

Simple neural substrate predicts complex rhythmic structure in duetting birds

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Horneros (*Furnarius Rufus*) are South American birds well known for their oven-looking nests and their ability to sing in couples. Previous work has analyzed the rhythmic organization of the duets, unveiling a mathematical structure behind the songs. In this work we analyze in detail an extended database of duets. The rhythms of the songs are compatible with the dynamics presented by a wide class of dynamical systems: forced excitable systems. Compatible with this nonlinear rule, we build a biologically inspired model for how the neural and the anatomical elements may interact to produce the observed rhythmic patterns. This model allows us to synthesize songs presenting the acoustic and rhythmic features observed in real songs. We also make testable predictions in order to support our hypothesis.

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I. INTRODUCTION

Birdsong is among the most beautiful and complex sounds of nature, arising from the interaction between neural circuits, body, and environment. Somehow, behavioral content of avian communication is elegantly translated into the musical constitutive elements: the rhythm and the melody.

Almost 40% of the bird species need some degree of tutoring in order to develop their songs. Learning birds are attracting a growing interest within the scientific community because they represent a wonderful test bench of how experience shapes the neural architecture to help the acquisition of a complex behavior. On the other hand, recent results [1] show that despite being nonlearners, the suborder of the *suboscines* can constitute a great model for studying the integration between auditory and motor pattern instructions.

Suboscine hornero (*Furnarius Rufus*) is a brownish, monogamous bird that lives in South America. Spreading all over the vast territory of the Pampas, their oven-looking nests can be easily recognized over trees and roofs. There is a remarkable ability of hornero's couples: during nest construction, reproductive period, while feeding offspring, at any season, horneros couples can be heard singing well coordinated duets.

Duetting male and female horneros are easily recognized in the frequency domain. A typical sonogram is displayed in Fig. 1, continuous traces are denoted as notes. Low frequency notes correspond to male vocalizations, whose songs are relatively simple, consisting of a unique syllable type (or note) repeated at an increasingly high production rate. On the other hand, the female notes are located at frequencies above the male register, presenting a more complex rhythmic structure. In the example of Fig. 1, the female seems to lose synchrony after the first few notes, increasing and decreasing the note production rate and giving rise to a complex sequence of coincidences between the male and the female notes.

Complex behavioral rhythms have been reported [2,3], but there are almost no examples coming from living interacting organisms. In a previous work [1], the rhythmic structure of horneros duets was studied in terms of their locking sequences. A mathematical structure emerged from this de-

scription, compatible with the subharmonic behavior of nonlinear forced systems.

In this work we study in detail the rhythmic organization of duets. In order to address the question of how a motor program for the duetting birds may encode and control different rhythmic patterns, we present a model compatible with the known suboscines anatomy. The model allows us to generate synthetic songs presenting both the rhythmic and the acoustical properties observed in horneros' duets. It also allows us to make predictions for the validation of the subharmonic hypothesis.

This work is organized as follows: in Sec. II we present a qualitative-quantitative description of the rhythms. In Sec. III we introduce a neural model driving the respiratory circuit. In Sec. IV we build the bridge between the neural activity and the sound, allowing us to generate synthetic songs. In this section we also propose the experimental tests to support our model's hypothesis. The last section contains our conclusions.

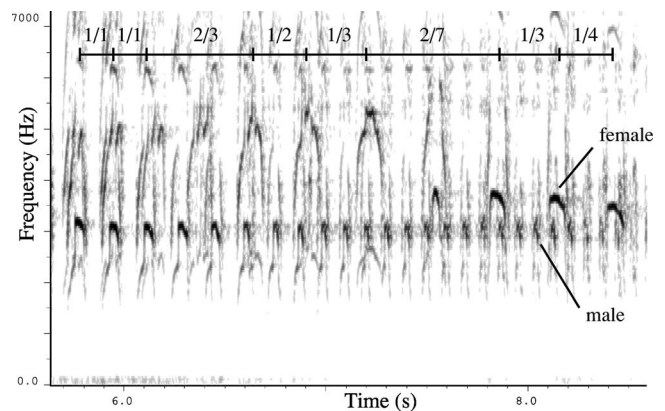


FIG. 1. Typical sonogram of a couple of duetting horneros (*Furnarius Rufus*). Lower frequency syllables correspond to the male song. As the duet evolves, the male increases the note rate production and his notes becomes shorter. On the other hand, female notes present a more complex temporal structure, locking to the male notes in a systematic way. The fractions shown correspond to the locking numbers r_{ap} .

