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Dynamical origin of complex motor patterns

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Abstract. Behavior emerges as the nervous system generates motor patterns in charge of driving a peripheral biomechanical device. For several cases in the animal kingdom, it has been identified that the motor patterns used in order to accomplish a diversity of tasks are the different solutions of a simple, low dimensional nonlinear dynamical system. Yet, motor patterns emerge from the interaction of an enormous number of individual dynamical units. In this work, we study the dynamics of the average activity of a large set of coupled excitable units which are periodically forced. We show that low dimensional, yet non trivial dynamics emerges. As a case study, we analyze the air sac pressure patterns used by domestic canaries during song, which consists of a succession of repetitions of different syllable types. We show that the pressure patterns used to generate different syllables can be approximated by the solutions of the investigated model. In this way, we are capable of integrating different description scales of our problem.

1 Introduction

Behavior in the animal kingdom is the result of an interaction between a complex nervous system, and a peripheral apparatus that needs to be controlled in a robust way. For this reason, motor patterns require some degree of simplicity and regularity. At the same time, the need to perform different tasks usually requires a diversity of qualitatively different motor patterns.

It was suggested, in different cases, that this diversity might be due to the existence of different solutions for the nonlinear dynamical system ruling the activity of a part of the nervous system. As an example, the spatio-temporal symmetries of the quadrupedal gaits walk, trot and pace have been interpreted as the symmetry breaking solutions of a dynamical system describing a symmetric central pattern generator [1]. More recently, the diversity of pressure patterns used by canaries (Serinus canaria) during song have been shown to be well approximated by the subharmonic solutions of a simple, low dimensional, nonlinear driven dynamical system [2]. Since the neural substrate involved in the generation of these motor patterns involves a large number of dynamical units (neurons, or subpopulations of synchronized neurons), it raises the question on how to achieve low dimensional, yet non trivial dynamics out of that complex neural architecture.

From a dynamical point of view, the problem of many interacting nonlinear units is an extremely difficult one. Kuramoto [3] proposed a simplified model to study the behavior of a large population of coupled biological oscillators. He described each unit in terms of its phase, assumed a single coupling coefficient, and also a simple functional form to describe the coupling between the interacting units. Under these assumptions, he was able to prove that whenever the coupling coefficient exceeds a threshold, mutual synchronization takes place. Since then, a variety of closely related problems were studied, the intuitive arguments suggested by Kuramoto were mathematically explored, and applications were proposed [4]. A breakthrough was presented in the field recently. Ott and Antonsen [5] showed that the Kuramoto model presents an invariant manifold (in many cases, an attracting one [6]) consisting of states for which the macroscopic dynamics becomes low dimensional. According to this framework, a population of interconnected communities of forced nonlinear units should be capable of displaying low dimensional yet non trivial dynamics [7].

Phase equations are not only an adequate representation for oscillatory dynamics. They can also describe the dynamics of a class of excitable systems. That is the case when a dynamical system is close, in parameter space, to experiencing a saddle node on a limit cycle bifurcation (SNILC). For those systems, in the unfolding of the bifurcation one finds two qualitatively different regimes. In the first one, a saddle and a node coexist, with the unstable manifold of the saddle belonging to the stable manifold of the attractor. In the second regime, the system displays oscillatory dynamics. The transition occurs as the saddle and the node collide. This dynamical scenario (known as class I excitability [8]) is present in a very common neural architecture called neural oscillator, which consists of a subpopulation of excitatory units coupled to another subpopulation of inhibitory ones [9]. In [9], a thorough description of the different dynamics presented by this array is discussed.

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In this work, we explore the dynamics presented by an infinitely large population of excitable units whose dynamics are described individually by phase equations, with global sinusoidal coupling, and external forcing. In terms of the previous discussion, this constitutes an idealization of a large array of coupled neural oscillators (each consisting of a subpopulation of excitatory units coupled to a subpopulation of inhibitory ones) which is periodically forced. We find that the average activity of the driven population obeys a low dimensional nonlinear equation capable of displaying non trivial solutions.

As a case study, we analyze air sac pressure data from singing domestic canaries. Some elements of the neuroanatomy of their pre motor brain areas suggest that it might be pertinent to analyze the data in the light of these results. We find that the pressure patterns used to generate different syllables can be approximated by the solutions of the equations obeyed by the order parameter describing the behavior of periodically forced networks of coupled excitable units.

