Synfire Waves in Small Balanced Networks

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Abstract

We study the problem of mixing rate and temporal codes in the same population at the same time. We use a balanced network, known to act well as a rate code model, and embed in it synfire chain connectivity. The propagation of a synfire wave on top of asynchronous background activity requires large networks. Here we show that this can be achieved also in small networks provided one adds inhibitory (shadow) pools to the excitatory ones. Correct adjustment of these pools is required to allow for synfire wave propagation.

1. Introduction

In a balanced network (BN) the mean inhibitory input to a neuron cancels the mean excitatory input [8]. BNs of Integrate-and-Fire (IF) neurons with sparse random connectivity have been shown [3] to have stable asynchronous states (AS). The statistics of the AS is closely related to that of cortical tissue. In addition, it has been shown on another model [9] of BN that the AS performs well in transferring rate code via population activity.

In this work, we seek a system that conveys information using both temporal and rate codes, perhaps even simultaneously. We adopt the BN model as the framework for rate coding, and the synfire [1] model as a framework for temporal coding.

In the synfire model, pools of excitatory neurons are connected in a consecutive manner to form a chain. All neurons in a pool project their output to all neurons in the consecutive pool. Diesmann et al [5], and more recently [4][7], have shown that above a critical pool size, pool activity ignited at the first pool propagates from one pool to the next, forming a synfire wave. The successful propagation is due to exact timing of the excitatory input, hence it reflects temporal coding.

Here, we embed a chain in the excitatory-to-excitatory connectivity matrix of the BN, and we look for conditions under which the AS of a BN is stable and, on top of it, a synchronized wave of activity can propagate along a chain. Since the connectivity matrix is not random anymore, and since there is feedback between the network activity and the chain (which is part of the network), it is not clear if such conditions exist. In a previous work [2] we have demonstrated that these conditions can be met by very large networks. Here we will demonstrate that an additional modification allows them to be met in small networks too.

2. The Problem: Too much excitement, the balance is broken.

The idea underlying the synfire model is that a stable and reproducible wave can propagate under noisy conditions, if strong excitatory input overcomes the noise and drives the correct neuron across threshold at the right time. The strong correlated excitatory input is obtained through converging connections from one pool of neurons to the next.
On the other hand, rate coding in general and BN in particular, requires random connectivity. Randomness is required for desynchronizing neurons, leading to a global asynchronous state that mediates a signal by means of population average.
We face two conflicting demands from the system: While synfire waves require ordered connectivity between pools of neurons, rate code requires random connectivity among neurons in a population.
In [2] we studied this problem and showed that there exists a scaling variable, relating the pool width and the general connectivity, to which the AS is sensitive. Below a critical value of the scaling variable both constraints can be satisfied, but above the critical value, global synchronized activity appears. This can be amended at the price of large number of neurons. With the neuronal model used, we needed 10^5 excitatory neurons in order to construct a system expressing the synfire temporal code on top of a global asynchronous activity.

Apart from being a computational challenge, the requirement for such a large number of neurons questions the biological relevance of this model. We propose a solution based solely on architectural modification, without any change to the simple Lapique IF neuronal model used.

3. A Solution: Casting Shadows

We define a modified synfire chain as follows: A pool of randomly chosen inhibitory neurons, a 'shadow' pool, is attached to each excitatory pool in a synfire chain. A neuron in an excitatory pool projects its output, not only to the next pool in the chain, but also to all neurons in its shadow pool. A neuron in the shadow pool, does not project it output in any ordered manner, but diffuses its output randomly to the rest of the network, as is in a completely random network. Similar connectivity, but for different reasons, was suggested in [6]. A sketch of the connectivity scheme of a modified synfire chain is shown in Figure 1.