II. RHYTHM ORGANIZATION

In a previous analysis [1], rhythmic features of the duets were quantified as follows. A coincidence was counted every time that the male note occurs within the duration of a female note, where the duration of the notes was taken as the time intervals in which the fundamental frequencies leave a trace in the sonogram.

Then, a ratio $r_{ap}=p/q$ was defined between the number p of female notes and the number q of male notes between consecutive male-female coincidences. Each duet was described by a sequence of rational numbers r_{ap} as displayed in the sonogram of Fig. 1 for a typical duet.

These quantitative indicators were then computed for a database of duets and plotted as a function of the interval between male notes (period). Remarkably, the numbers organized in a clear stairlike structure, presenting a typical fingerprint of periodically driven nonlinear oscillators: the devil's staircase. In Ref. [1] it was reported that the structure breaks down if surrogate data [4] are constructed and analyzed.

This description for the syllable-locking sequences was suggested by the rhythmic features of the duet, which were thought to depend exclusively on the frequency of the male production rate. The organization of the data required a normalization: the average time interval between male notes was normalized to the average of the corresponding female when locked to $r_{ap}=1/3$.

Building upon the evidence of a highly structured rhythmic organization, in this work we analyzed an extended database of hornero duets. Field recordings were performed at the Nature Reserve ECAS (Villa Elisa, Argentina). We selected a couple of horneros, banded them, and proceeded to record over a hundred duets during the nest construction, incubation, and feeding of the newborns, all these processes taking place between spring and summer seasons. The data were processed in order to compute the sequences of locking numbers for each duet.

In Fig. 2(a) we present our results for 20 duets in the following way: for each duet in the y axis we represent the locking states as points located at the corresponding period of the male (x axis). The qualitatively different locked states (i.e., the states with different values of r_{ap}) are represented with different point types.

The duets were sorted in order to obtain a "smooth" interface between the two largest locking states ($1/3$ and $1/4$). Smoothness was achieved by ordering the duets in such a way that the frequency values of the points in the interface between the largest regions would be a decreasing function of the duet number.

Remarkably, this sorting procedure left the other regions very well clustered. Moreover, as predicted by Ref. [1], the $2/3$ state lies between the $1/2$ and $1/1$ states, following the Farey rule of sum. Within this representation, data do not need further normalization in order to display a perfect clustered organization, as it was the case in Ref. [1].

III. MODEL

Compatible with this rhythm organization, we propose a neural model for the integration of auditory and motor control pathway in suboscines.

The level of detail captured by a neural model is question dependent. When a syllable is repeated, a basic rhythm has to be generated in order to set the motor instructions driving the production of sound. Moreover, many features of the syllable depend only on the phase difference between two gestures: the air sac pressure and the tension of muscles controlling the syrinx (i.e., the avian vocal organ) [5]. Both in oscine and nonoscine birds, these gestures are generated in well defined nuclei (set of interconnected neurons) [6].

The simplicity of this motor representation of acoustic features suggests that the mean activity of the neuron population at each of these nuclei could be an appropriate level of description for motor control in birdsong, and this is one of the hypotheses of this work. We model mean neural activities of the nuclei using one simple standard additive model [7].

Since we are mainly interested in the rhythmic structure of duets, we will first focus on the respiratory circuit: the one providing the rhythmic instructions controlling the expirations needed to induce phonation [6]. A set of brainstem nuclei has been reported [8] that can be associated to the physiological instructions governing respiration [6].

In Fig. 2(b) we sketch the anatomical elements involved in the respiratory circuit of suboscines. The air sacs are driven by inspiratory and expiratory muscles. These are enervated by motor neurons, driven in turn by medullar nuclei: the *parambigualis* (Pam), and the *retroambigualis* (Ram). These nuclei are enervated by the *dorsomedial nucleus of the intercollicular complex* (DM), believed to be the highest nucleus in the motor pathway of nonoscines (oscines have a set of telencephalic nuclei which are part of the motor control pathway).

We model the dynamics of the air sacs in terms of a variable describing the departure of their volumes from equilibrium values. A sac is idealized as a damped mass (m) subjected to the action of the respiratory muscles [Eq. (1)]. The activity of these muscles should be in turn proportional to the activities of the nuclei Ram (I_2) and Pam (I_1) innervating expiration and inspiration muscles, respectively. These two nuclei are thought to be mutually inhibitory [9]. Equations (2) and (3) describe the activities of these nuclei using a standard additive model [7].

