

Lateralization as a symmetry breaking process in birdsong

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The singing by songbirds is a most convincing example in the animal kingdom of functional lateralization of the brain, a feature usually associated with human language. Lateralization is expressed as one or both of the bird's sound sources being active during the vocalization. Normal songs require high coordination between the vocal organ and respiratory activity, which is bilaterally symmetric. Moreover, the physical and neural substrate used to produce the song lack obvious asymmetries. In this work we show that complex spatiotemporal patterns of motor activity controlling airflow through the sound sources can be explained in terms of spontaneous symmetry breaking bifurcations. This analysis also provides a framework from which to study the effects of imperfections in the system's symmetries. A physical model of the avian vocal organ is used to generate synthetic sounds, which allows us to predict acoustical signatures of the song and compare the predictions of the model with experimental data.

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I. INTRODUCTION

The acquisition of song by songbirds has been an active field of research. The learning of vocalizations by imitation of a tutor is shared by humans and just a few examples in the animal kingdom [1]. Another impressive analogy is functional lateralization of the brain, once considered exclusive to human language, and recently proved to play a role in song production by oscine birds [2]. Birds generate sounds by means of a bipartite organ called the syrinx [3]. A pair of labia in each juncture of the bronchi with the tract are set in motion when air passes through them. In contrast, the vocal source in humans consists of a unique pair of folds at the larynx.

The avian vocal organ is controlled by a set of muscles. Some of them affect the tension of the oscillating labia (and therefore the frequency of the resulting vocalization), while others control the air passage through the syrinx by actively closing or opening each side. Some species use one side predominantly, while in others both sides can be active sequentially or simultaneously. This behavior is puzzling due to the absence of an obvious asymmetry in the morphology of the system [4]. In this work we will study the mechanisms involved in the generation of different gating patterns.

We address this issue from the perspective of nonlinear dynamics. The activity of the neural circuits controlling the muscles responsible for the gating follows nonlinear rules. Therefore it can be described in terms of the solutions of a system of nonlinear equations. If such a system should present a symmetry, not all the solutions will necessarily reflect it [5]. This is the central hypothesis of this work: the spatiotemporal patterns of activity of the nuclei controlling the gating muscles can display different symmetries that those of the neural substrate that generates them. In this work we propose a simple neural model for the gating, analyze its solutions, and use them to drive a computational model of the syrinx. In this way, we are capable of predicting acoustic features of song revealing complex spatiotemporal patterns of bilateral gating activity.

II. NEURAL MODEL

The main acoustic features of the birdsong are determined by a few physiological parameters [6] (tension of the oscillating labia, respiratory rhythm, and gating). These gestures are controlled by a song program which is implemented by sets of interconnected nuclei, each of them containing several thousands of interconnected neurons. These nuclei are typically described as hierarchically organized. Activity generated at a high level of the hierarchy eventually activates neurons in a nucleus which acts as a "junction box," creating a pattern of activity that controls both the vocal organ and the respiration. The command of the vocal organ is carried out by a medullar nucleus called nXII_{ts} while the respiration is commanded through expiratory and inspiratory nuclei [7].

Each brain hemisphere holds a copy of this structure. In general, the activity within this network can make different contributions to each side of the vocal organ [8], which is consistent with the independence of the fundamental frequencies of the sounds produced by each sound source.

On the other hand, birds can actively control the gating [9]. As can be expected, the gating nuclei have to be strongly coupled with those controlling respiration. Since the respiratory activity is bilaterally symmetric, the question naturally arises of which mechanisms lead to the emergence of lateralized gating patterns in a system lacking obvious asymmetries, and strongly coupled to a symmetric driver.

In order to generate song, the birds produce a set of basic gestures: on one hand, the vocalization is the result of an increase in air sac pressure, and while the expiration takes place, the tension of the oscillating labia is controlled in order to shape the dynamics of the syllabic fundamental frequency [10]. The motor instructions of the respiratory muscles are bilaterally distributed, in contrast with those controlling the syrinx. This is particularly evident in the case of the instructions controlling gating muscles [11], which ultimately allow the air passage through each side of the syrinx.

