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Long and short-term synaptic plasticity and the formation of working memory: A case study

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Abstract

We study the collective behaviour of recurrent networks of integrate-and-fire neurons, connected by synapses whose efficacies are subjected to a spike-driven, and rate sensitive, Hebbian LTP and a homosynaptic depression, as well as a short-term, frequency dependent depression (STD). Through a mean field analysis, and numerical simulations of the coupled neural and synaptic dynamics, we show how repeated stimulations of the network can dynamically produce a synaptic structure supporting persistent, collective, stimulus-selective activity, that have been proposed since long as a substrate for 'working memory'. We discuss constraints relevant to the stability of the 'learning' process, and the related role of long-term synaptic depression as well as the effects of inclusion of STD. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Synaptic plasticity; LTP/LTD; STD; Spiking neurons; Working memory

1. Introduction

Hebbian-like mechanisms of synaptic plasticity, suitable for implementing stimulus specific, persistent states of neural activity in recurrent networks of spiking neurons have been mostly studied in terms of the network's dynamical scenarios *before* and *after* learning [2]. This implies making an a priori choice as to the synaptic structure which defines the "after learning" condition. Studying the process by which such synaptic structures can be dynamically built by the ongoing (stimulus-dependent) neural activity, is still largely an open challenge. We make in the present work a first

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step in this direction, sketching some general implications through a case study. Once a specific hypothesis has been made on how the synaptic dynamics depends on the pre- and/or post synaptic activities, the main source of difficulty in studying dynamic, *on line* learning has to do with (1) the stability of the network's activity and (2) the related stability of the memories embedded in the synaptic structure. Regarding point (1), neural activities drive the synaptic evolution, which in turn feeds back on the neural states, by modulating the afferent current to the neurons; the reaction of the latter can significantly change the rate of synaptic modifications, thus possibly igniting a chain reaction that can seriously challange the network's stability and can well prevent the network from reaching developed memory states, though they might be stable in terms of a static synaptic prescription. As we will see, since we work in the framework of spike-driven, but rate dependent, Hebbian plasticity, rate adaptation effects turn out to be very helpful in tempering some of the above instabilities. We choose as a candidate mechanism the recently observed "short term depression" (STD) effect [8,1]. Point (2) above refers to the trade-off that presents itself with the "stability-plasticity" dilemma: the synaptic structure has to be plastic on time scales comparable with the typical time a stimulus persists, in order to keep a memory trace of it, but the rate of stimulus induced synaptic changes has to be low enough in order to prevent new information from quickly erasing previously stored memories. The latter requirement suggests strategies of *slow learning* [3], all along the "learning trajectory" that the synaptic structure travels.

2. Context and tools for analysis

The model system we study is a recurrent network of (excitatory and inhibitory) integrate-and-fire (IF) neurons (both the usual leaky IF neurons and the "linear" IF neurons—with constant leakage introduced in [6]). Excitatory neurons are connected by plastic synapses, having two values of ('potentiated' and 'depressed') efficacy (PSP) which are assumed to be stable on the long time scale. Long-term synaptic dynamics, i.e. transitions between these two states, is driven by neural pre- and post-synaptic activities through a fast, spike-driven dynamics which affects a suitable analog, 'internal' variable of the synapse (for the original proposal of this type of synaptic device see [5,4]). Fig. 1 sketches the specific synaptic dynamics we adopt; on the left we show a sample evolution of the analog internal synaptic variable (middle) for given pre-synaptic (top) and post-synaptic (bottom) spike trains, together with the associated time course of the synaptic efficacy (light gray strip: potentiated; dark gray strip: depressed). Up (down) regulation of the internal variable occurs if a pre-synaptic spike comes within (beyond) Δt after the emission of a post-synaptic spike.[2] When the internal variable crosses a threshold from below (above) the efficacy gets potentiated

[2] As long as the time window available for down regulation is variable (equal to the ISI minus Δt) the qualitative behaviour of such a synapse does not change much if the dependence on the relative spike timings is reversed. The results reported here are qualitatively valid for a large class of spike-driven synaptic devices we have explored, in view of the different and still uncertain experimental indications.

