Signal detection in networks of spiking neurons with dynamical synapses

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Abstract. Using a realistic model of activity-dependent synapses, we study the detection of coincident spikes by a postsynaptic neuron. In this context, the interplay between short-term depression and facilitation is analyzed. We have computed, both numerically and analytically, the degree of correlation between the postsynaptic response and the input signal. Our study shows that facilitation strongly enhances spike detection compared with the situation in which depression is the only considered synaptic mechanism. In addition, facilitation determines the existence of an optimal input frequency value, which allows for the best performance within a wide (maximum) range of the neuron firing threshold. This fact could be important in coding relevant information in neural systems constituted by neurons with a high variability in their firing thresholds, as occurs in some cortical areas.


Keywords: short-term depression and facilitation, spike coincidence detection

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INTRODUCTION

It is known that postsynaptic membrane potentials recorded in cortical neurons present dynamical properties which are strongly dependent on the presynaptic activity [1, 2]. This behaviour is usually explained by means of several synaptic mechanisms such as short-term synaptic depression and facilitation. Synaptic depression occurs when the limited amount of neurotransmitters in the synaptic buttons disables the neuron to transmit the presynaptic signals for high input rates. This leads to a nonlinear behaviour of the system which is responsible for some complex emergent phenomena as, for instance, switching of the neural activity between different activity patterns [3] and enhancing the network sensitivity to external stimuli [4]. On the other hand, synaptic facilitation is a mechanism produced by the influx of calcium in the presynaptic neuron, near the synapse, after the arrival of an action potential. The extra calcium favours the release of neurotransmitters, which, in fact, increases the probability for synaptic transmission. This mechanism can explain several neural phenomena such as the efficient detection of activity bursts [5].

Here, 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). More precisely, we compute the conditions (that is, the regions in the space of 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, especially when the synapse does not have enough synaptic resources. In these conditions, depressing synapses are not able to perform well. Moreover, our study also reveals the existence of an optimal input frequency at which an efficient detection of presynaptic spikes occurs for a wide range of values of the neuron firing threshold. This resonant type of behaviour only occurs in the presence of facilitation and the particular value for this optimal frequency can be controlled by means of facilitation control parameters.

THE MODEL

Our starting point is a postsynaptic neuron which receives inputs from a set of $N$ presynaptic neurons, with a subset $M$ of them strongly correlated in time (signal term). The remaining $N-M$ neurons are totally uncorrelated and constitute a noisy background. Each synapse has its own dynamics described by the equations

$$
\begin{align*}
\frac{dx_i}{dt} &= \frac{z_i}{\tau_{\text{rec}}} - U(t)x_i\delta(t-t_{sp}) \\
\frac{dy_i}{dt} &= \frac{y_i}{\tau_{\text{in}}} + U(t)x_i\delta(t-t_{sp}) \\
\frac{dz_i}{dt} &= \frac{y_i}{\tau_{\text{in}}} - \frac{z_i}{\tau_{\text{rec}}}
\end{align*}
$$

(1)

where the variables $x_i, y_i, z_i$—that represent the state of the synapse $i$—are the fraction of neurotransmitters in the recovered, active and inactive state, respectively, being $\tau_{\text{rec}}$ and $\tau_{\text{in}}$ the time constant for recovering and inactivating processes. The system of equations (1) considers that the limited amount of neurotransmitters, in the synaptic buttons, causes a decrease in the stationary amplitude of the postsynaptic current when the frequency of the signal is high (synaptic depression). For depressing synapses, $U(t) = U_{SE}$ represents the maximum fraction of neurotransmitters released after a spike. Realistic values of the parameters for cortical synapses are $\tau_{\text{rec}} = 800 \text{ ms}$, $\tau_{\text{in}} = 3 \text{ ms}$ and $U_{SE} \sim 0.01 - 0.9$. In order to consider also synaptic facilitation, one can assume the more general assumption $U(t) = U_{SE} + (1-U_{SE})u(t)$, that is, a fraction of the available neurotransmitters is released after each incoming spike, namely, $U_{SE}$, and the remaining, namely, $(1-U_{SE})u(t)$ is released by means of facilitating mechanisms. Here, $u(t)$ follows the dynamics

$$
\frac{du(t)}{dt} = -\frac{u(t)}{\tau_{\text{fac}}} + U_{SE}[1-u(t)]\delta(t-t_{sp})
$$

(2)

and takes into account the influx of calcium ions into the cell through voltage-sensitive ion channels. This additional calcium favours the release of neurotransmitters to the synaptic cleft and, therefore, facilitates the signal transmission through the synapse. One can also assume that the generated postsynaptic current in each synapse is proportional to the fraction of active neurotransmitters, that is, $I_i = A_{SE}y_i$, where $A_{SE} \approx 42.5 \text{ pA}$ for convenience. The total postsynaptic current $I = \sum_{i=1}^{N} I_i$ generates a postsynaptic
membrane potential which is the result of integrating the equation

\[ \tau_m \frac{dV}{dt} = -V + R_{in} I. \]  

(3)

Here, we take \( R_{in} = 0.1 \, \text{G}\Omega \) and \( \tau_m = 15 \, \text{ms} \) that are typical values for cortical cells [6]. Following the dynamics (3), once \( V \) has reached a certain threshold \( V_{th} \), an action potential (AP) is generated and, suddenly, the membrane potential remains in zero during a refractory period \( \tau_{\text{ref}} \).