Despite the fact that the real mechanisms relating auditory and motor control pathways in birds are unknown, it has been noticed that the DM nucleus, which innervates Ram, lies adjacent to the auditory system. Yet, anatomical connections between auditory and vocal centers at the level of the brainstem have not been reported [10].

In our model, we assume that DM receives auditory input. Mathematically, we represent with a simple harmonic function the activity of nucleus DM in the female, induced by the auditory input. This periodic function represents the average activity of the whole population of neurons in DM, and its period is taken as the male production rate. This function is used to drive the activity in nucleus Ram [Eq. (3)] of the female hornero.

Translating this anatomical observations into a model for the respiratory system of the female hornero, we get

$$m\ddot{x} + kx + \mu\dot{x} = 3I_1 - 4I_2, \quad (1)$$

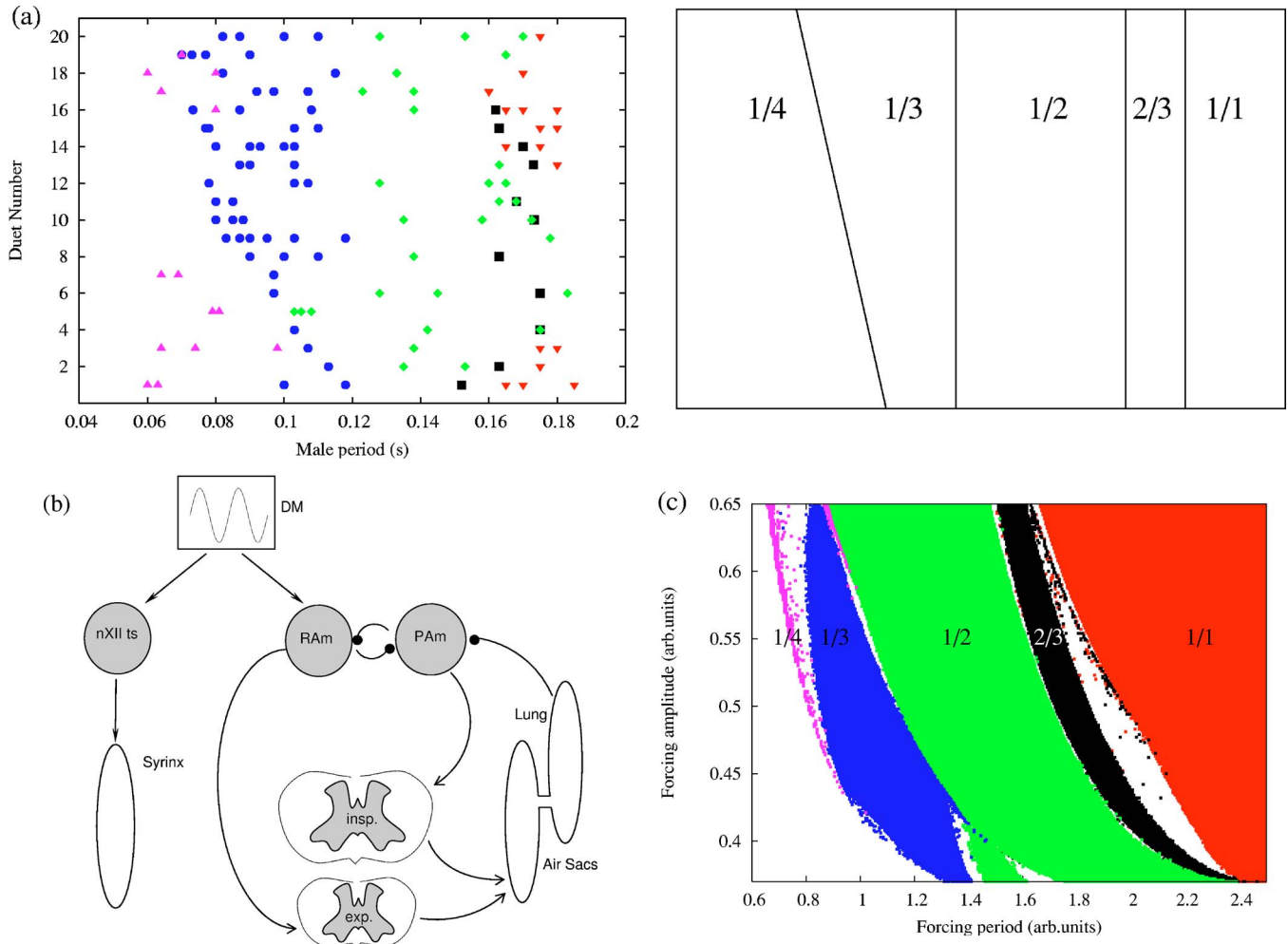


FIG. 2. (a) Left: a classification scheme for the different locking types found in 20 horneros' duets. Each female syllable is represented by a different type of dot located at the corresponding male period. The point type code indicates the different locking numbers. We use down triangles (∇) for $r_{ap}=1/1$, diamonds (\diamond) for $r_{ap}=1/2$, circles (\circ) for $r_{ap}=1/3$, up triangles (\triangle) for $r_{ap}=1/4$, and squares (\square) for $r_{ap}=2/3$. The locking regions are clustered. Right: schematic order of the locked regions. (b) Sketch of the proposed auditory-integrated respiratory and vocal model for the female hornero [Eqs. (1)–(3) and (5)]. Inhibitory connections are indicated by a solid black circle. (c) The model described by Eqs. (1)–(3) displays Arnold tongues when forced at different amplitudes and frequencies. Phase locking regions are organized in the same way as the experimental data displayed in inset (a).

$$\dot{I}_1 = 30[-I_1 + S(-1.43 - 18I_2 + 2I_1 - f(x))], \quad (2)$$

$$\dot{I}_2 = 30[-I_2 + S(-1.43 - 18I_1 + 2I_2 + A \cos(\omega t))], \quad (3)$$

where $S(x) = 1/(1 + e^{-x})$ is a standard saturating function [7]. The function $f(x) = 9x^3/(1 + x^3)$ represent the inhibitory effect of CO_2 sensors on the activities responsible for inspiration [9].

Disregarding the forcing term, this model displays excitability. Excitable behavior is characterized by a threshold separating two types of behavior: subthreshold perturbations leave the system close to the rest state, while upper threshold stimuli generate excursions through parameter space, decaying to the original quiescent state after a characteristic lifetime which is independent of the nature of the stimulus. It is important to realize that this excitability is a dynamical prop-