A muscle whose activity closes air passage through each

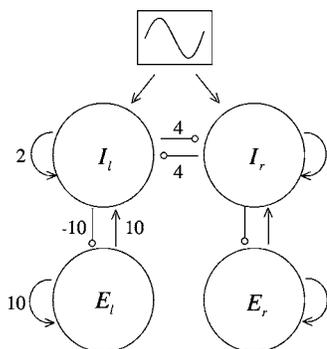


FIG. 1. Scheme of the neural architecture controlling the activity of the gating muscles (dS). Arrows stand for excitatory connections, circles indicate inhibition. The contralateral coupling constant was set to $c=4$. Notice that the results of the work are independent of details of the architecture chosen for the coupling. The upper panel displays the driving signal (related to respiratory activity). We model it as a harmonic function, since the spatiotemporal patterns arising through symmetry breaking bifurcations do not depend on the specific form of the forcing.

side is the *syringalis dorsalis*(dS) [4,12]. We propose a computational model for the subpopulations of neurons that innervate the gating syringeal muscles (which are part of the nXIIIts nucleus). The variables of our model describe the average rate activities of two neural populations for each side: left (right) excitatory motoneurons E_l (E_r) that controls the activation of adducting muscles, and left (right) inhibitory neurons I_l (I_r) [13].

In this work we are especially interested in testing the hypothesis that general properties of the neural architecture (as its symmetry) can account for the complex gating patterns that have been reported. For this reason we choose to write a simple model for the dynamics of the variables of interest. A well established description of average activity of neural populations is known as the additive model [14] which states that the activity in a nucleus converges to a saturating function of its total input.

The neural structure is sketched in Fig. 1, and the equations ruling their dynamics are

$$\tau \frac{dE_{l,r}}{dt} = -E_{l,r} + S(10E_{l,r} - 10I_{l,r}), \quad (1)$$

$$\tau \frac{dI_{l,r}}{dt} = -I_{l,r} + S\{-11 + 10E_{l,r} + 2I_{l,r} + A/2[1 + \cos(\omega t)] - cI_{r,l}\}, \quad (2)$$

where $S(x)=1/(1+e^{-x})$ is a continuous, monotonically increasing saturating function for the neural inputs [14]. The forcing term $A/2[1+\cos(\omega t)]$ represents the effect through the known connections between respiratory nuclei and nXIIIts [13]. A coordination between respiration and gating is necessary, and we model it requesting that for high values of either inspiration (negative pressure) or expiration (positive pressure), the activity of the inhibitory populations should be enhanced. In this way, the activity of the nuclei controlling

the muscles that close the air passage is inhibited as air is needed. For this reason, the forcing frequency in our model is twice as high as the respiratory frequency. In this way, a solution of period 2 of our model represents a solution of period 1 measured in units of the pressure periodicity. The parameter c accounts for the contralateral coupling between left and right sides through inhibitory neurons [13]. The choice of the parameters is dynamical in nature. Numerical values of coefficients in Eqs. (2) guarantee that changes in the respiratory forcing could induce transitions between an active and an inactive state [14], and without forcing, the system would remain in a closed state.

We have proposed a symmetrical mathematical model consistent with anatomical observations of the nuclei controlling the gating, intrinsically nonlinear due to the nature of the neural activity, and symmetrically forced due to the deep interaction between respiration and gating. In the next section we analyze the solutions that can be expected from such a model.

III. SOLUTIONS OF THE SYMMETRICAL SYSTEM

Any biological system will present a symmetry at most in an approximate way. Yet, the outstanding features of the spatiotemporal patterns will reflect the nature of the solutions of the perfectly symmetric case. The geometrical symmetry of the problem consists of the exchange operator e , which acts on the variables of the problem as follows: $e(E_l, I_l, E_r, I_r) \rightarrow (E_r, I_r, E_l, I_l)$. For the solutions of period 2, an additional symmetry operator (T) can be defined, which shifts $T(x(t)) \rightarrow x(t+2\pi/\omega)$, where x denotes any of the dynamical variables of the problem.

In Fig. 2 we display the portrait of the different solutions of Eqs. (1) and (2), in the space (ω, A) of forcing parameters. Solutions with a given periodicity and spatiotemporal symmetry can be found in the different regions plotted. The regions are labeled following the notation described above: $1e$ for solutions of period 1 with exchange symmetry, $2(e, T)$ for period 2 solutions left invariant under the joint operation of e and T , 1ℓ represents two different period 1 solutions with no exchange symmetry, and $2(\ell, T)$ a non symmetric period two solution. The insets show the projection of the solutions in the variables (E_l, E_r) . The solutions living in the diagonal $E_l=E_r$ correspond to simultaneous activity of both sides of the syrinx. Solutions close to either axis represent lateralized activity. Solutions exploring wider regions of the phase space projection describe gestures engaging both syringeal sides. An interesting gating pattern is associated with the solutions of panel $2(e, T)(II)$. These solutions correspond to inspiration carried out through the two sources with a minimal time delay between them, while the expiration takes place mainly through one source.