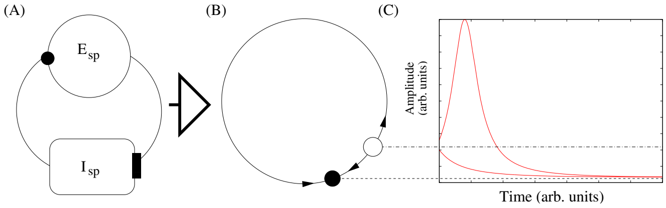

Fig. 1. (Color online) (A) Schematics of a neural oscillator. The circle on the top represents an excitatory subpopulation of neurons (E_{sp}) while the rectangle represents the inhibitory one (I_{sp}). (B) Mathematical representation of the neural oscillator by a phase oscillator. The main dynamical features of the neural oscillator close to a SNILC bifurcation are captured by this simple model. (C) Qualitative behaviour of the phase oscillator model. For initial conditions below the threshold (indicated by the dashed line) the solution is a rapid decay to the stable fixed point, while for initial conditions above this threshold the system performs a large excursion in phase space. This means that small perturbations from the stable fixed point will result in rapid decay to equilibrium. For perturbations that are large enough, the system response is qualitatively different.

2 The model

The study of the generic features presented by systems consisting of large number of coupled oscillators has a long history [4]. In part, this is due to the wide range of areas where this problem emerges. Kuramoto made a seminal contribution to the field by introducing a mathematical model which allowed some analytic treatment. The dynamics of each oscillator was described in terms of its phase, and the coupling between the different oscillators was assumed to be sinusoidal, what simplified the analysis of the model. By introducing a mean field function, he obtained an indicator of the coherence of the units. He found that the oscillators are forced by the mean field, and depending on its parameters, they can synchronize with it. Recently, Ott and Antonsen [5] found that the Kuramoto model presents an invariant manifold, i.e., a set of states for which the macroscopic dynamics becomes low dimensional. This strategy was later applied to solve closely related problems, as the dynamics of a set of periodically forced coupled oscillators [7].

In this work, we are interested in exploring the dynamics of a set of forced coupled excitable systems. As we mentioned in the introduction, it is common to find neural architectures consisting of coupled neural oscillators, i.e. interconnected subpopulations of excitatory and inhibitory neurons. For a wide region of their parameter space, neural oscillators present excitable dynamics: unless they are perturbed, they rest on their quiescent state; after being perturbed, the return to equilibrium can follow qualitatively different paths. In neural oscillators, excitability is lost in a SNILC bifurcation, giving rise to oscillations born with non zero amplitude and zero frequency [9]. A simple phase equation can account for this dynamics:

$$\dot{\theta} = \omega - \gamma \sin(\theta). \tag{1}$$

If $\frac{\omega}{\gamma} < 1$, the system has two fixed points, one stable and the other unstable. The separation between these fixed points depends on the $\frac{\omega}{\gamma}$ ratio. The qualitative behavior of this system is shown in Figure 1, where we display the response of the system to different initial conditions. If these are close to the quiescent state, the system rapidly decays to the stable fixed point, while for initial conditions above some threshold, the response of the system is a large excursion in the phase space.

In our study, the forcing units will be represented mathematically by phase oscillators. We assume that there is global coupling between all driven excitable units, global coupling between all forcing units, and a directed coupling from the driving units to the network of excitable, driven units.

In this way we have two sets of phase oscillators. Set 1 refers to the driving set, while set 2 refers to the driven set. We use Greek letters to indicate population number and Latin letters to index the elements within a population. Using this notation we have the full extended model,

$$\dot{\theta}_i^\sigma = \omega_i^\sigma - \gamma_i^\sigma \sin(\theta_i^\sigma) + \sum_{\sigma'=1}^{2} \frac{K_{\sigma\sigma'}}{N^{\sigma'}} \sum_{j=1}^{N^{\sigma'}} \sin(\theta_j^{\sigma'} - \theta_i^\sigma), \tag{2}$$

where for each population the natural frequency of the ith oscillator is denoted by ω_i^σ, the parameter ruling the excitable nature of the oscillator is γ_i^σ, the number of oscillators in the population is given by N^σ and $K_{\sigma\sigma'}$ stands for the connectivity matrix.

