Spike and burst synchronization in a detailed cortical network model with I-F neurons

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Abstract. Previous studies have suggested that synchronized firing is a prominent feature of cortical processing. Simplified network models have replicated such phenomena. Here we study to what extent these results are robust when more biological detail is introduced. A biologically plausible network model of layer II/III of tree shrew primary visual cortex with a columnar architecture and realistic values on unit adaptation, connectivity patterns, axonal delays and synaptic strengths was investigated. A drifting grating stimulus provided afferent noisy input. It is demonstrated that under certain conditions, spike and burst synchronized activity between neurons, situated in different minicolumns, may occur.

1 Introduction

The synchronized activity of the neurons in visual cortex is believed to contribute to perceptual grouping [14,20,21,22,24,28], see also [23]. It is also assumed that neurons in primary visual cortex have small and overlapping receptive field [8]. We assume also that local cortical connectivity (<300 μm) is dense [7]. Dense local connectivity should help neurons to synchronize their activities. This should mean that neurons with same or contiguous receptive fields are active in presence of stimulus.

Studies have shown evidence for long-range horizontal connections in primary visual cortex [10,13]. Recently Bosking et al. also showed evidence for modular and axial specificity of long-range horizontal connections in layer II/III, and suggested that these connections could help neurons respond to a stimulus, in part because they receive input from other layer II/III neurons [11].

We suggest that long-range horizontal connections that exist in layer II/III together with local connections can be used by the neurons for synchronization of their activities over distances of several millimeters on cortex surface.

This follows the same ideas as earlier network model simulations where horizontal connections [16,17,19,25, 27] and synchronization [15,18,26] play an important role.

2 Network Model

We have built a biologically plausible, but sub-sampled, network model. The network consists of neurons situated in six cortical minicolumns (orientation columns), having the same orientation preference. The minicolumns were lined up with a distance of 0.5 mm between two successive ones. We assume that minicolumns are co-linearly positioned in adjacent hyper-columns [8]. The cylinder shaped minicolumns had a height of 300 μm [7] and diameter of 50 μm [8].

Each of the six minicolumns was composed of 12 layer II/III pyramid cells. The neurons were positioned stochastically to fill up the volume of a minicolumn. Connection probability between two neurons was a function of the distance between them [7]. This resulted in a very spread connection probability of 15-80% for neuron pairs, and led to a connectivity of 50-60% between neurons inside a minicolumn [8].

Long-range horizontal connections were defined as connection between two neurons situated in different minicolumns. We computed the connection probability between such pairs of neurons by extrapolating the reported connection probabilities (<500 μm) by Hellwig [7] so that they fitted the findings by Bosking et al. [11]. This resulted in a smooth transition between local and long-range connection probabilities. In average a neuron received 6.2 intra-columnar inputs and 2.1 inter-columnar inputs.

We implemented a leaky Integrate-and-Fire model neuron with noise [1,2]. It was modified to allow adaptation of the membrane time constant [3]. Adaptation is very crucial for the dynamics because of the fact that our network, as many others, does not have inhibitory interneurons. The neuron population was heterogeneous with all values sampled from a uniform distribution with a deviation of 10%.

An axonal diameter of 0.3 μm [8] resulted in a spike propagation velocity of 0.85 m/s [5]. This value together with distances between neurons, and the synaptic delay, resulted in maximum delay inside a minicolumn of approximately 1.36 ms. Maximum delay between neurons situated in two minicolumns was approximately 3.96 ms. This delay corresponds to a distance of approximately 2.52 mm. Maximum values of EPSP:s were in the range of 0.5-2.2 mV for intra-columnar connections and three times those values for inter-columnar connections [4]. The simulation time step was 0.5 ms.

