

Improvement of spike coincidence detection with facilitating synapses

Jorge F. Mejías and Joaquín J. Torres

*Department of Electr. and Matter Physics, and Institute Carlos I for Theoretical
and Computational Physics, University of Granada, E-18071 Granada, Spain*

Abstract

A realistic model of activity dependent dynamical synapses is used to study the conditions in which a postsynaptic neuron detects temporal coincidences of spikes arriving from N different afferents. We analyse the interaction between synaptic depression and facilitation, which are known to be important short-term mechanisms for synaptic transmission. Compared with the case of only depressing synapses, our results show that facilitation improves the detection of correlated signals arriving from a subset of presynaptic excitatory neurons, as well as presynaptic firing rate changes. In addition, facilitation determines the existence of an input frequency value which allows the best performance for a wide (maximum) range of the neuron firing threshold. This could be important for the detection of relevant information in neural systems constituted by neurons showing a high variability in firing threshold as occurs in some cortical areas.

Key words: Short-term depression and facilitation, spike coincidence detection.

1 Introduction

In recent years it has been reported that postsynaptic membrane potentials recorded in cortical neurons present dynamical properties which are strongly dependent on the presynaptic activity [8,1]. This behaviour can be explained by considering several synaptic mechanisms such as short-term synaptic depression and facilitation. The former is well known to be responsible of several emerging complex phenomena as, for instance, cortical gain control [1], and complex switching behaviour between activity patterns in neural network models [7,2]. It considers that synaptic buttons contain only a limited amount of neurotransmitters ready to be released. This fact turns into a situation in which the neuron is unable to transmit the incoming spikes if the presynaptic firing rate is too high. Therefore, the resulting dynamics are highly nonlinear

and strongly dependent on presynaptic activity. Moreover, synapses in cortical neurons also exhibit synaptic *facilitation*. This mechanism takes into account that the influx of calcium ions through voltage-sensitive channels favours the neurotransmitter vesicle depletion. As a consequence facilitation is able to explain several relevant behaviour observed in real neural tissue, such as the efficient detection of bursts of action potentials (AP) [4].

In this work we use a phenomenological model of dynamic synapses, which takes into account the two mechanisms explained above, to theoretically study their influence on the spike coincidence detection (CD). With preciseness, we compute the conditions (that is, the regions in the space of the relevant parameters of the model) in which a postsynaptic neuron can efficiently detect temporal coincidences of spikes arriving from N different afferents. Our study shows that facilitation improves the detection of these correlated spikes, specially when the synapse does not have enough synaptic resources. In these conditions, depressing synapses are not able to perform well. In addition, facilitation also reveals the existence of a certain frequency value which allows the best performance for a wide range of values of the neuron firing threshold. This optimal frequency can be controlled by means of facilitation control parameters. Finally, we observe that the inclusion of the facilitation mechanism yields to a better detection of changes in the presynaptic firing rate, for certain conditions in which only depression does not perform well.

2 Model

We consider a postsynaptic neuron receiving signals from N presynaptic neurons through excitatory synapses. In order to approximately model experimental data, we assume that the activity of each presynaptic neuron can be viewed as a temporal Poisson spike train with mean frequency f . The state of the synapse i is given by [8]

$$\begin{aligned} \frac{dx_i}{dt} &= \frac{z_i}{\tau_{rec}} - U_i(t)x_i\delta(t - t_{sp}) \\ \frac{dy_i}{dt} &= -\frac{y_i}{\tau_{in}} + U_i(t)x_i\delta(t - t_{sp}) \\ \frac{dz_i}{dt} &= \frac{y_i}{\tau_{in}} - \frac{z_i}{\tau_{rec}} \end{aligned} \tag{1}$$

where x_i, y_i, z_i are the fraction of neurotransmitters in a recovered, active and inactive state, respectively. This model assumes that every time an AP arrives at $t = t_{sp}$ to the synapse, a certain fraction $U_i(t)$ of neurotransmitters that are in the recovery state (that is, neurotransmitters that are ready to take part in the synaptic transmission) are released to the synaptic cleft. Then,

