Highly Structured Duets in the Song of the South American Hornero

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The South American Hornero (*Furnarius rufus*) is a suboscine bird widely known for its mud-made, oven-looking nest. Beyond their architectural skills, the male and female Horneros sing in highly structured duets. The analysis of field recordings reported in this work reveals that as the male increases the note production rate the female responds by switching to different locking states: the ones predicted by the theory of nonlinear forced oscillators. This gives the duet a most appealing rhythm, and unveils the nonlinear nature of the underlying brain activity needed to generate the song.

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Complex rhythms arising from nonlinear processes are frequently found in living organisms [1,2]. *In vitro* experimental systems have revealed their nonlinear nature after being driven by periodic stimuli [3–7]. However, rhythms in animals interacting with their natural environment have been more complex to understand [1]. In this work, we analyze recorded duets of a South American bird, the suboscine Hornero (*Furnarius rufus*), and show that the phase-locking organization between male and female voices is that of nonlinear driven oscillators [8]. This constitutes an example of synchronization of physiological rhythms in a natural behavior.

The couples of Hornero sing in well coordinated duets. The male begins the vocalizations at a note production rate of approximately 6 Hz and, in the time course of approximately 5 s, monotonically increases the note production rate about 200%. The duration of the note also decreases. The time evolution of note production rate of the female response presents a larger diversity, and soon after beginning the duet the female seems to lose synchrony [9]. Yet, the timing of the duet between male and female notes is highly structured.

We performed our study in the Nature Reserve ECAS (Villa Elisa, Argentina), where duets between male and female Horneros were recorded. We computed a sonogram for each recording, displaying only the fundamental frequencies, as shown in Fig. 1(a). The continuous traces represent notes. The time intervals in which two notes are present are those in which the two duetting birds are vocalizing simultaneously. In order to characterize the duet, we worked with the sonograms of our recorded songs. We first defined a coincidence as an event in which the maximum of a male note occurs within a time interval in which the female is vocalizing a note. We then defined a number that describes the locking between male and female voices. This number r_{ap} is the quotient between two integers p/q, where q stands for the number of male notes between consecutive male-female coincidences, and p is the number of female notes between consecutive male-female coincidences. The same numbers are computed on synthetic data in Fig. 1(b). In Fig. 2(a) we plot r_{ap} as a function of the normalized average time interval between male notes T_{male} for $n = 11$ duets (from at least ten Hornero couples), in order to inspect the female response. We normalized the average time interval between male notes to the average time interval between notes of the corresponding female when locked with $r_{\mathrm{ap}} = 1/3$ (every female locked with $r_{\mathrm{ap}} = 1/3$ at least once). A clear stairlike structure emerges, with steps at several values of p/q. Notice that some values of p are different from 1. These are located at the regions predicted by the Farey sum rule [8]. For example, we found a number $r_{\mathrm{ap}} = 2/7$; it fell between $r_{\mathrm{ap}} = 1/3$ and $r_{\mathrm{ap}} = 1/4$. A segment with $r_{\mathrm{ap}} = 3/10$ was also found, located between $r_{\mathrm{ap}} = 1/3$ and $r_{\mathrm{ap}} = 2/7$.

This organization is typical of nonlinear oscillators. Nonlinear and linear oscillators react under periodic forcing in a qualitatively different way. Linear oscillators end up following the forcing, while nonlinear ones display a wide variety of subharmonic behaviors, depending on the amplitude and frequency of the forcing. If the frequency of the forcing is similar to the natural frequency of the forced oscillator, they will lock in a one-one regime for a wide range of parameter values. However, if the frequency of the forcing is larger than the natural frequency of the forced oscillator, other behaviors can be found. In the case the forcing amplitude is not too large, periodic and quasiperiodic motions are possible. The periodic behavior can be characterized by the rotation number r, a quotient of integers $r = p/q$ in which q is the period (measured in units of the forcing period), and p stands for the number of oscillations that the forced system performs in a time equal to q times the forcing period [8]. The regions in parameter space where different rotation numbers occur present universal features, regardless of the details of the forced system (that

