Modelling Neural Systems with Short-Term Depression and Facilitation

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Abstract. We review some computational properties of neural model systems with activity-dependent synaptic connections. In particular, we study the interplay between short-term depression and facilitation concerning signal detection, stochastic resonance and global behaviour of attractor neural networks. We discuss on the computational and biological relevance of the competition between depression and facilitation.

INTRODUCTION

It has recently been reported that postsynaptic potentials recorded in cortical neurons present dynamical properties which depend on the presynaptic activity [1, 3, 2]. This behaviour can be understood by the action of different mechanisms at the synaptic level, as for instance, short-term depression and/or facilitation. Depression seems to the due to a limited amount of available neurotransmitters in the synaptic button. Thus, the neuron needs some time to recover before transmiting the next incoming spike. The synapse dynamics is thus an activity-dependent mechanism producing a non-trivial effect in the postsynaptic response. This picture differs from the classical synaptic description which considers the synaptic strengths as static identities with only possible time modifications due to the (relatively) very slow learning processes, as described for instance by Hebb [24]. Synaptic facilitation takes into account that the influx of calcium ions through voltage-sensitive channels favours the neurotransmitter vesicle depletion. Moreover, it is well known that short-term depression plays an important role in several emerging phenomena in the brain [22, 21], such as selective attention [5, 6], cortical gain control [2], and complex switching behaviour between activity patterns in neural network models [7, 9]. Facilitation yields to relevant behaviour in synchrony and selective attention [5], in detection of bursts of action potentials (AP) [10, 11] and in the efficient transmission of temporal correlations between spikes trains arriving from different synapses [12]. However, a full description of the consecuences of competition between the mechanisms present during synaptic transmission on pyramidal neurons is still lacking.

We shall describe here some of the computational properties found in realistic models of dynamic synapses and their implications in the global behaviour of neural networks. In particular, we analyse the interplay between short-term depression and facilitation among different computational tasks. We start focusing at detection of weak signals, detection of changes in the input properties (e.g. input frequency) and synchronization of the postsynaptic neuron with the input for different frequencies. We then review the dynamical properties found in attractor neural networks for the case in which the synapses present short-term depression and facilitation. We show in examples that the effect caused by the competition between the two mechanisms could be of computational and biological relevance in a wide variety of systems.

DETECTING AND PROCCESING SIGNALS WITH DYNAMIC SYNAPSES

In a real tissue, neurons are usually exposed to hundreds of stimuli. Each neuron must be able to distinguish the relevant information, and also to separate it from the noisy environment caused by the presence of other neurons. It is also known that the presence of noise can enhance the signal level and allow the neuron to detect weak signals. This phenomena, known as stochastic resonance (SR), has been measured in experiments in neurons in different areas of the brain [13, 14]. In this context, the dynamic properties of the synapses seems to be relevant. Since the behaviour of real synapses depends on presynaptic activity, this characteristic could regulate the level of the noisy environment
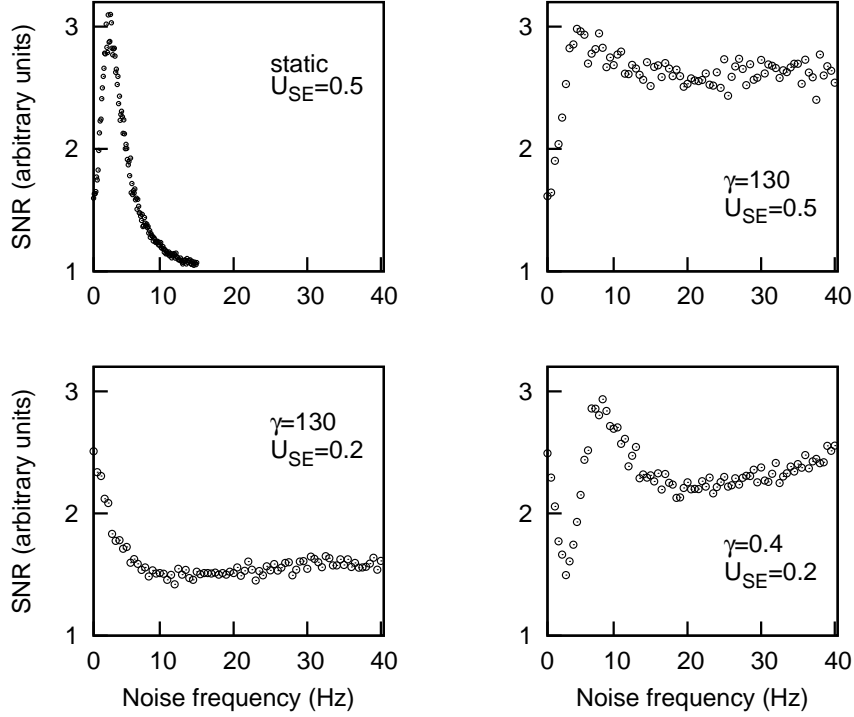
FIGURE 1. SNR as a fuction of the mean frequency of the neurons that constitutes the noisy background. One can see that the effect of including depression is to enhance the response of the neuron to the weak signal, via stochastic resonance. This effect is maintained when facilitation is added, even for low values of U_{SE}.