3 Simulation Results

We did three simulations series to demonstrate the influence of long-range horizontal connections on spike and burst synchronization. The initial simulation was done to show that, for our network, synchronization between neurons situated in different minicolumns is not possible, in the absent of the long-range horizontal connections. The network was tested on two different types of inputs. A drifting grating stimulus, modeled as a constant current [6], and a moving bar stimulus, modeled as a Poisson spike train with maximum frequency defined in a Gaussian manner [6]. We saw that in the absence of long-range horizontal connections, the neurons in different minicolumns were not synchronized with each other (Fig. 1). Although the response of the network to the two inputs was different, spike synchronization between neurons inside a minicolumn was present in both cases, especially for constant current input.

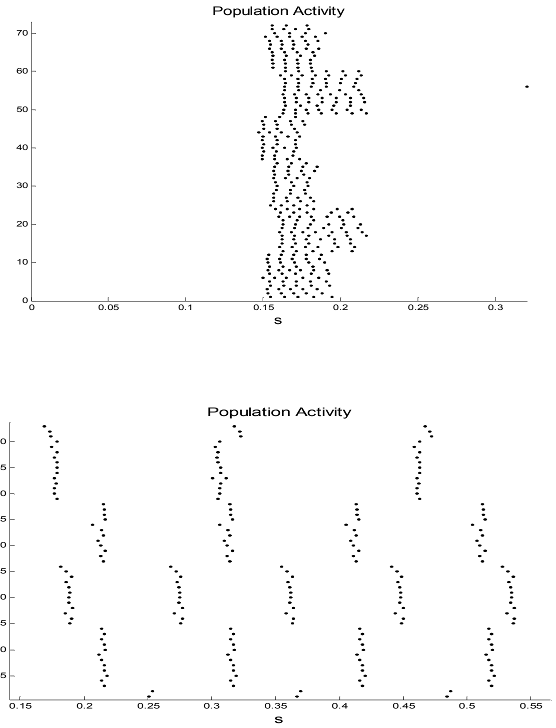

Fig. 1. Population activity in the absent of long-range horizontal connections. Poisson spike train input (*above*), Constant current input (*below*).

The following two simulations were done with the same two input types as described above, and in the presence of long-range horizontal connections. A drifting grating stimulus (constant current) resulted in both spike and burst synchronization for different values on input currents. In the first part of this simulation all the neurons received constant current. Some of the cells displayed repetitive bursting, for higher values of input current, synaptic weights or more dense connections. Spike synchronization as well as burst synchronization could be seen (Fig. 2). It is assume that the repetitive bursting behaviour contributes to synchronous oscillation of the population [12]. But this behaviour destroyed high precision spike synchronization (Fig. 2). In the second part of this simulation we fed only neurons in minicolumns one, two, five and six with constant current to see if neurons in minicolumns one and six still were correlated with each other. Observe that there were no direct connections between minicolumns one and six during this particular simulation, and neurons in the two middle minicolumns were not spiking (not shown here). Spike synchronization between neurons in minicolumn one and six was however present (Fig. 3). There was a tendency for a lag of a couple of millisecons if synaptic weights were low or connections were sparse (not shown here). Observe that the shortest possible delay between two neurons situated in minicolumn one and six was 2.75 ms. Gamma-band oscillation (20-70Hz) could be generated with different values on current input, and we assumed that oscillation was a property of the network.