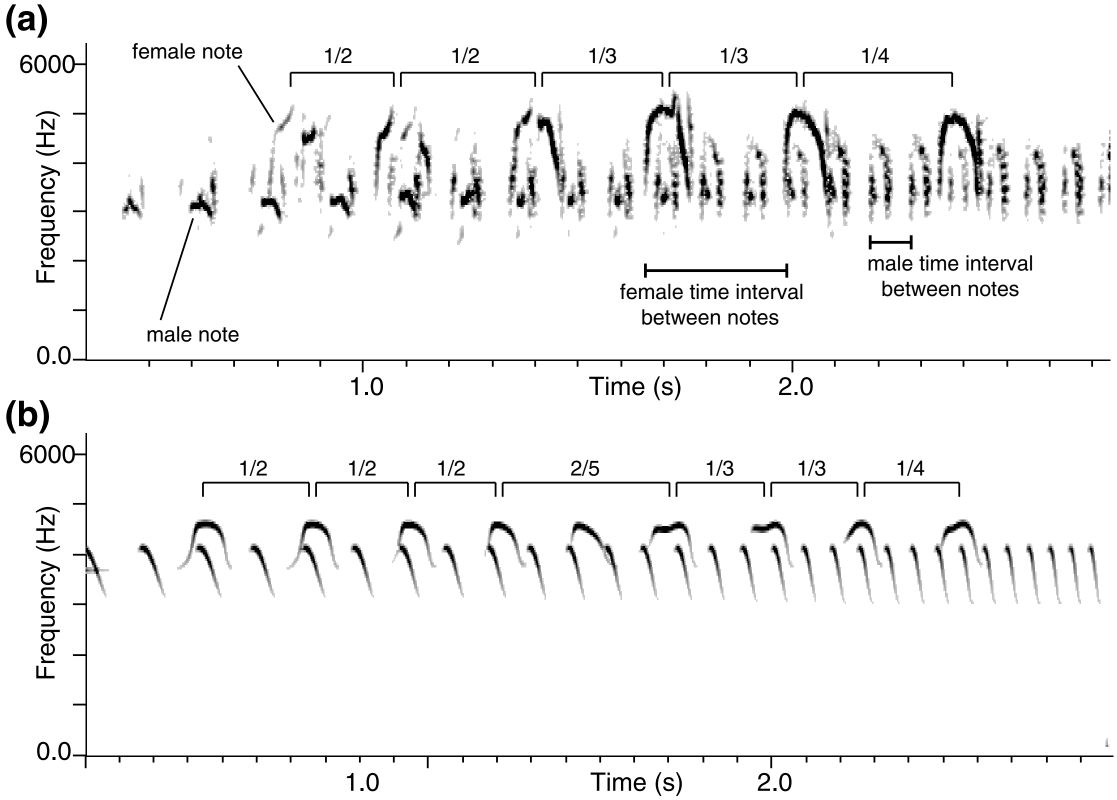

FIG. 1. Duet sonograms. (a) Sonogram of a typical duet of the suboscine Hornero (*Furnarius rufus*). Male and female voices are easily distinguished, due to the differences in their spectral and temporal features. Time measurements were taken from the sonogram (uncertainty: ±0.005 s). The male begins the vocalization, monotonically increasing the note production rate as the duet develops. The female, on the other hand, may respond with increasing, decreasing, or nonmonotonically varying note production rate, but their notes lock in a systematic way. The locking sequence of this duet is shown above the sonogram. (b) Sonogram of a synthetic duet. Female syringeal and respiratory gestures were simulated by a nonlinear oscillator subjected to a periodic forcing of increasing frequency. The oscillator used was $u' = 75\{u - u^3 + 0.5\cos[w(t)\,t] + 0.5\}$, $v' = 6(u + 0.7 - 0.8v)$, with $w(t)$ varying linearly in the range (6 Hz, 12.5 Hz). The driving variables for the female's syrinx were $f = u - v$, $g = u + v$, which allow one to generate realistic looking female syllables. Both periodic forcing and forced nonlinear oscillators were used to drive the physical model of the syrinx to generate male and female notes, respectively. Parameter values in Eq. (1) are $b = 0$ and $c = 2 \times 10^9\ \mathrm{s}^{-1}\,\mathrm{cm}^{-2}$. Parameter values in Eq. (2) are $p_0 = 100\ \mathrm{s}^{-1}$, $p_1 = 1000\ \mathrm{s}^{-1}$, $k_0 = 5.0 \times 10^8\ \mathrm{s}^{-2}$, and $k_1 = 5.2 \times 10^8\ \mathrm{s}^{-2}$ for the male, and $p_0 = 170\ \mathrm{s}^{-1}$, $p_1 = 100\ \mathrm{s}^{-1}$, $k_0 = 6.5 \times 10^8\ \mathrm{s}^{-2}$, and $k_1 = 0.75 \times 10^8\ \mathrm{s}^{-2}$ for the female.

