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Comparative study of synfire chain and ring attractor model for timing in the premotor nucleus in male Zebra Finches

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Abstract. Timing is crucial for the generation of a wide range of sensorimotor tasks. However, the underlying mechanisms remain unclear. In the order of milliseconds, premotor nucleus HVC (proper name) in male zebra finches is an outstanding model in studying the sequential neuronal activity encoding action timing. Current computational models of HVC rely on the synfire chains, which are not robust to noise and function for a narrow range of weights. An alternative with robust functional properties [11][5] are attractors. Here, we compare the two models and show that not only the ring attractor is more robust, but can also reproduce the brief activity bursts of HVC neurons.

1 Introduction

Timing is crucial for a wide range of sensorimotor tasks, including speech and birdsong production, which require precise temporal control at the scale of tens to hundreds of milliseconds for the essential tight coordination of vocal muscles. In songbirds, temporal precision is managed by a localized timing area, the premotor nucleus HVC (proper name), which projects to a downstream motor nucleus, RA (robust nucleus of the acropallidum) responsible of controlling syringeal and respiratory muscles. The projection neurons HVC_{RA}, fire in a time-locked manner during singing, producing a single $\approx$ 10 ms long burst of 3-6 spikes [4]. To simulate neuronal dynamics giving rise to motor timing at this scale, several computational models have been proposed i.e. ramping models, internal clocks, population clocks, labeled-line models and multiple-oscillator models [3, 2]. Among these, population clocks and in particular synfire chains are most commonly used to model the particular dynamics of the aforementioned nucleus HVC.

A synfire chain [8] is a feedforward network of excitatory neurons organized in sequentially connected layers (or pools), with neurons in the same layer firing in an almost synchronous manner [8, 6]. However, the purely feedforwad connection pattern of synfire chains does not appear compatible with the connectivity patterns revealed experimentally in cortical networks, which typically entail high levels of reciprocal connectivity [10]. Additionally, synfire chain networks are sensitive to noise and not very robust to weight variability, requiring

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precisely tuned synaptic strengths to avoid runaway excitation (saturation) or decay.

We propose attractor models as an alternative since their dynamics provide both robustness to noise and high accuracy. Linear attractors, also referred to as ring attractors [11][5], in the case of asymmetric connections, can drive a drifting activity bump, with robust and resilient properties thanks to recurrent connections [5]. However, it remains unclear whether attractors with structured connectivity can accurately represent HVC dynamics underlying song timing as HVC song-related activity is very sparse and the underlying activity bump is very narrow; the timescale of neuronal dynamics may impose a limit on bump width in this model. We propose that this narrow bump of activity could be the result of sparse, strong excitatory connections, organised as a function of the neurons' preferred timing. In the present work, we compare synfire chains and the ring attractor model, their output and robustness and propose a Ring Attractor model with a narrow Gaussian pattern of connectivity to model HVC neuronal dynamics.

2 Methods

2.1 Synfire Chain

To investigate synfire chains and assess their properties, we implement a synfire chain model with adaptive exponential integrate and fire (AdEx) neurons (eq. (1)). We build a network of 3000 neurons, consisting of 120 layers and 25 neurons per layer. Every neuron on one layer has an excitatory synaptic connection (weight) to each neuron of the next layer (all to all connectivity). All synaptic weights are identical and the value is such as to ensure proper activity progagation. The parameter values are the same as the ones reported in [9] and the adaptation parameters were adjusted to generate bursts of 4 spikes. The AdEx model is described as below:

$$C\frac{dV_i}{dt} = -g_L(V_i - E_L) + g_L\Delta_T e^{(\frac{V-V_T}{\Delta_T})} - w + I_{syn} + I_{ext,i}(t) + \sqrt{\tau_n}\sigma\eta_i(t),, \tag{1}$$

$$\tau_w\frac{dw}{dt} = a(V - E_L) - w + b\tau_w\delta(t - t^f),, \tag{2}$$

where C is the membrane capacitance and V is the membrane potential. On the right hand side (rhs) of Eq. (1), g_L is the leak conductance, E_L the leak reversal potential, V_T the threshold, Δ_T the slope factor, I_{ext} the external input, I_{syn} the synaptic input and w the adaptation variable. The last rhs term is a zero-mean Gaussian white noise. In Eq. (2), τ_w equals 100 ms, a is -0.5 nS and b 0.5 nA. When the membrane potential crosses the threshold potential ($V > V_T$), the above parameters are updated: $V \to V_r, w \to w + b$, where V_r is the reset potential and the update parameter b (0.01 nA) is the spike triggered adaptation.

