Heterogeneous networks of spiking neurons:
self-sustained activity and excitability

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Abstract

Cortical neuron networks are able to maintain self-sustained activity in the absence of any input, while exhibiting a high sensitivity to external stimulation. An attempt to aggregate both behaviors is presented in this paper, based on a hybrid network which combines both a resonant and an integrator component. Resonance is shown to contribute to self-sustained activity, while the integrator component, coupled with resonance, can render the network more responsive to input. Simulation results show that the self-sustained regime can still be maintained, even when introducing a significant integrator component in the network. The analysis of the responsiveness to input reveals also other interesting phenomena, related to some experimental findings in real biological circuits, like ON- and OFF-response properties.

1. Introduction

The study of large-scale networks of spiking neurons is relevant for understanding brain function and discovering new paradigms of computation [12], while providing the basis for the implementation of biologically inspired artificial intelligence [6]. Such networks have been studied in the context of biologically realistic modeling, ranging from persistent neural activity [1] to generic models of computation [13] and even robot control [4].

Unlike neurons in classical artificial neural networks, spiking neurons incorporate spatial-temporal information in computation [17]; their output is expressed in terms of *spikes*. Since they are based on dynamic event-driven processing, spiking neurons open up new horizons for superior models with an increased computational power. Moreover, spiking neuron models are closer to their biological counterparts [8] than classical models of artificial neural networks.

One of the key properties of biological neurons is their ability to integrate incoming electrical signals (called "postsynaptic potentials"). In the classical view, neurons change their membrane potential according to excitatory or inhibitory incoming postsynaptic potentials, such that their probability of firing spikes (also called "action potentials") is increased or decreased, respectively [2]. Apart from the integrative behavior, neurons can also display resonant activity; they exhibit a preference to input stimulation of a given frequency [5], [10].

It has been suggested that resonant behavior can contribute to dynamical homeostasis of the activity of large-scale recurrent networks of neurons, regulating excitability and stabilizing network activity, to avoid "epileptic" explosions [14], [15]. However, in general, resonance at the neuron level keeps network responsiveness to input low, dampening especially high frequency stimulation. On the contrary, networks of integrator neurons tend to be very responsive to input but highly unstable [16].

Here, we study how the combination of resonance and integration can yield stable dynamics as well as responsiveness to external input in heterogeneous networks of resonant (RES) and regular spiking (RS) neurons [11]. We show that self-sustained behavior can be preserved in the hybrid network, in certain conditions and that the response profile of the network reproduces some patterns found experimentally, in real neural circuits. We conclude that the resonator population plays a central role in the network dynamics and that the interaction between RS and RES neurons contributes to network responsiveness.

2. The spiking neuron model

One of the first models describing the process of action potential generation has been the one introduced by

Hodgkin and Huxley [9]. Since then, several spiking neuron models have been proposed. They tried to preserve, as much as possible, the neural dynamics of the initial model, while reducing its computational complexity as to make it feasible for large scale simulation. The spiking neuron model considered here is part of the same category. Introduced by Izhikevich in [11], it is a two-dimensional approximation of the Hodgkin Huxley model. This particular variant was preferred due the fact that it can reproduce a rich set of dynamical behaviors of the cortical neurons, while remaining simple enough to be computationally feasible. The model is defined by a system of differential equations:

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

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

where

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

When the membrane potential reaches the value of $30mV$, a spike is recorded, the membrane potential is reset to its rest value, and the recovery variable is updated:

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

where c - rest potential, d - a parameter of the recovery variable.

Various settings for the parameters a, b, c and d give different dynamic behaviors, such as adaptation, or post-inhibitory rebound. This study focuses on two particular configurations for the parameters, namely the ones corresponding to the regular spiking regime ($a = 0.02$, $b = 0.1$, $c = -65mV$, $d = 8$) and the resonator regime ($a = 0.1$, $b = 0.26$, $c = -65mV$, $d = 2$).

The behavior of the RS neuron is not that of a true integrator; instead, its dynamics is intermediary -between an integrator and a resonator- exhibiting adaptation [11], [15]. The resonator component of the RS regime had to be considered when analyzing the dynamics of the heterogeneous network of spiking neurons. Consequently, a simpler integrator model was needed as reference for the comparison - the leaky integrate-and-fire model.

