A Neural Microcircuit Model for a Scalable Scale-invariant Representation of Time

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Abstract

Scale-invariant timing has been observed in a wide range of behavioral experiments. The firing properties of recently described *time cells* provide a possible neural substrate for scale-invariant behavior. Earlier neural circuit models do not produce scale-invariant neural sequences. In this paper we present a biologically detailed network model based on an earlier mathematical algorithm. The simulations incorporate exponentially decaying persistent firing maintained by the calcium-activated nonspecific (CAN) cationic current and a network structure given by the inverse Laplace transform to generate time cells with scale-invariant firing rates. This model provides the first biologically detailed neural circuit for generating scale-invariant time cells. The circuit that implements the inverse Laplace transform merely consists of off-center/on-surround receptive fields. Critically, rescaling temporal sequences can be accomplished simply via cortical gain control (changing the slope of the f-I curve). Because of the generality of the Laplace transform and the flexibility of this neural model, this neural architecture could contribute to many neural computations over functions.

Keywords: time cell, scale-invariance, rescaling, gain control

Introduction

Numerous behavioral experiments in human and other animals suggest that time is represented in the brain in a scale-invariant fashion. Recent neurophysiological recordings of *time cells* provide a possible neural substrate of this behavior (Pastalkova, Itskov, Amarasingham, & Buzsaki, 2008; MacDonald, Lepage, Eden, & Eichenbaum, 2011; Salz et al., 2016; Tiganj, Kim, Jung, & Howard, 2017; Tiganj, Cromer, Roy, Miller, & Howard, 2018). To account for scale-invariant behavior, time cells should exhibit the scalar property: the width of their firing fields should scale up linearly with the peak time so that all neurons in the sequence have the same coefficient of variation (CV). While neural data are qualitatively consistent with these properties, it is unclear how the brain could construct scale-invariant time cells.

Chaining model breaks scale-invariance

We first rule out 1D chaining models where every synapse is modeled as the same synaptic kernel (Goldman, 2009) as a mechanism for scale-invariant temporal sequences. In this model the neural activity of the i th neuron is $g_i(t) = \int_{-\infty}^{t} g_{i-1}(t')K(t-t')dt'$. We notice that, up to a constant factor, g_i is the probability distribution of the sum of two random variables whose probability distributions are g_{i-1} and K respectively. If K has mean m and variance σ, then by central limit theorem, for large i, g_i will have mean im and variance $\sqrt{i}\sigma$; the coefficient of variation (CV) scales as $\sqrt{i}$ for different neurons along the chain. Since the CV is not a constant, 1D chaining models cannot generate scale-invariant sequences. We instead propose a feedfoward network architecture that implements an approximated inverse Laplace transform using a set of leaky integrators with a spectrum of functional time constants.

The network model

Our neural network model consists of three layers. The layer I neurons have exponentially-decaying firing rates with long time constants. This is achieved by the dynamics of the calcium-nonspecific cationic (CAN) current (Tiganj, Hasselmo,

& Howard, 2015). The layer I neurons project to the layer II neurons via NMDA synapses with uniform connectivity. The layer II neurons and the output layer neurons are connected via NMDA and $GABA_a$ synapses with connectivity given by the inverse Laplace transform, so that the firing rates for the output layer neurons approximate $T_s(t) = \frac{(-1)^k}{k!} s^{k+1} \frac{d^k f_s(t)}{ds^k}$ where $f_s(t)$ is the firing rate of an layer I neuron indexed by its rate constant s. This is the approximation of the inverse Laplace transform proposed in (Post, 1930), where k indexes the accuracy of the transform. The connectivity matrix $\mathbf{W}_k$ is given by discretizing the derivative in the previous equation, $\mathbf{T}(t) \approx \frac{(-1)^k}{k!} \mathbf{s^{k+1}} \odot \mathbf{D}^k \mathbf{f}(t) \equiv \mathbf{W}_k \mathbf{f(t)}$, where $\odot$ represents element-wise multiplication, and $\mathbf{s^{k+1}} = [s_1^{k+1}, s_2^{k+1}, ... s_N^{k+1}]^T$. When $\Delta s \to 0$, it can be shown that the connectivity matrix is symmetric and has an on-center, off-surround shape.

Simulation

Figure 1 shows the activity of the simulated time cells (the output layer neurons). They fire sequentially, with timescales of seconds to hundreds of seconds, and they have the same form of firing rates when rescaled by peak times. These results are consistent with neural data.

In addtion, this network can readily produce the "time rescaling" phenomenon, where the firing fields of time cells are rescaled by the length of the delay interval (MacDonald et al., 2011; Mello, Soares, & Paton, 2015; Wang, Narain, Hosseini, & Jazayeri, 2018). In previous work based on reservoir computing frameworks, rescaling requires learning new sets of weights (Hardy, Goudar, Romero-Sosa, & Buonomano, 2017; Goudar & Buonomano, 2017; Wang et al., 2018). On the contrary in the current framework, rescaling of the neural sequence is achieved simply by cortical gain control, i.e., a global change in the slope of the f-I curves among all the layer I neurons. Figure 2 shows the results of two simulations where the speed of the sequence was rescaled by $\alpha = \frac{1}{2}$ and $\alpha = 2$ by changing the cortical gain of all the layer I neurons.

Indeed as shown in Figure 2a,b changing the slope of the f-I curves changes the time constants of layer I neurons. Figure 2c shows the firing rates of the same time cells before and after the change in α. Their firing fields appear rescaled by the scaling factor $\frac{1}{\alpha}$, in accordance with observation (MacDonald et al., 2011; Mello et al., 2015).