erty of the average activity over the respiratory system, and does not relate directly to the excitability of the individual neurons.

In our case, the excitable behavior depends in an essential way on the interaction of the air sacs and the neural substrate. Opposed to the case of respiration in mammals, where expiration is essentially driven by mechanical restitution of the lungs, the dynamics of the air sacs in birds is ruled by both inspiratory and expiratory nuclei (Ram and Pam), and feedback from the physical system is needed in order to reconstitute the system back to the initial state.

The dynamics of nonlinear oscillators and excitable systems are usually explored through the application of a periodic driving. Qualitatively different solutions appear, including phase locked periodic solutions, quasiperiodic ones, and even chaotic solutions. In particular, locked periodic solutions can be characterized by the rotation numbers $r = p/q$, where q is the period and p the number of large variable

explorations taking place in a time window of one period.

Organization of subharmonic periodic behavior is usually described as a function of the amplitude and period of the forcing. A structure of stable subharmonic regions appears, displaying universal properties, independent of the particular forced system. The organization of the locking regions is known as Arnold tongues.

In Fig. 2(c) we show tongues of period up to 3 (and the case $r=2/3$) generated by the respiration model [Eqs. (1) and (2)].

Remarkably, the relative order of the different tongues generated by the model is the same as for the clustering found in real horned duet [Fig. 2(a)], revealing that respiratory patterns organize themselves as the subharmonic solutions of a periodically driven nonlinear system.

It could be tempting to directly identify the locking numbers r_{ap} with the rotation numbers r . However, it should be noted that there is a fundamental difference between the way in which Figs. 2(a) and 2(c) are constructed. In Fig. 2(c), rotation numbers r were computed from solutions of the theoretical model after the transients. On the other hand, intercoincidence syllable numbers r_{ap} are computed from real duets while the forcing frequency is continuously increasing. Therefore transients are present, giving rise to an error in the computation of the locking numbers r_{ap} , which are approximants of the rotation numbers r . The error is inversely proportional to the length of the transient. Therefore the similarity presented between the organization of the tongues and the arrangement of experimental data suggests the system behind the female's respiratory gestures should present a highly dissipative behavior.

