membrane undermines the assumption that the source of sound is a membrane constrained like a pinned drum. Again, the most compelling evidence has come from Goller, who recently removed this membrane entirely, without detriment to song production [11].

We now turn from the physics of labial oscillation to consider the neural control of the vocal apparatus. Among the variety of learned behaviors in the animal kingdom, the learned vocalizations of song birds are attractive for mechanistic study because the behavior is generated by a relatively

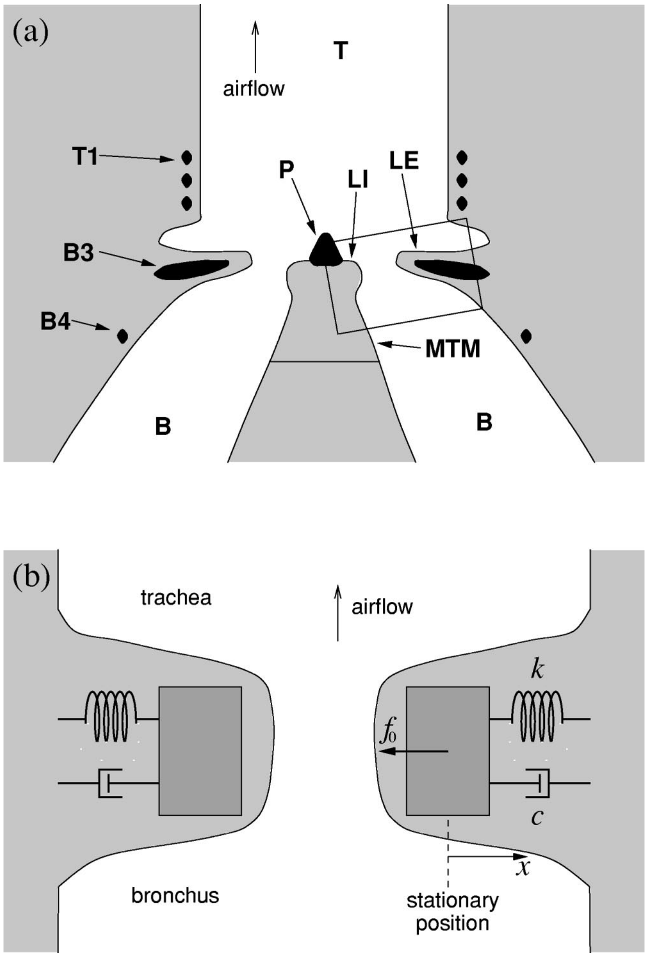

FIG. 2. (a) Schematic picture of the syrinx in the phonatory position (frontal section), showing its main components involved in the production of sound. Abbreviations: LE, labium externum; LI, labium internum; MTM, medial tympaniform membranes; T, trachea; B, bronchus; T1, first tracheal ring; B3, third bronchial ring; B4, fourth bronchial ring; P, ossified pessulus. (b) A diagram of the terms in the model (enlarged from the figure above).

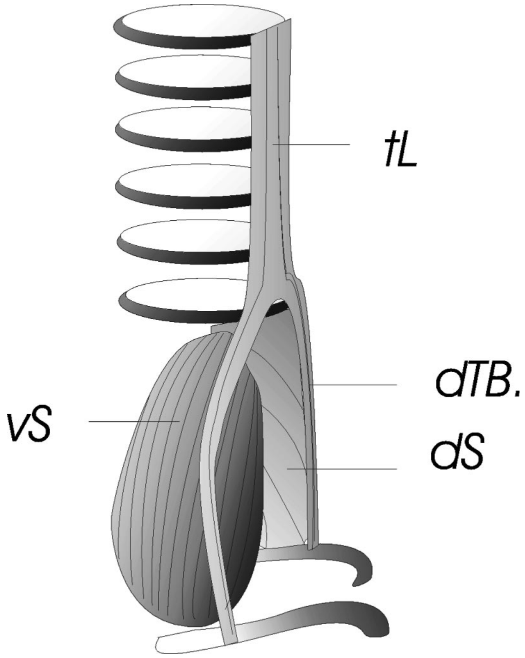

FIG. 3. The muscles controlling the syrinx (antero-lateral view), as described in the text, adapted from an original by Franz Goller.

small set of muscles. The relevant muscles are believed to be seven muscles in the syrinx, the muscles controlling inspiration and expiration, and muscles controlling the beak aperature. Unlike human speech, the diversity of vocal forms is primarily a product of syringeal variations rather than vocal tract reconfigurations.

