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Dynamical systems techniques reveal the sexual dimorphic nature of motor patterns in birdsong

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In this work we analyze the pressure motor patterns used by canaries (*Serinus canaria*) during song, both in the cases of males and testosterone treated females. We found a qualitative difference between them which was not obvious from the acoustical features of the uttered songs. We also show the diversity of patterns, both for males and females, to be consistent with a recently proposed model for the dynamics of the oscine respiratory system. The model not only allows us to reproduce qualitative features of the different pressure patterns, but also to account for all the diversity of pressure patterns found in females.

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I. INTRODUCTION

Birdsong is an interesting example in the animal kingdom to explore a variety of neuroethological issues that range from learning to functional lateralization [1]. One of these is sexual dimorphism. In many species, only the males sing, and moreover, in songbirds, sex difference in singing behavior has been found to have a parallel with sex differences in the brain [2,3].

Even in species for which song is mainly restricted to males, like canaries, the treatment of females with testosterone leads towards typical malelike singing behavior [4]. Moreover, this behavioral hormone induced change correlates with changes in the brain [4–8]. Female canaries present the same song system but with several morphological differences. For example, differences in the volume of the song related nuclei and in the neuron number of these nuclei [9–11].

The main difference between the vocalizations produced by males and females treated with testosterone consists in the variety of syllables used in the songs, with females using a smaller number of syllables than males [6]. Remarkably, the malelike syllables uttered by females share many acoustical and rhythmic features with the male syllables. This could suggest that the motor patterns used to generate the song are similar to those used by the males. Yet, the recording of the pressure patterns used by singing males and females shows that there is a qualitative difference in the way they produce their vocalizations.

We imported from the theory of dynamical systems a series of tools to analyze the recorded patterns and found that, consistent with recent work [14], the males presented pressure patterns that could be interpreted as subharmonics of a nonlinear system under periodic forcing. Remarkably, the analysis of female song revealed that in order to generate the same rhythms as males, females use harmonic pressure patterns. Moreover, with a recently proposed model for the dynamics of the oscine respiratory system, we could reproduce the diversity of patterns observed in males and females.

The work is organized as follows. The experiments are described in Sec. II, where we also describe the topological description of the patterns used to assess the qualitative difference between males and females pressure patterns.

In Sec. III we discuss the experimental results in terms of a computational model of the oscine respiratory system. Sec. IV contains our conclusions.

II. THE EXPERIMENTS

The experiences were carried out with ten canaries, seven males and three females. Both groups were topically treated with testosterone (20 mg in a daily application). The dose of testosterone applied to females was adjusted in order to mimic the plasma testosterone level of male canaries in the reproductive season [4].

As a result of 25 days of this treatment the female canaries showed singing behavior similar to males singing, regarding its loudness and its stereotypical nature. In the case of males the addition of testosterone increased the rate of song production and drove the birds to a crystallized song pattern characteristic of the breading season [12].

Furthermore, the air sac pressure was recorded for each one simultaneously with their song. The air sac pressure was registered by the insertion of a cannula (venisystems Abbocath-T) through the abdominal wall just posterior to the last rib, so that it extended a few millimeters into a thoracic air sac. The free end of the cannula was connected to a miniature piezoresistive pressure transducer (Fujikura model FPM-02PG), which was mounted on the bird's back. The signal was amplified and modulated in order to record it using a PC with a sound card (MAYA1010). The same card was used to record the ambient sound. The cannula used in this work was considerably thinner than the silastic tubing used in previous studies [14]. Yet, the results were similar for males (which were studied in [14]), which allows us to infer that the measurements do not affect qualitatively the normal behavior.

Typical records are displayed in Fig. 1. Figures 1(a) and 1(b) display the sonograms of two pieces of song, uttered by a male and a female, respectively. Each one consists of two different syllable types, downsweeps (the frequency of the sound at the beginning of each syllable is larger than at the end) and upsweeps. Downsweeps (A and C) are uttered at half the syllabic rate of upsweeps (B and D). Despite the rhythmic and partial acoustical similarity, the inspection of the pressure patterns unveils a qualitative difference between the male and female vocalizations.