and allows the neuron to detect a weak signal. This is particularly interesting under high levels of input noise, that is, when the mean firing rate of the neurons which contribute to the noisy background is high. To analyse the influence of dynamic synapses on the detection of weak signals, we employ the model and parameters of dynamic synapses presented in [1] and a standart FitzHugh-Nagumo model, in order to qualitatively reproduce the basic features of neurons as excitable elements. The synapse model is

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

where x_i, y_i, z_i are the fraction of neurotransmitters in a recovered, active and inactive state, respectively. Here, τ_{in}, τ_{rec} and τ_{fac} are the inactivation, recovery and facilitating time constants, respectively. Depressing synapses are obtained for $u(t) = U_{SE}$ constant, which represents the maximum amount of neurotransmitters which can be released (activated) after the arrival of each presynaptic spike. The facilitation mechanism is introduced with the dynamics of u_i, which is a dynamical variable which takes into account the influx of calcium ions into the neuron near the synapse through voltage-sensitive ion channels [15]. The postsynaptic current can be written as $I_{noise} = \sum_i^M A_{SE} y_i$, where $A_{SE} \approx 42 \ pA$ is the maximum postsynaptic current and M is the number of presynaptic afferents [8]. It is useful to define the balance
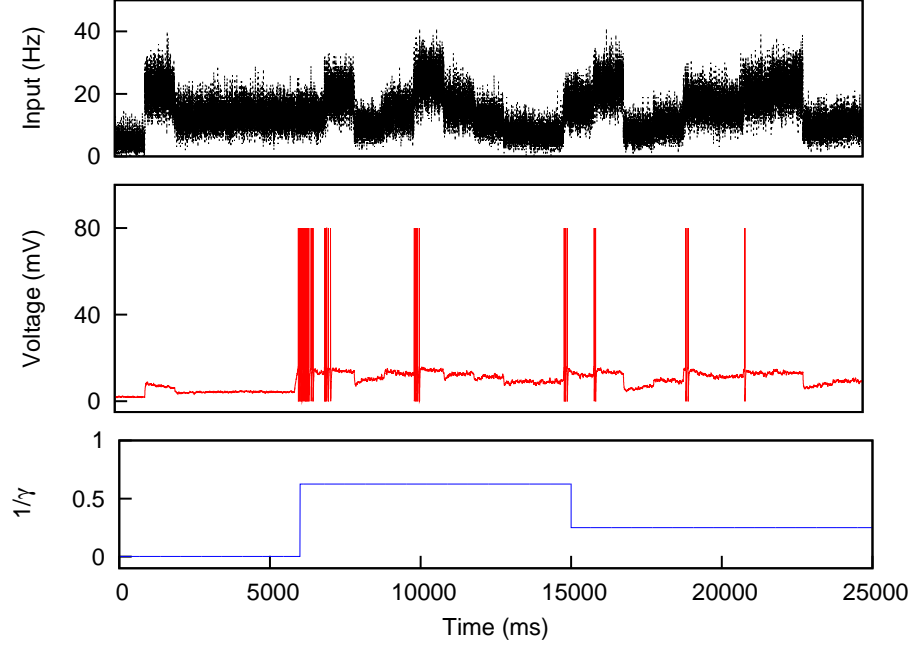
FIGURE 2. Detection of firing rate changes with depressing and facilitating synapses. The top panel shows the mean firing rate of the $M = 1000$ presynaptic neurons as a function of time. Middle panel shows the response of the postsynaptic membrane potential for different levels of balance (bottom panel), with $U_{SE} = 0.1$. Detection of variations onto lower frequencies are not possible with these synaptic mechanisms.