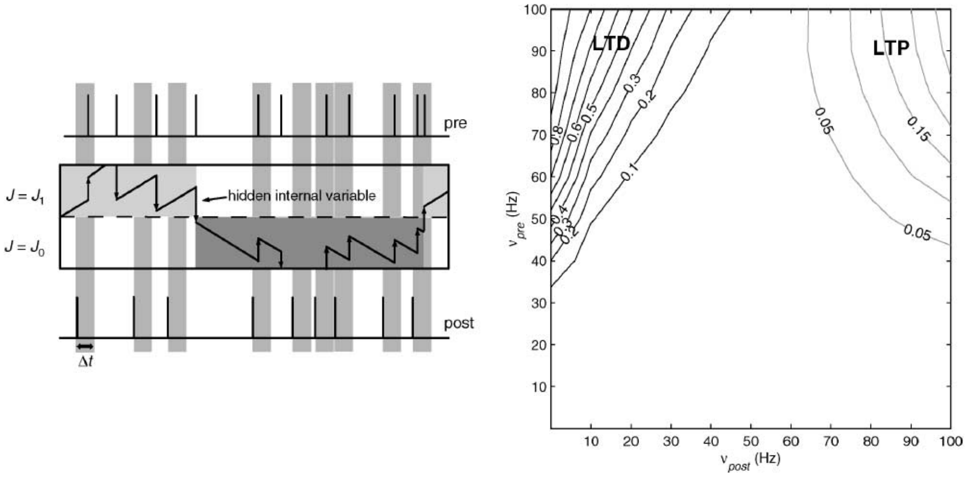

Fig. 1. The spike-drive synapse. Left: sample evolution of the internal synaptic variable, and the associated efficacy. Right: rate dependence of LTP and LTD.

(depressed). Because of the stochasticity of the spikes in the network (due to features like the random pattern of connectivity) such synaptic transitions are themselves stochastic, and are characterized by a (frequency dependent) 'transition probability'. We stress that such a synaptic device, though driven by spike timings, acts as frequency meter of the pre- and post-synaptic neurons, and implements a rate dependent, Hebbian LTP and a homosynaptic LTD, as illustrated in Fig. 1, right, where we show curves of equal (up and down) transition probabilities for such a synapse with Poisson, independent pre- and post-synaptic spike trains.

For a network with N neurons the analysis of the coupled neural and synaptic dynamics requires to solve a system of $O(N + N^2)$ coupled equations. Standard approaches to the numerical integration of those equations imply a prohibitive $O(N^3)$ computational load. We therefore use the event-driven approach to simulation introduced in [7], which lowers the complexity to $O(N^2)$. On the other hand, predictive, analytical tools are needed in order to choose interesting regions in the huge parameters space of the neural and synaptic dynamics. Under suitable hypotheses the "extended mean field theory" (MFT) approach [2] proved to be very useful and, as long as the characteristic times of synaptic changes are much longer than those of neural dynamics, it still serves as a precious tool in the present scenario. Assuming that synapses undergoing Hebbian potentiation and those homosynaptically depressed all share the same average efficacies (J_{p} and J_{d}, respectively), a compact representation (extending the one adopted in [2]) can be devised, exposing in the plane $(J_{\mathrm{p}}, J_{\mathrm{d}})$ the nature of the stable collective states predicted by MFT (Fig. 2). We will be seeking learning trajectories bringing the network from a totally unstructured synaptic state (the lower right corner in the plane) to a state supporting a low rate, unspecific "spontaneous" state coexisting with a selective, higher rate, state to be interpreted as

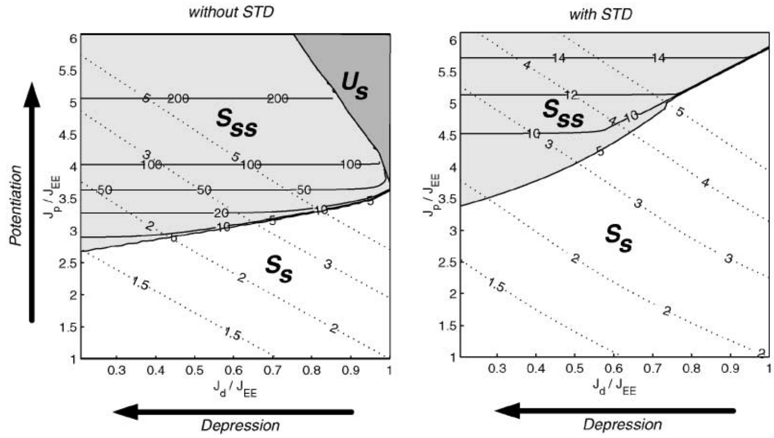

Fig. 2. J_p–J_d plane. J_{EE} is the average efficacy of the unaffected synapses. Dotted (solid) contour lines are iso-frequency curves for spontaneous (selective) activity. For white regions (marked $\mathbf{S_S}$) MFT predicts only stable spontaneous states; for light gray regions (marked $\mathbf{S_{SS}}$) there are both spontaneous and selective stable states, while for the dark gray region (marked $\mathbf{U_S}$) the spontaneous activity is unstable. Initial, unstructured networks are identical in the two cases.

the neural substrate of a "working memory" state (light gray region in the plane). To take STD into account in the MFT description, we adopt the model introduced in [8], and calculate the corrections to the mean and variance of the afferent currents (the needed ingredients for MFT) due to inclusion of STD (details will be given in a forthcoming paper). The resulting scenario is illustrated in (Fig. 2), right.