As we show here, and elsewhere [10], for many songs the syringeal variables can be reduced to an even smaller number of control parameters. To the extent that the function of these muscles can be understood, we can hope to interpret the various modes of neuromuscular control in the developmental time course of song ontogeny. While the muscles involved in song production are few, they still are a system of much higher dimension than the time series of pressure measured with a microphone. Clearly, an analysis of muscle activity during song production must accompany an acoustic analysis of the sound if we hope to learn more about the various modes of neuromuscular control employed in song learning and song maintenance.

To advance this understanding of the muscular physiology in song production, a few groups have placed pressure, flow, and electromyographic sensors in the syrinx during song production. From the pressure studies, we have learned that songbirds do not complete a song with a single breath at the beginning. In between syllables, songbirds usually take minibreaths. Even in singing canaries producing up to 27 syllables per second, (EMG) analysis of abdominal expiratory activity gives evidence of minibreaths [15]. That is, each syllable is accompanied by a pulse of air pressure, and each silence by a pressure fall below atmospheric pressure.

At the level of muscular control in the syrinx, active research is ongoing. Goller and Suthers have observed EMG activity in most of the muscles of the syrinx, in a variety of species. In conjunction with airflow measurements, these data have been used to discern the action of a number of principle syringeal muscles. One study by Goller and Suthers [9] examined syringeal control during song in nine different brown thrashers (*Toxostoma rufum*). Roughly, they found muscles involved in the active closing of the syringeal lumen (adduction of the labia), muscles involved in the active opening of the syringeal lumen (abduction of the labia), and muscles which do not participate in the gating of the airflow but whose activity is closely related to the frequency of the vocalization. More specifically, the study could establish that the role of dorsal muscles (such as the large *m. syringealis dorsalis dS*) is adduction (see Fig. 3). They noticed that bursts of electrical activity were synchronized with decreasing airflow. The role of the *tracheobronchialis ventralis vTB* is active abduction. This muscle appears to be involved in the opening of the syringeal lumen for short inspirations. The study also established that a muscle which does not seem to have an active role in closing or opening the airflow is, on the other hand, crucial for the production of birdsong: the *syringealis ventralis* vS. This muscle likely controls the tension of the oscillating labia by altering their stiffness, since its activity is directly correlated to the fundamental frequency of the produced sound [16].

In the following sections, we draw from these electrophysiological measures to describe a simple model of song production, which is applicable to the songs of many birds.

III. THE MODEL

As we have described, recent experiments established that the bird's vocal organ, known as the syrinx, generates sound primarily through oscillation of the medial and lateral labia, which open and close the air passage from the lungs to the trachea. The character of this constriction is homologous in function to the human vocal chords, and for this reason, models of self-oscillations in the human vocalfolds can be adapted to birdsong. A variety of models exists in the literature to account for the self-oscillation of the human vocal chords. In a classic work by Ishizaka and Flanagan [18], a two-mass model for the folds was proposed to account for its dynamics. This model has been recently used [19] to explain the existence of period doubling in the song of the zebra finch (*Taeniopygia guttata*), and has been recently revised by Mergell *et al*. [20].