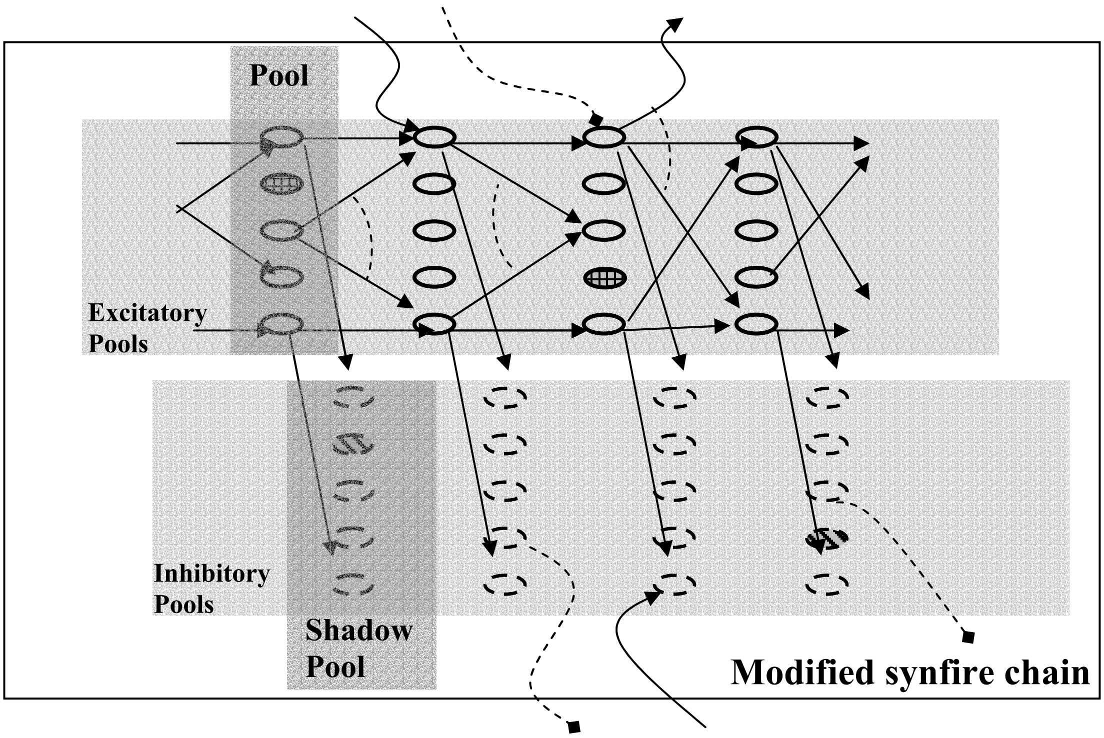

Figure 1: The connectivity of a modified synfire chain. Only representative connections are shown. Excitatory (Inhibitory) neurons and connections are in solid (dashed) lines. Each neuron in an excitatory pool projects its output to all neurons in the next pool and to all neurons in the shadow pool. In addition, each neuron receives inputs from, and projects to, many other neurons in the network (indicated by curved lines). Note that a neuron can participate in many pools (indicated by neurons with same pattern).

These inhibitory pools do not carry specific information down the chain, as is the case for the excitatory pools, but rather echo a synchronized activity of their attached excitatory pool. The role of the 'shadow pools' is to guarantee a correct amount of inhibition during the propagation of the wave. The excess of converging connections in the network, due to the embedded chain, induces excess of correlated excitation, which may in turn, transform to global excitation [2]. The sole purpose of the shadow pools is to cancel that excess of excitation.

In Figure 2, we demonstrate that increasing the size of shadow pools, decreases the globally synchronized activity.

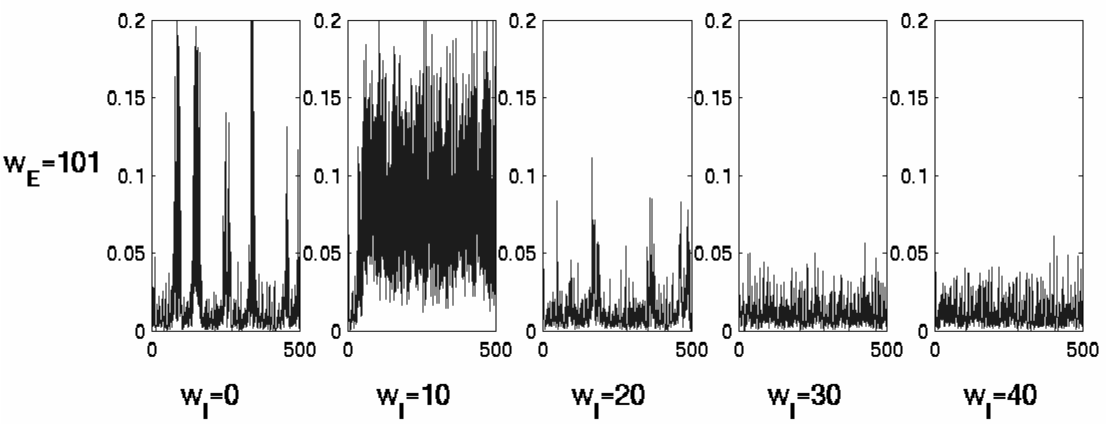

Figure 2: Excitatory population activity for different shadow pool sizes. Population activity is the fraction of neuron that fires in 0.2ms. In each panel, y-axis is the population activity and the x-axis is time in ms. Panels, from left to right, are for shadow pools of size, w_I= 0, 10, 20, 30 and 40. The excitatory pool size, w_E, is 101. Size of excitatory (inhibitory) population: 10,000 (2,500). Chain length: 50.