The integrate-and-fire model has become ubiquitous in practice, as one of the simplest representations of neuronal dynamics. It is a class 1 excitable system; it shows a monotonic increase in response when increasing the stimulation frequency. In an electrical interpretation, the model corresponds to a capacitor and a resistor connected in parallel (in our case, $R = 1M\Omega$, $C = 10\mu F$). The IF formalism models only one variable, namely the membrane potential (v) of neurons:

$$\tau \frac{dv}{dt} = -v + R \cdot I \quad (4)$$

where

- v - membrane potential,
- $\tau = R \cdot C$ - membrane time constant (typically $10ms$),
- R - membrane resistance,
- I - total post-synaptic current.

In all cases, the total input current (I) received by the neuron is computed as the sum of all post-synaptic currents (psc) contributed by each synapse:

$$psc(t) = A_{syn}W_{syn}g_{syn}(t-1) \cdot (E_{syn} - U_{post}(t-1)) \quad (5)$$

$$g_{syn}(t) = g_{syn}(t-1) \cdot e^{-\frac{1}{\tau_{syn}}} \quad (6)$$

where: psc - post-synaptic current, A_{syn} - maximal synaptic amplitude, W_{syn} - the synaptic strength ($W_{syn} \in [0, 1]$), g_{syn} - the instantaneous synaptic conductance, E_{syn} - the reversal potential of the synapse ($0mV$ for excitatory synapses and $-90mV$ for inhibitory synapses), U_{post} - the membrane potential of the post-synaptic neuron, τ_{syn} - the time constant for the decay of the synaptic conductance after the neurotransmitter release (typically $10 - 20ms$).

Each time an afferent spike reaches the synapse, the instantaneous conductance is incremented:

$$g_{syn} = g_{syn} + 1 \quad (7)$$

3. Experimental work and results

The network structure considered in this study is heterogeneous, including RS and RES neurons in certain well-established proportions ($0 - 100\%$, with a 20% increment). Following the biological model, 20% of all neurons are inhibitory, while the remainder population is excitatory. Efferent synapses of a neuron are all of a single type, as specified by Dale's law. Inhibitory neurons are randomly selected from the global neuron population, with a uniform distribution. Synaptic connectivity is 10%, selected at random; the same configuration applies also in the case of the input connections. The bias of randomly selecting the connectivity and neuron types is reduced by averaging the results for experiments performed on various network connectivity patterns and, for each such configuration, taking several random assignments of the spiking neuron types (10
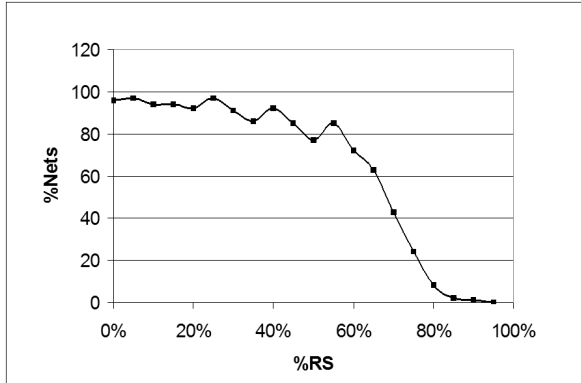
Figure 1. Percentage of hybrid networks that reach a self-sustained regime, for various RS proportions.
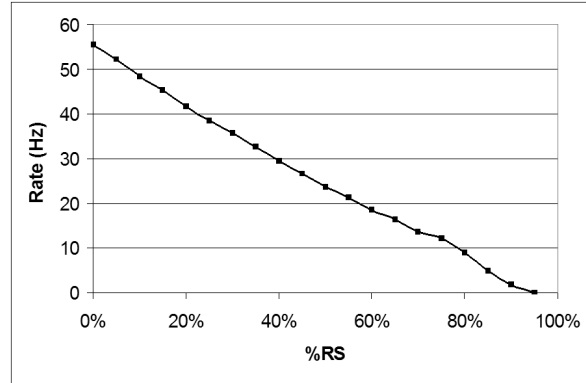
Figure 2. Population rate in the stable regime, as measured when varying the RS proportions.

network structures x 10 type assignments = 100 trials per experiment).

For the analysis presented here, the synaptic amplitude is tuned as to obtain a stable self-sustained dynamics in the case of the resonant-only network. Future analysis should include a study of the behavior of the network, as the synaptic amplitude is varied.

3.1. Resonance and self-sustained behavior

Recent literature recognizes that most activity in the brain is internally generated [16], thus emphasizing the importance of self-sustained activity in modeling neural circuits.

In order to achieve a self-sustained regime, excitation should be able to maintain firing levels high enough as to prevent the global network activity from dying out. At the same time, inhibition should prevent an explosion of the activity, owed to the recurrent network connectivity. Considering these two aspects, it appears that a precise balance between excitation and inhibition is required for achieving self-sustainability. However, other solutions have been proposed in the literature; most of them impose some structural constraints on the network architecture.

