An Important Role of Spike Timing Dependent Synaptic Plasticity in the Formation of Synchronized Neural Ensembles

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Abstract

Synchronous neural activity plays an important role in the functioning of the brain. In this paper we study the entrainment of a heterogeneous network of electrically coupled neurons by synapticaly mediated periodic stimulation. We demonstrate by computer simulations that input synapses with spike timing dependent plasticity (STDP) greatly enhance the coherence of spiking activity in the network as compared to the case of input with constant strength. We also show that synchronization in the network stimulated through STDP synapses is much more robust to the variability of network properties. The observed mechanism may play a role in synchronizing the activity of a hippocampal network.

Key words: Synchronization, spike timing dependent plasticity, hippocampus

1 Introduction

Synchronous neural activity plays an important role in the functioning of the brain. It is a robust phenomenon, frequently observed across populations of neurons with diverse membrane properties and intrinsic frequencies. In the light of such diversity it remains unclear how can precise synchronization be achieved in heterogeneous networks. Several mechanisms were suggested and many of them require unreasonably high degree of network homogeneity or

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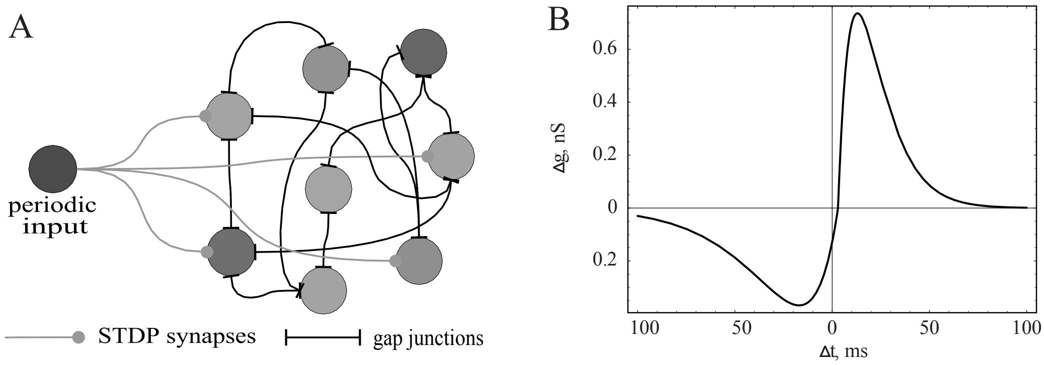

Fig. 1. (A) Configuration of the model: heterogeneous network of tonically spiking pyramidal neurons stimulated by external periodic input through a set of STDP synapses. (B) The curve illustrating the learning rule used in simulations of STDP.

very strong connectivity to achieve coherent neural activity. Recently, it was demonstrated in computer simulations and in experiments with hybrid neural circuits that in a network of two synaptically coupled neurons spike timing dependent plasticity (STDP) of the synapse leads to the dynamic self-adaptation of synaptic conductance to the value that is optimal for the entrainment of the postsynaptic neuron (6; 5). In this paper we study the entrainment of a heterogeneous network of electrically coupled neurons by periodic external stimulation. Only a fraction of neurons in the network receive stimulation. We show by computer simulations that such network oscillates with much higher degree of coherence when it is subject to the stimulation that is mediated by STDP synapses as compared to the case of stimulation through static synapses. We also study how the observed phenomenon is influenced by the number of stimulated neurons, strength of electrical coupling and the degree of heterogeneity.

2 Description of the Model

Our computational model consists of 50 one-compartmental pyramidal neurons (3) randomly connected by 1750 gap junctions (Fig. 1(A)). Conductances of the gap junctions are taken to be relatively small and chosen randomly from the interval $g_{gj} \pm 50\%$ with $g_{gj} = 0.1\, nS$. Each neuron is spiking tonically with a period randomly chosen from the interval $T_2 \pm 30\%$ with $T_2 = 35\, ms$. The network receives periodic input ($T_1 = 25\, ms$) through a number of excitatory STDP synapses. Initial conductances of the input synapses are chosen at random from the interval $g_{in} \pm 50\%$ with $g_{in} = 2.5\, nS$.