factor $\gamma \equiv \tau_{rec}/\tau_{fac}$, since our goal is to study the interplay between depression and facilitation. The associated neuron model is

$$
\begin{aligned}
\varepsilon \frac{dv}{dt} &= v(v-a)(1-v) - w + S(t) + R_{in}I_{noise}(t) \\
\frac{dw}{dt} &= bv - w,
\end{aligned}
\tag{2}
$$

where v is the postsynaptic membrane potential and w is a slow recovery variable. In these equations, $S(t)$ is the signal term, $R_{in}I_{noise}$ is the noise term and $a = 0.001$, $b = 3.5$ and $\varepsilon = 0.0015$ are other neuron parameters to put the model in the excitable regime.

In order to study the detection of a weak signal of low frequency ($f_s = 1 \ Hz$) we compute the signal-to-noise ratio (SNR) of the output [16], for different values of the synaptic parameters. The result is shown in Fig. 1. For static synapses (top left panel) the system has a well known SR peak around $\sim 3Hz$ for the noise frequency (f_N). If we increase the depression characteristic time (top right) we can see that the resonance is maintained for much higher values of f_N ($\sim 40 \ Hz$ in the plot), allowing the neuron to detect a weak signal over a wide range of noise intensity. However, this is only valid for high values of U_{SE}. If it takes low values, around 0.1, the neuron becomes unable to detect the input signal for any value of noise intensity (bottom left). By including the facilitation mechanism (bottom right) one can recover the maintained resonance. Therefore, depending on the value of U_{SE} a balance between depression and facilitation should be useful to obtain optimal SNR values over a wide range of noise frequencies [19]. Since these frequencies are within the physiological range, dynamic synapses could allow neurons to work even with high frequency values without annoying to other neurons in the network.

Dynamic synapses are also relevant in order to respond to changes in the input properties of the signals. Related to this, a realistic assumption is to consider the presynaptic firing rate as a dynamic variable as it happens in real neuronal tissue. The rate changes during normal functioning of neural systems in the presynaptic current leads to a transient behaviour in the excitatory postsynaptic potential (EPSP) which could cause a burst or an AP in the postsynaptic neuron [1, 12, 2]. The question that arises is if the postsynaptic neuron is able to detect synchronous
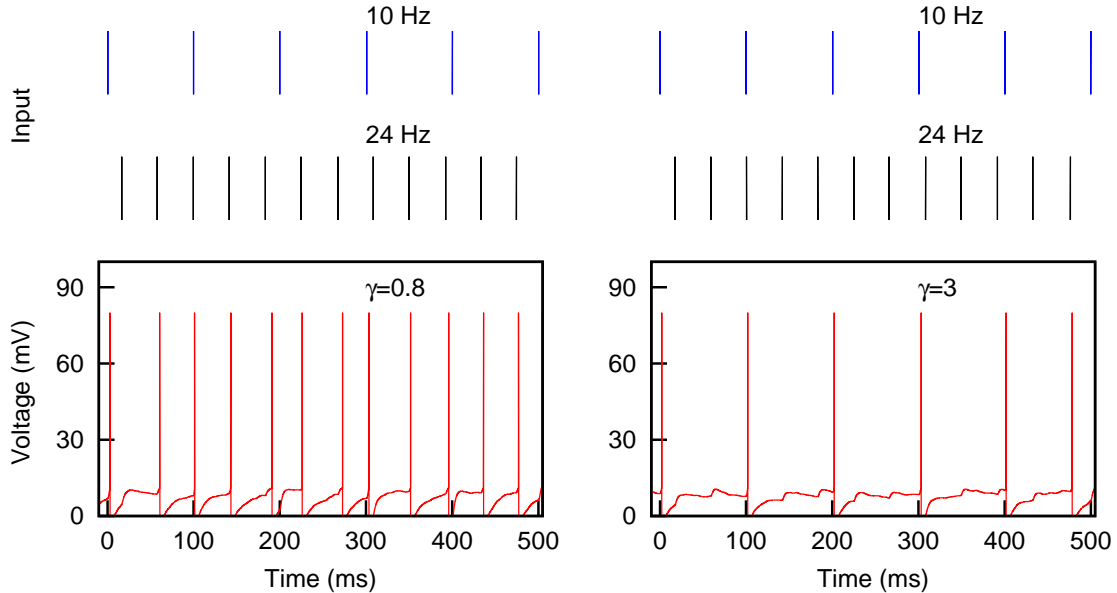
FIGURE 3. Selectivity among different frequencies embedded in the same input signal. Depending on the level of facilitation, the neuron synchronizes its activity with the higher frequency (right panel, for high γ values) or the lower frequency (left panel, low γ values).

