Short-term synaptic depression: implications for learning

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Abstract

We investigate the implications of the recently observed short term synaptic depression (STD) occurring for rapid pre-synaptic firing, for the properties of the working memory states in a recurrent network of spiking neurons. To this end, starting from the phenomenological model proposed by Tsodyks and Markram, we calculate an 'exact' analytical expression for the time evolution of all the moments of the variable expressing the amount of synaptic resources involved in each spike transmission. Using this result, we develop an 'extended' mean field theory, and perform simulations. We argue that the frequency adaptation under stimulation brings about a smooth dependence of the frequencies of the stable fixed points for the collective states of the network on the average level of synaptic potentiation.

1 Summary

A recent series of experiments showed *in vitro* that the synaptic efficacy between pyramidal neurons undergoes a 'fast' depression, for high rates of pre-synaptic spikes (see for instance Thomson & Deuchars, 1994, Markram & Tsodyks, 1996 and Abbott, Varela, Sen, & Nelson, 1997). The typical manifestation of this short-term, adaptation mechanism is the rapid decrease in the successive values of EPSPs induced by a fast, regular pre-synaptic train, until a stationary value of the EPSP is reached. After no pre-synaptic spikes occur for about 1 *sec.*, the full, maximum EPSP is 'recovered'.

In this contribution we study some implications of the above mechanism for the properties of *working memory* states produced by *stochastic* learning (Amit & Fusi, 1994), with Hebbian long-term potentiation and homosynaptic long-term depression, through repeated stimulation of a recurrent network of spiking, *integrate–and–fire* (IF) neurons. In the considered scenario, learning is accomplished by a stimulus–induced random walk through a discrete set of stable values for the synaptic efficacy; synapses eligible for changing their efficacy on the basis of their pre- and post-synaptic activities, do change with an activity-dependent 'transition probability' (see the other contribution to the conference (Del Giudice & Mattia, 2000)).

To this end, we start from a phenomenological model proposed by Tsodyks and Markram (1997), able to fit the above findings (together with other, facilitation, effects that will not be considered here) with a small number of functionally meaningful parameters.

We first improve on the mean field formulation in Tsodyks, Pawelzik, and Markram (1998), relaxing one of the approximations involved; then the learning scenario is examined in the light of the STD effects, both in mean field theory and in simulations. We will argue that frequency adaptation brought about by the inclusion of STD tempers the growth of the current circulating in the population of stimulated neurons, resulting in turn from the increased average synaptic efficacy produced by learning.

In particular, STD is expected to avoid a fast growth of the rates under stimulation. This puts the transition probabilities under easier control, and widens the available range allowing for the coexistence of enhanced frequency, selective states with low frequency states of spontaneous activity.

The model proposed by Tsodyks and Markram (1997) is described in terms of synaptic *resources*, a fraction U of which is first activated by each pre-synaptic spike (at time t_s), then inactivated with a very short characteristic time ($\tau_i, \mathcal{O}(ms)$)and finally recovered with a much longer time constant ($\tau_r, \mathcal{O}(s)$).

The assumption $\tau_i \ll \tau_r$, allows to reduce the model to the following equation for the recovered fraction of the synaptic resources, R:

$$\frac{dR}{dt} = \frac{1-R}{\tau_r} - U \sum_k R(t_k^-)\delta(t-t_k) \quad (1)$$

$R(t_k^-)$ is the value of R just before the arrival of the k-th spike. Assuming stochastically distributed spikes arrival times t_k, the above equation describes a stochastic process with multiplicative noise. Assuming the R process to be statistically independent from the pre-synaptic (Poisson) process, Tsodyks et al. (1998) get an equation for $\langle R\rangle$ and derive its stationary solution $R_\infty =$

$1/(1 + U\tau_r\nu)$.