The time dependent conductance of STDP synapses $g(t)$ is influenced by the spike timings of pre- and postsynaptic neurons. For each pair of nearest pre- and postsynaptic spikes, $g(t)$ is changed by $\Delta g(t)$ which is a function of the

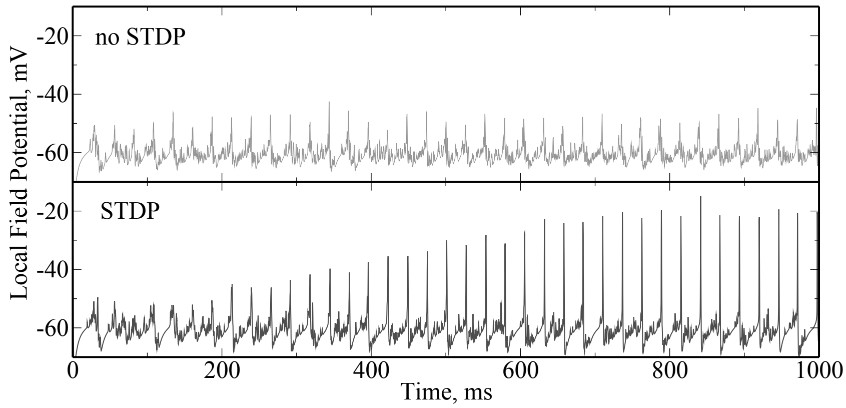

Fig. 2. Time dependence of the local field potential in networks with constant (top) and STDP-mediated (bottom) inputs.

time difference $\Delta t = t_{post} - t_{pre}$ between the spikes. We use additive update rule with a linear superposition of conductance changes and a small shift of the curve, τ_0 (Fig. 1(B)):

$$\Delta g = G(\Delta t) = \begin{cases} A_+ \frac{\Delta t - \tau_0}{\tau_+} e^{-(\Delta t - \tau_0)/\tau_+} & \text{for } \Delta t > \tau_0 \\ A_- \frac{\Delta t - \tau_0}{\tau_-} e^{(\Delta t - \tau_0)/\tau_-} & \text{for } \Delta t < \tau_0 \end{cases} \tag{1}$$

with the following values of parameters: $A_+ = 2\,nS$, $A_- = 1\,nS$, $\tau_+ = 10\,ms$, $\tau_- = 20\,ms$, $\tau_0 = 3\,ms$.

3 Results

As Fig. 2 illustrates, the amplitude of network oscillations as measured by the local field potential (LFP) remains constant throughout the response in the case of constant input conductances and exhibits growth and saturation at much higher values in the case of input synapses with STDP. The explanation for such behavior of LFP amplitudes is evident from Fig. 3 where the dynamics of synaptic conductances in the case of STDP-mediated inputs is plotted. As one can see, these conductances change dynamically at the beginning of the response and in a relatively short time reach location-specific steady state values. So, as it was shown in (6; 5) for the case of two neurons, input synapses provide forcing of the strength which is appropriate for synchronization of presynaptic and postsynaptic spike trains at each site of the network.

Let us investigate the role of different parameters of the model. In order to quantify the ability of STDP synapses to mediate an efficient entrainment

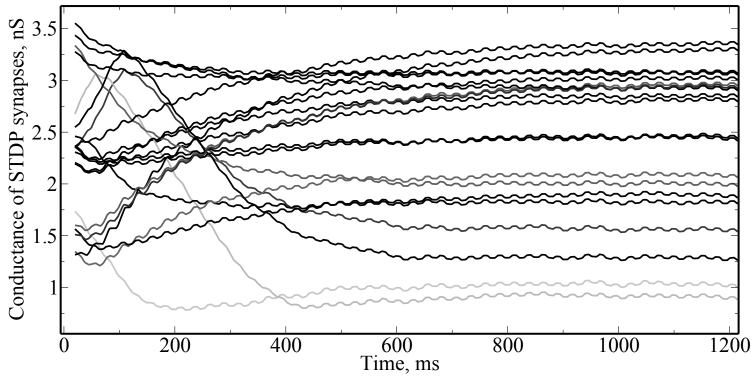

Fig. 3. Dynamics of conductances of input synapses with STDP.

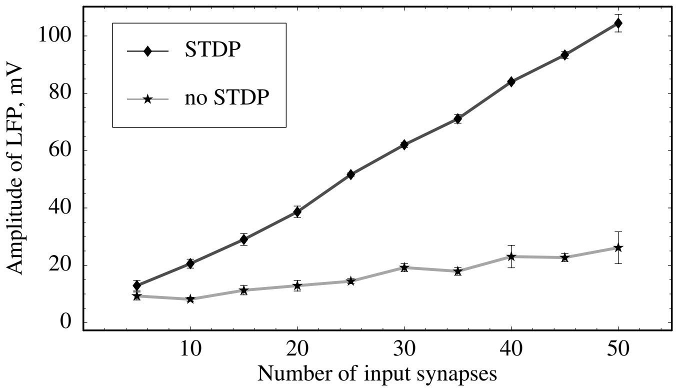

Fig. 4. Dependence of the amplitude of network's local field potential on the number of input synapses.