changes (increases) in the afferent firing rates, as a function of the facilitation parameters. Here, we try to answer this question by studying the effect of increasing facilitation in spite of depression in the optimal detection of rate changes in the presynaptic current.

We assume a population of M afferents firing uncorrelated Poisson spike trains with a certain frequency f (which changes its value every $1000\,ms$) into a postsynaptic neuron. We use an integrate-and-fire model $dv/dt = -v + R_{in}I(t)$ for the postsynaptic membrane potential. The Fig. 2 shows the behaviour of the postsynaptic neuron for different levels of facilitation. Simulations show that facilitating synapses ($\tau_{fac} = 500\,ms$) allow for a better detection of rate changes, and over a large range of frequencies, than depressing synapses. In general, the regions in which depressing and facilitating synapses perform well can vary. For instance, there are particular situations where facilitation is needed to detect presynaptic rate changes.

Another situation that should be taken into account is that presynaptic spike trains could contain much information in it, and in some cases the neuron must be able to distinguish between different patterns of activity encoded in a single signal. Since short-term depression works as a gain modulator [2], one could expect that the inclusion of facilitation has also an effect in the signal detection depending on the embedded frequency. To test this hypothesis, we have considered two different population of correlated neurons firing spikes periodically to a postsynaptic one, including also a noisy background with fixed frequency f_N. The neurons of a given population j fire spikes simultaneously with a certain frequency f_j. Therefore, the postsynaptic neuron receives signals from both populations, resulting in a nontrivial input spike train. The results of this study are shown in Fig. 3. We take a fixed value for $\tau_{rec} = 800\,ms$ and $U_{SE} = 0.05$. From the figure, one can see that the effect of modifying the balance between depression and facilitation is the synchronization of the postsynaptic neuron with the frequency of population 1 or 2. That is, depending on the level of facilitation, the neuron will detect the spikes of one of the populations and ignore the spikes from the other. Therefore, facilitation works as a selectivity mechanism between signals with different frequencies encoded in the same input spike train.