can be either a nonlinear oscillator or an excitable system) and the nature of the periodic forcing (a harmonic function, a sequence of impulses, etc.). The organization of the rotation numbers as a function of the forcing period is known as the "devil's staircase": a complex structure where the steps are rational numbers, as displayed in Fig. 2(b).

The detailed physiological studies of peripheral motor function in birds during singing performed in recent years [10] have led to the formulation of theoretical models of birdsong production [11–13]. These models suggest that many features of birdsong are determined by the phase difference between the motor instructions controlling respiratory and syringeal activity [14]. In oscines, these gestures are expected to be strongly coupled since they originate at regions within the robustus nucleus of the archistratum coupled by long-range inhibitory interneurons [15]. Oscines constitute approximately 4000 out of the around 10 000 species of birds known to exist, and are highly studied since they need some level of exposure to a tutor in order to learn their vocalizations. In suboscines (a largely tropical group of about 1000 species which are thought to sing "innate" songs), the underlying neural template is less well understood [16], but the generators of these motor instructions should be coupled at some level since they are able to generate stable, repetitive notes. We interpret the existence of a staircase in the duets as a consequence of the male notes acting as a unidirectional forcing on the female motor control through an auditory pathway. Since the female notes manage to lock properly, both the respiratory and syringeal gestures should constitute an oscillator, suggesting that at some level the corresponding motor neurons should be closely connected.