In the limit $N^\sigma \rightarrow \infty$, these populations can be described in terms of density probability functions $f^\sigma(\theta, \omega, t)$, with $\sigma = 1, 2$. The evolution of f^σ is given by the continuity equation,

$$\frac{\partial f^\sigma}{\partial t} + \frac{\partial}{\partial \theta}(f^\sigma v^\sigma) = 0, \tag{3}$$

where the velocity v is given by:

$$v^\sigma(\theta^\sigma,\omega,t) = \omega^\sigma - \gamma^\sigma \sin(\theta^\sigma) + \sum_{\sigma'=1}^{2} K_{\sigma\sigma'} \int_{-\infty}^{\infty}\int_0^{2\pi} \sin(\theta' - \theta^\sigma) f^{\sigma'}(\theta',\omega,t) d\theta' d\omega. \quad (4)$$

In this way, the state of the system, is described by the density functions f^σ. We have defined f in such a way that the fraction of oscillators with phases between θ and $\theta + d\theta$ and natural frequencies between ω and $\omega + d\omega$ is given by $f(\theta,\omega,t)d\theta d\omega$. Therefore, in order to close the system we need that the following equations are satisfied:

$$\left\{ \begin{array}{ll} \int_{-\infty}^{\infty}\int_0^{2\pi} f^\sigma(\theta,\omega,t)\, d\theta d\omega = 1 & \\ \int_0^{2\pi} f^\sigma(\theta,\omega,t)\, d\theta & = g^\sigma(\omega) \end{array} \right\}.$$

As suggested by Kuramoto we define the system complex order parameter,

$$r^\sigma(t) = \sum_{\sigma'=1}^{2} K_{\sigma\sigma'} z^{\sigma'}, \quad (5)$$

where z^σ is the complex average of the oscillators in σ-th population given by the following equation:

$$z^\sigma = \int_{-\infty}^{\infty}\int_0^{2\pi} e^{i\theta} f^\sigma(\theta,\omega,t) d\theta d\omega. \quad (6)$$

With these definitions, the velocity (4) simplifies to:

$$v^\sigma(\theta^\sigma,\omega,t) = \omega^\sigma + \frac{\gamma^\sigma}{2i}(e^{i\theta^\sigma} - e^{-i\theta^\sigma}) + \frac{1}{2i}(e^{-i\theta^\sigma} r^\sigma - e^{i\theta^\sigma} r^{\sigma^*}), \quad (7)$$

where the super index * denotes complex conjugation. Let us assume that it is sufficient to characterize the forcing population by a harmonic fluctuation. We represent this by making $\gamma^{\sigma=1} = 0$ and $K_{12} = 0$. In this way we reduce this population to one behaving as in the case described by Kuramoto. It is known that above a certain threshold in the coupling strength K_{11}, the oscillators synchronize. In this way we obtain the desired coherent fluctuations needed to represent a harmonic driving. Also, by changing this parameter we can control the amplitude of the fluctuations. We simplify the notation and leave $\gamma^{\sigma=2} = \gamma$ as a parameter of the model.

It is a conventional strategy to address this problem by expanding f^σ in a Fourier series in θ,

$$f^\sigma(\theta^\sigma,\omega,t) = \frac{g^\sigma(\omega)}{2\pi}\left[1 + \sum_{n=1}^{\infty} f_n^\sigma(\omega,t) e^{in\theta^\sigma} + c.c.\right], \quad (8)$$

with *c.c.* denoting complex conjugation. Replacing (8) and (7) into (3) one obtains, in principle, an infinite dimensional system of equations for f_n^σ.