In a different approach, [15] it is suggested that the property of resonance of neurons could play an important role in the homeostasis of neuronal activity. The study shows that large microcircuits of resonant neurons can exhibit stable activity even in the absence of external stimulation. Moreover, the self-sustainability of such networks is very robust and, unlike other models, does not require a precise balancing of excitation and inhibition. In this context, it is interesting to study to which extent this behavior can be preserved in heterogeneous networks.

The paper analyzes a range of heterogeneous networks; we measure the self-sustainability state and its corresponding stable rate, while varying systematically the proportion of RS neurons. A network is considered to have left the self-sustained regime either when the population rate is null for some specified time-interval (the network has 'died out'), or when the rate is maintained over a certain high threshold for the same duration (saturation). A value of $40ms$ was set for both intervals, in our case. For each self-sustained network, the population rate in the stable regime is estimated as an average over the last $50ms$ of the trial, using a sliding window technique [3]. As described before, 100 trials are generated for each proportion of RS neurons, to yield a better rate estimation. Each trial lasts $1s$, time being discretized in $1ms$ units. Results of this experiment are presented in figures 1 and 2.

The average rate for the entire population decreases linearly when the number of RS neurons is increased. The explanation of this phenomenon resides in the reduced responsiveness of the RS population, the overall dynamics of the system being driven by the resonant component, as will be detailed in the following section.

3.2. Network responsiveness

A wide range of models have been proposed for explaining the input sensitivity of neural networks. A smaller number of solutions achieve a self-sustained activity, but it is difficult to find models that encompass the two dimensions together. This is most unfortunate, since an aggregated analysis of both aspects is critical for a better understanding of how higher level cognitive functions are achieved in the neural circuits [16].

In the input sensitivity analysis for the model, the response to a a Poisson input is measured for various RS-
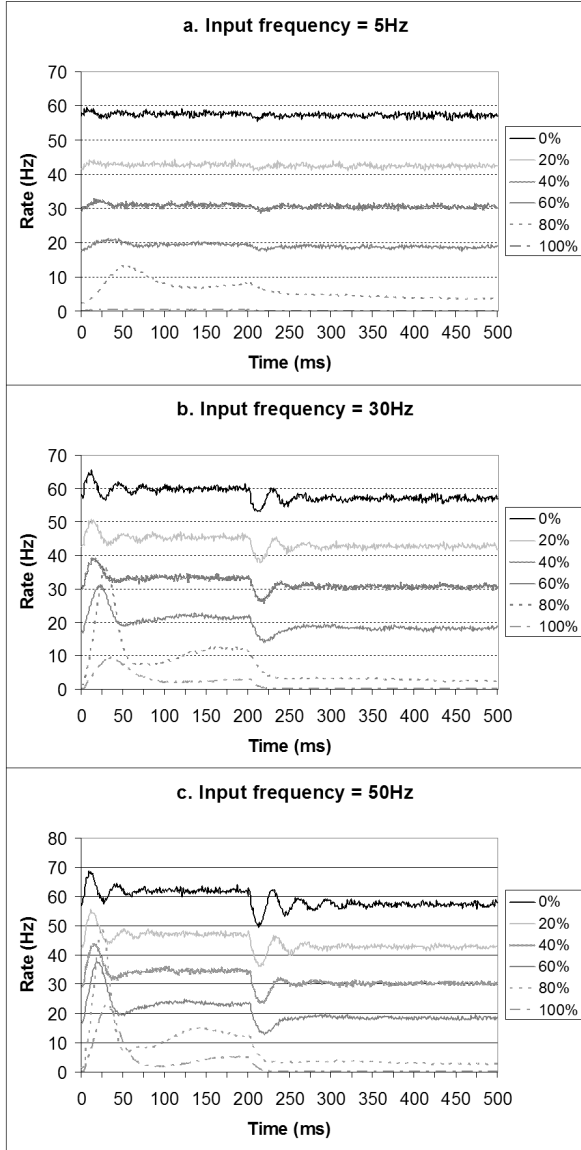
Figure 3. Post-Stimulus Time Histogram averaged over 100 hybrid networks, for a Poisson input and various RS proportions. a. Input frequency = 5Hz. b. Input frequency=30Hz. c. Input frequency=50Hz.
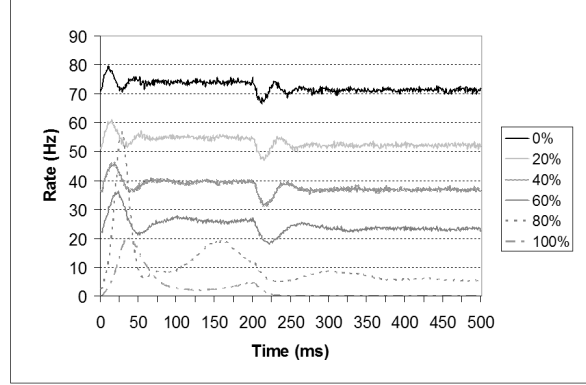
Figure 4. Average PSTH for hybrid networks with no inhibitory neurons (as function of %RS). The input frequency is 30Hz.

