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The generation of respiratory rhythms in birds

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Abstract

The generation of precise respiratory rhythms is vital for birds, which must generate specific pressure patterns to perform several activities, song being one of the most demanding ones. These rhythms emerge as the interaction between a peripheral system and a set of neural nuclei which control the action of expiratory and inspiratory muscles. A computational model was proposed recently to account for this interaction. In this work, we describe the set of solutions that this model can display as its parameters are varied, and compare experimental records of air sac pressure patterns with the predictions of the model.
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Keywords: Birdsong; Respiratory system; Rate models

1. Introduction

The generation of a behavior involves interactions between the nervous system, the morphology of the peripheral system and the environment. The biomechanics of a peripheral system imposes constraints on the neural control, and also provides opportunities for the emergence of complexity in behavior [1]. A rich example is birdsong, where neural instructions drive a complex respiratory system in order to activate the vocal organ. The dynamical state of the respiratory system feeds back into the nuclei in charge of expiration and inspiration, and therefore the emerging dynamics can be potentially extremely rich.

Recently, the interaction of brainstem nuclei and the peripheral respiratory apparatus was shown to be capable of generating complex respiratory patterns in duetting sub-oscines [2]. The example is interesting, since these birds lack the telencephalic nuclei that oscine birds have [3], and therefore the complex patterns cannot be the result of a complex forcing on the respiratory system. At the respiratory level, the neural organization of oscines and sub-oscines is equivalent. With this precedent, we inspect the respiratory patterns that can be generated as the result of the interaction of the respiratory nuclei and the respiratory peripheral system.

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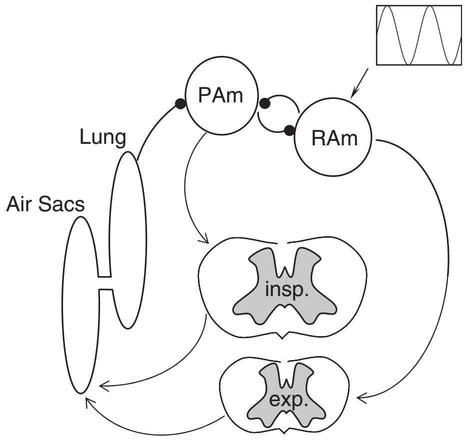

Fig. 1. A schematic diagram of the nuclei and peripheral system involved in our model.

2. The neural control of birdsong

The respiratory gestures of all birds are controlled by inspiratory and expiratory muscles. These muscles are innervated by neurons in the spinal chord. The premotor neurons activating them are located in the medulla. The bulbospinal neurons projecting to the region of the spinal chord containing motorneurons innervating expiratory muscles are concentrated in the nucleus retroambigualis (RAm), while the nucleus parambigualis (PAm) contains premotor neurons of the inspiratory muscles. We call this part of the respiratory system lower respiratory system (LRS).

In Fig. 1 we sketch the elements involved in the respiratory circuit of birds. In order to perform a computational implementation of this model, the dynamics of the air sacs is described in terms of a variable accounting for 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 [4]. Eqs. (3) and (2) describe the activities of these nuclei using a standard additive model [5].

Translating these anatomical observations into a model for the respiratory system, we get:

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

$$\dot{I}_1 = 30[-I_1 + A_1\cos(\omega t) + S(E_1 - 18I_2 + 2I_1 - f(x))], \tag{2}$$

$$\dot{I}_2 = 30[-I_2 + S(E_2 - 18I_1 + 2I_2 + A_2\cos(\omega t))], \tag{3}$$

where $S(x) = 1/(1 + e^{-x})$ is a standard saturating function [5]. The function $f(x) = 9x^3/(1 + x^3)$ represents the inhibitory effect of CO_2 sensors on the activities responsible for inspiration [4]. We will neglect the inertia of the air sacs, therefore reducing the dimensionality of the dynamical system to three.

The parameters E_1 and E_2 are basal activity levels for nuclei PAm and RAm. These nuclei are, in turn, driven by rostral nucleus of the ventrolateral medulla (RVL) (modeled as the forcing term $F_i(t) = A_i\cos(\omega t)$, $i = 1, 2$), responsible for generating or conveying a basic oscillatory rhythm. The complexity of the solutions displayed by Eqs. (1)–(3) with $A_i = 0$ anticipates an extremely rich set of respiratory solutions. Recently, a wide diversity of pressure gestures used to generate different syllables during song was explained in terms of the subharmonic solutions of Eqs. (1)–(3) when the parameters were such that for $A_i = 0$ the system displays excitability [6]. For these reasons, we study in detail the solutions of (1)–(3) with $A_i = 0$.

3. The solutions of the model

In Fig. 2 we display a detailed bifurcation diagram of the model for $\mu = 1$, $k = 0.2$, with E_1 and E_2 the bifurcating parameters. There are 11 regions of the parameter space with qualitatively different solutions.

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