An important breakthrough in the analysis of the problem was introduced by Antonsen and Ott, who [5] noticed that the following ansatz $f_n^\sigma(\omega,t) = (\alpha_\sigma(\omega,t))^n$ would satisfy all the amplitude equations as long as certain equations would be satisfied by α_σ, namely:

$$\left\{ \begin{array}{l} \dot{\alpha_1} = -i\omega\alpha_1 + \frac{K_{11}}{2}(\alpha_1 - \mid \alpha_1 \mid^2 \alpha_1) \\ \dot{\alpha_2} = -i\omega\alpha_2 + \frac{\gamma}{2}(1 - \alpha_2^2) \\ \qquad + \frac{K_{22}}{2}(\alpha_2 - \mid \alpha_2 \mid^2 \alpha_2) + \frac{K_{21}}{2}(\alpha_1 - \alpha_1^* \alpha_2^2) \end{array} \right\}. \quad (9)$$

By further assuming that $g^\sigma(\omega)$ is a Lorentzian,

$$g^\sigma(\omega) = \frac{\Delta^\sigma}{\pi\left[(\omega - \omega_0^\sigma)^2 + (\Delta^\sigma)^2\right]}, \quad (10)$$

and that $\alpha_\sigma(\omega,t)$ satifies certain analyticity conditions in the complex $\omega-$plane, Ott and Antonsen [5] evaluated equation (9) by contour integration. Multiplying both sides of (9) by $g^\sigma(\omega)$ and using the residue theorem we have the following equations for the evolution of $\alpha_\sigma(\omega,t)$:

$$\left\{ \begin{array}{rl} \dot{\alpha_1}(\omega_0^1 - i\Delta^1, t) = & -i(\omega_0^1 - i\Delta^1)\alpha_1 \\ & + \frac{K_{11}}{2}(\alpha_1 - \mid \alpha_1 \mid^2 \alpha_1) \\ \dot{\alpha_2}(\omega_0^2 - i\Delta^2, t) = & -i(\omega_0^2 - i\Delta^2)\alpha_2 \\ & + \frac{\gamma}{2}(1 - \alpha_2^2) + \frac{K_{22}}{2}(\alpha_2 - \mid \alpha_2 \mid^2 \alpha_2) \\ & + \frac{K_{21}}{2}(\alpha_1 - \alpha_1^* \alpha_2^2) \end{array} \right\}. \quad (11)$$

We can include a *dc* level for the forcing (i.e., and additive constant) by including in our description a third population characterized by a constant α_0, coupled through a coefficient K_{20} to the driven set of excitable units. The full model we worked with is finally given by:

$$\dot{\alpha_1} = -i(\omega_0^1 - i\Delta^1)\alpha_1 + \frac{K_{11}}{2}(\alpha_1 - \mid \alpha_1 \mid^2 \alpha_1) \quad (12)$$

$$\dot{\alpha_2} = -i(\omega_0^2 - i\Delta^2)\alpha_2 + \frac{\gamma}{2}(1 - \alpha_2^2) + \frac{K_{22}}{2}(\alpha_2 - \mid \alpha_2 \mid^2 \alpha_2) + \frac{K_{21}}{2}(\alpha_1 - \alpha_1^* \alpha_2^2) + \frac{K_{20}}{2}(\alpha_0 - \alpha_0^* \alpha_2^2), \quad (13)$$

where we dropped the arguments in α_σ to ease notation. The exact distribution function of the oscillators can be obtained by performing the summation in equation (8) as discussed in [5]. The order parameter of each subpopulation is given by (5). By using the Fourier expansion (8) of the distribution function and the ansatz in (6), we have the relation between the distribution function and the order parameters for each set of units:

$$z^\sigma(t) = \int_{-\infty}^{\infty}\int_0^{2\pi} e^{i\theta} f^\sigma(\theta,\omega,t)\, d\theta d\omega = \int_{-\infty}^{\infty} \alpha_\sigma^* g^\sigma(\omega)\, d\omega = \alpha_\sigma^*(\omega_0^\sigma - i\Delta^\sigma, t). \quad (14)$$

We can write the order parameter in its Eulers form as, $z^\sigma(t) = \rho^\sigma(t) e^{i\theta^\sigma(t)}$. The average position of the oscillators