RES heterogeneous networks; the input frequency ranges between 5 and $50Hz$. We compute the *Post-Stimulus Time Histogram* (*PSTH*) of the network for a time interval of $500ms$. The stimulus length is $200ms$; to avoid superimposing effects, a $1s$ interval is established between each two subsequent input presentations. Results are averaged over 20 trials. The initial stimulus is presented only after the network activity has stabilized, to eliminate any bias induced by the initial RES activity.

The PSTH is computed as an average over the population of networks and the stimulus presentations. Each bin i of the 500 bins, measures an estimate of the number of spikes occurring i ms after the initial stimulus presentation. In the end, the PSTH is computed, as:

$$PSTH(i) = \frac{\#spikes_i}{N \cdot N_{trials} \cdot T_{bin}} \quad (8)$$

where

- $\#spikes_i$ - total number of spikes for bin i;

- N - population size (100);

- N_{trials} - number of trials (20, in our case),

- T_{bin} - bin size, expressed in seconds (10^{-3} in our case).

The results of the study are presented in figure 3.

The first observation is that the global rate of the population decreases (almost linearly) as the proportion of RS neurons is increased. This result is consistent with the analysis presented for the case of self-sustained regime, when no input was presented to the network.

Secondly, there is a large increase in the amplitude of the population rate after the initial stimulus presentation (the
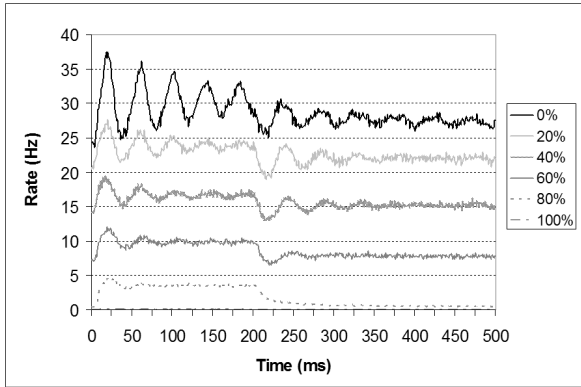
Figure 5. Average PSTH for hybrid networks with strong inhibition, when varying RS percentage. The input frequency is 30Hz.
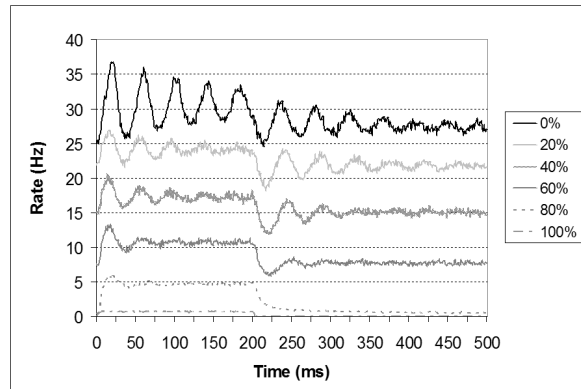

Figure 6. PSTH results in the RES/IF hybrid network, for a 30Hz Poisson input and various RS percentages.

first $10 - 50ms$). This phenomenon is consistent with biological recordings (what is referred in the literature as the *ON-response* [7]). The initial peak is followed by a stabilization of the global population rate, through a damped oscillation. A similar dynamics appears immediately after the stimulus is removed ($t = 200ms$), a phenomenon called *OFF-response*. After a temporary fall in activity, a new population rate peak occurs (OFF-response), smaller than the one for the ON-response, after which the network reaches a new stable regime. The plots show that periods of higher activity correspond to times of disruption, which require some system reorganization; when such variations occur, the network increases its rate to adapt to the new conditions. Response amplitudes are larger for high frequencies, probably owed to the fact that higher inputs induce larger disruptions in the system.