A simpler model was proposed by Titze [21], valid for folds supporting both a lateral motion of their centers of mass together with an upward propagating surface wave. This ''flapping'' motion allows one to easily understand the transfer of energy from airflow to folds: if the vocalfolds have a convergent profile while opening, and a divergent profile while closing, the pressure in between the folds will be larger when they depart from each other than when they approach each other. In this way, there will be a net energy transfer from airflow to labia in a cycle of oscillations. Taking a spatial average of the driving pressure between the folds, Titze arrived at a simple equation for the variable x describing the departure of the midpoint of the folds from the prephonatory position for small oscillations. The flapping mode of oscillation is consistent with recent videography of the avian vocal organ [22,19], and a model based on the Titze's full aerodynamic term leads to reasonable reproductions of a variety of birdsong forms [10]. In this paper, we further simplify Titze's aerodynamic forcing term to arrive at the simplest possible description of the physics. Up to linear terms, the dynamics for the midpoint of the folds is given by $Mx''+Kx+Bx'=0$, where M and K stand for the mass of the fold and stiffness, respectively. The constant B is the difference between the linear damping constant and a linear function of the lung pressure (all three constants are defined per unit area). Simple as it is, this model reproduces appropriate frequencies for realistic parameter values. In order to extend this model to account for the large amplitude oscillations in the syrinx, the first element to be added is a nonlinear dissipation [10,23]. Physically, a high dissipation takes place when either the labia meet each other or the containing walls. In order to contain the possibility of an independent control of the stationary position of the labia, a constant force should also be included in the description. Adding all these elements together, a simple toy model for the dynamics of the departure x of the midpoint of the labia from the prephonatory position can be written as

$$\dot{x}=y, \tag{1}$$

$$\dot{y}=-kx-cx^2y+by-f_0, \tag{2}$$

where k is the restitution constant, c is the nonlinear dissipation constant, b is a linear function of the net driving pressure, and f_0 is the constant force term (notice the minus sign in its definition). All four constants are defined per unit mass of the labium. The dynamics of this system of equations is simple to understand. Notice that it is the standard form [24] of the following system (a slight perturbation of the van der Pol oscillator)

$$\dot{u}=v-cu^3/3+bu, \tag{3}$$

$$\dot{v}=-k(u+f_0/k), \tag{4}$$

after writing $x\equiv u, y\equiv \dot{u}$. For $f_0=0$, the system displays relaxation oscillations whenever $b>0$ (i.e., whenever the transfer of energy exceeds the dissipative losses). Oscillations stop in the case f_0 is in modulo larger than $k\sqrt{b/c}$, due to the syrinx being either very closed (f_0 positive) or wide open (f_0 negative). The disappearance of the oscillations occurs in an inverse Hopf bifurcation.

The behavior of the system of Eqs. (1) and (2) as a function of the parameters b, f_0, and k is summarized in Fig. 4 (parameter c is kept fixed at 10^8 [(dyn s)/(cm^3 g)] throughout this paper). In Fig. 4(a), we display the projection of the phase portrait into the (b,k) parameter space ($f_0=0$ dyn/g). For positive values of b the system displays oscillations. The dotted-line curves in the region of oscillation are iso-frequency contours. Notice that the larger the value of the k parameter (restitution constant), the larger the frequency.

In Fig. 4(b), we display a projection of the phase portrait into the (b,f_0) parameter space [$k=10^9$ dyn/(cm g)]. The nonshaded region (large values of f_0) corresponds to a region of the parameter space for which no oscillations take place. Physically, a large constant force pulls the labia together, closing the syrinx and preventing oscillation. As the constant force decreases, oscillations are born in Hopf bifurcations. Iso-frequency contours are displayed as dotted-line curves.

At the point of instability, or Hopf bifurcation, the oscillation is born without any power in the overtones. For larger oscillations, the nonlinear term generates harmonic content in the oscillation. In general, we can not expect a toy model to produce an exact match of the spectral content, and indeed for a system symmetric around $x=0$, the odd nonlinear term we included here generates only odd harmonics. However, the constant force f_0 breaks the symmetry around zero, and the model produces both even and odd harmonics.

