

Resonance as an effective mechanism of dynamical stability in large microcircuits of spiking neurons

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1. Introduction

Self-sustained activity of the cortical circuitry is a known property in the brain. It is manifested both during spontaneous activity and delay periods [2]. The spontaneous activity is characterized by a very stable low firing regime (1-5 Hz) in which neurons tend to maintain a constant, homeostatic firing level. To account for it, most modeling studies dealing with spontaneous self-sustained activity have assumed an external “background” current [1]. The main argument rendering the above assumption reasonable is that neurons in the cortex seem to spike in an apparent random fashion [8, 9]. However, it has also been shown, that completely deterministic networks of spiking neurons can produce pseudo-random activity patterns, also called “network effect” [3, 5]. Moreover, the assumption of an independent, external, random drive is not only questionable, but it also changes the statistics of neural firing in a way that is not dependent on the states of the network. Thus, we propose, that at least to some degree, a large cortical circuit must be able to maintain its activity independently of any external stimulation.

There have been many attempts to build self-sustained networks of spiking neurons. Most studies have been conducted using integrate-and-fire neurons and have failed, since the network either tends to “die out” or to “explode”, firing in saturation. A precise balance of excitation/inhibition or special structured receptive fields [10] are required in order to avoid the above-mentioned effect. The inhibition/excitation balance is however very difficult to maintain since it depends on the dynamical patterns of activity which are continuously changing. We propose that resonating neurons can overcome the instability effects in such networks and effectively contribute to the maintenance of ongoing self-sustained dynamics.

2. The resonator model

Experimental evidence suggests that cortical neurons exhibit frequency dependent behavior, having preferred stimulation frequencies in the range of 5-20 Hz for pyramidal neurons and 5-50 Hz for interneurons [4]. Recently, a biologically plausible neural model has been proposed, that is easy to simulate and is able to produce resonating behavior [6, 7]. The Izhikevich model [6] mentioned here is explicitly modeling the membrane potential (v) of the neuron and a recovery variable (u):

$$\frac{dv}{dt} = 0.04v^2 + 5v + 140 - u + I \quad (1)$$

$$\frac{du}{dt} = a \cdot (bv - u) \quad (2)$$

where v – membrane potential, u – recovery variable, I – total post-synaptic current, a, b – parameters.

When the membrane potential reaches a value larger than 30 mV, a spike is recorded and the membrane potential is reset to its resting value, while the recovery variable is increased by a given amount:

$$v = c; \quad u = u + d \quad (3)$$

where c – resting potential, d – a parameter that is added to the recovery variable.

Depending on the concrete value of the four parameters (a, b, c, d), the model can reproduce a plethora of cortical neuron behaviors, like adaptation, post-inhibitory rebound, etc [6]. Here we are interested in the resonator regime, obtained with the following parameters: $a = 0.1$, $b = 0.26$, $c = -70$ mV, $d = 2$.

We also model the total input current (I) that a neuron receives as being the sum of all post-synaptic currents (psc) contributed by each synapse:

$$psc = A_{syn} \cdot W_{syn} \cdot g \cdot (E_{syn} - v_{post}) \quad (4)$$

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$$\frac{dg}{dt} = -\frac{g}{t_{syn}} \quad (5)$$

where, p_{sc} – post-synaptic current, A_{syn} – an amplitude parameter that determines the maximal amplitude of the p_{sc} , W_{syn} – the synaptic strength ($W_{syn} \hat{I} [0..1]$), g – the instantaneous synaptic conductance, E_{syn} – the reversal potential of the synapse (taken 0 mV for excitatory synapses and -90 mV for inhibitory synapses), v_{post} – the membrane potential of the post-synaptic neuron, t_{syn} – the time constant for the decay of the synaptic conductance after the neurotransmitter release (typically 10-20 ms).

Each time an afferent spike reaches the synapse, the instantaneous conductance is raised by a constant value (here 1):

$$g = g + 1 \quad (6)$$

First, we studied the responsiveness of the resonator neuron to spike trains of various frequencies. The input spike train consists of a fixed number of spikes, separated by a fixed inter-spike interval determined for each stimulation frequency. The same total number of input spikes is delivered to the post-synaptic neuron, for each frequency, in order to allow us to compare the number of fired output spikes for different frequencies. The afferent stimulation is delivered through an excitatory synapse with $A_{syn} = 0.45$, $t_{syn} = 20$ ms, $W = 1.0$.

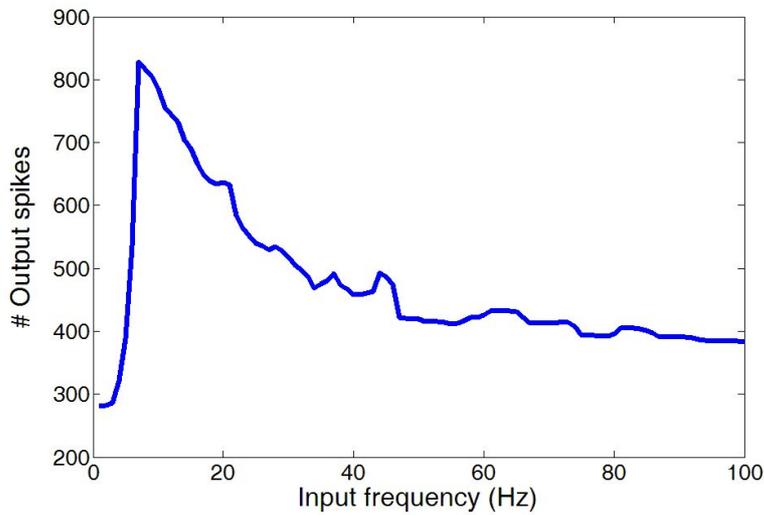


Fig. 1. Frequency response of the resonator neuron to input spike trains with fixed number of spikes, but different frequencies. It is obvious that the model prefers low frequencies while it dampens the effect of high input bombardment.