For large enough shadow pools, the AS is stable. We believe that it is the excess of correlated inhibition that balances an excess of correlated excitation. The inhibition, however, need not target specific neurons in the network.
In Figure 2, panel w_I=10, spontaneous waves keep forming, creating an illusionary high activity AS. The raster plot of that case, is similar to that of Figure 3A.
If the size of the shadow pools is too large, a desired synfire wave may cause an excess of inhibitory input, which leads to its own termination. This is demonstrated in Figure 3C.

As seen in Figure 3B, there is a size of the shadow pools that is not too small and not too large, for which the system allows propagation of synfire waves on top of asynchronous activity. This demonstrates temporal coding in a population that performs rate coding.

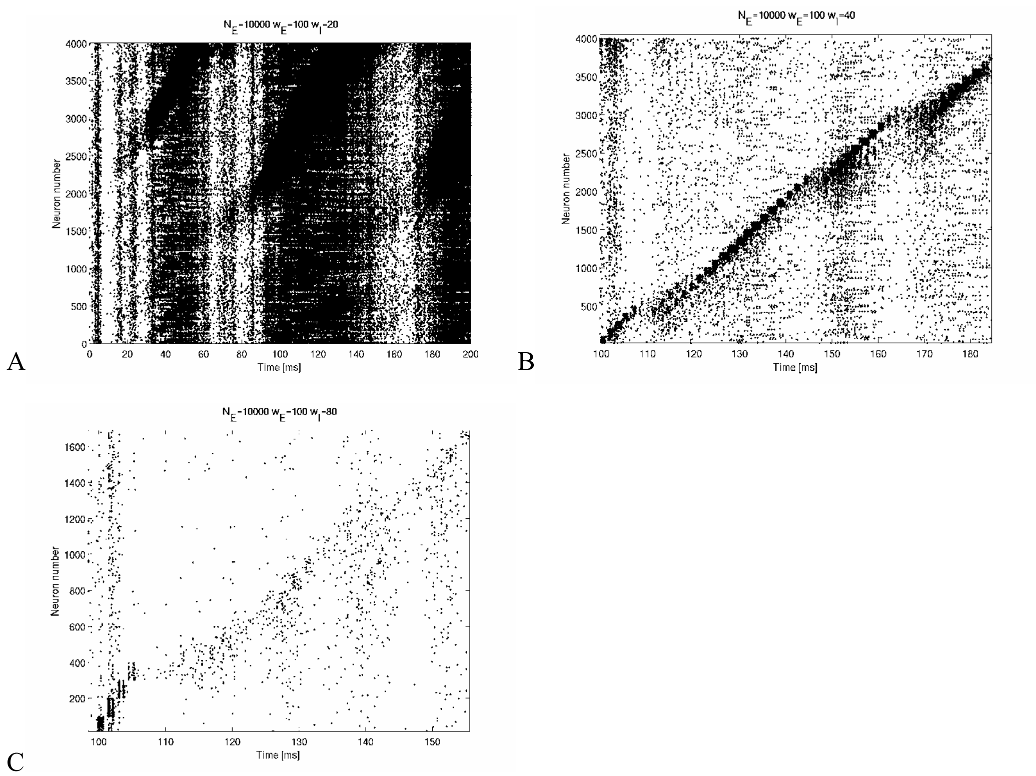

Figure 3: The effect of the shadow pool size on a synfire wave. In these raster plots, neurons are ordered according to their participation in the chain. The shadow pool size is (A) 20, (B) 40 and (C) 80. Three panels display three possible scenarios: (A) global excitation, (B) stable propagation together with stable global AS, (C) wave dissolve in a stable global AS. Parameters as in Figure 2

4. Summary

To allow temporal coding on top of a rate-coding system, we introduced a double-balance requirement: At the macroscopic level, inhibitory input cancels mean excitatory input, providing a global asynchronous state. At the microscopic level, inhibitory pools counteract synchronized excitatory synfire pools.

Acknowledgements

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