Figure 2b shows the peak times of 55 time cells before and after rescaling. The linear relationship indicates that the time cells indeed code relative time during an interval.

Discussion

Although we emphasize on the network's ability to generate a representation of time, the functional capability of the neural circuit can be generalized in two important ways. First of all, the rescaling mechanism mentioned above gives the neural circuit the ability to compute Laplace transform over other variables. For example, if the rescaling factor above is controlled by instantaneous velocity (i.e. $\alpha(t) = \frac{dx}{dt}$), this neural circuit computes the Laplace transform with respect to position and is able to construct one-dimensional place cells (Howard et al., 2014). Second, functions represented in the Laplace domain can be manipulated more easily. For example, by flexibly modulating the weights in our neural circuit one can translate the functions to simulate future (Shankar, Singh, & Howard, 2016).

This model motivates experiments to find persistent firing neurons with a systematic broad spectrum of time constants and when techniques are available for measuring connectivity between functionally identified neurons, to test the predicted pattern of connections between the persistent firing neurons and time cells.

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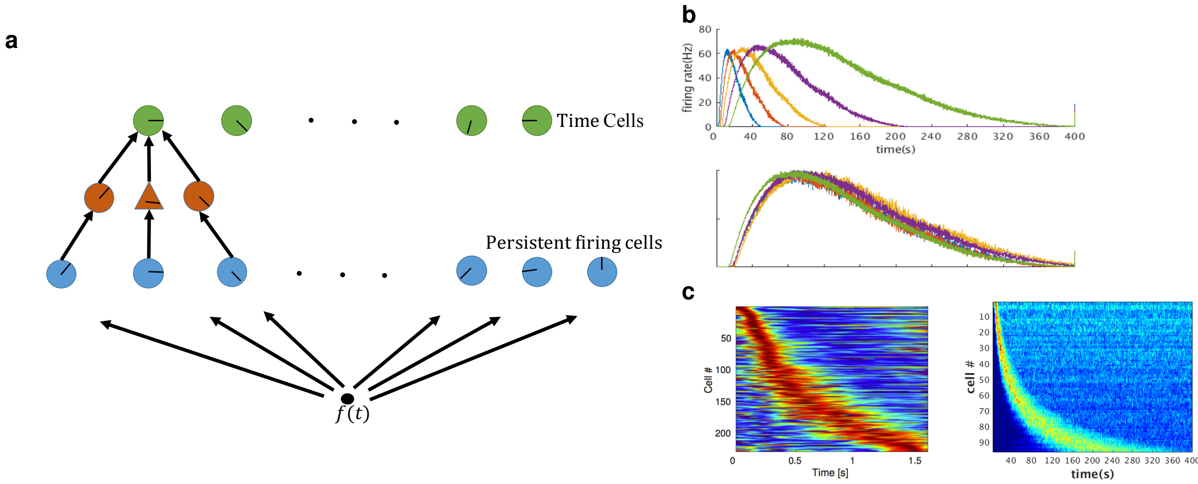

Figure 1: **a.** A schematic drawing of the network. The direction of the “clock hand” indicates cells with different intrinsic timescales. Triangle and circle refer to neurons with excitatory (NMDA) and inhibitory (GABAa) synapses, respectively **b.**Top: postsynaptic firing rates for 5 simulated time cells;Bottom: Postsynaptic firing rates rescaled by peak times **c.** Left:Recording data from monley lPFC during a delay match to category task (Tiganj et al., 2018) Right: The heatplot of simulated time cells. Each row represents the firing rate of one time cell.

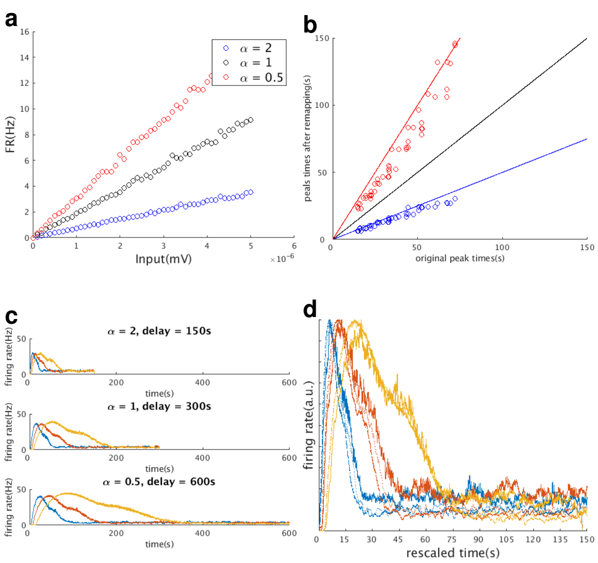

Figure 2: **a**. Three f-I curves of the same layer I cells when the delay interval is changed to half (blue), twice (red), and the same as the original. This results in the rescaling of the peak times of all the time cells. **b**. Red: peak times become twice the original, blue: peak times become half the original. Three straight lines indicate $y = 0.5x$(blue), $y = x$(black) and $y = 2x$(red). **c**. Firing rates of 3 representative time cells under different delay length. **d**. The firing rates of the same time cell under different delay lengths coincide when the time axis is rescaled according to the peak times . Color indicates the same cell in (**c**), thick line: $\alpha = 2$, dotted line: $\alpha = 1$, thin line: $\alpha = 0.5$)

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