Results in fig. 1 suggest that the resonator model prefers low frequency inputs in the range of 8-10 Hz. For high input spike rates, the neuron gets less and less responsive. Such properties render the neuron ideal for stabilizing the dynamic activity of a network. When the input is weak (small frequency) the neurons are very sensitive and more excitable. As the activity in the network builds up, the neurons get less and less responsive favoring the automatic normalization of activity and avoiding an exponential buildup that could eventually result in saturation (as is the case with integrate-and-fire neurons).

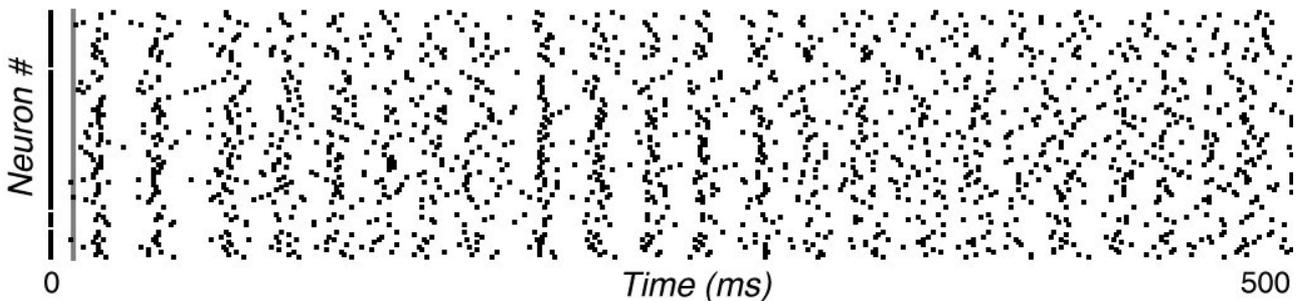


Fig. 2. Self-sustained dynamics of a 1000 resonator neuron microcircuit (100 neurons plotted).

During a first phase, lasting 20 ms, the network was stimulated with a 50 Hz Poisson input spike train. After that, the microcircuit stops receiving external stimulation and it is able to robustly sustain its activity at an average level of 20-30 Hz, usually as long as the simulation lasts (even hours). Moreover, the

network occasionally develops rhythms in the gamma band (40 Hz) due to the coupling between excitatory and inhibitory neurons.

Finally, we monitored the survival time of 50 resonator microcircuits as a function of the excitatory synaptic amplitude. As suggested by fig. 3, the survival reliability of the networks is increasing for stronger excitatory synapses. At the same time, for the range of parameters considered, the microcircuits never showed tendencies to saturate. In fact, the activity plot in fig. 2 is produced with $A_{syn} = 0.01$ which is at the high end of the tested parameter space. For excitatory synapses with $A_{syn} = 0.01$ or larger, the networks always self-sustain and fire reliably for as long as the simulation lasts.

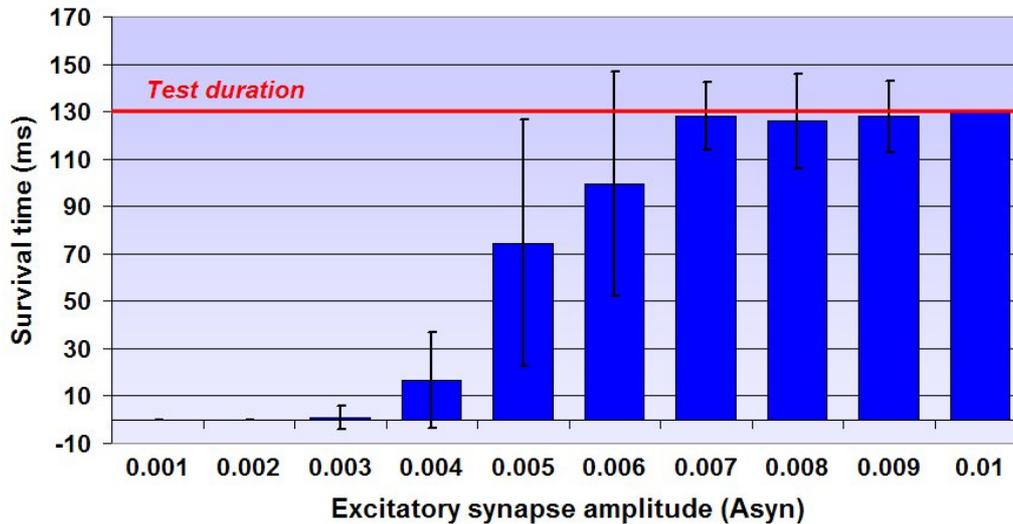


Fig. 3. Survival time of a resonator microcircuit as a function of excitatory synapse amplitudes. The total simulation time is limited to 130 ms.

3. Conclusion

The resonance property of neurons could play an important role in the homeostasis of neuronal activity. In the context of self-sustained dynamics, we have shown that large microcircuits of resonating neurons exhibit stable activity even in the absence of any external stimulation. Moreover, the self-sustainability of such networks is very robust, for a wide range of parameters and does not require a precise balancing of excitation and inhibition.

4. References

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