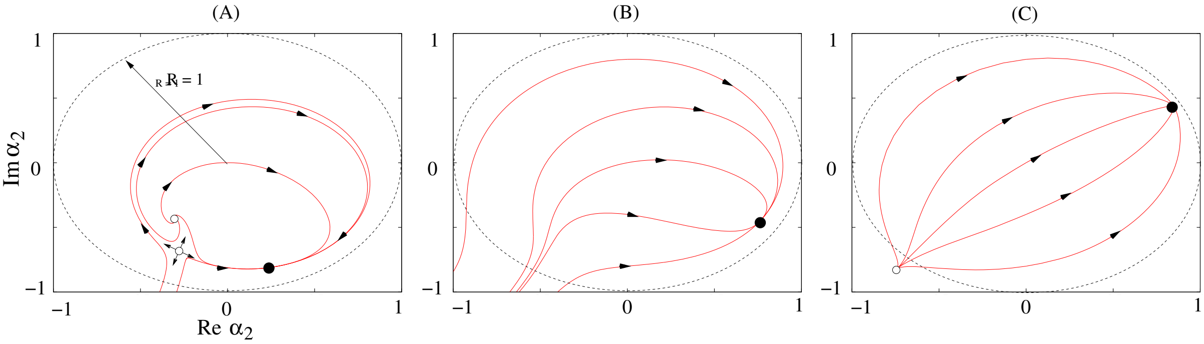

Fig. 2. (Color online) Phase diagrams of α_2 when uncoupled to α_1. We set $K_{21} = 0$ in equation (12) and show the phase diagram for different values of α_0. (A) $\alpha_0 = 0$. (B) The on state, $\alpha_0 = 1 + i1$. (C) The off state, $\alpha_0 = 10 + i10$.

is given by $\theta^\sigma(t)$ while the modulus $\rho^\sigma(t)$ measures how peaked the distribution is. In this work we deal only with the order parameters. Finally, we can define $x(t)$ as the projection of population 2 order parameter:

$$x(t) = \rho^{\sigma=2}(t) \sin(\theta^{\sigma=2}(t)). \tag{15}$$

If we think that the dynamical units presenting excitability are neural oscillators (i.e., coupled subpopulations of excitatory and inhibitory neurons), such a projection of the order parameters describes the macroscopic behavior of the excitatory subpopulation.

Let us display some solutions of this system of equations. In Figure 2 we show three panels that display the real and imaginary parts of α_2, for different values of the *dc* component of the input. For computing the displayed trajectories, there was no periodic component of the forcing. The parameters where fixed to the following values: $\omega_0^2 = 2.9$, $\gamma = 2.96$, $K_{11} = 8$, $K_{12} = 0$, $K_{22} = 6, K_{20} = 1$, $\Delta^1 = 1$, $\Delta^2 = 1$. The parameters that were left unfixed are the natural frequency of population 1, ω_0^1 and the connectivity between population 2 and 1, K_{21}.

In Figure 3, bottom panels, we show the solutions of the model when there is a forcing including a *dc* component and a sinusoidal one. The parameters of the forcing (ω_0^1 and K_{21}) are displayed in the caption of the figure. The three solutions of the bottom panels were generated with different values of the coupling and the forcing frequency. The solutions in (A) and (B) correspond to period one solutions, i.e., the periodicity of the forcing coincides with the periodicity of average activity of the driven network. The case of panel (C) is different: it is a period two solution, i.e., one that repeats itself after twice the period of the forcing. In summary, the average activity of our periodically forced coupled network is capable of displaying low dimensional and yet non trivial dynamics. Subharmonicity arises from the competition between the time scale of the forcing frequency and the one associated with the forced network.

