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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.

Song system

Neural architecture model

Left hemisphere

Right hemisphere

Modeled pressure patterns of canary song

Serinus canaria

Sensorimotor integration; dynamical systems; birdsong

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

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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 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 remains elusive is the connectivity between neurons that could, in principle, generate networks of different topologies. On the other hand, at the other end of the central nervous system (CNS), the respiratory and the syringeal muscle activation patterns can be

considered good proxies of the song system's output. Moreover, they can be measured during the generation of behavior, e.g. [32–37]. Therefore, a model written in terms of average activities of neural populations could involve variables to be compared with actual observables. Typically, these models are phenomenological in nature [38]. Yet recently, techniques have been developed that allow computing measures of global activity from coupled excitable units [39]. The dynamics derived from first principles for those collective variables is similar to the one displayed by the variables of the phenomenological rate models.

The motor patterns used to generate song can be successfully reproduced by a low dimensional dynamical system [40–42]. In Figure 2a we show a representative respiratory pattern used by canaries during singing. This pattern can be thought as a proxy for the average activity of an expiratory related brain area, which is known to consist of interconnected excitatory and inhibitory neural populations. This structure is known in the literature as a *neural oscillator* and can display a variety of different dynamics as fixed points or oscillations (see Figure 2b and [43]). To test the hypothesis that a circular architecture can give rise to the observed respiratory patterns, the input functions that would be necessary for driving the neural oscillator were identified [40]. Then, it was shown that those inputs could be embedded in a circular topology.

The modeling starts by identifying the plausible dynamical responses of a neural oscillator to changes in the input parameters. The bifurcation diagram of the driven dynamical system (displayed in Figure 2b) serves as a map during this procedure. Canary syllables are generated with four basic respiratory patterns [44]. Syllables A, B, C and D in Figure 2a are representative examples. The illustrated paths in parameter space (Figure 2b) were used to synthesize the pressure gestures shown in Figure 2c. For syllables C and D, a structured input is needed (blue and red paths in parameter space). The blue lines represent an input from the brainstem, while the red lines, the input from the telencephalon. Remarkably, it is possible to generate the input to the neural oscillator from the telencephalon with the same initial pulse of activity responsible for the brainstem input. In this way, a unique initial command is responsible for a direct effect on the neural oscillator, and the indirect one as well. During this indirect path, the signal gets enriched. For one class of pressure patterns, the time traces predicted by the model are shown in Figure 3.

Describing the song system by means of population activity averages allows the output of the CNS to smoothly couple with models for the vocal organ. This biomechanical device has been modeled as a nonlinear oscillator whose time dependent parameters can be related to CNS output [45,46]. In this way, it is possible to build a bridge that connects the CNS with the body to generate the appropriate behavior. The song system is close to provide such a description, as has been recently shown [47].

Beyond reproducing an observable, this operational model can lead to quantitative and precise predictions. It allows, for example, to revisit quantitatively the effect of cooling HVC. Since cooling would imply not only slowing down the dynamics in HVC, but that of its synaptic inputs as well, the model predicts which syllables would break and how (see [31,40] for more details).

Conclusions

Despite the deeply interconnected nature of the song system, there is a widely accepted “top-down” view in the birdsong community. According to this view, birdsong is encoded primarily in a dedicated cortical brain area. We adhere to an integrated hypothesis of the song system, in which brainstem and telencephalon interact to generate behavior. This is a natural way to integrate an evolutionarily new function (the production of a learned behavior) with older ones, vital to the animal’s survival, as respiration or non-learned (innate) vocalizations. Also, with an integrated view, inter-hemispheric coordination between telencephalic areas emerges naturally.

It is difficult to imagine that we will be able to understand birdsong motor production isolated from the integration with its auditory processing, or from the signals that the brainstem sends to the cortical areas. Low dimensional models could act as conceptual tools to orient these inspections, allowing to test the consistency of all these concurrent signals in the brain regions where they are integrated. An auditory signal triggered by a syllabic onset, for example, could be easily integrated into a motor coding if HVC receives a sparse notice of the syllable onset from the brainstem.

