Effects of Pruning on Phase-Coding and Storage Capacity of a Spiking Network

Silvia Scarpetta^{1,3} and Antonio De Candia^{2,3,4}

¹ Dipartimento di Fisica "E.R. Caianiello", Università di Salerno, Italy
 ² Dipartimento di Scienze Fisiche, Università di Napoli Federico II
 ³ INFN, Sezione di Napoli e Gruppo Coll. di Salerno
 ⁴ CNR-SPIN, Unità di Napoli
 sscarpetta@unisa.it, decandia@na.infn.it

Abstract. Synaptic pruning is a crucial process during development. We study the imprinting and replay of spatiotemporal patterns in a spiking network, as a function of pruning degree. After a Spike Timing Dependent Plasticity-based learning of synaptic efficacies, the weak synapses are removed through a competitive pruning process. Surprisingly, after this pruning stage, the storage capacity for spatiotemporal patterns is relatively high also for very high diluition ratio.

Introduction

The capacity to code and memorize information is fundamental to normal cognition. Here we study the effects of Synaptic pruning — the elimination of synapses — on the information processing capacity. The study of the relation between synaptic efficacy and synaptic pruning suggests that the weak synapses may be modified and removed through competitive learning. In our strategy the strength of connections is determined by a learning rule based on spike-time-dependent plasticity (STDP), with an asymmetric time window depending on the relative timing between pre- and post-synaptic activity. After storage of multiple spatiotemporal patterns, we apply a synaptic pruning strategy, eliminating the weaker connections. We eliminate all the weaker connections, in such a way that at the end each neuron is connected only to a small number $z \ll N$ of other neurons. We find that the ability to replay the stored spatiotemporal patterns is relatively high also for very small value of z.

In this paper we analyze the role of synaptic pruning, eliminating the weaker connections after a learning rule based on STDP, in storing multiple phasecoded memories as attractor states of the neural dynamics. The framework of storing and retrieval of memories as attractors of the dynamics is widely accepted, but the effects of pruning on such dynamical periodic spatiotemporal patterns haven't been investigated before.

In Section 1 we present the model, the learning rule and pruning rule. In Section 2 we introduce some parameters which will be useful to study the capacity of the network. Lastly, in Section 3 we report a summary of the obtained results along with a short discussion.

125

1 The Model

We consider a network of N spiking Leaky Integrate and Firing (LIF) neurons, with N(N-1) possible directed connections J_{ij} . The fully-connected model has been studied in [16]. Here we study the effect of pruning. Briefly, the postsynaptic membrane potential of a neuron *i* is given by:

$$h_i(t) = \sum_j J_{ij} \sum_{t^*_j > t^*_i} \epsilon(t - t^*_j),$$
(1)

where i = 1, ..., N, J_{ij} are the synaptic connections, the sum over t^*_j runs over all pre-synaptic firing times following the last spike of neuron i, and $\epsilon(t)$ describes the response kernel to incoming spikes on neuron i:

$$\epsilon(t - t^*{}_j) = K\left[\exp\left(-\frac{t - t^*{}_j}{\tau_m}\right) - \exp\left(-\frac{t - t^*{}_j}{\tau_s}\right)\right] \Theta(t - t^*{}_j)$$
(2)

where τ_m is the membrane time constant (10 ms), τ_s is the synapse time constant (5 ms), Θ is the Heaviside step function, and K is a multiplicative constant chosen so that the maximum value of the kernel is 1, as in [4,16]. When the membrane potential $h_i(t)$ exceeds the spiking threshold θ_{th} , a spike is scheduled, and the membrane potential is reset to the resting value zero. The STDP learning rule used to determine the synaptic efficacy has been introduced in [7,10,11,15,21,12,17,19,18,20]. After learning a spatiotemporal periodic pattern μ , the synaptic efficacies are:

$$J_{ij}^{\mu} = \frac{1}{N} \sum_{n=-\infty}^{\infty} A(t_j^{\mu} - t_i^{\mu} + nT^{\mu})$$
(3)

where $t_i^{\mu} = (\phi_i^{\mu}/2\pi)T^{\mu}$ is the spike time of unit *i* in the pattern μ .

The kernel $A(\tau)$ is the STDP measure of the strength of synaptic change when a time delay τ occurs between pre and post-synaptic activity. We use the kernel introduced and motivated by [23], $A(\tau) = a_p e^{-\tau/T_p} - a_D e^{-\eta\tau/T_p}$ if $\tau > 0$ and $A(\tau) = a_p e^{\eta\tau/T_D} - a_D e^{\tau/T_D}$ if $\tau < 0$, with the same parameters used in [23] to fit the experimental data of [6], $a_p = \gamma [1/T_p + \eta/T_D]^{-1}$ and $a_D = \gamma [\eta/T_p + 1/T_D]^{-1}$ with $T_p = 10.2$ ms and $T_D = 28.6$ ms, $\eta = 4$, $\gamma = 42$. This function satisfies the balance condition $\int_{-\infty}^{\infty} A(\tau) d\tau = 0$. Notably, when

This function satisfies the balance condition $\int_{-\infty}^{\infty} A(\tau) d\tau = 0$. Notably, when $A(\tau)$ is used in Eq. (3) to learn phase-coded patterns with uniformly distributed phases, then the balance condition assures that the sum of the connections on the single neuron $\sum_{j} J_{ij}$ is of order $1/\sqrt{N}$, and therefore, it assures a balance between excitation and inhibition [16].