The model described above accounts for the oscillation of the labia. But in birdsong it is important to take into account the filtering process that takes place in the upper part of the vocal organ (trachea, beak). In principle, the pressure waves

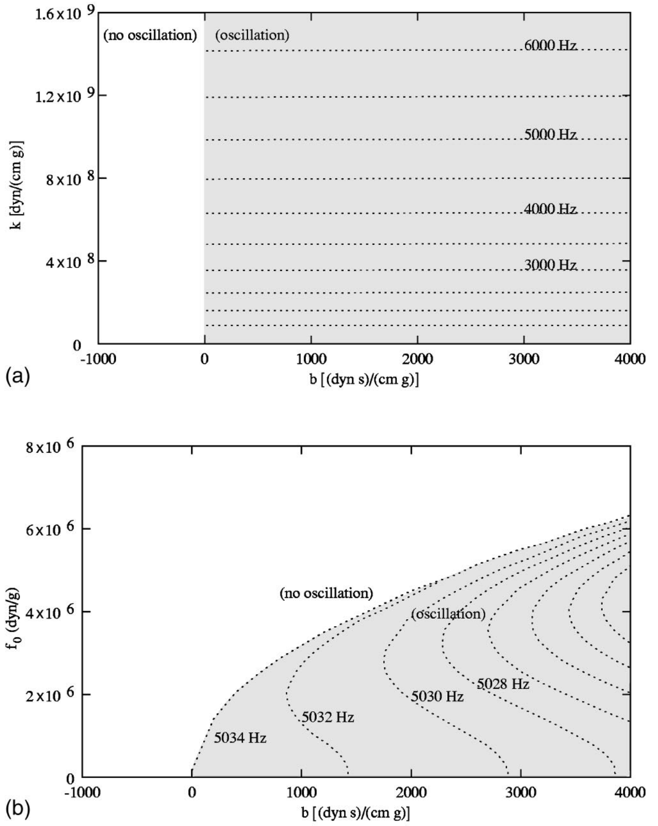

FIG. 4. Bifurcation diagram of the model. Parameter c is kept fixed throughout this paper, $c = 10^8$ $[(\text{dyn s})/(\text{cm}^3\ \text{g})]$. (a) Solutions in (b,k) parameter space at $f_0 = 0$ dyn/g. The system displays oscillations if $b > 0$. Dotted-line curves (which appear as almost straight lines at this scale) are iso-frequency contours. (b) Solutions in (b,f_0) parameter space at $k = 10^9$ $[\text{dyn}/(\text{cm g})]$. The upper region (large f_0) corresponds to active adduction (syrinx closed, no labia oscillation). Oscillation occurs in the lower region ($f_0 < k\sqrt{b/c}$). Dotted-line curves are iso-frequency contours.

traveling back to the labia might affect their dynamics. Yet, recently it has been shown that this effect could only give rise to nontrivial dynamics for a high degree of coupling between source and filter [25]. A high degree of coupling is given, among others things, by a very small A/L ratio (vocal tract cross section to vocal tract length). Since the syrinx sits deep in the thoracic chamber of songbirds, this ratio can be an order of magnitude larger for some birds than for humans. It remains an interesting possibility that some of the complex elements of bird vocalizations (such as subharmonics and aperiodic oscillations) could be the result of these feedback interactions. However, for the vocalizations studied here, these complex dynamics are not present, and our simulations suggest that significant coupling between the vocal tract and the labia are not an issue. Therefore, as it is usually assumed for human-voiced sounds, we work within the source-filter theory (i.e., the source produces oscillations of high-spectral content which are responsible for the creation of pressure perturbations at the origin of the tract. The vocal tract then linearly filters the signal without perturbing the dynamics of the source). The filtering of the vocal tract for birdsong is important if we want to synthetically produce realistic sounding solutions (*http://www.nld.df.uba.ar/~mindlin/birdsong)*. In this paper, we used a simple one-tube approximation for the tract of length $L = 1.9$ cm [10].

The model for the labia can be linked to the activity of the muscles controlling the syrinx, as reported experimentally. We saw that large positive values of f_0 represent active closing of the syrinx, since it prevents oscillations and corresponds to the labia at their minimum separation. Large negative values of f_0, on the other hand, also prevent oscillations by active opening of the syrinx (the labia at their maximum separation). Therefore, f_0 will be large whenever the activity of dS is large, and f_0 will be negative but large in absolute value whenever the activity of vTB is large. The details of the mechanics are not completely known, but dS presumably rotates the bronchial ring pushing the outer labium into the lumen (see Fig. 3) [11].