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Synaptic input is a function of synaptic weights and post-synaptic potential:

$$I_{syn} = \sum_j W_{ij} \sum_k \Theta(t - t_j^k)\, e^{\frac{-(t-t_j^k)}{\tau_s}}, \tag{3}$$

where $\Theta(t - t_j^k)$ is a step function and t_j^k denotes the $\mathrm{k^{th}}$ spike of the $\mathrm{j^{th}}$ neuron.

2.2 Ring Attractor with a Spiking Neural Network

We consider a discrete population of N = 3000 adaptive exponential integrate-and-fire neurons that are able to display a burst activity as it has been observed in HVC. The dynamics of each AdEx neuron $i \in \{1, 2, ..., N\}$ in the network are given by Eq. (1). The equations governing adaptation and synaptic input are as in the synfire chain model, respectively described in Eq. (2) and Eq. (3). The weight matrix W is chosen of the following form:

$$W_{ij} = W_0 + W_2 \frac{1}{\sigma\sqrt{2\pi}} e^{-\left(\frac{i-j+\beta}{2\sigma}\right)^2} . \tag{4}$$

As HVC microcircuitry does not display spatio-temporal organization, W is defined based on the neurons' preferred timing and not their spatial position. W_0 represents global inhibition, W_2 the excitation factor and σ the standard deviation of excitation. The β (bias) term makes the connectivity pattern asymmetric.

2.3 Simulations

In both models, the simulation time and network size are identical, 350 ms and 3000 neurons respectively. We also adjust the parameters and layer size to get a similar propagation speed in both. All simulations were performed with Euler integration and a timestep (dt) of 0.01 ms for the synfire chain and 0.1 ms for the ring. In the synfire chain we inject a current only to the first layer (12 nA for 1 ms) and in the ring attractor only to one neuron (1.9 nA for 15 ms). Additionally, a constant input is needed in the ring to preserve the bump activity (0.7 nA). Parameter values for the simulations are detailed in the code in Github.

2.4 Robustness protocols

We design two test protocols, compatible with both models, to evaluate the robustness of the network under possible perturbations. One test corresponds to noise injection in the synaptic weights while the second corresponds to an inhibitory input injected on random neurons in the population. In the first test, random synaptic weights, with a total of at least 10 percent are affected. The amount of noise is set to be a function of the weights (30 percent). In the second test, we start by affecting only 5 percent of the population with an inhibitory input of an amplitude equal to 10 percent of the excitatory starting input.

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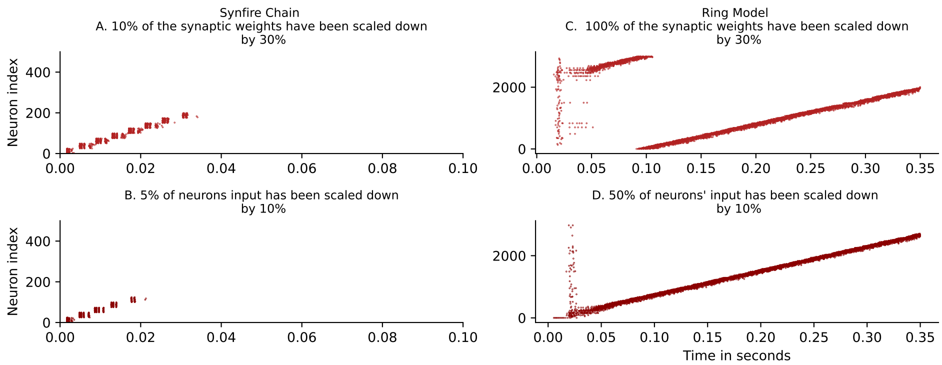

Fig. 1: **Synfire Chain and Ring Attractor models.** Representation of spiking dynamics of both models and their robustness.(A) Behavior of the synfire chain facing a decrease in synaptic weights. There is a stop in propagation. (B) Behavior of the synfire chain facing external inhibition. There is a stop in propagation when 5 percent of the population is affected. (C,D) same as (A,B) but for the Ring Attractor. Neurons inhibited in both models are not functionally clustered; they are randomly chosen in the network. Note: In panels A and B, we show a zoomed in version to illustrate where propagation stops.

3 Results

In the ring attractor model, recurrent connections allow for the formation of an activity bump that remains stable across a wide range of weights [5]. To ensure propagation across stable states and consequently generate sequential activity, several approaches have been identified [5], including using a moving stimulus as an external drive, an asymmetric connectivity profile and adaptation. The first two have, respectively, a linear and quasi-linear relationship with the speed of the bump. Adaptation can ensure bump propagation through delayed, local inhibition [5].