these neurotransmitters become inactive during a characteristic time constant τ_{in} . After a certain period of recovery (typically τ_{rec}), the synaptic resources are reloaded and the synapse returns to its initial state. Since the fraction of available neurotransmitters is limited, the strength of the synapse can decrease for rapid repetitive presynaptic activity, yielding to the well known depression phenomena. Depressing synapses are obtained for $U_i(t) = U_{SE}$ constant, which represents the maximum amount of neurotransmitters which can be released after the arrival of each presynaptic spike. Typical values of the parameters in cortical depressing synapses are $\tau_{in} = 3 \text{ ms}$, $\tau_{rec} = 800 \text{ ms}$, and $U_{SE} = 0.5$ [8]. The synaptic facilitation mechanism can be introduced assuming that $U_i(t)$ has its own dynamics related with the release of calcium from intracellular stores and the influx of calcium from the extracellular medium each time an AP arrives. We consider the dynamics proposed in [8] which assume $U_i(t) \equiv U_{SE} + u_i(t)(1 - U_{SE})$, with

$$\frac{du_i(t)}{dt} = -\frac{u_i(t)}{\tau_{fac}} + U_{SE}[1 - u_i(t)]\delta(t - t_{sp}). \quad (2)$$

Here, $u_i(t)$ is a dynamical variable which takes into account the influx of calcium ions into the neuron near the synapse through voltage-sensitive ion channels. These ions usually bind to some acceptor which gates and facilitates the release of the remaining available neurotransmitters, namely $(1 - U_{SE})x_i(t)$. A typical value for the facilitation time constant is $\tau_{fac} = 530 \text{ ms}$ [3]. We assume that the postsynaptic current due to a particular synapse i is given by $I_i(t) = A_{SE} y_i(t)$, and the total postsynaptic current can be written as $I_{total}(t) = \sum_{i=1}^N I_i(t)$. This approach can be valid for $V < V_{th}$ and $\tau_m \gg \tau_{in}$. Then, the parameter A_{SE} is the maximum postsynaptic current that a synapse can generate (we choose $A_{SE} \approx 42.5 \text{ pA}$). The corresponding postsynaptic membrane potential is modeled using an integration-and-fire (IF) neuron model

$$\tau_m \frac{dV(t)}{dt} = -V(t) + R_{in} I_{total}(t), \quad (3)$$

where $R_{in} = 0.1 \text{ G}\Omega$ and $\tau_m = 15 \text{ ms}$ are, respectively, the input resistance and the membrane time constant. These typical values have been taken also from pyramidal cells [8]. The IF model assumes that once $V(t)$ reaches a certain threshold V_{th} , an AP is generated and after that $V(t)$ resets to zero. We consider also a refractory period of $\tau_{ref} = 5 \text{ ms}$ during which $V(t)$ remains to zero after the generation of each AP.

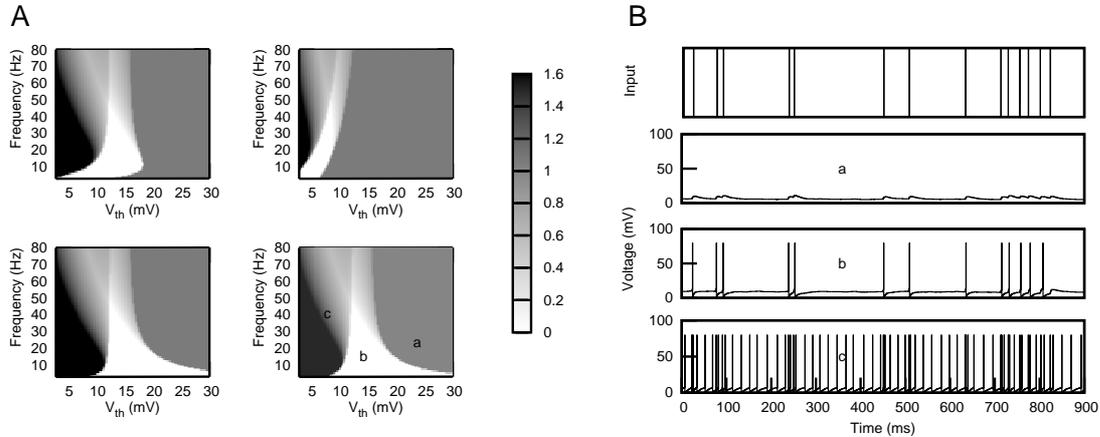


Fig. 1. (A) Coincidence detection maps for a system with facilitating-depressing (left) and only-depressing (right) synapses for $U_{SE} = 0.05$ (top) and 0.5 (bottom). The inclusion of facilitation allows for a better CD for relative small U_{SE} and the same performance for relatively large U_{SE} . (B) Postsynaptic membrane voltage time series for the conditions marked by letters in the CD maps of panel A.