Birdsong has gained much and valuable information from single unit measurements, just like physics could have not advanced without describing the dynamics of a single point-like particle. Yet, understanding the emergence of behavior will require moving beyond single unit measurements, widening our perspective to integrate different time scales, brain areas and functions, just like physics had to move towards thermodynamics to explain macroscopic machines. To move forward in this direction, we propose a model for the song system in terms of set-average quantities integrating different areas. Lower resolution inspection of the whole system could be appropriate to advance into the understanding of this complex animal model.

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Highlights

- Birdsong as a model to study the generation of a complex motor task.
- We discuss an integrated hypothesis for sensorimotor coding in songbirds.
- Low dimensional models as conceptual tools to explore whole-brain interactions.

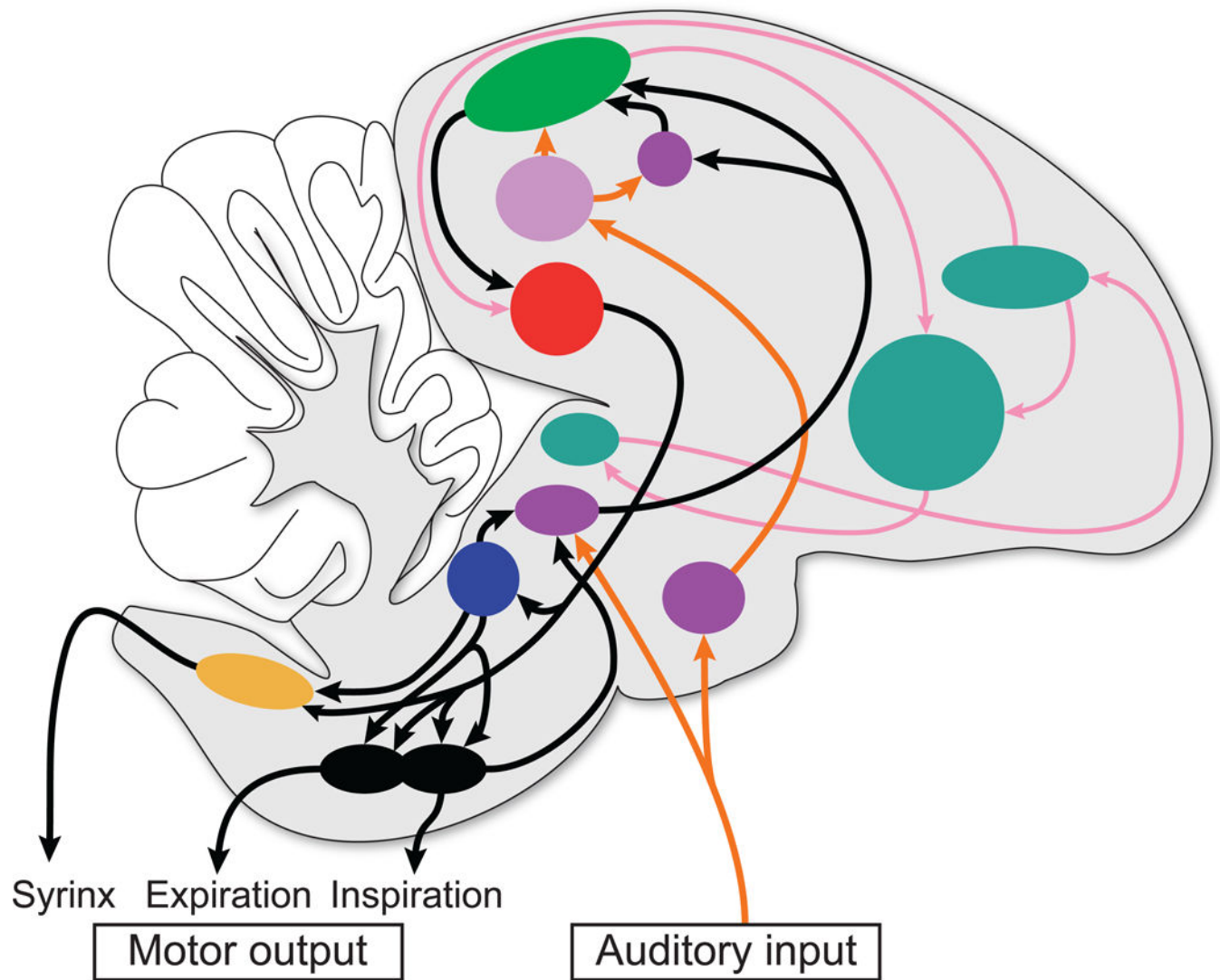


Figure 1. Schematic of songbird's song system and sensory pathways

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: nXIIts (whose motor neurons innervate the syringeal muscles), RA_m 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: nXIIts, tracheosyringeal portion of the hypoglossal nucleus; RA, Robust nucleus of the arcopallium; DM, dorsomedial

intercollicular nucleus; RAm, nucleus Retroambigualis; PAm, nucleus Parambigualis; Uva, nucleus Uvaeformis; Nif, nucleus interfaccialis of the nidopallum; 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.

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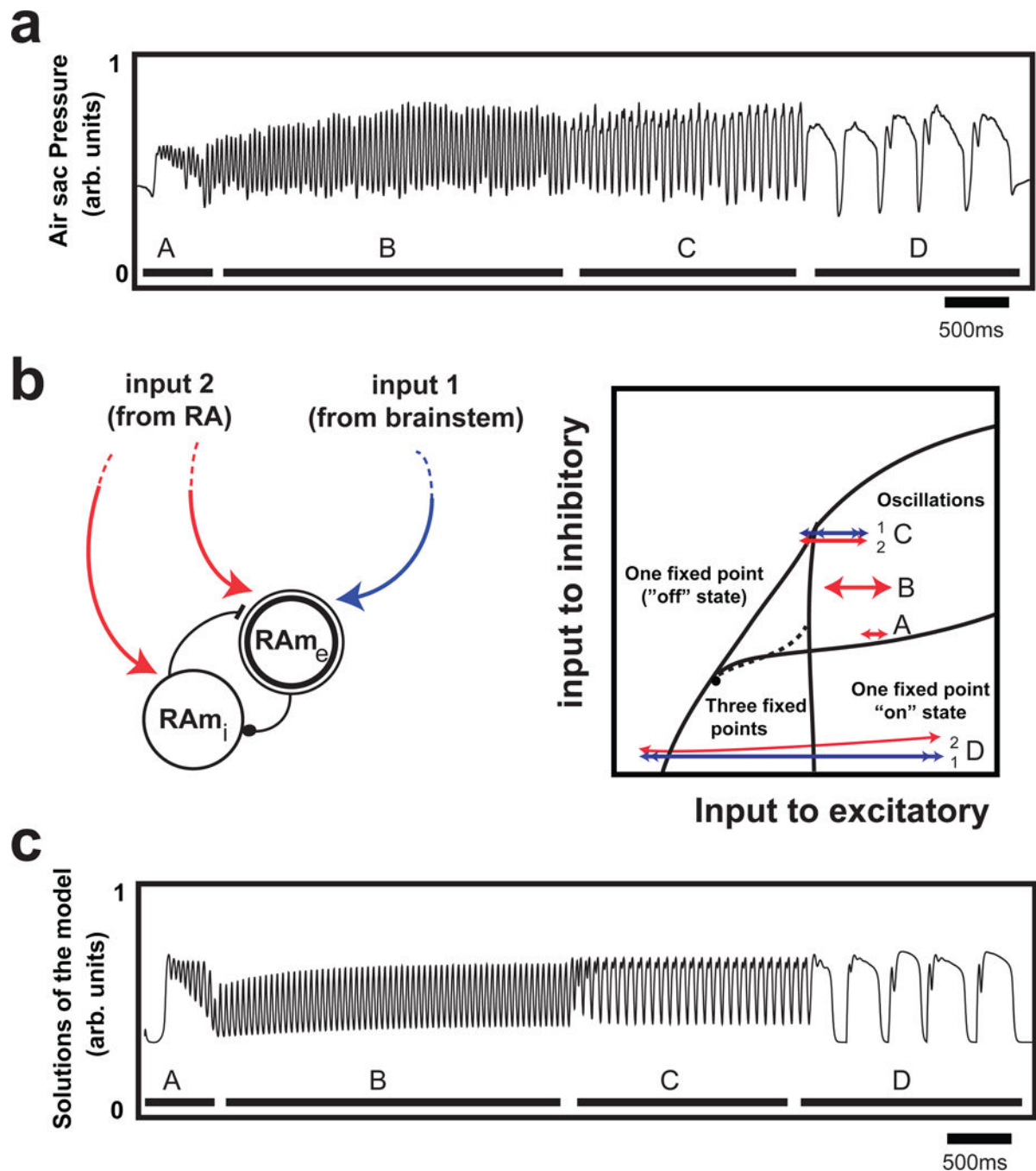