In Fig. 3, we show some time series corresponding to solutions type $2(e, T)$ and $2(\ell, T)$, which were generated with the model of Eqs. (1) and (2) at parameter values indicated as **A** and **B** in Fig. 2. Notice that for the solution corresponding to the parameter value **A** we observe alternation of activity in the excitatory variables E_l, E_r . In terms of our description, this implies that the bird uses one syringeal side during ex-

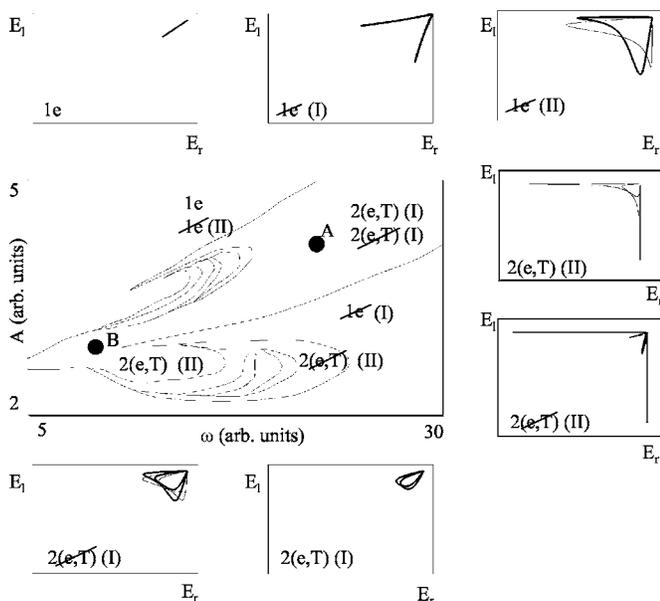


FIG. 2. Portrait of the different solutions found at different parameter values of the forcing. The particular parameters of our dynamical model were chosen to guarantee that the labia are closed unless forced to be opened by respiratory requirements. In order to do so, we related the variables in the neural model ($E_{l,r}$) with the mechanical parameter $\delta_{l,r}$ as $\delta_{l,r} = 33 \times 10^6 / 2 \times 10^8 (1 - E_{l,r})$. The time scale of Eqs. (1) and (2) was $\tau = 30$. The insets display projections of the solutions within the different regions onto the excitatory variables (E_l, E_r). **A** and **B** label two particular sets of parameters: **A**: $(\omega, A) = (22.00, 2.75)$; **B**: $(\omega, A) = (12.50, 2.75)$. We follow the notation used in the text to characterize the different symmetry types of the solutions: $1e$ is used for solutions of period 1 with exchange symmetry, $2(e, T)$ for period 2 solutions left invariant under the joint operation of e and T , $1\dot{e}$ represents two different period one solutions with no exchange symmetry, and $2(\dot{e}, T)$ a nonsymmetric period 2 solution. For the nonsymmetric solutions, the conjugate pairs are illustrated with different line types. A and ω are expressed in arbitrary units. A measures the relative strength of the forcing with respect to the activities of the nuclei involved, and ω measures the relative timing of the forcing with respect to the natural frequencies of the neural gating oscillators.

piration and the other during inspiration (Fig. 3, case B). This is a case in which the vocalization is executed with only one syringeal side. Fig. 3, case A, displays a time series data corresponding to a solution integrated with parameters at point A in Fig. 2. Notice that both sides are used to generate the syllables. Remarkably, the lack of exchange symmetry in the solution will leave its fingerprint in the acoustic features of the syllable. Moreover, as the different symmetry types are found at different values of the forcing frequencies, we can expect the syllabic rates to be a quantifier in terms of which comparisons between theory and experiment can be performed. This case has been reported in the literature [1].

IV. SONG SIMULATION

Recently, a simple model was proposed to synthesize birdsong, with biologically sensible parameters [8,15–20].