The relationship between the model parameters and the activity of vS is simpler. As we mentioned above, vS activity is correlated with the frequency of the vocalization [16], and not correlated with the gating of airflow. It is likely that longitudinal tension of the labia, caused by muscle contraction, alters their elasticity. Therefore, it is natural to associate it with restitution constant k in the model.

In summary, the rough picture is that two families of syringeal muscles affect the production of birdsong. One family pushing the oscillating folds either to or away from each other, and another family involved in the control of the tension of the labia and, in this way, in the frequency of the resulting vocalization. These two effects are controlled in the model by the parameters f_0 and k, respectively. With these elements, we will show how to construct curves in parameter space of the model that will generate vocalizations with desired spectral evolution.

IV. PATHS IN PARAMETER SPACE

A birdsong is composed of a sequence of simple elements known as syllables. In the standard representation of sound frequency as a function of time, they are continuous segments that are reliably (or recognizably) reproduced with similar form from one song to another. In Fig. 5(a) we display a typical sonogram of a syllable. It represents a brief vocalization of 0.3 sec, and the frequency monotonically increases from 4000 to 5000 Hz. As it was mentioned in Sec. II, it is typical to find that the bird takes mini breaths between syllables. With these elements in mind, we will build a possible path in the parameter space of our model that will generate a signal with a similar sonogram. Since for the moment we attempt to fit only the time course of the fundamental frequency, we will only describe the dynamics of the sound source. We will leave a complete description of the source and filter for Sec. V, where an actual vocalization is analyzed. Since the many songs are composed of repetitions of similar elements, the basic structure of the paths in parameter space associated with a syllable should be cyclic [10]. After [9], we know the way in which the syringeal events take place. The cycle begins with a breath: air sac pressure is slightly negative and the labia are in their rest position (not

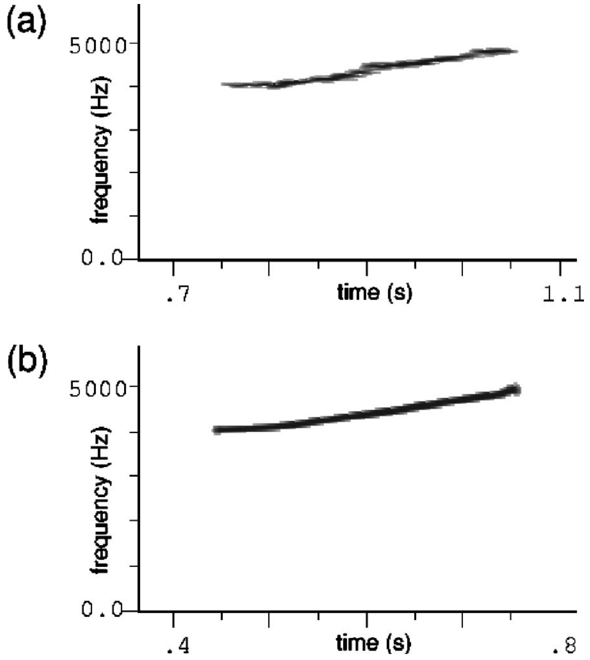

FIG. 5. (a) Sonogram of an actual birdsong syllable. (b) Sonogram of a simulated syllable, obtained by integrating the model equations along the path shown in Fig. 6.

adducted nor abducted, the syrinx is open). After the inspiration air sac pressure starts to build up, while the syrinx is actively adducted with the help of the *dS* muscle, in order to prevent an early oscillation. At a certain point, the activity of the *dS* falls, allowing the lumen to open. The labia begin to oscillate, at a frequency determined by the activity of the *vS* muscle. At the end of the syllable, the activity of the *dS* muscle increases shortly again, closing the syrinx to stop the oscillation. The lumen of the syrinx is then opened, and pressure drops below zero as the bird makes the next inspiration, completing the cycle.