Finally, we would like to point out that normal quiet respiration requires a basic rhythmic oscillation. Our model, however, is an excitable one: unless the male song provoke a vocal response on the female motor control, respiratory system is at rest state. Excitable systems become oscillators for some values of their parameters, but unfortunately, this is not a biological meaningful mechanism to account for normal respiration. There are other brainstem nuclei involved in basic respiratory activity (ventrolateral nucleus of the rostral medulla, RVL, nucleus infraolivaris superior, IOS, and nucleus parabranchialis ventrolateralis, PBvl). Dynamics of this respiratory circuit can be included to the one presented here in order to account for both normal and singing respiratory patterns [11].

Moreover, the respiratory model presented here can be further simplified by neglecting the inertial and dissipative terms of the air sacs ($\mu/k, m/k \ll 1$), which are thought to passively follow the activities of inspiratory and expiratory muscles.

The rhythmic structure of the duets can be characterized by a sequence of approximants r_{ap} to the rotation numbers r characterizing the subharmonic solutions of nonlinear forced systems [1]. Compatible with this underlying dynamical rule, we constructed a model presenting the anatomical elements involved in the respiratory system, from which the temporal pattern of birdsong primarily arises.

In the next section we will develop a full model for birdsong sound generation. This will allow us to make an experimental prediction to test the hypothesis of how subharmonic

behavior may leave its fingerprint in the physiological parameters.

IV. SYNTHETIC PHYSIOLOGICAL INSTRUCTIONS AND SONGS

The avian vocal organ (syrinx) generates sound through flow-induced oscillations of the labia, a bilateral structure of tissue folds that cyclically open and close the air passage from the bronchi.

Recently, a model for the physical processes taking place at the syrinx was proposed [12]:

$$\ddot{z} - [p(t) - b]\dot{z} + k(t)z + cz^2\dot{z} = 0. \quad (4)$$

Transference of energy from the air flux to the tissue arises from the competition between air sac pressure $p(t)$ and dissipation b , setting up sustained oscillations of the labia. Labial stiffness is characterized by $k(t)$ and the coefficient c represents a nonlinear dissipation constant. This model has been tested using real inputs $p(t)$ and $k(t)$ from electromyographic data in good agreement with experimental recordings [13].

Syringeal and respiratory gestures are set to

$$k(t) = k_0 + k_1 f(t), \quad (5)$$

$$p(t) = p_0 + p_1 g(t) \quad (6)$$

with $f(t)$ and $g(t)$ functions accounting for the recurrent gestures needed to generate song. We generated male notes with qualitatively the same acoustical content as the real ones by driving Eq. (4) with $f(t)$ and $g(t)$ simple harmonic functions of the form $\cos(\omega(t))$, with $\omega(t)$ an increasing function of time. Parameters were chosen in order to produce songs in the correct frequency ranges (see caption of Fig. 3).

Female song, on the other hand, is more complicated. Nucleus DM innervates the nXIIIts [Fig. 2(b)] which in turn project to the muscles controlling the tension of the labia. Here, we assume that the activity of nXIIIts passively follows the forcing of DM, and therefore $f(t)$ is the same harmonic function as for the male.

The function $g(t)$ can be associated to the displacement of the air sacs x [Eq. (1)]. The pressure of the air sacs relative to atmospheric pressure is inversely proportional to the volume of the sacs. For simplicity, we choose $g(t) = -x$. In this way, pressure patterns $p(t)$ can present a variety of subharmonic solutions.

In Fig. 3(a) we display a sonogram for a real duet when locked to $r_{ap} = 1/3$. In order to test our model, we integrated Eq. (4) for the dynamics of the labia, driven by $p(t)$ and $k(t)$ as described for male and female birds.

For the male period and amplitude, the respiratory system for the female [Eqs. (1) and (2)] is located in the region $r = 1/3$ of Fig. 2(c). The locking structure of the notes is $r_{ap} = 1/3$. A sonogram of the resulting synthetic duet is displayed in Fig. 3(b).

Figure 3(c) corresponds to the pressure time course of the male and female horned duet during the duet as generated by the abstract model [Eqs. (1) and (2)]. The right insets show