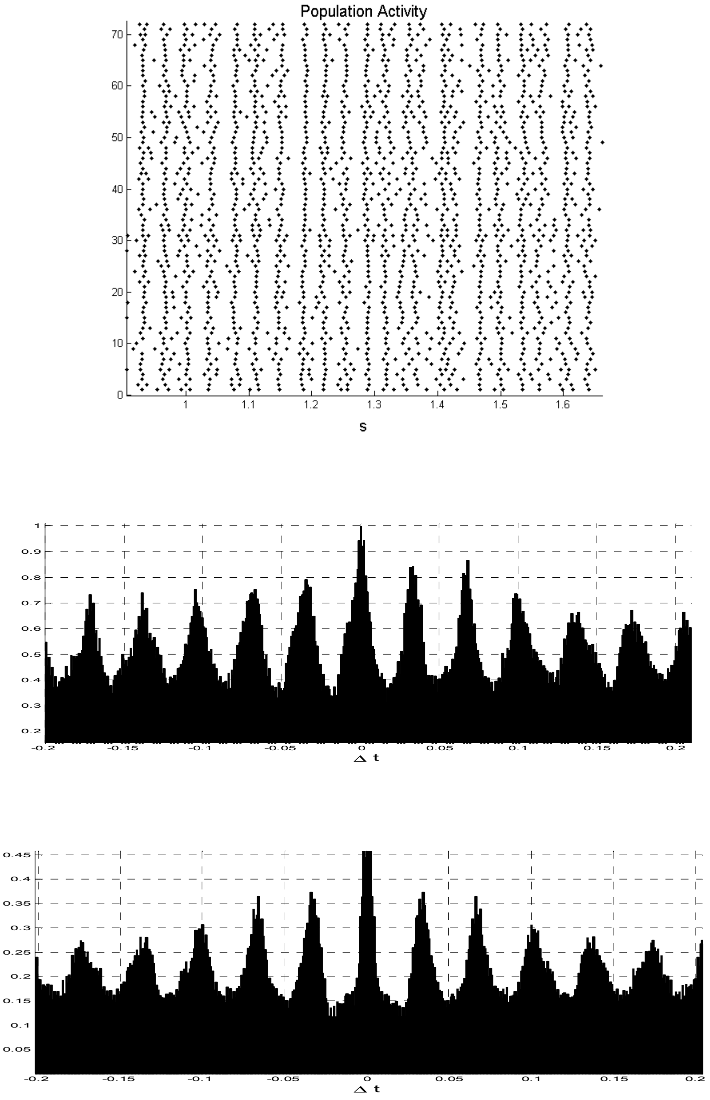

Fig. 2. Population activity (*top*), and cross-correlation (*middle*) between minicolumn one (neurons 1-12) and six (neurons 61-72). Auto-correlation on minicolumn six (*bottom*).

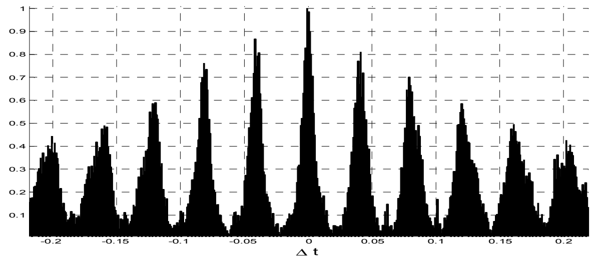

Fig. 3. Cross-correlation between minicolumn one and six. Neurons in the two middle minicolumns were not receiving current input, and were not spiking throughout the simulation. Oscillation frequency is 25 Hz.

The intention of the moving *one* bar-stimulus simulation was to show that, it is possible for neurons to respond to a stimulus that they are not receiving directly. In this simulation all neurons received constant current input. However this input was not sufficient for generating a spike, and corresponded to lowering of the thresholds. Neurons in minicolumns one, two, five and six received uncorrelated Poisson spike trains for a short period of time (80-100 ms) as described above. Poisson spike EPSP:s were in the range of 0.05mV. On average neurons received 65 of these spikes. We saw that neurons in minicolumns three and four were activated by other neurons, with a lag of approximately 4 ms (Fig. 4 and 5).