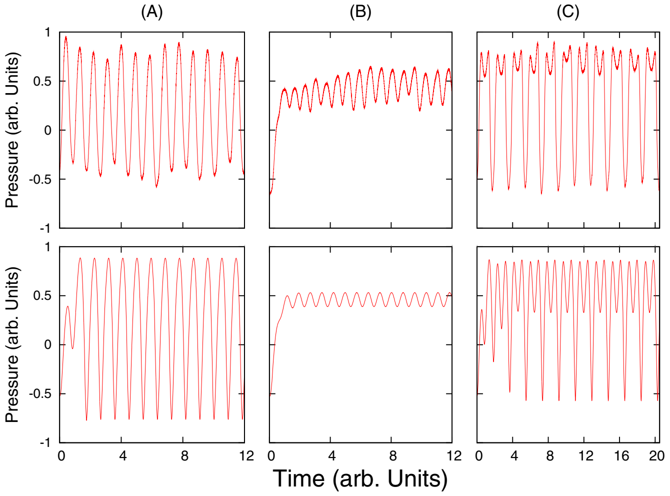

Fig. 3. (Color online) Comparison of experimental measurements with solutions of the model. Top panels, experimental time series of pressure patterns in the air sacs of a singing canary. Lower panels, solutions of the model that locally minimize the cost function. (A) Periodic activity spanning the full range of pressure values. The parameters of the fitting solution are $\omega_0^1 = 6.834$ and $K_{21} = 6.533$. (B) Small oscillations mounted on a constant value. The parameters are $\omega_0^1 = 8.238$ and $K_{21} = 0.981$. (C) Periodic pressure pattern presenting wiggles. The fitting solution corresponds to a subarmonic response of population 2 to the forcing by population 1. The activity of population 2 is twice the period of the activity in population 1 (not shown). The fitting parameters are $\omega_0^1 = 6.808$ and $K_{21} = 5.522$. All the solutions were obtained fixing $\alpha_0 = 1 + i1$ (on state).

3 A case study

Birdsong is a complex behavior, which has been widely studied in the last years. For many bird species learning plays a role in the acquisition of their normal vocalizations. For this reason, songbirds have become an ideal animal model to understand some aspects of vocal learning. Physics has participated in this collective effort by integrating a large body of experimental work with the expected bio mechanical processes involved in birdsong production.

For the oscine birds cases (which account for about 40 percent of the known species known to exist, the domestic canaries in this study among them), experimental work and theoretical analysis have highlighted the role played by different motor patterns [10,11]. The activity of syringeal muscles, for example, is fundamental in the frequency control of the syllables and the airflow gating. But the process of vocalizing itself does not start until the bird generates respiratory pressure sufficiently high to allow the onset of the labial oscillations within the vocal organ. We will concentrate on the physiological gestures necessary for the generation of the air sac pressure pulses needed for vocalizing.

In this section we will first introduce our data. Then, we will discuss the elements that suggest that it might be pertinent to interpret the data in terms of the previous model. Comparisons between the solutions and the model will close this section.

Simultaneous recordings of sound and sub syringeal air sac pressure were made in an adult male canary (*Serinus canaria*). It was given water and seed ad libitum, housed in an individual cage ($30\times25\times30$ cm) and maintained in a 14:10 h light/dark cycle. A microphone in front of the cage recorded the produced song with a sound card (MAYA 1010, 44.1 kHz sample rate) directly onto a computer.

The time series corresponding to air sac pressure was registered by the insertion of a cannula (venisystemsAbbocath-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 birds back [12]. The signal was amplified and modulated in order to record it onto a computer with the same sound card used to record sound. The insertion of the cannula was made with the bird anesthetized with intramuscular injection of Ketamine/Xilazyne. Birds usually start singing 1–2 days after the surgery. In this way, we generated time traces corresponding to pressure in arbitrary units sampled at 44.1 kHz. A typical time series is displayed in Figure 4. Notice that it consists of a succession of repeated syllables.

The brain structure controlling song production in songbirds consists of sets of neurons called nuclei, and axons interconnecting them, forming a circuit known as the motor pathway. One of these nuclei is called HVC (for high vocal center), which presents high levels of activity during song. It connects to a set of neurons in the telencephalon called retroambigualis (RA), with neurons projecting to respiratory nuclei and neurons projecting to the nuclei which ultimately innervate the muscles in the vocal organ. In other words, the nucleus HVC generates neural activity patterns that will affect the dynamics of the syringeal and respiratory muscles. It is in the most dorsal region of RA (i.e., the region closer to the back of the animal) that one finds neurons projecting to the respiratory premotor nuclei; Ram and Pam (for retroarambigualis and parambigualis respectively). This is the region of the brain relevant for the generation of the motor patterns that will ultimately control the pressure pulses during birdsong. In other words, the activity in HVC is processed to be eventually is transduced into motor patterns.