In Figs. 1(c) and 1(d) we display typical pressure patterns recorded for a male and a female, respectively. Notice that the pressure pattern of group A in Fig. 1(c) has a fine structure [see arrow in Fig. 1(c)] that does not appear in the pres-

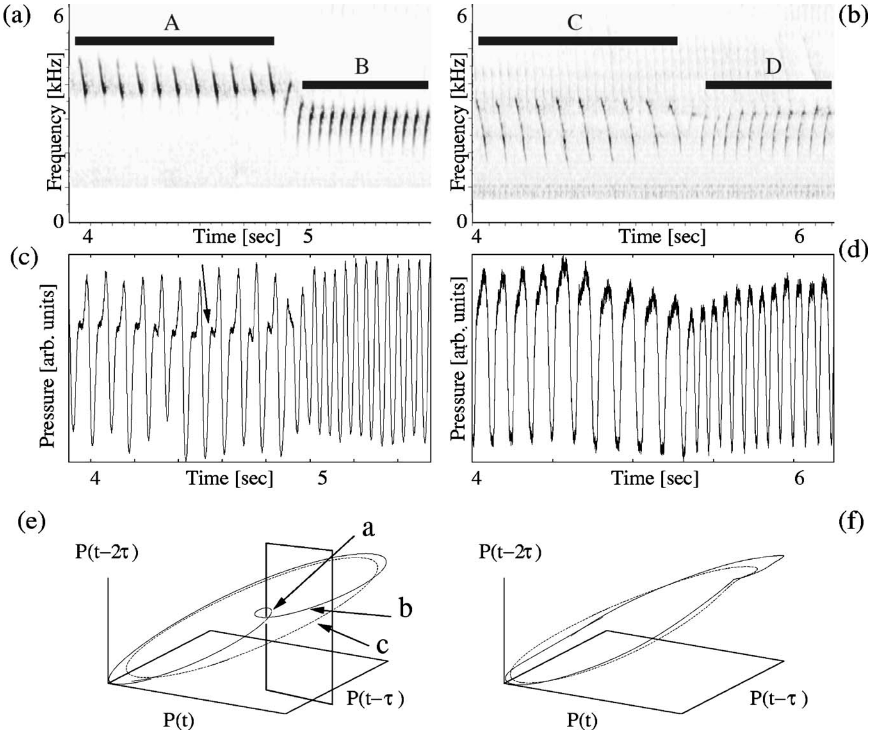

FIG. 1. Similar songs uttered by a male (a) and a testosterone treated female (b), with their respective pressure patterns, (c) and (d). The embedded orbits of this segments are shown in (e) for the male and in (f) for the female. In (e) we show the orbit of period two for the segment A in the song and the orbit of period one for segment B. This is not observed in (f) where the segments C and D have both orbits of period one. A Poincare section is used to characterize topologically the segments of the pressure recorded from the males. The strands starting in the three points where the orbits cross the section (see arrows in the figure) are labeled with the starting points a, b, and c. Following the prescription of Ref. [24], the arrangement of strands is characterized by the word $\sigma_{cb}\sigma_{bc}\sigma_{ba}$, which is the word of a braid describing a period one orbit, and a period two orbit bifurcating from it in a period doubling.

sure patterns of group C [see Fig. 1(d)]. In fact, this feature is not present in any pressure pattern of any syllable uttered by the females in the study.

In order to characterize these features, we imported some data analysis techniques from nonlinear dynamics. Treating the pressure patterns as approximate periodic orbits, we selected time series segments and embedded them in a three-dimensional space through time delays, i.e., $x(t)\rightarrow[x(t),x(t-\tau),x(t-2\tau)]$ (see [13]). The results are shown in Figs. 1(e) and 1(f). The embedded segments displayed in Fig. 1(e) look similar to solutions of periods 1 and 2 of a forced nonlinear dynamical system [14]. Beyond this similarity, other more complex pressure patterns displayed by males also look like higher period orbits. In Fig. 2(a) we show a pressure pattern of another male canary while singing. To identify segments that could be associated with higher period orbits we show a close return pattern in Fig. 2(b). The method consists in plotting a dot at a position (i,j), whenever $|x(i)-x(j)|<\epsilon$ (see [15,16]). To complete the analysis we extracted the time series segment E displayed in Fig. 2(a) and embedded the orbit as shown in Fig. 2(c) (left). The embedding of the segment F [Fig. 2(a)] is displayed in Fig. 2(c) (right). The period of a segment in the second syllabic group is three times that of a segment in the first group, as it can be concluded from the close return plot displayed in Fig. 2(b). Notice that the embedded segment of Fig. 2(c) presents a complex structure.

