

From perception to action in songbird production: Dynamics of a whole loop

Ana Amador, Santiago Boari and Gabriel B. Mindlin

Abstract

Birdsong emerges when a set of highly interconnected brain areas manage to generate a complex output. This consists of precise respiratory rhythms as well as motor instructions to control the vocal organ configuration. In this way, during birdsong production, dedicated cortical areas interact with life-supporting ones in the brainstem, such as the respiratory nuclei. We discuss an integrative view of this interaction together with a widely accepted “top-down” representation of the song system. We also show that a description of this neural network in terms of dynamical systems allows to explore songbird production and processing by generating testable predictions.

Addresses

Department of Physics, FCEyN, University of Buenos Aires, and IFIBA Conicet, Int. Guiraldes 2160, Pab. 1, Ciudad Universitaria, 1428 Buenos Aires, Argentina

Corresponding author: Mindlin, Gabriel B (gabo@df.uba.ar)

Current Opinion in Systems Biology 2017, 3:30–35

This review comes from a themed issue on **Mathematical modelling, Dynamics of brain activity at the systems level (2017)**

Edited by **Marcelo O. Magnasco**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 1 April 2017

<http://dx.doi.org/10.1016/j.coisb.2017.03.004>

2452-3100/© 2017 Elsevier Ltd. All rights reserved.

Keywords

Sensorimotor integration, Dynamical systems, Birdsong.

Introduction

Birdsong is an attractive model to study the neurobiology of behavior. Several elements contribute to its particular appeal: the stereotyped nature of this behavior, its complexity, and that some degree of learning is involved for approximately forty percent of the known bird species. As learned vocal production occurs very rarely in the animal kingdom, songbirds have been the focus of active research. The approach from neuroethology stresses how this complex behavior emerges from the interaction between the nervous system, the body and the environment.

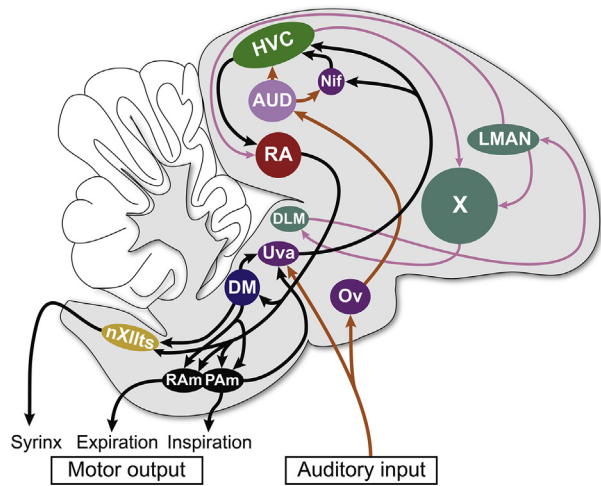
Specialized neural circuitry is dedicated to vocal learning and production, presenting strong similarities to mammalian brain pathways (e.g. [1]). This neural

architecture is known as the *song system* (see [Figure 1](#)) in which the telencephalic nucleus HVC (used as proper name) is a site where motor and auditory representations of song merge. HVC neurons display song motor-related activity and can be excited by auditory presentation of the bird’s song (BOS) [2–5]. This property is extended to all the nuclei of the song system downstream from HVC, and the neural response is stronger to BOS than to any other auditory stimuli (e.g. [6–8]). This selective response to BOS emerges during learning and is preserved in adulthood [9–11]. Damage to the vocal periphery results in altered auditory tuning of BOS-selective neurons [12,13]. Moreover, HVC neurons show auditory-vocal mirroring properties, i.e., the same pattern is generated when singing and hearing the BOS [5,14], with no delay between the auditory and the motor pattern. In this way, HVC constitutes a good candidate to explore sensorimotor integration. Being a cortical structure has also been an advantage for neurophysiological recordings. Therefore, there has been a bias towards focusing in cortical structures, positioning HVC at the top of the hierarchy of motor control and sensory processing. In this review, we present two current hypotheses for sensorimotor coding in songbirds, and show how dynamical systems modeling can be used to generate testable hypothesis to guide future experiments and advance neuroscience.

The “top-down” view

The telencephalic nucleus HVC and the Robust nucleus of the arcopallium (RA) (see [Figure 1](#)) are required for normal song production; bilateral lesions of either of these nuclei cause severe song disruptions [15]. Electrical stimulations during singing showed different functionalities for these nuclei: stimulating RA distorted acoustical properties of the ongoing syllable, while stimulating HVC altered the whole song program [16]. At the beginning of this century, technology allowed to record single neurons within cortical nuclei during singing. In nucleus HVC there are two distinct populations of neurons: projecting neurons and interneurons (see detailed description in [17]). The projecting neurons burst sparsely during song production, and engage neurons downstream the neural pathway [18]. Ultimately, they affect the rhythmicity of the respiratory nuclei and the motor neurons controlling the configuration of the vocal organ. After these experiments, a “top-down” picture emerged, in which the motor patterns were fully coded by the specialized cortical area HVC [19]. Confidence on this paradigm was built