It is possible to reproduce these gestures in terms of the model. Let us assume that we begin the cycle with a breath, as in the experiments we described above. The pressure should therefore be slightly negative, and the labia should be relaxed ($k=0$) and not adducted, nor abducted ($f_0=0$). As b is built up to positive values, the value of f_0 is increased (to at least a minimum value of $k\sqrt{b/c}$), in order to close the syrinx. When b has already built up to a certain value, the parameter f_0 vanish and the oscillations begin. The evolution of the oscillation frequency will then be given by the time evolution of the k parameter. To end the vocalization, the parameter f_0 is increased again for a short time, and then pressure decreased (to allow the following mini breath). In this way, the cycle is closed.

In Fig. 6, we show a simple, continuous, cyclic path in parameter space compatible with the description given above. A two-dimensional projection into the (b,k) plane of the cycle is displayed in Fig. 6(a), while a three-dimensional view is shown in Fig. 6(b). Notice that it corresponds to a very simple curve: an ellipse [10]. The frequency of the phonation raises from a lower value at the beginning to a higher value at the end, therefore the resulting vocalization is an upsweep. For the figures in this paper, the rate at which an ellipse is traversed is chosen to be either a linear function of time, or a hyperbolic tangent (some parts of the ellipse are traversed rapidly, others more slowly). We integrated our model equations along this path to generate a synthetic signal with a sonogram similar to the one displayed in Fig. 5(a). The resulting synthetic syllable is shown in Fig. 5(b).

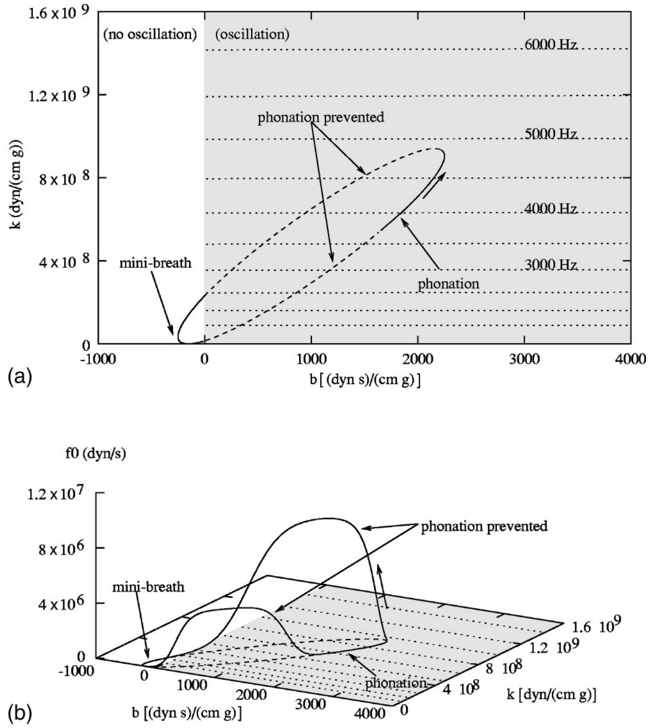

FIG. 6. Path in (b,k,f_0) parameter space leading to the synthetic syllable of Fig. 5(b). (a) Two-dimensional (2D) projection into the (b,k) space. Dashed-line sections of the curve correspond to large f_0 values (active adduction, syrinx closed, no oscillation). Phonation occurs along the solid-line section of the ellipse in the oscillation region. Direction of traversal is indicated by an arrow. Time parametrization is not illustrated; solid-line sections are traversed more slowly than dashed-line sections. (b) 3D view. The ellipse is evident at the bottom plane.

This description assumes that the control parameters are swept much slower than the oscillations of the labia. This is an appropriate assumption, since a typical syllable lasts approximately 100 ms, while the frequency of the oscillations is on the order of the 5 kHz.