3 Results

We have studied the postsynaptic response of a neuron receiving input signals from $N = 1000$ excitatory synapses, with a subset of $M = 200$ synapses stimulated by identical spike trains. These strongly correlated afferents can be considered as a *signal* term. The remaining $N - M$ synapses receive uncorrelated spike trains (*noisy* term). We have investigated spike coincidence detection (CD) experiments by computing CD *maps*. In these maps, we computed the fraction of errors committed by the postsynaptic neuron in the detection of the signal for a wide range of values for the relevant parameters, that is, the incoming frequency f and neuron threshold V_{th} [6]. An appropriate error coefficient is defined as $\Delta = (N_{false} + N_{failure})/N_{input}$, where the number of false, failure and input spikes are computed. Although other definitions could be used, the coefficient proposed here is convenient since the regions of false spikes (low threshold values) and failures (high threshold values) are clearly separated. The main results are showed in figure 1A. The light area corresponds to regions where the postsynaptic neuron is able to efficiently detect the coincidence-input-events and to generate a postsynaptic response strongly correlated with the input signal (situation marked by "b" in the figure 1B). On the other hand, dark areas are regions with a high percentage of errors (situations "a" and "c"). Then, the inclusion of facilitation improves the detection of correlated signals in regions where only-depressing synapses do not perform well. This improvement is observed for any value of U_{SE} and τ_{fac} , but is more evident for moderate values of U_{SE} (< 0.1) and high values of τ_{fac} . Concretely, for a fixed τ_{fac} the increment of U_{SE} leads to an enlargement

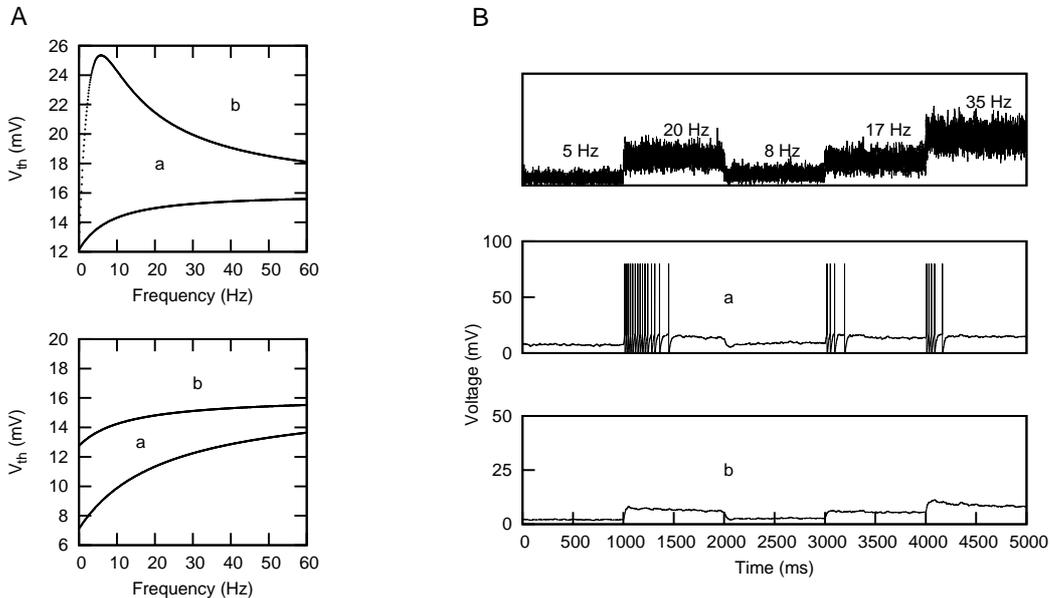


Fig. 2. (A) FRCD maps for a system with facilitating-depressing (top) and only-depressing synapses (bottom). (B) Time series of the postsynaptic membrane potential under the firing rate change protocol showed in the top panel for the situations marked with letters in graph A.

of the light area, allowing a better CD for higher thresholds. This fact is also observed when one fixes U_{SE} and varies the facilitation time constant τ_{fac} . A detailed observation of figure 1 also shows the existence of a certain frequency which allows a good performance for a wide (maximum) range of values of V_{th} (see threshold range for $f = 10 Hz$ in top left CD map). This feature could be relevant for information processing in real neural systems constituted by neurons with different values of the firing threshold. The results obtained above have been numerically tested and are the same for more realistic situations as, for instance, when signals arriving from different synapses are not totally correlated in time [5].