Figure 1



Schematic of songbird's song system and sensory pathways. The song system is comprised of the song motor pathway (SMP, black arrows) and the anterior forebrain pathway (AFP, pink arrows). In the "top-down" view of the SMP, activity originates at HVC and projects downstream to RA. RA projects to DM in the midbrain and to brainstem nuclei: nXIIIts (whose motor neurons innervate the syringeal muscles), RAm and PAm which control expiration/inspiration, respectively. An integrated view of the SMP takes a recurrent motor pathway into account, which connects both DM and PAm indirectly to HVC via Uva. The AFP presents an indirect pathway from HVC to RA, resembling cortical-basal ganglia loops in mammals. AFP is crucial for song learning and adult song maintenance. Additionally, HVC receives auditory information from two pathways (orange arrows). In one pathway, auditory information is transmitted through Uva to HVC both directly and indirectly via Nif. The other pathway sends the auditory input through Ov. Ov projects to highly-interconnected nuclei dedicated to auditory processing (Field L, CM and NCM, represented as "AUD" in the figure). Abbreviations: nXIIIts, tracheosyringeal portion of the hypoglossal nucleus; RA, Robust nucleus of the arcopallium; DM, dorsomedial intercollicular nucleus; RAm, nucleus Retro-ambiguus; PAm, nucleus Parambiguus; Uva, nucleus Uvaeformis; Nif, nucleus interfascialis of the nidopallium; Ov, nucleus Ovoidalis; LMAN, lateral magnocellular nucleus of the anterior nidopallium; DLM, dorsal lateral nucleus of the medial thalamus; CM, caudal mesopallium; NCM, caudal medial nidopallium.

through thermal manipulations in HVC [20]. Cooling HVC would slow down the time scale associated with the structure at the top of the hierarchy, what would in turn, stretch the song. The actual stretching of song under cooling in zebra finches (*Taeniopygia guttata*) gave support to the "top-down" view of this neural architecture.

An integrated approach

The inspection of the song system's anatomy suggests a more integrated view. The output of the song system is given by nuclei at the brainstem controlling muscles that affect syringeal configuration and respiration [21]. These nuclei receive motor commands from nucleus RA, which is innervated by nucleus HVC. There are also several pathways linking the brainstem back to HVC

(see Figure 1) defining a looped network. The anatomical evidence has been strengthened with physiological evidence. Electrical stimulation applied to the thalamic nucleus Uvaeformis (Uva) activated HVC and the vocal motor pathway, including tracheosyringeal motor neurons that innervate the bird's vocal organ [22]. Spiking activity in Uva can modulate forebrain activity: single Uva spikes suppress and spike bursts enhance spontaneous and auditory-evoked bursts in HVC and RA neurons [23]. Uva lesions permanently disrupted vocal production [22,24], while chronic multiunit recordings from Uva during singing show bursts of premotor activity that lead the onset of some song components. Also, larger bursts marked the end of complete song motifs [22]. Further physiological evidence suggested that the song system is organized as a recurrent pathway, with no structure at the top of the hierarchy [25–27]. Another aspect that builds confidence towards an integrated approach is inter-hemispheric coordination. HVC activity is synchronized between hemispheres during song production despite the absence of commissural connections between these two nuclei or any other forebrain song control nuclei [28]. This observation suggests that the bilaterally projecting brainstem nuclei may provide a synchronizing signal to the forebrain song system [29].

To test the integrative hypothesis, the thermal manipulation work was revisited. It was observed that if song timing was controlled by coupled chains within HVC, the focal cooling of HVC should cause a much greater stretching than observed experimentally. This would be compatible with the stretching predicted if HVC was part of a several nodes brainstem-forebrain network [30]. Moreover, it was reported that cooling the thalamic nucleus Uva slows song tempo in a manner consistent with a distributed timing mechanism. The cooling experiment was also revisited for a different species [31]. Canaries (*Serinus canaria*) showed an initial stretching of song when cooling down HVC, but when the temperature dropped below a critical point, the "breaking" of some syllables occurred. This syllable deformation could be explained if an additional effect was considered: the slowing down of the synaptic inputs into HVC. Altogether, these experiments suggest that a more integrated architecture is needed to reproduce how temporal features of the song are affected by thermal manipulations.

Towards dynamical modeling

An operational model capable of reproducing observed physiological quantities could allow us to illustrate how an integrated model could work. Yet, building a dynamical model for the song system is a difficult task. The knowledge of different areas is disparate and the measurement of single units involves just a few neurons among thousands. Another piece of information that

Download English Version:

<https://daneshyari.com/en/article/8918160>

Download Persian Version:

<https://daneshyari.com/article/8918160>

[Daneshyari.com](https://daneshyari.com)