The fine structure present in some of the vocalizations of the males [Figs. 1(c) and 2(c) (right)] could be either interpreted as oscillations of low fundamental frequencies with a rich harmonic structure, or as the signatures of subharmonicity. In a previous work [14] evidence supporting the second hypothesis was presented. This study was performed with a population of birds that had no contact with those used in [14] and yet their pressure patterns present exactly the same topological structure after being embedded. The topological characterization between reconstructed and embedded segments was computed and found to be in agreement with those of [14]. The characterization of time series segments through topology is a technique imported from the field of nonlinear dynamics [16]. A three-dimensional time delay embedding is constructed from each selected pressure pattern. The collection of curves is then described topologically. To do so, one defines a Poincare section (a semiplane crossed by the curves, as defined in [16,13]), and the curves are split in strands (segments of the curves which start and end in the Poincare section). The characterization of the set of strands is performed by associating them with a word. The words are symbols that account for which strand passes over which in the embedded space [16,13], as described in [24]. In the field of nonlinear dynamics, the characterization of orbits in this way is used to build confidence, or refute, models proposed for experimental time series data [15]. We imported these techniques in the same spirit.

According to our experiments, females manage to emulate similar syllables as those produced by males, by changing dramatically the fundamental frequency of simple oscilla-

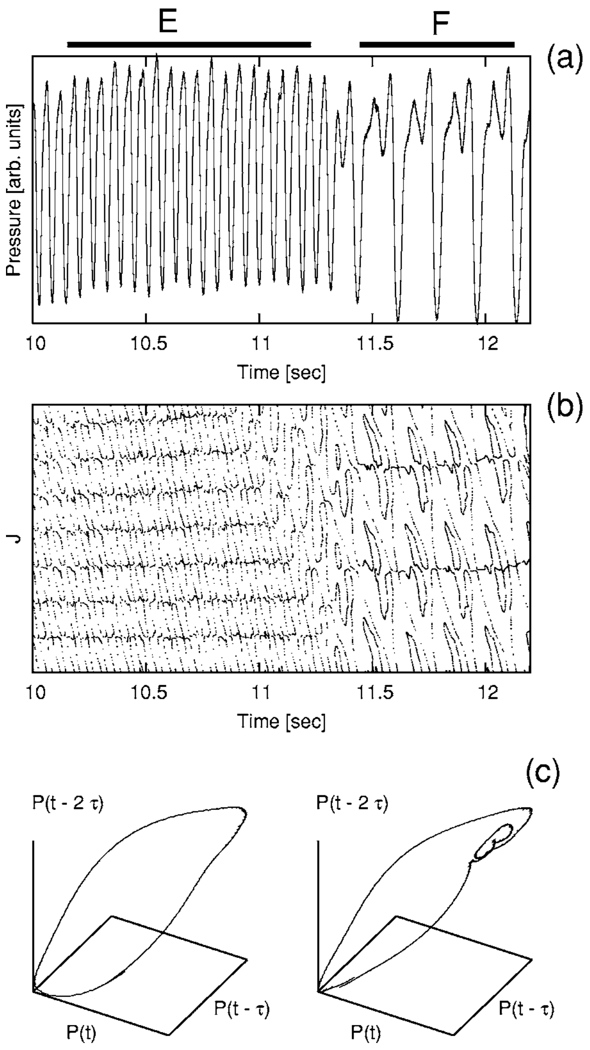

FIG. 2. Complex pressure pattern of a male canary while singing (a). To analyze this pattern we used the method of close returns (b) and embedding in a three-dimensional space through time delays (c). From this analysis we could deduce that the segment E corresponds to a period one and the segment F to a period three.

tions, without presenting, in any of the records, evidence of subharmonic orbits. The specific structure of the pressure patterns present in males was found to be consistent with the solutions of a model describing the dynamics of air sacs and respiratory nuclei [14].

III. INTERPRETATION

Recently, a model was proposed to account for the mechanisms responsible for the respiratory patterns during song [14,17]. Dynamically, this model displays excitability for a network of nuclei that incorporates biologically meaningful respiratory and neural components. The interpretation of the complex respiratory patterns as subharmonics of a nonlinear system allowed us to account for a wide diversity of structures used by singing male canaries.