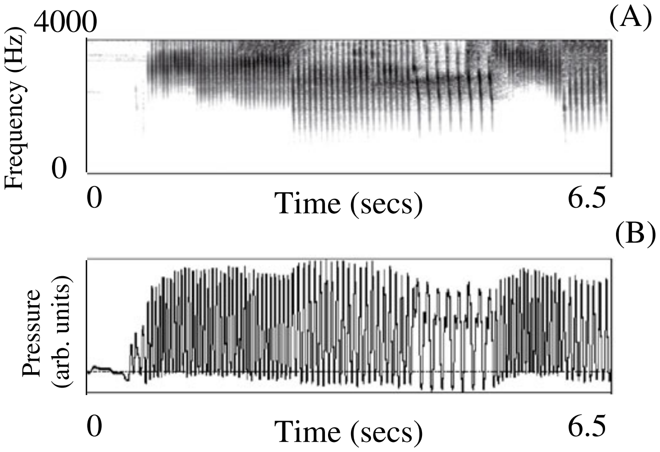

Fig. 4. The song of a canary (upper panel (A)) and the air sac pressure used to vocalize (bottom panel (B)). The song is represented by a sonogram: the signal is partitioned up into small, overlapping segments, and Fourier transformed to calculate the magnitude of the frequency spectrum for each one. The spectrum for each segment then corresponds to a vertical line in the image, providing a measurement of spectral content of the signal as a function of time. In the bottom panel, the air pressure, measured as discussed in the text. The air sac pressure needs to overcome a threshold value so that labia in the birds vocal organ (which are located at the junctures of the bronchii with the trachea) start to oscillate. The modulations of the airflow by these oscillating labia are responsible for the sound.

For the case of canaries, the respiratory activity during song production has been already studied. In [2,13] it was shown that the respiratory gestures used to utter different syllables could be well approximated by subharmonic solutions of forced low dimensional dynamical systems. In [13] a simple dynamical system was proposed in order to mimic the rate activities of different nuclei in the motor pathway, and its solutions were found to be similar to the measured pressure patterns. The subharmonic solutions emerged as periodic instructions from RA forced the lower respiratory system, which presented excitable dynamics. It is worth pointing out that subharmonic behavior could also be found in a model where periodic HVC activity forces an excitable network in RA [2]. At present, it is not possible to perform direct measurements which would allow us to choose between these alternative hypothesis. Yet, for the purpose of our study both mechanisms are dynamically equivalent.

In both cases, the actual neural substrate responsible for the instructions controlling both respiration and muscle activity consists of thousands of interconnected neurons. Even if the motor output of this pathway is a repertoire of solutions of a low dimensional dynamical system, the large number of units involved is likely to provide robustness as well as an opportunity for fine tuning during learning. Some neurons of the motor pathway are in fact innervated by the output of a different set of neural nuclei (called the anterior forebrain pathway) which play a crucial role during vocal learning, through a delicate code which is still far from being understood [15].

Since the neural substrate of the song pathway does involve thousands of nonlinear units, we are interested in testing the hypothesis that a periodically forced network of excitable units can display an average activity capable of approximating our measured pressure patterns. This requires an average activity which is both low dimensional and non trivial. Could the parameters of a system like the one derived in (12), designed to describe the average activity of a generic forced excitable network, be fitted so that its solutions approximate the measured respiratory activity of singing canaries?

To find the best fit of the data, with solutions of the model, we proceeded as follows. First, the experimental data was re sampled to 2800 Hz in order to fit the time scales of the system to those of the experiment. This is the same as fixing the time scale of the model with a multiplicative constant. Then, segments of the time series corresponding to a unique syllabic type were selected.

For each experimental time series segment we define the cost function:

$$c(\omega_0^1, K_{21}) = \frac{1}{T_{exp}} \int_0^{T_{exp}} (x(t) - p(t))^2 dt, \qquad (16)$$

where $p(t)$ is the experimental time series in consideration, T_{exp} is its duration and $x(t)$ are the solutions of the model to be compared, which depend on parameters and initial conditions. An inspection of the cost function in our parameter space revealed a complex structure, reflecting the diversity of qualitatively different solutions presented by the system for different parameters. Yet, close to a global minimum, the cost function displayed a smooth behavior. A gradient descend method was implemented in order to obtain the parameters that locally best fit the experimental time series, i.e. the parameters that minimize the cost function. Three representative solutions and the corresponding time series are shown in Figure 3. The numeric values of the parameters are shown in the figure caption. A second fitting procedure was implemented: a genetic algorithm [16] (200 chromosomes, 50 generations, crossing rate $cr = 0.8$ and mutation rate $m = 0.1$) allowed us to obtain the same fitting values.