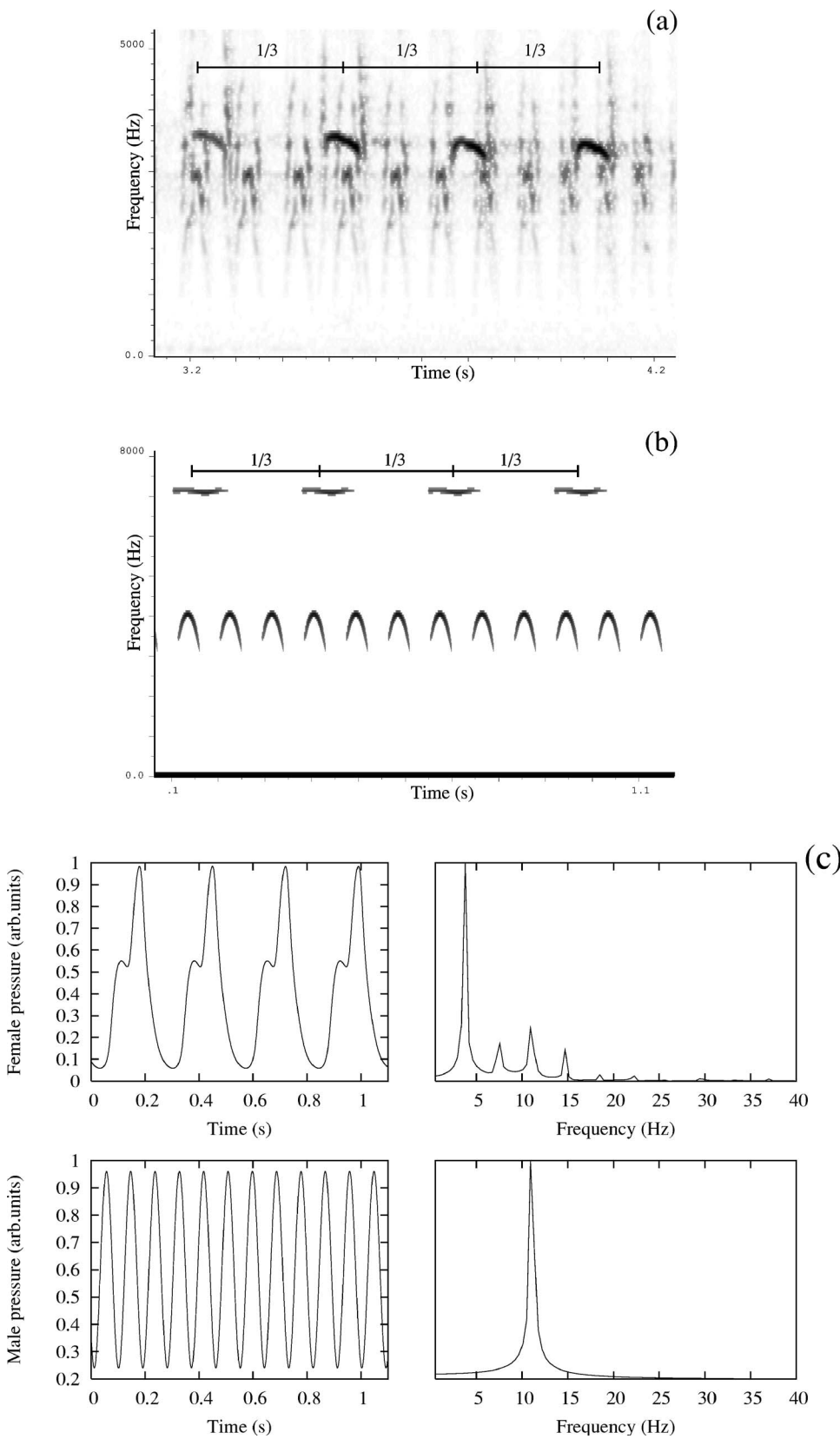


FIG. 3. A sonogram segment presenting a 1/3 locking structure for a real duet (a). A sonogram generated from a synthesized song using our model at the same locking state (b). The parameters used in our simulations are $m=0.0024$, $k=1.5$, $\mu=0.86$ in Eq. (1); $A=0.6$, $w=6.98$ in Eq. (3) to generate a 1/3 locking; and in Eqs. (5) and (6), $k_0=4.8 \times 10^7$, $k_1=8.4 \times 10^7$, $p_0=2.5 \times 10^3$, and $p_1=7.0 \times 10^3$ for the male and $k_0=2.0 \times 10^8$, $k_1=1.0 \times 10^6$, $p_0=-4.0 \times 10^2$, and $p_1=1.10^3$ for the female. Throughout this work, $c=2.0 \times 10^9$. Inset (c) shows the female and male air sac pressure predicted by the model, and FFT transforms of each pressure signal. Pressure activity at thirds the fundamental frequency of the male are predicted for the female signal.

the FFT analysis of the pressure patterns for both birds. This figure can be interpreted in two different ways. In the most parsimonious one, a female pressure signal of fundamental frequency f_f is one third the fundamental of the male, f_m