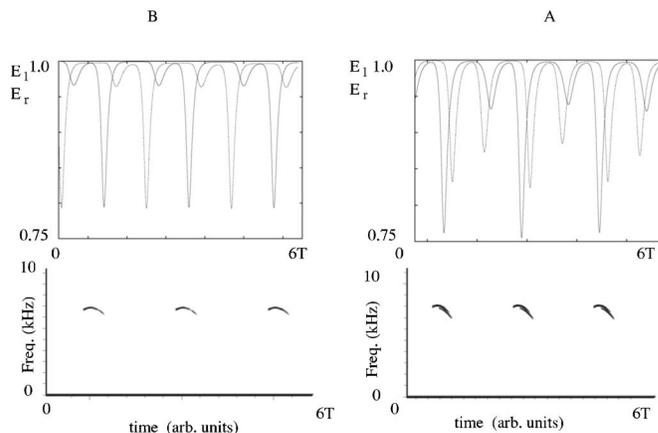


FIG. 3. Time series for E_l and E_r obtained integrating 1 and 2, with the parameters **A** (a) and **B** (b). The sonogram of a song consisting in three repetitions of a syllable obtained driving a syringeal model with the solutions in (a), and three syllables using the solutions in (b). Notice the different syllabic rates, and the difference in continuity of the trace describing the fundamental frequency.

The model, describing the dynamics of the labial displacement x_l (x_r) at the left (right) sound source, can be written as

$$\ddot{x}_{l,r} + \kappa(t)x_{l,r} - \beta(t)\dot{x}_{l,r} + \gamma x_{l,r}^2 \dot{x}_{l,r} - \delta_{l,r} = 0, \quad (3)$$

where $\delta_{l,r}$ represents the action of the syringealis ventralis muscle activity, a parameter such that for values above a threshold prevents vocalizations [8,16]. The parameter $\beta(t)$ represents the periodic respiratory forcing which, at the syllabic period, drives the syringeal model in and out of an oscillatory regime associated with the vocalizations [10]. We fed this model with the time series generated by 1 and 2 to emulate the values of $\delta_{l,r}$ (see Fig. 2 caption for details). In this way, we generated synthetic songs.

Integrating these equations for parameter values represented by **A** and **B** in Fig. 2, we generated a song whose sonogram is displayed in the lower panels of Fig. 3. Notice that as the syllabic rate is changed, different symmetry types are visited. The first syllables of the sonogram are characterized by a continuous trace. The second set of syllables, on the other hand, is characterized by a discontinuous trace. This acoustic feature is a signature of the gating parameter symmetry type. As we discussed above, the spatiotemporal pattern of Fig. 3(b) presents out of phase expirations. The delay between the expirations translates into a discontinuity in the fundamental frequency trace.

V. EXPERIMENTAL DATA

In this section we present data of bilateral airflow recorded for this study as well as review the data previously published in the literature, and discuss it in the framework of our model. Different gating patterns measured for several bird species are classified according to our spontaneous symmetry breaking scheme. In Fig. 4 we illustrate gating patterns with different symmetry types. The left column displays bilateral airflow (F_l for left; F_r for right) and air sac pressure

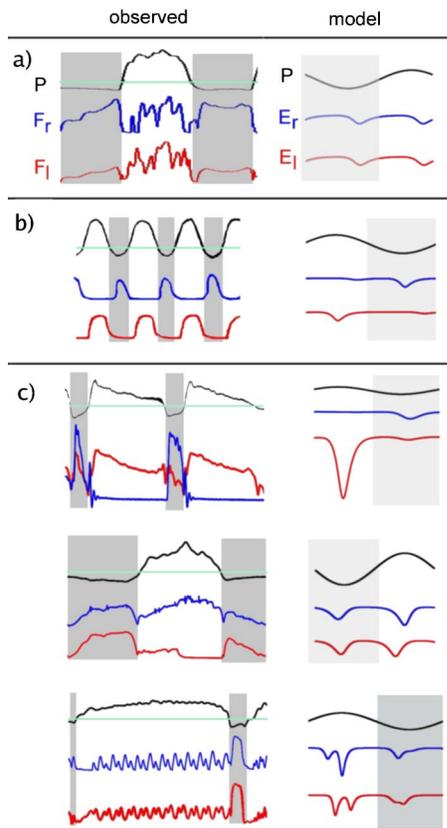


FIG. 4. (Color online) Different gating patterns measured for several bird species, and their relationships with the solutions of the proposed model. Parameters (A, ω) for the theoretical solutions displayed in (a) $(5.5, 30)$, (b) $(3.2, 20)$, and (c) $(2.6, 18)$ (top), $(4.31, 20)$ (middle) and $(4.5, 10)$ (bottom).

(P) data for song segments illustrating the various symmetry type solutions: $1e$, American robin, Fig. 4(a); $2(e, T)II$, Waterslager canary, Fig. 4(b), data redrawn from [21]; and, in Fig. 4(c), (top) cardinal, redrawn from [22], corresponding to symmetry type $2(e, T)II$, (middle) American robin and (bottom) white-crowned sparrow, data recorded for this study, both of them corresponding to symmetry type $2(e, T)II$. The middle panel and the bottom panel correspond to solutions of different Arnold tongues, and therefore present different degrees of internal structure.