Beyond the similarity between the experimental segments and the solutions of the model, it is worth mentioning that the different solutions correspond to different subharmonics of the driven network. The solution shown in $3(C)$ corresponds to a subharmonic response of the second population. Its period is twice the period of the input signal coming from the first population. This is consistent with previous results [2] that have suggested that the diversity of pressure patterns used during the song of the domestic canary are not arbitrary, but are the subharmonic solutions of a simple driven low dimensional differential equation.

4 Discussion and conclusions

Motor patterns require some degree of simplicity and regularity. At the same time, the need to perform different tasks usually requires a diversity of qualitatively different motor patterns. The theory of (low dimensional) dynamical systems has offered, in the last years, a natural paradigm to address this issue: non linear systems can display qualitatively different solutions for different parameters. Yet, motor patterns emerge as large numbers of neurons interact.

In this work, we investigated the dynamics of a network of globally coupled excitable units under the effect of a periodic forcing. We simplified the analysis by assuming sinusoidal coupling, and a phase representation of the dynamical units. Following Ott and Antonsen [5] we could obtain a low dimensional dynamical system for the order parameter that describes the macroscopic behavior of the network. As it was suggested in [5], non trivial solutions exist. This problem can be thought as an idealization of a forced network of neural oscillators (each one consisting on subpopulations of excitatory and inhibitory neurons), since these present type I excitability (i.e., excitability that can be destroyed, as parameters are varied, through a saddle node bifurcation on a limit cycle). In that framework, the existence of sub harmonic solutions in the average activity of the network allows to have diverse solutions for different parameters, as well as robustness (the qualitative features of a solution would not change within an open set of the parameter space).

As a case study, we analyzed experimental data of air sac pressure patterns recorded from singing domestic canaries. The existence of a driver, and a driven network built out of excitatory and inhibitory neurons suggested that it might be reasonable to test whether the data could be approximated by the solutions of the equations of the average activity of a driven network of type I excitable units. The results are quite satisfactory: it is possible to fit the equations to have solutions similar to the experimental ones.

A model with global coupling between the interacting units can be used to test some hypothesis pertinent for neuroscience. In our case, whether it is possible to achieve, in average, activity displaying non trivial low dimensional dynamics, without complete synchronization. Notice that in our problem, as long as γ is not zero, the order parameter does not remain constant: a periodic solution of the averaged activity requires periodic fluctuations in the degree of synchrony of the population. In other words, global coupling does not imply synchronized activity unless $\gamma = 0$. Yet, global coupling is a rough approximation for many realistic neural architectures, and therefore it remains an open and interesting problem to systematically study how other connectivities affect the dimensionality of the averaged network activity.

Mathematically, our model is equivalent, before forcing, to the problem analyzed by Childs and Strogatz in [7]. They discussed the periodically forced Kuramoto model which, in a frame co rotating with the drive, is equivalent to the homogeneous part of our model. Childs and

Strogatz did a thorough study of the bifurcations present in the problem and described a situation where a cusp and a Hopf bifurcation collide. On the other hand, in a previous work [2], we showed that the pressure patterns used by domestic canaries during singing could be approximated by a simple forced nonlinear equation. The forced equation was required to present, precisely, a cusp and a Hopf colliding. This is the mathematical common theme in this problem. We selected three segment of the pressure data for one bird in our case study. In [2] we studied several patterns, for several birds. Since the underlying mathematical structure behind these patterns in the phenomenological model in [2] and in the one discussed in this work are equivalent, as discussed above, we do not repeat an extensive study over many syllables. In fact, the topological features of the solutions in the phenomenological model [2] and those of our average equations will be identical [14].

Our results suggest then, that the pressure patterns used during song are not a succession of arbitrary time traces. Moreover, a given dynamical system generates solutions that are linked and knotted in phase space in a very precise way. Therefore, it is not the case that, by changing parameters, a unique ODE could be used to fit an arbitrary collection of curves.

In this work, we followed a strategy recently proposed in the field of dynamical systems, which allowed us to us go from a idealized microscopic model to the macroscopic variables relevant for behavior. Work along these lines will allow to integrate efforts carried out at different scales in a variety of biological problems.

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