of the postsynaptic network we compare the coherence of network oscillations (as measured by the amplitude of LFP) for the cases of constant and STDP-mediated inputs. First, let us see how the coherence of oscillations is influenced by the number of inputs. To account for the role of parameter heterogeneity we simulate 5 random networks for each data point. As one can see in Fig. 4, the coherence in STDP-stimulated networks growth much faster with the number of input synapses. Interestingly, the network without STDP shows a relatively low degree of coherence, even when each neuron in the network is stimulated. This is because conductances of input synapses do not depend on the differences of presynaptic and postsynaptic frequencies and hence provide inadequate forcing strengths.

Let us now look at the role of g_{gj} - average conductance of the gap junctions. In Fig. 5 we plot the LFP amplitudes for different values of g_{gj} obtained in simulations of a network with 50 input synapses. Notice that in the case of STDP-mediated stimulation the amplitude of LFP is almost independent of g_{gj}. The difference between the amplitudes is especially profound in weakly coupled networks in which gap junctions play no role in synchronization.

Finally, we investigate the role of network heterogeneity by simulating net-

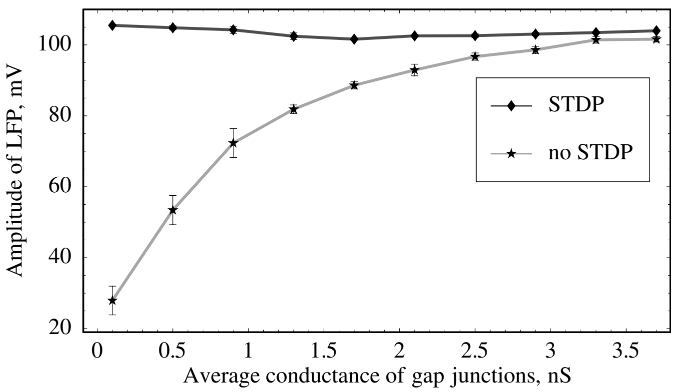

Fig. 5. Dependence of the amplitude of network's local field potential on the average conductance of gap junctions.

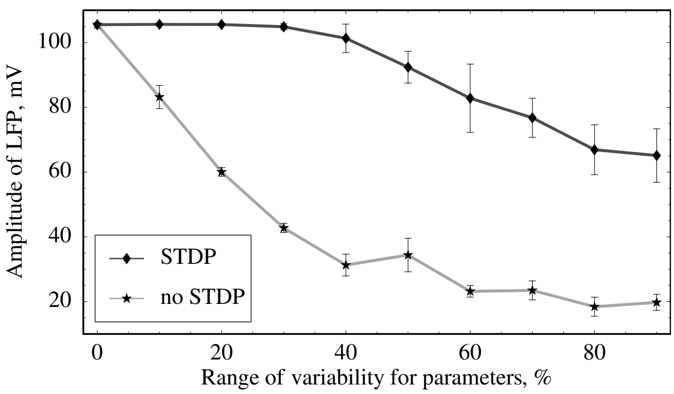

Fig. 6. Dependence of the amplitude of network's local field potential on the variability of network parameters.

works with 50 input synapses and varying the range of variability for the conductances of gap junctions, conductances of input synapses and spiking periods of the neurons. As Fig. 6 illustrates, coherent oscillations in STDP-stimulated networks are much more robust to the variability of network properties. They are robust because conductances of STDP synapses reach optimal for synchronization values regardless of the mismatch in membrane properties.

4 Discussion

Due to the heterogeneity of the network, stimulation of different strength is needed at different sites of the network to bring it into synchronized state. We have demonstrated that STDP leads to such specificity of stimulation by dynamically adjusting the strength of each synapse to the value that is optimal for entrainment. On the other hand, stimulation through static synapses is, in general, not site specific and can not provide adaptive level of stimulation. As a result, coherence of network oscillations is much higher when it is stimulated by STDP synapses as compared to the case of stimulation by static synapses. The difference in coherence is maximal for weakly coupled networks. Also, as we have shown, coherent oscillations in STDP-stimulated network are much more robust to the variability of network properties.

Recent experiments with connexin36 knock out mice (1; 2) and modeling studies (4) suggest that electrical coupling between hippocampal pyramidal cells is responsible for the formation of synchronized gamma-band activity in hippocampus, while gap junctions between interneurons exert modulatory effect. Taking into account the fact that processes that synapse onto pyramidal cells exhibit STDP, we suggest that the described above mechanism may play a role in effective entrainment of the hippocampal network by the input from upstream areas of the brain.

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