3. On-line learning: The role of LTD and STD and a feasibility proof

From Fig. 2, left, we see that, despite the wide region allowing for coexistent spontaneous and selective activity, its frontier, that the learning trajectories have to cross from below, has a very steep rise with respect to J_p; this, in view of the discussion in the Introduction, is a candidate source of instability in the dynamic scenario. If the increase of J_p is not adequately balanced by increased depression, the spontaneous activity is easily destabilized. The stabilizing role of the LTD is such that the lower J_d/J_{EE} (higher depression) the wider the regions of the synaptic space in which the spontaneous and selective activities coexist; the region of instability shrinks. Including STD, we see from Fig. 2, right, that the spontaneous activity is virtually unaffected, and is kept stable in a much wider region of the plane, while the rates of the selective states have now a very smooth dependence on J_p, suggesting that, as simulations will confirm, on-line learning will be kept more easily under control. Fig. 3 illustrates how large scale simulations of the ongoing neural and synaptic dynamics (diamonds in the plot) meet the above expectations. We demonstrate how an initially unstructured network, after repeated presentations of five different stimuli, exhibits a stimulus

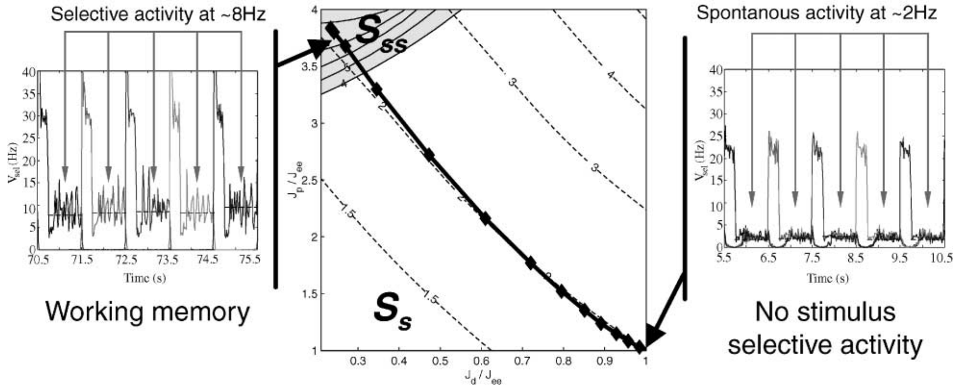

Fig. 3. A 'successful' learning trajectory (see text of explanation).

selective activity in the delay periods between two successive stimulations. Extensive explorations of learning scenario suggest and support the following heuristic characterization of 'interesting' learning trajectories:

- Keeping spontaneous activity stable during learning implies that synapses driven by low neural activity should not change. It also implies that during learning a sufficiently intense synaptic long-term depression should take place, in order to compensate for synaptic potentiation, pushing the network towards higher spontaneous frequencies.
- Selective, working memory rates should not provoke long-term synaptic changes; if this were not the case, we would have the network continuously restructuring its synaptic matrix in the reverberant state induced by the last stimulus, which tends to destroy the synaptic trace of past stimuli;
- The finite number of neurons in the network produces in general a *distribution* of frequencies inside a population, and this can provoke unwanted synaptic changes. In particular, potentiating synapses that should be depressed can result in uncontrolled excitation destabilizing the network, while depressing synapses that should be potentiated can prevent the formation of working memory states. The dynamics of the synapse should be highly sensitive to small variations of the pre- and post-synaptic frequencies, in the critical regions where, e.g., the opposite tails of the frequency distributions can come close for neural populations to be regarded in a very different way by the synapse.
- In the initial, unstructured synaptic state, the rates under stimulation should be high enough to produce 'slow' stochastic learning (high memory capacity [3]). Besides, for the structured synaptic matrix, selective rates should stay lower than those under stimulation, while the latter should not grow too much, in order to keep low the transition probabilities. So, for the hierarchy of spontaneous, selective and stimulated frequencies, synaptic dynamics should be such as to have negligible, negligible and low transition probabilities, respectively, all along the learning path.

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