In Fig. 3 we show the elements considered in our model of the respiratory system. A variable x measuring the departure from the volume of the sacs at atmospheric pressure describes the dynamics of the air sacs. In Eq. (1) we model the sacs as a damped mass (m), driven by inspiratory and expiratory muscles. The activities of these muscles are assumed to be proportional to the activities of brainstem nuclei parambigualis PAm (i_1) and retroambigualis RAm (i_2), respectively [18,19], which are thought to be mutually inhibitory (see Fig. 3). These nuclei are the premotor nuclei for the spinal motor neurons controlling inspiration and expiration, respectively. The activity of these nuclei are assumed to present a dynamics obeying one of the simplest neural additive models [Eqs. (2) and (3)] [20]. A harmonic function is used as a simple input in our model to emulate the oscillatory telencephalic activity triggering birdsong production [21,22]. Translating these anatomical observations into a mathematical model, we get

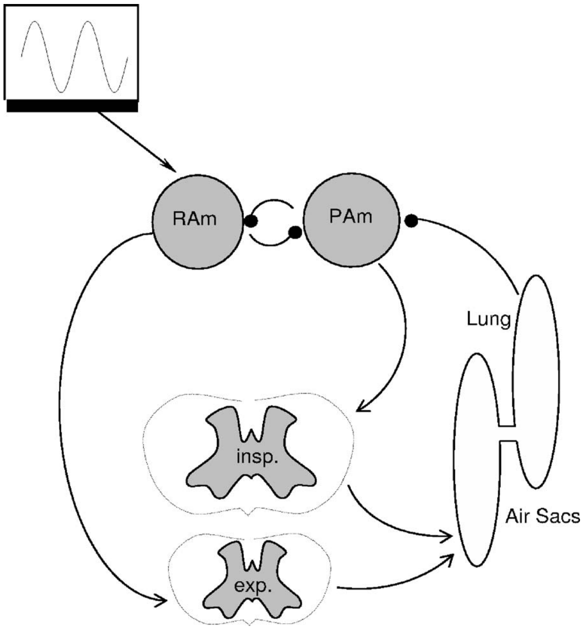

FIG. 3. Scheme of the respiratory system in birds. Excitatory connections are indicated by arrows and inhibitory connections by filled circles. The nuclei parambigualis PAm and retroambigualis RAm control inspiration and expiration, respectively. The input is modeled by a sinusoidal oscillation generated by telencephalic nuclei.

$$m\frac{d^2x}{dt^2} + kx + \mu\frac{dx}{dt} = I_a i_1 - I_b i_2, \tag{1}$$

$$\tau\frac{di_1}{dt} = - i_1 + F[E_1 - I_c i_2 + I_d i_1 - f(x)], \tag{2}$$

$$\tau\frac{di_2}{dt} = - i_2 + F[E_2 - I_c i_1 + I_d i_2 + A\cos(\omega t)], \tag{3}$$

with $F(x)=\frac{1}{1+\exp(-x)}$ representing a saturating function for the neural activities, A and ω representing, respectively, the amplitude and frequency of the telencephalic forcing, $f(x)=\frac{9x^3}{1+x^3}$ representing the inhibitory effect of volume [23], and

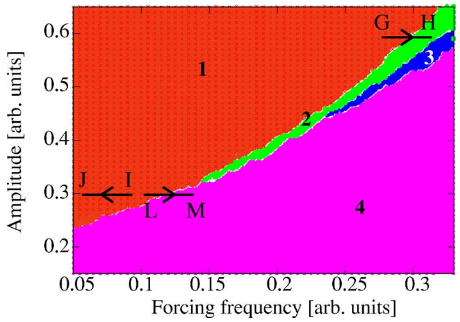

FIG. 4. (Color online) The parameter space of the model defined by Eqs. (1)–(3). The amplitude A and forcing frequency ω stand for the amplitude and forcing frequency of the respiratory system by the activity of telencephalic nuclei. The numbers show the different periodical solutions, measured in units of the forcing period: (1) for large period one, (4) for small period one mounted in a dc level, (2) for period two, and (3) for period three. The arrows indicate possible parameter variations in the case of males (GH) and females (IJ, LM). The fixed parameters used in Eqs. (1)–(3) are $m=0.5$, $k=1$, $\mu=4$, $I_a=4$, $I_b=1$, $\tau=1$, $I_c=18$, $I_d=2$, $E_1=-1.3$, and $E_2=-1.5$.

CO_2 sensors on the activity of the neurons responsible for inspiration (which is mediated by the vagal nerve).

As the parameters A and ω are varied, qualitatively different solutions can be observed. They can be classified by their period measured in units of the forcing period $T_f=2\pi/\omega$. In Fig. 4 we show the values of A and ω where solutions of different periods are founded. This behavior is typical from a nonlinear system presenting either excitability or relaxation oscillations, under forcing. In our case, excitability is the dynamical feature presented by the model which is responsible for the behavior under the forcing [17,20].