$= 1/3 f_m \sim 10$ Hz. On the other hand, under the subharmonic paradigm, the female's pressure spectral content should be interpreted as the signature of the subharmonic behavior of her respiratory system, with coincident fundamen-

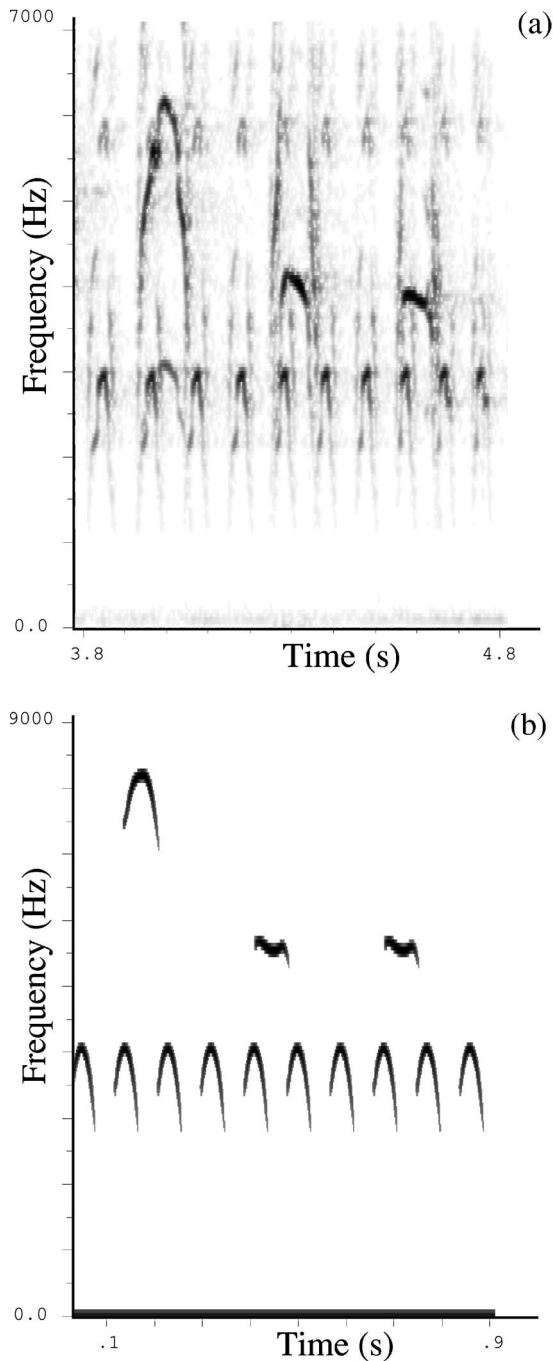


FIG. 4. Two syllable types can be recognized for the female song. In suboscines, the syrinx is in contact with the interclavicular sacs. Our model assumes that, as the duet evolves, the pressure decreases affecting the tension of the labia at the syrinx. Equation (4) is integrated for the female hornero using $k_2=2.0$ for $t \leq 0.3s$ and $k_2=1.1$ thereafter, giving rise to the different syllables in (b). The neural parameters [Eqs. (1), (2), and (4)] remain unchanged in this case.

cies $f_f=f_m \sim 10$ Hz [third peak of the female and first of the male in Fig. 3(c)], constituting a fingerprint of the $r=1/3$ subharmonic.

The spectral power of the female pressure signal should be essentially condensed in the peaks below the fundamental