V. AN EXAMPLE: THE CHINGOLO SPARROW (*Zonotrichia capensis*)

Among songbirds, species differ in the variety of their song (i.e., in the size of their repertoire). As Brown thrashers might have a repertoire of more than 2000 songs, the Chingolo sparrow has only one type of song. Yet, the details and degree of variability of this unique song has been well studied. The reason is the following: it has been conjectured that song learning might have evolved as a means of matching song to habitat, and the dialect system of the Chingolo [26] shows a strong association between dialect and habitat. Be-

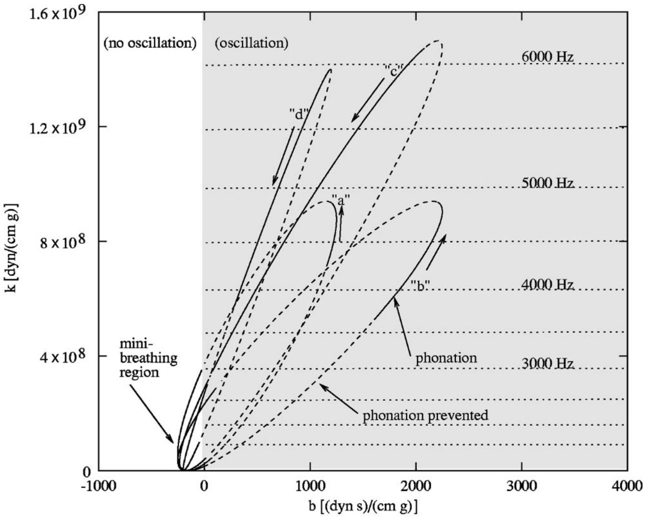

FIG. 7. Continuous path in parameter space leading to the simulated Chingolo's song of Fig. 1(b). Ellipse labeled "a" corresponds to the song's first syllable, and so on. Ellipses corresponding to consecutive syllables are smoothly matched in the mini-breathing region. Dotted line: large f_0 value (labia adducted, syrinx closed). Solid line: $f_0 = 0$ (syrinx open). As in Fig. 6, phonation occurs along the solid-line arcs in the oscillation region. Time parametrization is not illustrated; solid-line sections are traversed more slowly than dashed-line sections.

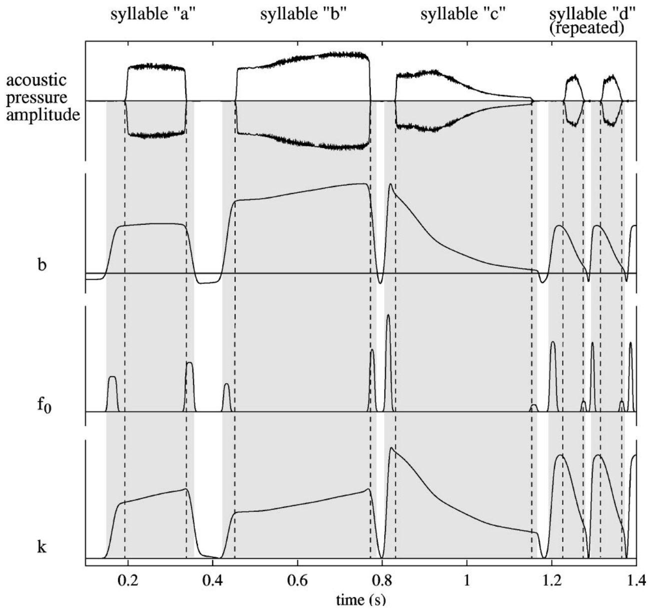

FIG. 8. Time series of b, k, and f_0 parameters for the continuous path shown in Fig. 7. Each syllable is initiated and terminated with a "burst" of f_0 parameter. Notice that both k and f_0 are near zero during the mini breaths.

yond the biological interest in the details of this song, we chose it as an example to test our model for its simplicity. The fact that the Chingolo has only one song might be useful for further experimental validation.

The sonogram and pressure time series of a typical song of the Chingolo is shown in Fig. 1(a). It has a clear introduction consisting in three syllables (two upsweeps and a downsweep), and a trill of several rapid downsweeps.

All the elements in the sonogram vary between 3 and 6 kHz, and the whole song lasts not much more than 2 s. All the syllables have their spectrum enhanced around the 4.5 kHz. This is consistent with the fact that the trachea of the Chingolo is ~ 1.9 cm long, which has a fundamental frequency near that value.