In Ref. [14] the diversity of patterns used by singing male canaries was associated with different solutions of this system of equations, for *the same value of the forcing amplitude*, as the *forcing frequency* was varied. In the literature, the anatomical changes induced in female brains after treatment with testosterone was thoroughly discussed [4,5]. These works point at a growth of the telencephalic nuclei HVc, which is part of the song motor control pathway. Yet, these nuclei do not reach the same size as those of the males [6,7]. With this observation in mind, we hypothesize the telencephalic forcing on the respiratory system of testosterone treated females to be smaller than in the case of males. Therefore we explored the model used to generate respiratory gestures in a wider region of the parameter space than the one discussed in [14]. The result is shown in Fig. 4, where the regions of parameter space (amplitude and frequency of the telencephalic forcing) displaying different subharmonics are drawn in different point types. For small values of the amplitude the width of the tongues with complex subharmonics (period higher than one) shrink. This is consistent with our observations: the females could only generate simple harmonic pressure patterns. According to the model they could produce a pattern of small syllabic rate by decreasing the telencephalic forcing frequency (as in path IJ in Fig. 4), as opposed to males, who could diminish the syllabic rate by increasing the telencephalic forcing and driving its respiratory system to a region of the parameter space displaying subharmonics (as in path GH in Fig. 4).

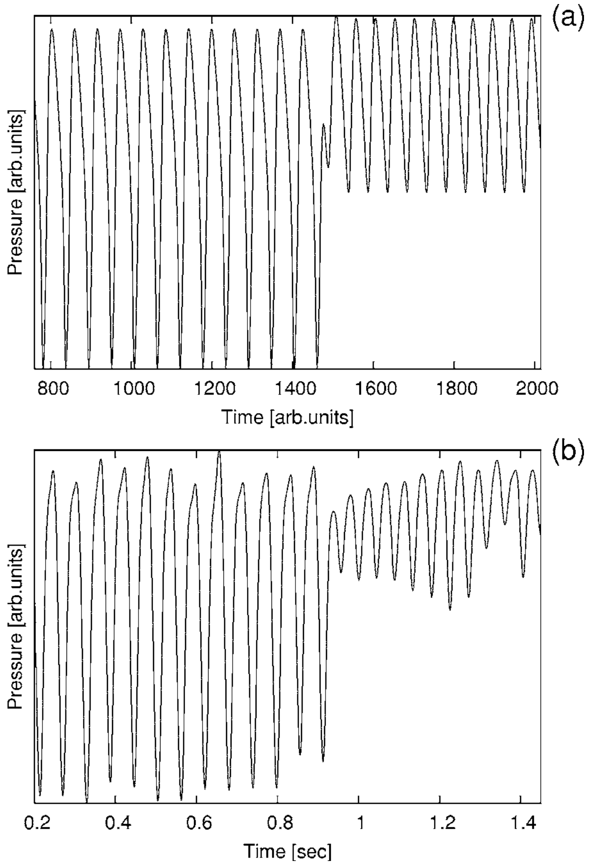

FIG. 5. Synthetic solution of the model as the forcing frequency is increased in the path LM (see Fig. 4) (a) and experimental pressure patterns in a testosterone treated female (b).

Notice that under this hypothesis, the females should be in principle capable of generating a second qualitatively different pressure pattern: a small oscillation mounted on a dc level. In Fig. 5(a) we show the synthetic pressure patterns in a transition corresponding to the path LM in the parameter space of Fig. 4. Notice that (as opposed to what happens in males), the frequency of the small oscillations has only slightly changed. We looked experimentally for such patterns in the testosterone treated females, and the results are shown in Fig. 5(b). This pressure gesture was found in all the females analyzed. Notice that both in the case of males and females, the syllabic frequencies are such that they operate near the boundary between the two period one orbits.

IV. CONCLUSIONS

In this work we have analyzed the pressure patterns used by male and females during song. We noticed that there was a qualitative difference between them, even when syllables of similar rhythmic (and to some extent, acoustic) features were produced. The difference between some of these syllables was qualitative: in their time delay embeddings they displayed different topological features.

We were capable of showing that these results are compatible with a recently proposed model for the respiratory system of oscine birds, under the hypothesis that the telencephalic forcing on the respiratory pathway was smaller in the case of females, which is consistent with anatomical evidence.

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[23] J. Keener and J. Sneyd, *Mathematical Physiology* (Springer, New York, 1998).
[24] A braid is a set of strands. It can be characterized in an algebraic way by associating a word to each braid. These words are built by a sequence of symbols $\sigma_{i,i+1}$, ($\sigma_{-1,i,i+1}$) where i, $i+1$ denote consecutive starting points of the crossing strands with the strand starting at $i+1$ (i) crosses over the strand starting at i ($i+1$).