**DETECTION OF COINCIDENT SPIKES**

In order to visualize the capacity of the postsynaptic neuron to detect the coincident spikes (signal term), we computed coincidence detection (CD) maps. That is, our interest is to determine the values of the relevant parameters—the input frequency \( f \) and the membrane threshold \( V_{th} \)—which allow for a strong correlation between the input signal and the postsynaptic response. An example of CD map is shown in figure 1. The light zones correspond to areas in which the postsynaptic neuron is able to efficiently detect the input signal. On the other hand, dark zones are regions with a high percentage of errors. These errors are caused by failures in the detection of input spikes (grey zones in the high threshold region) or by the generation of false spikes which do not correspond to presynaptic input events (black zones in the low threshold region). Then, by means of the CD maps, we can characterize the behaviour of the postsynaptic neuron for any set of values of the input frequency and the neuron firing threshold.

Figure 2 shows the effect of including facilitation in a system with only depressing synapses. For high values of the parameter \( U_{SE} (\sim 0.5) \), there is not any effect due to facilitation and the CD map looks very similar with that computed with only depressing synapses. However, if \( U_{SE} \) takes lower values (\( \sim 0.05 \)) one can see that facilitation improves the input signal detection. Moreover, for high enough values of the facilitation characteristic time \( \tau_{\text{fac}} \), one recovers the results obtained for high \( U_{SE} \), that is, the maps with the largest light area for depressing synapses, even if we have low values of \( U_{SE} \). This means that a sustained facilitation during a long time induces an additional depression neglecting the positive effect due to facilitation. Therefore, we can conclude that facilitation improves the detection of coincident signals for most of the values of the relevant parameters.

**OPTIMAL FREQUENCY**

One of the most interesting conclusions that arise from the study of CD maps with only-depressing synapses is the existence of certain threshold value (\( \sim 13 \, \text{mV} \)) which allows a good performance in the detection of signals for a wide range of frequencies [7]. Similarly, our study revealed, for a system with facilitating-depressing synapses, the existence of an optimal value of the input frequency, namely \( f_{\text{opt}} \), at which the postsynaptic neuron efficiently detects signals for a wide (maximum) range of membrane threshold values, namely \( \Delta V_{\text{max}} \). It is shown, for instance, in the figure 1 (upper-left plot in panel
A), where $\Delta V_{\text{max}}$ is obtained for $f_{\text{opt}} \sim 10 \text{ Hz}$. $f_{\text{opt}}$ is always zero for a system with only depressing synapses, as we can see in the right plots in panel A. As a consequence, in a system with a high heterogeneity for the $f$ ring-thresholds, only embedded signals with very low mean $f$ ring rate can be detected. However, if we include facilitation, the optimal frequency can be tuned to higher values by means of facilitation parameters $\tau_{\text{fac}}$ and/or $U_{SE}$, and this allows for a better performance in the processing of signals with high mean $f$ ring rates. For a better quantification of this effect, we represent in figure 3 the behaviour of $f_{\text{opt}}$ (left panel) and $\Delta V_{\text{max}}$ (right panel) as a function of $\tau_{\text{fac}}$ and/or $U_{SE}$. The figure shows that the lower $\tau_{\text{fac}}$ is, the higher value of $f_{\text{opt}}$ is obtained. However, since the limiting case $\tau_{\text{fac}} = 0$ is equivalent to only-depressing synapses, for very low values of $\tau_{\text{fac}}$ the optimal frequency goes to zero. Therefore, there is a certain level of facilitation which allows to have nonzero optimal frequencies, since very high values of $\tau_{\text{fac}}$ induces in the system the additional depressing phenomena explained above. On the other hand, $\tau_{\text{fac}}$ also influences $\Delta V_{\text{max}}$. As we can see in figure 3(right), this magnitude increases with the facilitation characteristic time, that is, for sustained facilitation. The control of $f_{\text{opt}}$ by means of facilitation parameters could be important for the processing of relevant information, codified in the mean-$f$ ring rate of spike trains in actual neural systems constituted, for instance, by neurons with a high variability in their $f$ ring threshold [8].
FIGURE 2. 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 $U_{SE}$.

**DISCUSSION**

In this work, we have shown that the inclusion of synaptic facilitation in neural networks enhances their performance during the transmission of information embedded in spike trains. Moreover and contrary to what it happens with only depressing synapses, the performance of the network with facilitating synapses is even higher when the amount of available neurotransmitters is limited. A particular interesting effect due to facilitation is that neurons, with a priori very different firing thresholds, can detect the same signals when they arrive through synapses with similar degree of facilitation. Some results of our study can be useful for a better understanding of the behaviour of actual neural systems constituted by neurons with different firing-thresholds, as in some cortical networks [8]. Moreover, a more detailed theoretical study of the complex interplay between different synaptic mechanisms and their competition could be important to understand the basis of working memories in the prefrontal cortex, which has been reported to be constituted by several subnetworks with different types of facilitating and depressing synapses [9].
FIGURE 3. Left: Dependence of $f_{opt}$ (left) and $\Delta V_{max}$ (right) (as explained in the text) with $\tau_{fac}$, for different values of $U_{SE}$.

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