Figure 2. Modelling respiratory patterns of canary song

(a) Recorded air sac pressure. Canary song is composed of the repetition of different subunits (syllables) at a given syllabic rate. Syllables of canary song repertoire can be classified using topological tools and PCA, defining the 4 types of pressure patterns shown here (black bars): (A) Pulsatile, (B) P1, (C) P2 and (D) P0 solutions. (b) Diagram of expiratory neural nucleus RAm as populations of inhibitory and excitatory units driven by inputs from brainstem and RA (left). The activities of the excitatory and inhibitory populations (x_1 and x_2 , respectively) are prescribed by an additive model: $\dot{x}_i = -x_i + S(\rho_i +$

$\alpha_{1i}x_1 + \alpha_{2i}x_2$ with $i=1,2$ and $S(x) = 1/(1 + e^{-x})$; $\rho_1(t)$ and $\rho_2(t)$ are the inputs to the excitatory and inhibitory populations, and the constants α_{1i} and α_{2i} describe the architecture of the array. For parameter values see [40]. (Right) Bifurcation diagram in terms of inputs to inhibitory and excitatory populations. Bifurcations (black lines) separate regions of parameter space with qualitatively different behaviors (shown in figure). Color-coded, named arrows show the corresponding parameter space paths for the inputs to RAM necessary to obtain the respective solution shown in (c). Adapted from [42]