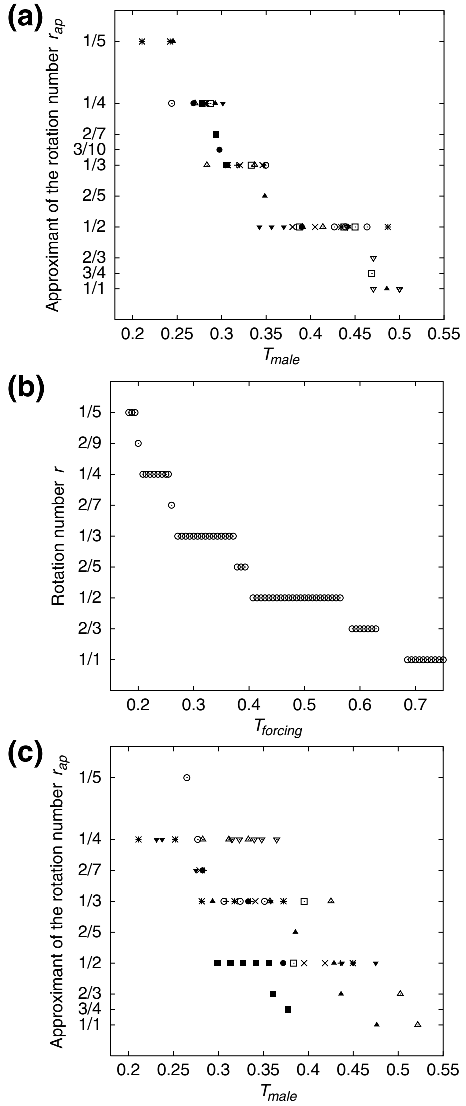

FIG. 2. Locking organization. (a) Approximant of the rotation number r_{ap} as a function of the normalized average time interval between male notes T_{male}, for $n = 11$ Hornero duets. The bottom axis is normalized for each male to the average time interval between notes of the corresponding female when locked with $r_{\mathrm{ap}} = 1/3$. Not every couple played the complete locking sequence from 1/1 to 1/5, but all of them played 1/3 at least once. (b) Rotation number r as a function of forcing period T_{forcing}, for a nonlinear oscillator subjected to a periodic forcing. This steplike organization is known as the devil's staircase. The bottom axis is normalized to the natural period of the driven oscillator. (c) Surrogate random duets (see text for details). The steplike structure is lost. For a quantitative measure of the staircase structure, we defined ϕ as the average overlap between steps, using the 1/2, 1/3, and 1/4 steps (the only steps we approximately know their length). The ratio of the overlapped length to the average step length is computed between the 1/2 and 1/3 steps, and the same is done between the 1/3 and 1/4 steps. The two ratios are then averaged to give ϕ. In the case of the surrogate duets (bottom panel), the average overlap ϕ is almost 70%, while in the case of the original duets (top panel) ϕ is less than 20%.

In order to check the plausibility of the proposed mechanism, we generated synthetic duets with a theoretical model. A physical model of the syrinx was recently proposed [13], which reads

$$\ddot{x} - [p(t) - b]\dot{x} + k(t)\,x + c\,x^2\dot{x} = 0, \tag{1}$$

where $p(t) - b$ stands for the difference between bronchial pressure and linear dissipation, $k(t)$ for the syringeal labia stiffness and c for a nonlinear dissipation constant, all per unit mass of the labia. We generated male notes by driving Eq. (1) with a periodic forcing of increasing frequency; that is, we set male syringeal and respiratory gestures to

$$k(t) = k_0 + k_1\,f(t), \qquad p(t) = p_0 + p_1\,g(t), \tag{2}$$

where $f(t)$ and $g(t)$ were of the form $\cos(\omega t)$ with ω an increasing function of time (see parameter values in the caption of Fig. 1). Analogously, we generated female notes by driving Eq. (1) with Eq. (2), but this time $f(t)$ and $g(t)$ were a nonlinear oscillator forced in turn by the male gestures. The synthetic duet is displayed in Fig. 1(b). In this sonogram we see that different lockings occur at $r_{\mathrm{ap}} = 1/2$, 1/2, 1/2, 2/5, 1/3, 1/3, and 1/4. It should be pointed out that, despite the fact of having a natural frequency, the time interval between notes of the simulated female is not constant during the duet.

In order to check that Fig. 2(a) is not an effect of a simple mismatch between frequencies changing independently, we built surrogate duets and analyzed them. Surrogate duets were assembled by first taking two randomly chosen duets. The time scales were shifted until the first locked note of the males of each duet would start simultaneously. Then, the male notes from the first duet and the female notes of the second duet were eliminated. In this way, 11 random surrogate duets were built and subjected to the same analysis performed to the original duets. As shown in Fig. 2(c), the structure of the devil's staircase is lost in the surrogate data.

There is an important difference between the way in which Figs. 2(a) and 2(b) were constructed. In order to generate Fig. 2(b), for each value of the forcing frequency a transient is disregarded, and the rotation number of the asymptotic locked orbit is plotted as a function of the forcing frequency. Estimating the rotation number with a small transient gives rise to an error (inversely proportional to the length of the transient) [17]. Figure 2(a), on the other hand, displays the sets of r_{ap} numbers obtained from different duets. Since within each duet the syllabic frequency of the male song varies, we are looking at nonstationary data and r_{ap} can only be seen as an approximant of the rotation number. The difference between r_{ap} and the rotation number will be smaller, the larger the system's dissipation. Therefore, the similarity between the well defined devil's staircase and the observational arrangement of r_{ap} as a function of the frequency suggests that a highly dissipative nonlinear mechanism is involved in the generation of the gestures driving the female's vocal organ in order to produce her part of the duet.

Despite sustained evidence of the importance of nonlinearities in the generation of biological rhythmic behavior, most of the work has been based on *in vitro* preparations. In this work we have analyzed recorded duets of the suboscine Hornero (*Furnarius rufus*), showing the existence of a signature of nonlinearity in a bodily rhythm that emerges in a natural environment, as part of a natural behavior.

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