3.1 Robustness

With the first robustness check protocol, we show in Fig. 1 (A) that in the synfire chain with a 10 percent involvement of the population, propagation stops. In contrast, in the ring 1 (C), we can go up to 100 percent and there is only a slight delay in initiation of the activity, but no effect in the propagation. Results are similar in the second protocol, which is taken as a proxy for local inhibition, as neurons are chosen randomly based on their preferred timing, but could be considered as spatially correlated. Here, the synfire chain shows a cease in propagation 1 (B) at a 5 percent involvement, in contrast to up to 50 percent with the ring model 1 (D).

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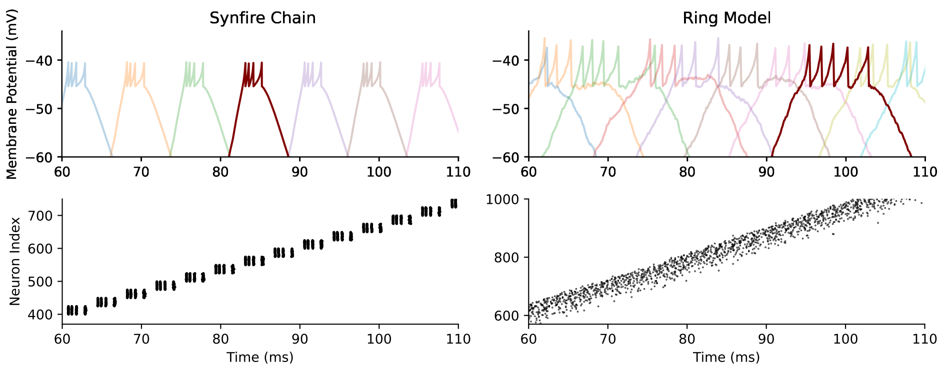

Fig. 2: **Spiking dynamics in the Synfire Chain (left) and Ring Model (right).** In the four panels a specific time in the sequence is chosen (60 -110 ms) and the activity (voltage traces, above) and raster plots (below) for each model are shown. A typical burst generated by the synfire chain lasts 4 ms and contains 4 spikes, whereas the one generated by the ring model 6- 10ms, with 3- 6 spikes. The different colors represent different neurons and in both models, every 50 neurons, a neurons voltage trace is plotted (i.e, neuron 50, 100 etc.).

3.2 Reproducing HVC spiking dynamics

We show that the two models are able to reproduce HVC dynamics as shown in Fig. 2. The ring model shows a continuous propagating activity across the population, whereas the synfire chain is more discrete due to its layered structure. We also show the burst patterns, duration and number of spikes per burst, which in the ring seem closer to experimental observations ([4], Fig.2).

4 Discussion

HVC neuronal recordings reveal bursts of 3-6 spikes lasting 6-10 ms, time-locked to the song. In this study, we implement two models, aiming to capture the sequential neuronal activity of HVC, while preserving these individual neuronal properties. We use a spiking model and as previous evidence [7] has shown that HVC bursts are mediated by calcium spikes, we add adaptation[1], which can account for ionic channel activity, depolarizing currents (parameter a in Eq.2) and calcium dependent potassium channels (parameter b). Our findings provide clear evidence with two robustness protocols that the ring attractor model is more robust in modelling HVC dynamics, compared to a synfire chain. Thereby, in the synfire chain, it emphasizes the fine tuning necessary for the weights, which does not support possible weight modifications possibly occuring due to developmental, seasonal, experiential factors. It also shows high sensitivity to a local inhibition with small size and low magnitude. Since HVC is not topologically organized, the neurons affected by this inhibition would not be functionally correlated and a preservation of timing is expected, especially with a small size and low magnitude. However, in both cases the ring model is robust and only displays a delay in activity initiation, even at higher perturbation size and magnitude. Furthermore, we compared the spiking dynamics produced from the synfire chain model and the ring attractor with an asymmetric connectivity profile. With both models, we generate sequential activity and spiking dynamics similar to the ones shown in HVC recordings [4]. A possible limitation of our model could be adaptive learning, which entails learning to modify the duration of a syllable, without affecting the other syllables. This has been shown to be the case in songbirds and it has also [9] been shown that only the synfire chain, and not attractors, can accomplish adaptive learning. However, as a structured attractor, the ring model could perform differently, which remains yet to be explored.

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