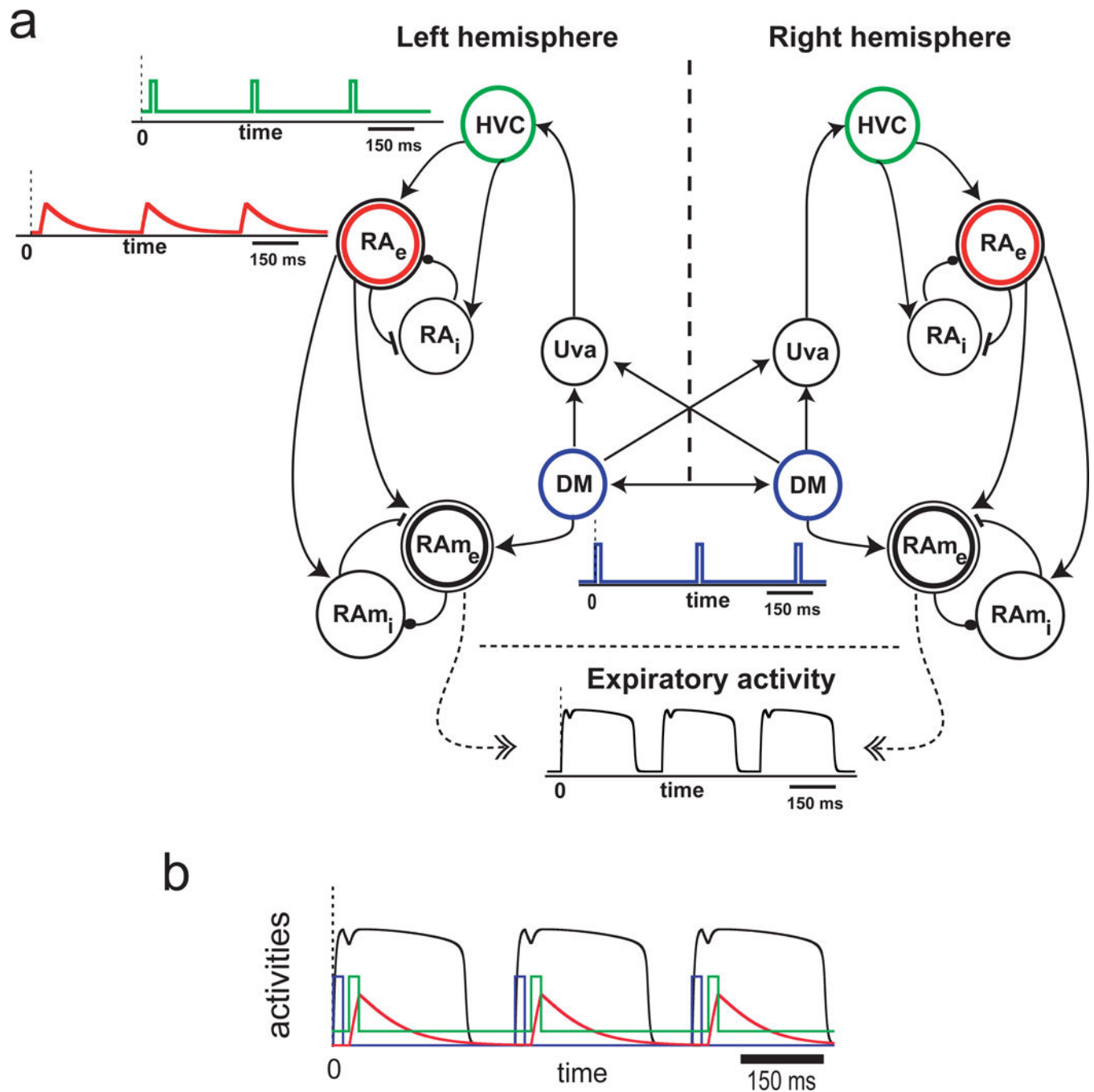


Figure 3. A circular model for birdsong motor control

(a) Minimal neural architecture description including a looped connectivity that can reproduce measured pressure patterns of canary song. Circles represent neural nuclei included in the model. Some nuclei (RA, RAm) are represented as an interconnected set of excitatory (-e) and inhibitory (-i) populations. Bilateral connections are considered in the description. DM has been proposed as the common input to the expiratory-related area (putatively nucleus RAm) and to HVC via Uva. Color-coded time traces represent the population activity (arb. units) of the nucleus of the same color. At $t=0$ a pulse of excitatory

activity is sent to RAm and Uva. HVC activity is modeled as a combination of a continuous component (notice activity baseline) and sparse peaks provided by the input from DM via Uva (notice the time delay). Modelling RA as a neural oscillator allows it to respond to HVC input with a sharp growth followed by an exponential decay that projects to RAm. In this way, RAm has a primary, direct input from DM and a secondary input that consists of the processed signal through telencephalic nuclei. Finally, RAm drives the expiratory activity necessary to produce song. (b) Superimposed time traces shown in (a). This solution represents a modeled P0 pressure pattern of canary song. For this syllable type (P0), the model presents a specific prediction of HVC activity timing: a sharp peak near syllable onset. Adapted from [40] and [47].