The panels in the right column illustrate the solutions of the proposed model, corresponding to the panels in the left column. The first trace corresponds to the forcing (P), while the other two account for the activities of the neural populations assumed to drive gating muscles on the left and right sides ($E_{l,r}$, respectively). High values of these variables are interpreted as closing the controlled valve. The model output is driven by sinusoidal changes between expiratory and inspiratory pressure rather than the less symmetrical pressure cycles of the recorded data, and therefore is not intended to replicate the precise temporal aspects of the observed flow patterns but shows qualitative gating patterns that match those found in singing birds. For example, the number of pressure modulations is restricted in comparison to the recorded data of the white-crowned sparrow syllable. The

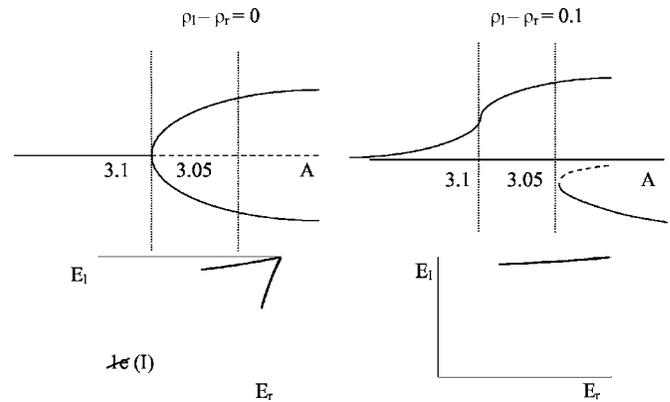


FIG. 5. The effect of an imperfect symmetry in the problem is illustrated in the case of the transition from a solution with symmetry $1e$ to the pair of conjugate solutions of symmetry type 1ℓ in the symmetric case (left panel) and in the imperfect case (right panel). In an open range of parameters, only one of the conjugate solutions survives.

qualitative similarity in out-of-phase fluctuations in left and right gating is, however, preserved.

The methods for recording bilateral airflow and air sac pressure were previously described in detail in [23].

VI. IMPERFECT SYMMETRIES

Throughout this work we made a strong hypothesis: that both the neural circuitry and the vocal organ are perfectly symmetric. We show that even in this perfectly symmetric configuration, the solutions can display a wide variety of spatiotemporal patterns, as those reported in the literature.

It is natural to ask what is the effect of slight imperfections on the system, as it could be expected to be the case in any biological organism. In this case it is expected that some solutions will disappear, and others will survive. Yet, it is important to notice that the surviving solutions will present spatiotemporal features preserving the fingerprint of the perfectly symmetric problem. As an example, we perturbed the dynamical system used to model the activity of the neural circuits controlling the gating in Eqs. (1) and (2). In particular, we added in Eq. (1) the effect of a slightly asymmetric input, leading to

$$\tau \frac{dE_{l,r}}{dt} = -E_{l,r} + S(\rho_{l,r} + 10E_{l,r} - 10I_{l,r}). \quad (4)$$

with $\rho_l = \rho_r + \epsilon$. The analysis of the solutions of this slightly perturbed system indicates that out of pairs of symmetrically conjugated solutions, some disappear in saddle node bifurcations, while the symmetric solutions of the perfectly symmetrical system survive the perturbation (slightly deformed). Figure 5 illustrates this phenomenon. For values of ϵ as small as 0.1, out of the pair of conjugate asymmetric solutions $2(e, T)II$ in Fig. 2, only the solution with $x_r \approx 1$ survives. The annihilation of complete sets of asymmetric solutions (for example, those involving mostly the activation of one side of the syrinx) is suggestive. It is known that lateralization in songbirds ranges from species presenting a clear unilateral

dominance (as white crowned sparrows, chaffinches) to others with approximately equal contributions from each syringeal side (as in brown thrashers, gray catbirds, and zebra finches). It is tempting to speculate that these species might present a different degree of departure from a perfectly symmetric neural substrate.

VII. CONCLUSIONS

In this work we emphasize that even when dealing with perfect symmetries, spontaneous symmetry breaking allows

a diversity of spatiotemporal respiratory patterns. Recently [24], it was shown that a diversity of respiratory gestures can be achieved as subharmonic solutions of a simple neural substrate. Spontaneous symmetry breaking [25] is another example of how nature can achieve complex solutions with minimal physical requirements.

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