Several potential mechanisms could be proposed to explain the phenomena described above. The interplay between excitation and inhibition is one possible candidate; another is the resonator component of the regular spiking neuron and the coupling between different neuron populations. Each of the alternatives is explored in a series of experiments, presented in the following.

In the initial experiment, inhibition was set to be lower than the level of excitation. Two different settings were also analyzed. In the first trial, the inhibition was eliminated completely, as shown in figure 4. It can be seen that removing inhibition does not significantly alter the initial result.

The same conclusion can be reached when increasing inhibition to the level of excitation (figure 5). In this case, the dynamic interplay between excitation and inhibition leads to *oscillations* in the population, but the ON-response phenomenon still occurs. Oscillations occurring in spiking neu-
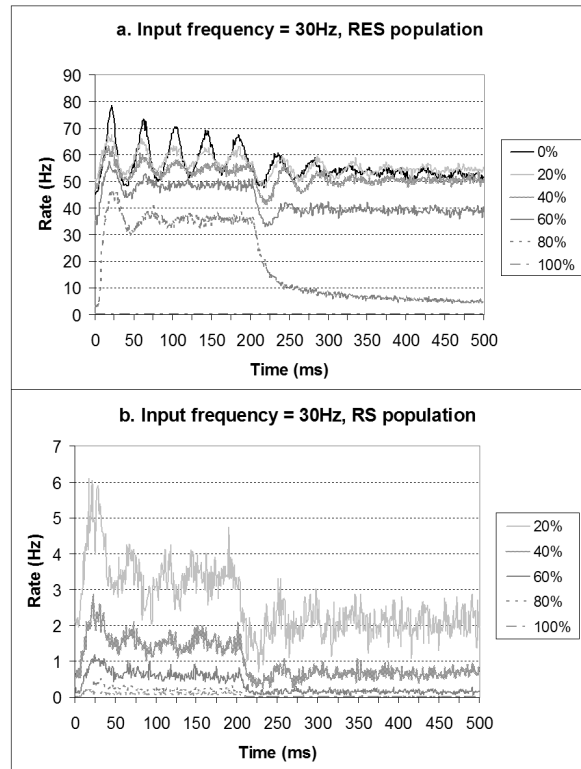
Figure 7. Population PSTH for the RES/RS network, with strong inhibition, for different RS%.

ron networks have been previously described in the literature [16]; they are reported to increase when strengthening the inhibitory component, which was also the case in our experiment. We conclude that the interplay between inhibition and excitation does not account for the generation of ON-/OFF-responses. However, it does contribute to the oscillatory activity of the network.

In the third experiment (figure 6), the RS neurons were replaced by IF, to eliminate completely the resonator behavior in the integrator population. Again, the change did not affect in any way the network ON-response characteristics.

Lastly, we have measured the PSTH of the individual RS and RES populations (figure 7). The results of this experiment show distinctively that the RES population is the one inducing the global network response, since the RS activity is significantly smaller than that of RES. The ON-response in the RES population is consistent in all the parameter range considered; the OFF-response is less visible for some values at the boundaries of the parameter space.

If small enough ($20 - 30\%$), the RS population shows an ON-response characteristic similar to that of RES, which is slightly shifted in time, relative to the RES peak; this suggests that it may be a result of integration owed again to the high RES activity.

4. Conclusions

This paper has attempted to determine how the combination of resonance and integration can yield both stable dynamics and responsiveness to external input in heterogeneous networks of resonant and regular spiking neurons.

It was shown that the self-sustained regime can still be maintained in the hybrid network, even when introducing a significant integrator component. As a general conclusion of the responsiveness experiments, it may be stated that the ON- /OFF-response effects in the described neural architecture are mediated by the resonator population. However, at this stage, it is still unclear if the response properties are directly influenced by the coupling between resonant and integrator populations. For example, the large ON-responses observed when the RS population dominates (see figure 3.c., when 80% of neurons are RS) cannot simply be explained in terms of integrator responsiveness (as shown in figure 7). It might be that external excitation leads to a slight activation of the RS population, which in turn could mediate the rapid formation of more active groups of RES neurons, thus explaining the fast rise of activity during the ON-response.

Even though the networks presented here have a simple, random architecture, they are able to reproduce interesting experimental observations about the response properties of cortical networks. Not only they exhibit ON- and OFF-responses, but they also display a pronounced dip in the PSTH response following the initial peak, similar to that reported for the cat and monkey visual cortex [7].

Further studies are required to elucidate the mechanism of ON-/OFF-responses in such networks, including an analysis of the evolution of hybrid networks as a function of the strength of the synaptic connectivity.

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