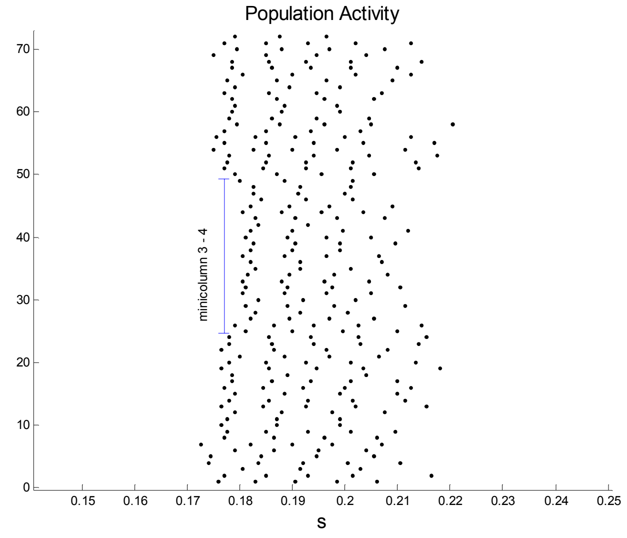

Fig. 4. Population activity. Notice how minicolumns three and four lagged behind.

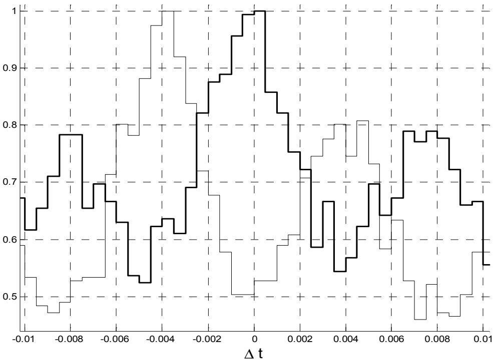

Fig. 5. Cross-correlation between neurons 1-24 and 49-72 (*thick line*). Cross-correlation between neurons 1-24 and 25-48 (*thin line*) for the trial shown in Fig. 3.

High precision spike synchronization was present only during the first two spikes (Fig. 4). With lower values on Poisson spike EPSP:s or larger deviation for the Gaussian distribution high precision spike synchronization could be achieved for longer durations (not shown here). However we could see that burst synchronization and oscillation was present (Fig. 6).

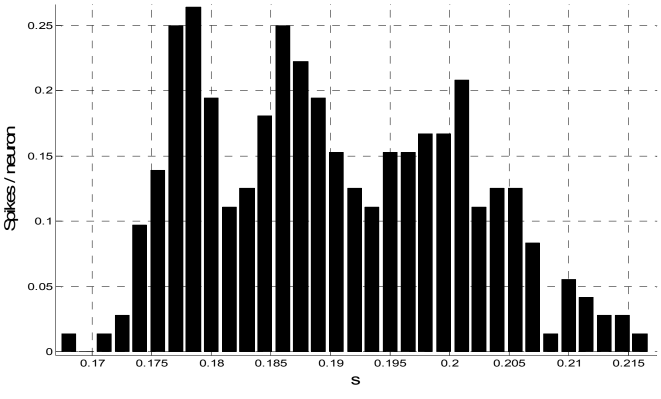

Fig. 6. Average PSTH of six trials.

4 Conclusion

We have shown that phenomena like spike and burst synchronization is possible to simulate with a biologically detailed network of I-F neurons. High precision spike synchronization (<10 ms) was possible to achieve with a constant current input. With increased input some of the neurons displayed repetitive bursting, which helped population oscillation but destroyed high precision spike synchronization.

We saw also that the network behaviour was rather independent of the input type. We assume that more pronounced spike synchronization could be achieved for the one bar stimulus simulation, if the stimulus configuration was different, as stated before.

The long-range horizontal connections played an important role for synchronization. Even with very few connections it was possible to spike synchronize neurons situated in minicolumns 2.5 mm from each other. We would like to stress the fact that, on average, there were at maximum two connections between neurons in minicolumn one and six during the simulations. Spike synchronization was tighter between neurons spatially closer to each other and decreased with distance.

Direction of our future research is to make the network model even more realistic. We are currently testing the network model with Poisson neurons. Cortical neurons are known for their irregularity of the interspike interval [3,9]. Preliminary results have shown that oscillation is possible to achieve with our network using Poisson neurons. Our intention is to expand the model with inhibitory neurons as well. We believe that inhibition will contribute to synchronized activity [4].

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