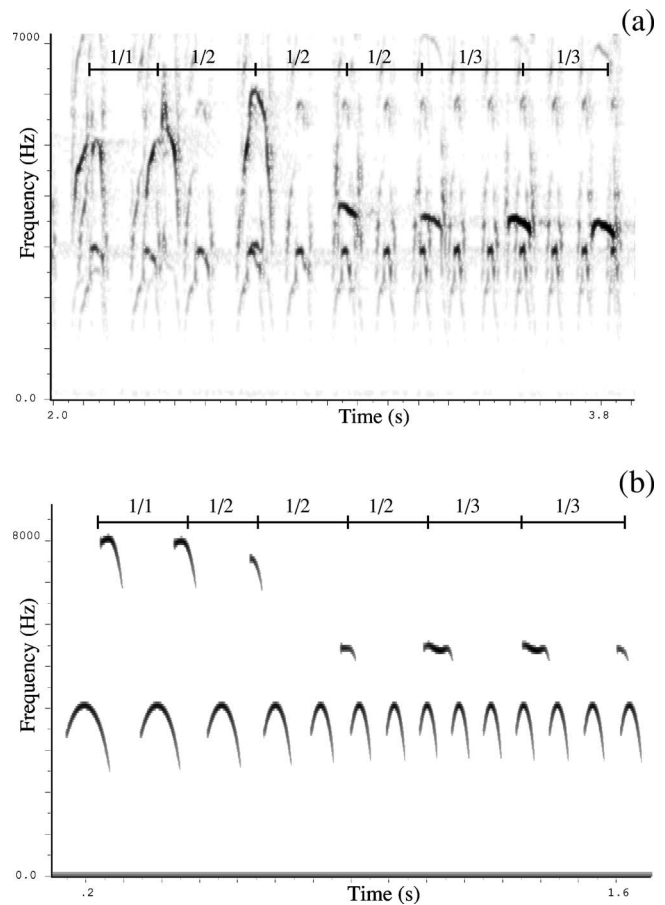


FIG. 5. A duet sonogram. The locking structure is indicated by the locking numbers r_{ap} (a). A synthesized sonogram with the same locking structure. The model was integrated by increasing the male note production rate $w(t)=3+2.5\{1+\exp[(1-t)/2.3]\}^{-1}$ (b).

frequency. Subharmonic behavior would then be evidenced by the appearance of equally spaced peaks in the female spectrum below a peak where female and male fundamental frequencies coincide. The simultaneous measurement of pressure patterns in air sacs [14] of a duetting couple would allow us to test the proposed theory: the pressure pattern of the female should present a spectral signature associated with the syllabic frequency of the male, in the form of subharmonics.

Let us turn briefly into the issue of the acoustical features of the duet. Although acoustical content of the syllables is relatively simple, the female typically presents two different syllable types [Figs. 1 and 5(a)]. At the beginning of the song, the fundamental frequency trend can be characterized by an wide upswEEP followed by a downswEEP. After a while, the female notes become almost constant. The transition between syllables is clear in the detail of the sonogram presented in Fig. 4.

In suboscines, the interclavicular sac is likely to interact with the syrinx, as in other examples of birds with tracheal syringes [15]. In order to account for this effect, we include an additional contribution to the tension due to the syrinx compression by pressure. This contribution is modulated by the parameter k_2 ,

$$k(t) = k_0 + k_1 f(t) + k_2 g(t). \quad (7)$$

As the duet evolves in time, the pressure decreases and consequently k_2 decreases. Figure 4(b) presents the sonogram for the simulated song. We changed the parameter from $k_2=2.0$ to $k_2=1.1$ at $t=0.3s$.

Finally, we simulated a song presenting a nontrivial locking sequence. In Fig. 5(a) a real duet is displayed, along with its locking sequence. For the simulation, we increased the male note production to match the observed one, obtaining the same locking sequence. The sonogram of Fig. 5(b) should be interpreted as a sequence of transients reflecting the subharmonic behavior of the respiratory system when unidirectional forcing of the male is exerted through auditory input. Acoustical features, on the other hand, were included accounting for the tension and pressure components acting on the syrinx.

V. CONCLUSIONS

In this work we show how a complex temporal plot can be generated by virtue of the subharmonic responses of a simple neural substrate. Organization of experimental rhythmic data is compatible with that of forced excitable systems when analyzed in the period-amplitude phase space. High dimensional systems present a complex subharmonic organization. The evidence presented in this work is likely to correspond to low dimensional dynamics, making unlikely that the rhythmic structure depended on the action of an extensive system.

Compatible with this nonlinear rule, we suggest a simple model integrating anatomical and neural centers for the female respiratory system. In this way, a wide variety of rhythmic structures can be generated by a female hornero with a simple neural substrate, provided it is sensitive to the range of the male note production rate.

Finally, we presented a testable prediction towards the validation of the subharmonic paradigm, measuring pressure patterns in air sacs of a duetting couple. As shown in our simulations, the pressure pattern of the female is expected to present a spectral signature associated with the syllabic frequency of the male, in the form of subharmonics.

In this work we showed that the rich rhythmic structure of duetting horneros can be interpreted as the signature of the subharmonic behavior of a simple neural substrate. Using the known biologically relevant elements, we constructed a respiratory neural model which is compatible with this dynamical paradigm. Nonlinear mechanisms are beginning to be recognized as an important source of complexity of neural pattern generation. The present example provides evidence in this direction, identifying a possible general mechanism for the generation of different rhythmic patterns in living interacting animals.

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