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Self-sustained activity of low firing rate in balanced networks

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Self-sustained activity in the brain is observed in the absence of external stimuli and contributes to signal propagation, neural coding, and dynamic stability. It also plays an important role in cognitive processes. In this work, by means of studying intracellular recordings from CA1 neurons in rats and results from numerical simulations, we demonstrate that self-sustained activity presents high variability of patterns, such as low neural firing rates and activity in the form of small-bursts in distinct neurons. In our numerical simulations, we consider random networks composed of coupled, adaptive exponential integrate-and-fire neurons. The neural dynamics in the random networks simulates regular spiking (excitatory) and fast spiking (inhibitory) neurons. We show that both the connection probability and network size are fundamental properties that give rise to self-sustained activity in qualitative agreement with our experimental results. Finally, we provide a more detailed description of self-sustained activity in terms of lifetime distributions, synaptic conductances, and synaptic currents.

1. Introduction

Self-sustained activity (SSA), where neurons display persistent activity even in the absence of external stimuli [1,2], is observed in diverse situations such as in *in vitro* cortical cultures and in slice preparations [3–5], in *in vivo* cortical preparations [6], in slow-wave sleep [7], in anesthesia [8], and in the resting state [9,10]. Electrophysiological recordings of SSA states show irregular neural spiking, typically with low average frequencies of a few Hertz, obeying long-tailed distributions [11–13].

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Many works have modelled neural networks with SSA by using random networks composed of excitatory and inhibitory leaky, integrate-and-fire (LIF) neurons with external background input [14–19]. Other studies have considered networks with non-random architectures, composed of LIF neurons [20–24] or nonlinear, two-dimensional integrate-and-fire neuron models [25–30]. Both the architecture and neuron types that comprise the network play an important role in SSA states. Such states are generated and maintained by recurrent interactions within networks of excitatory and inhibitory neurons. A stable SSA state is related to strong recurrent excitation within the neural network, which is restrained by inhibition to prevent runaway excitation. The balance between excitation and inhibition in neural networks is considered critical to maintain a SSA state [5,14,31–34]. Kumar et al. [17] studied the effects of network size on SSA states. Barak and Tsodyks [35] shown that combinations of synaptic depression and facilitation result in different network dynamics. Triplett et al. [36] analysed spontaneous activity in developing neural networks and shown that networks of binary threshold neurons can form structured patterns of neural activity.

In this work, we verify the existence of SSA in a random network composed of neurons with different intrinsic firing patterns (the so-called electrophysiological classes [37]). We consider the adaptive, exponential integrate-and-fire (AdEx) [38] model with cortical neurons modelled as regular spiking (RS) cells with spike frequency adaptation and fast-spiking (FS) cells with a negligible level of adaptation. In such networks, depending on the excitatory synaptic strength, neurons can exhibit a transition from spiking to bursting synchronisation [39,40] and bistable firing patterns [41]. We find conditions in which unstructured, sparsely connected random networks of AdEx neurons can display low frequency, self-sustained activity.

In particular, we show that not only the balance between excitation and inhibition but also the connection density and network size are both important factors for low frequency SSA. In balanced networks, high mean node-degree connectivity is necessary to give rise to low mean neural firing rates, and for such high values, large networks are necessary to support SSA states. In our computer simulations, we obtain qualitatively similar results to the ones we observed in our experimental recordings, where we use CA1 neurons whole-cell recordings in rats to demonstrate the possible variability of firing rate patterns observed in the brain. Our intracellular recordings show high variability of spontaneous activity patterns including low and irregular neural firing rates of approximately 1 Hz and spike-train power spectra with slow fluctuations [23], and small-bursts activity in distinct recorded neurons. Interestingly, we show that these results can be reproduced qualitatively by our model with cortical neurons modelled as regular spiking (RS) cells with spike frequency adaptation and fast-spiking (FS) cells with a negligible level of adaptation.

The paper is organised as follows: in Section 2, we introduce the neural network model and in Section 3, the various quantities used to study self-sustained activity in our numerical simulations and the details of our electrophysiological experiments. In Section 4, we present our results on self-sustained activity in the numerical simulations and experimental data, and in the last section we discuss them and draw our conclusions.

2. Neural network model

We start by building a random neural network of N AdEx neurons by connecting them with probability p, where p is the probability that any two neurons in the network are connected, excluding autapses (i.e. neurons connected to themselves, thus self-loops are not allowed). The N neurons are split into excitatory and inhibitory neurons according to the ratio 4:1 (meaning that 80% are excitatory and 20% are inhibitory), following [42]. The connection probability p and the mean connection degree K are associated by means of the relation

$$p = \frac{K}{N-1}. \tag{1}$$

The dynamics of each AdEx neuron $i = 1, \ldots, N$ in the network is given by the system of coupled equations [27]

$$C\frac{dV_i}{dt} = -g_L(V_i - E_L) + g_L\Delta_T \exp\left(\frac{V_i - V_T}{\Delta_T}\right) - \frac{1}{S}\left(w_i + \sum_{j=1}^{N} g_{ij}(V_i - E_j) + \Gamma_i\right), \tag{2}$$

$$\tau_w\frac{dw_i}{dt} = a(V_i - E_L) - w_i, \tag{3}$$

where V_i and w_i are, respectively, the membrane potential and adaptation current of neuron i, g_{ij} the synaptic conductance of the synapse from neuron j to neuron i, and Γ_i the external perturbation applied to neuron i. The synaptic conductance g_{ij} has exponential decay with synaptic time-constant τ_s. The parameter values in Eqs. (2) and (3) are given in Table 1. These values have been chosen so that the system can reproduce the spiking characteristics of RS (excitatory) and FS (inhibitory) neurons observed in experiments with real neurons [27].

When the membrane potential of neuron i is above a threshold potential ($V_i(t) > V_{\text{thres}} = -30$ mV), the neuron is assumed to generate a spike and the following update conditions are applied

$$V_i \rightarrow V_r = -60\,\text{mV}, \tag{4}$$

$$w_i \rightarrow w_i + b, \tag{5}$$

$$g_{ji} \rightarrow g_{ji} + g_s, \tag{6}$$