Another interesting approach to real situations is the assumption that the presynaptic firing rate is a dynamic variable in real neuronal tissue, not a fixed parameter. These rate changes leads to a transient behaviour in the EPSP which could cause a postsynaptic response [8,6,1]. That is, the neuron is able to detect synchronous changes (increases) in the afferent firing rates. To study this in the case of facilitating synapses, we assume a population of $N = 1000$ afferents firing uncorrelated Poisson spike trains with a certain frequency f into a postsynaptic neuron. This population changes its firing rate on periodic time intervals, in such a way that increases and decreases are produced (cf. figure2 top panel of B). We can theoretically compute the regions for detection of firing rate changes (FRCD) in an approximate way. Thus, to allow FRCD the threshold must satisfy $Cf_2\omega(f_1) > V_{th} > Cf_2\omega(f_2)$, where f_1 is the initial

rate, f_2 the final rate, $C = R_{in}N\tau_{in}$ a constant and $\omega(f) = A_{SE}U_{stationary}/(1 + f\tau_{rec}U_{stationary})$ is the synaptic strength –which can be easily computed from 1. This condition assumes that the synaptic strength varies slowly compared with the characteristic time for the transition between two firing rate values. If we fix the frequency step $\delta f = f_2 - f_1$, the resulting expressions lead to a close area of good FRCD between the two curves. These regions are showed in figure 2A for both facilitating-depressing and only depressing case. The shape and extension of both regions are drastically different. Thus, cooperation between depression and facilitation should be important to obtain good FRCD for the maximum range of conditions.

4 Discussion

This study shows that the inclusion of facilitation mechanisms enhances the performance of cortical neural systems in the transmission of information embedded in spike trains. Contrary to what it happens with only depression, the presence of facilitation makes not necessary to have a high value for the maximum amount of active neurotransmitters to have a good CD. Moreover, facilitation enhances good detection even when the correlation between different presynaptic afferents is not too strong. Facilitation also reveals the appearance of an optimal frequency and allows to control it by tuning the facilitation parameters. This result could be important to understand how real neural systems –where different types of neurons may have non-identical firing thresholds– can self-organize to efficiently detect and process correlated signals. Finally, facilitating synapses enhance the detection of rate changes for certain conditions, which could lead us to think that both depression and facilitation can cooperate in order to compute efficiently information for a wide range of conditions.

5 Acknowledgments

This work was supported by the *MEyC-FEDER* project FIS2005-00791 and the *Junta de Andalucía* project FQM-165.

References

- [1] L.F. Abbott, J.A. Varela, K. Sen, S.B. Nelson, Synaptic depression and cortical gain control, *Science* 275 (5297) (1997) 220–224.

- [2] J.M. Cortes, J.J. Torres, J. Marro, P.L. Garrido, H.J. Kappen, Effects of fast presynaptic noise in attractor neural networks, *Neural Comp.* 18 (2006) 614–633.
- [3] H. Markram, Y. Wang, M.V. Tsodyks, Differential signaling via the same axon of neocortical pyramidal neurons, *Proc. Natl. Acad. Sci. USA* 95 (1998) 5323–5328.
- [4] V. Matveev, X.J. Wang, Differential short-term synaptic plasticity and transmission of complex spike trains: to depress or to facilitate?, *Cerebral Cortex* 10 (2000) 1143–1153.
- [5] J.F. Mejias, J.J. Torres, The role of synaptic facilitation in coincidence spike detection, to be published (2006).
- [6] L. Pantic, J.J. Torres, H.J. Kappen, Coincidence detection with dynamic synapses, *Network: Comput. Neur. Syst.* 14 (2003) 17–33.
- [7] J.J. Torres, J. Cortes, J. Marro, H. Kappen, Competition between synaptic depression and facilitation in attractor neural networks, to be published (2006).
- [8] M.V. Tsodyks, H. Markram, The neural code between neocortical pyramidal neurons depends on neurotransmitter release probability, *Proc. Natl. Acad. Sci. USA* 94 (1997) 719–723.