In order to build a curve in parameter space which would lead to the production of a synthetic song with a sonogram similar to the experimental one, we follow the ideas discussed in the previous section. For each syllable, we take an ellipse in the (b,k) space (see Fig. 7). The ellipses are chosen to be skewed to the right. In this way, it is possible to reproduce upsweeps and downsweeps without changing the sense in which the ellipses are traversed (always counterclockwise).

Notice that the time evolution in the (b,k) space is simultaneous with a time evolution of the f_0 parameter. Therefore, if f_0 falls below $k\sqrt{b/c}$, phonation takes place. In the ellipse labeled "a" in Fig. 7(a) (corresponding to the first syllable in the song), the phonation occurs while the value of k is increasing. This is represented by the solid line arc in the phonation region.

All the ellipses displayed in Fig. 7 have a common point corresponding to the situation in which the mini breath is taken (b slightly negative, and $k=0$, $f_0=0$). The amplitudes in k are related to the maximum frequencies of the corresponding syllables (in the experiments [9] there are no peaks of vS activity before or after phonation). The amplitudes of the ellipses in the b axis are given by the relative sound intensity between syllables. The ellipses corresponding to consecutive syllables are smoothly matched in the region where the mini breaths take place, to form a continuous trajectory in parameter space.

The time series of the three parameters are shown in Fig. 8. Time evolution of f_0 is proportional to the activity of the adducting muscles. Notice that for all the downsweeps (third syllable and trill syllables), the activity is higher at the beginning of the syllable. The dynamical reason is simple: the minimum value of f_0 needed to prevent oscillations is $f_0 = k\sqrt{b/c}$. In this way, the higher the k (i.e., the higher the frequency of the oscillation being born), the higher the value of f_0. The converse holds for the upsweeps (first and second syllables). This feature is an intrinsic characteristic of this simple model, and therefore constitutes a testable prediction.

With the paths in parameter space described above, we integrated the equations of our model to produce a synthetic song. Both the pressure waveform and its sonogram is shown in Fig. 1(b), which show a remarkable agreement with the recordings. The sound files are available at *http://www.nld.df.uba.ar/~mindlin/birdsong.htm*.

VI. CONCLUSIONS

A primary motivation in the study of birdsong is the potential it holds for illuminating the nature of vocal learning. Studies of birdsong employ a wide variety of techniques, and address the roles of many structures from the syrinx to neural centers in the song control pathway of a songbird's brain.

Since the acoustic waveform of the song is readily accessible for measurement, it is the sound, rather than the muscular events producing the sound that have been most often studied in an analysis of song learning, or central motor control. However, in the process of deciphering the various phases of song learning, a knowledge of the muscular acts necessary to produce a given song element is essential. The considerable technical difficulties of studying a vocal organ which may only be a millimeter or two in diameter have made the physiology of the syrinx a rare subject, characterized by a history of wide speculation. As described above, a number of recent *in vivo* syringeal measurements performed by Suthers and Goller have considerably expanded the subject of the motor control of song [27]. In this paper, and in previous work [10], we have built models for the dynamics of the oscillating labia in the syrinx which are qualitatively based on these *in vivo* measurements. In the first study, we demonstrated that some phrases of canary song could be produced by simple harmonic oscillations of pressure and syringeal tension. Natural variations occurred with small changes in the relative phase of the oscillators. In this paper, we present a model of the syrinx which is even simpler than the first, to demonstrate how little is required of the underlying equations of motion. At the same time, we have introduced the activity of a second syringeal muscle which controls the resting position of the labia. This simple modification extends the range of vocalizations that can be addressed with the model. We analyzed a particularly simple song, and built a path in parameter space able to reproduce the observations. We propose how to interpret the parameters of this model in terms of the activity of the muscles involved in the production of birdsong, and thus some qualitative features of the curves in parameter space lead to testable predictions. The curves in parameter space needed to reproduce a song are very simple. In fact, the basic control needed to produce a variety of calls or songs is simply a smooth oscillation of the three parameters in the model. Variations, such as a transition from upsweep to downsweep are simply produced by shifts in the relative phases of these oscillators.

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