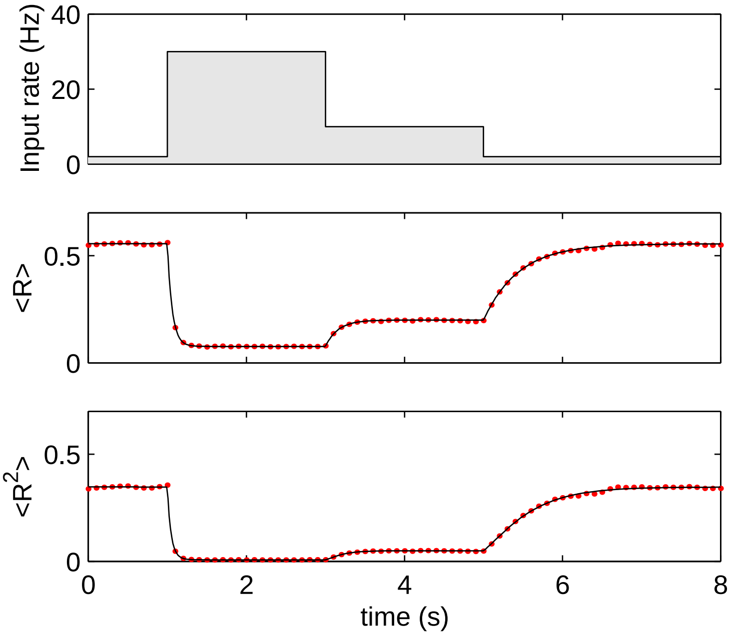

Figure 1: Match between simulations (dots) and theory (solid lines).

We start over from Eq. 1 to study the time evolution of the probability density function (pdf) of the process R. We reformulate the problem in terms of the *additive* process for $X = -\log R$, and show that the latter is amenable to a description in terms of a Kolmogorov equation for the pdf of X. From this equation it is straightforward to prove that the stationary solution for $\langle R\rangle$ found in Tsodyks et al. (1998) is *exact*. Furthermore, it is possible to derive a recursion relation for the time evolution of all the moments of R:

$$\frac{d\langle R^k\rangle}{dt} = \frac{k}{\tau}\left(\langle R^{k-1}\rangle - \langle R^k\rangle\right) - \nu\left[1-(1-U)^k\right]\langle R^k\rangle. \qquad (2)$$

The resulting values $\langle R^k\rangle_\infty$ of the moments at equilibrium are

$$\langle R^k\rangle_\infty = \frac{k\langle R^{k-1}\rangle_\infty}{k + (1-(1-U)^k)\,\nu\tau_r}. \qquad (3)$$

The above equations have been extensively checked against simulations, in which many realizations of the R process are generated, as shown in Fig. 1, and the averages $\langle R\rangle$ and $\langle R^2\rangle$ are calculated.

$\langle R\rangle$ and $\langle R^2\rangle$ are the ingredients needed to incorporate STD effects in the *extended* mean field (Amit & Brunel, 1997) description of a network of

IF neurons, in which both the mean and the variance of the afferent current enter the self-consistency equations which determine the frequencies of the stable collective states of the network.

The learning scenario that emerges in the mean field description, going from the "standard" to the STD case, is characterized by a virtually unaffected rate for the state of spontaneous activity, a smooth dependence of the selective rates on the level of synaptic potentiation and, therefore, a much smaller gap between the frequencies of the spontaneous and the selective states. Furthermore, STD entails a remarkably smooth dependence of the rates under stimulation on the potentiation level. This in turn is crucial to have a controlled and essentially uniform speed of learning (Del Giudice & Mattia, 2000).

We have performed simulations of large networks of leaky IF neurons, incorporating STD. The emerging phenomenology is quite complex and interesting; we limit ourselves, in this contribution, to show how mean field predictions are essentially confirmed by simulations if τ_r is smaller than a few tens milliseconds. Larger values of τ_r appear to weaken the basins of attraction of the stable states foreseen by the mean field calculation; a related feature brought about by large values of τ_r is an increased propensity of the network to ignite large fluctuations of the global activity. It seems likely that further mechanisms, like those related to the dynamics of NMDA receptors, might play a regulatory role helping stabilizing the network.

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