Finally, we explore the effects of including dynamic synapses in recurrent networks, as a first approach to model the behaviour of real systems constituted by a large number of neurons. The most simple way to do this is to work with an attractor neural network, which is able to capture some basic features of real systems, such as associative memory, with an extremely simple neuron dynamics. This simplicity allows to obtain approximate theoretical results to compare with the simulations [17]. The inclusion of depression and facilitation in attractor neural networks leads to a phenomenon of switching between patterns of activity, previously stored in the network via the Hebb rule [17, 7].
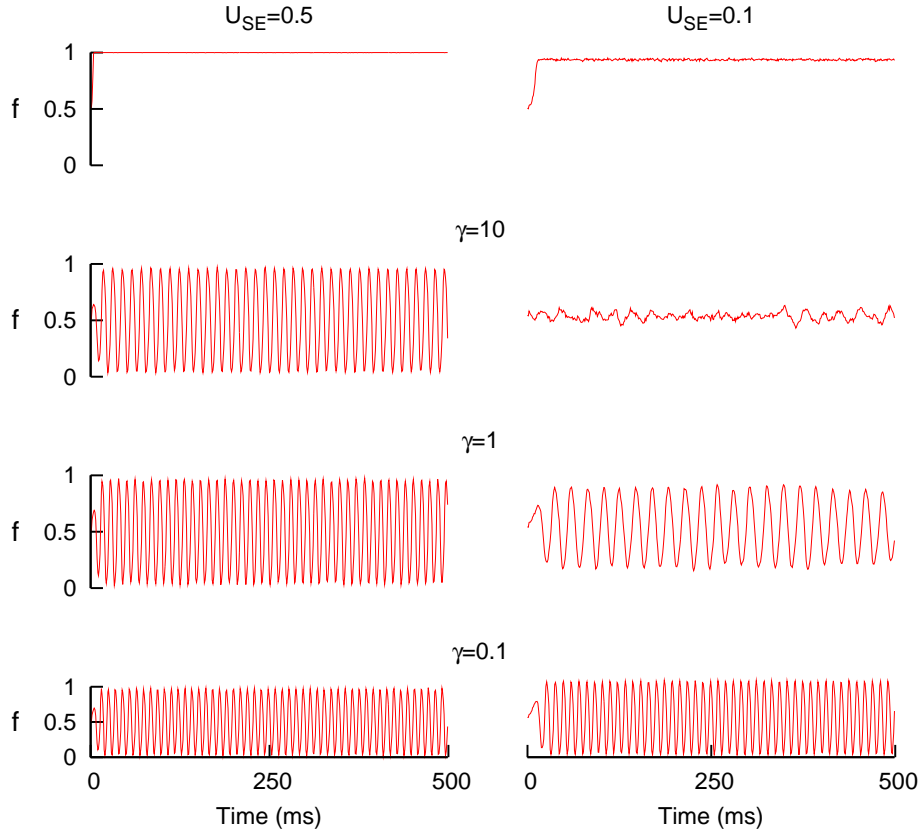
FIGURE 4. Time evolution of the mean firing rate of the network for U_{SE} high (left panels) and low (right) and different levels of facilitation, in several phases. One can see that low values of U_{SE} lead to a richer phenomenology, including oscillations with different mean frequencies (the two lowest panels on the right).

Here, we focus on the role of facilitation in this switching phenomena. An example of this behaviour is shown in Fig. 4. The state of a network of N neurons at instant t is characterized by his mean firing rate $f \equiv (1/N)\sum_i s_i$, where $s_i = 0, 1$ denotes if the neuron i is silent or firing, respectively. One can see that for high values of U_{SE} (when only depression is relevant) and increasing the level of facilitation, the system can only be in two phases, the retrieval phase (top left panel) and the oscillatory phase (the other panels on the left). However, if U_{SE} takes lower values, the facilitation mechanism becomes relevant, and phases of retrieval, non-retrieval and oscillatory behaviour appear (right panels, from top to bottom). One may think, therefore, that the inclusion of facilitation could help to explain the rich phenomenology of oscillations measured in different brain areas [18]. Detailed observations [17] reveal that facilitation also contributes to enhance the sensibility to external stimuli and to obtain a better recovery of the patterns (in a short time scale) than depression.

DISCUSSION

In the last years, there has been an increasing interest in the study of the computational functionality of synaptic activity dependent processes, as synaptic facilitation and depression, in real systems and neural networks models [20, 11, 17, 12]. In this work we have reviewed some of the computational properties found in models of neural systems which exhibit activity-dependent synaptic mechanisms. In particular, we studied the interplay between short-term depression and facilitation for different computational tasks. It has been shown that dynamic synapses enhance the SNR allowing the neurons to have a good performance in signal detection over a wide range of noisy levels, via stochastic resonance [19]. This fact could be of interest in order to understand how networks self-organize to allow neurons work freely within an apropiate noise level, that is, without interfere between them. Dynamic synapses also

appear useful to detect changes in the presynaptic firing rate, which is a realistic assumption and could help to understand the behaviour of real systems in non-stationary conditions. In addition, the role of facilitation as an active selectivity mechanism between signals of different frequencies should be of much importance in actual problems in neural computation, to clarify how the neuron encode and filter the information embedded in spike trains. Looking at the level of networks, dynamic synapses reveal a rich phenomenology observed in some cortical areas [18], and a clear role for facilitation mechanism appears. In particular, the transition between the different possible dynamical phases and their nature depends strongly on the interplay between depression and facilitation. This could be of computational and biological relevance for a wide variety of neural systems.

ACKNOWLEDGMENTS

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