The phases ϕ_j^{μ} of the spikes in the periodic spatiotemporal pattern are randomly chosen from a uniform distribution in $[0, 2\pi)$. When multiple phase coded patterns are stored, the learned connections are simply the sum of the contributions from individual patterns, namely

$$J_{ij} = \sum_{\mu=1}^{P} J_{ij}^{\mu}.$$
 (4)



Fig. 1. Dynamics of the network with N = 10000 neurons, z = 100 positive connections per neuron, P = 10 stored patterns, after a stimolation with M = 300 consecutive spikes with the phases of one of the patterns. On the vertical axis the phase of the spiking neuron in the replayed pattern is shown.

Previous works [11,16] showed that multiple items can be memorized in such fully connected LIF model, in such a manner that the intrinsic network dynamics recall the specific phases of firing when a partial cue is presented, if spiking threshold is in a proper range of parameters. A critical value of spiking threshold exists[18,19], such that for value higher of this critical value no persistent replay is possible. Here we study the effects of a stdp-driven pruning process. After the STDP-based learning Eq. (4), both positive and negative weak synapses are removed through a competitive process.

After learning P stored patterns, we start the pruning process, deleting the weaker syapses. We delete both negative and positive synapses with low values of $|J_{ij}|$. We prune a fixed percentage of positive connections, so that each unit has z positive outgoing connections. We then prune a variable percentage of negative connections, to ensure that sum of negative outgoing connections is equal to the sum of positive outgoing connections.

Notably, even for $z \ll N$, there's a range of spiking threshold θ_{th} , in which the response of the system to a cue external stimulation, in absence of noise, shows the replay of one of the stored pattern. A short cue with M = 300 spikes with the proper phase relationship is able to induce the selective persistent replay of the stored pattern similar to the cue, even when $z \ll N$. For example when z is as small as z = 100 in a network with N = 10000 units and P = 10 patterns are stored, the dynamics after the cue is shown in Fig. 1.

2 Storage Capacity of the Pruned Network

We study here the storage capacity of the network in the case of pruning, as a function of the number z of surviving connections. The storage capacity is defined, as usual, as the maximum number of patterns that can be stored and succesfully selectively retrieved, when the network respond to a short cue stimulation. To measure quantitatively the successfull of retrieval we introduce an order parameter m^{μ} , which measure the similarity between the network activity during retrieval dynamics and the stored pattern, defined as [18,16,19]:



Fig. 2. The capacity P_{max} as a function of spiking threshold of the units, for different values of connections z per neuron, in a network made up of N = 10000 neurons. Succesful retrieval is indicated in red, while failure in blue. (a) Pruned network with z = 50, and (b) pruned network with z = 100.



Fig. 3. The capacity P_{max} as a function of the number z of positive outgoing connections per unit, in a network with N = 10000 units

ı

$$m^{\mu}(T^{w}) = \frac{1}{\langle N_{s} \rangle} \left\langle |M(t, T^{w})| \right\rangle$$
(5)

where

$$|M^{\mu}(t,T^{w})| = \left| \frac{1}{N} \sum_{\substack{j=1,\dots,N\\t < t_{j}^{*} < t + T^{w}}} e^{-i2\pi t_{j}^{*}/T^{w}} e^{i\phi_{j}^{\mu}} \right|$$
(6)

where t_j^* is the spike timing of neuron j during the spontaneous dynamics, and T^w is an estimation of the period of the collective spontaneous periodic dynamics, the average $\langle \cdots \rangle$ is done on the starting time t of the window, and $\langle N_s \rangle$ is the average number of spikes on a window of time T^w . This quantity is maximal (equal to one) when collective activity is periodic and the ordering of spiking times coincide with that of the stored pattern, and is order $\simeq 1/\sqrt{N}$ when the spike timings are uncorrelated with the stored ones. For instance, if the retrieval of pattern $\mu = 1$ (out of 3) is successful, the overlap values will be $|m^1| >$ $0, |m^2| \simeq 0, |m^3| \simeq 0$. In the following we consider a pattern perfectly retrieved when order parameter |m| > 0.5 for at least 3 over 5 different realizations.

We consider a network of N = 10000 neurons, and we study network dynamics for different degree of pruning. In Fig. 2 we plot the maximum capacity P_{max} as a function of θ_{th} for different values of z. Througut the paper we use N = 10000, $\omega^{\mu} = 3Hz$, and a cue stimulation with M = 300 spikes with phases equals to the phases of pattern 1, and frequency $\omega^{cue} = 20Hz$.

To see how storage capacity changes as a function of the degree of pruning, we plot in Fig. 3 the storage capacity at optimal spiking threshold as a function of z. The number of patterns is well fitted by the function $P_{\text{max}} = 1.1 z^{0.56}$.

3 Summary and Discussion

In this paper we study the effects of synapses pruning in an oscillatory network, with particular attention to the function of storage and recall of phase-coded patterns of spikes. Oscillations are ubiquitus in the brain[2,9]. In the spatiotemporal patterns we consider the information is encoded in the phase-based timing of firing relative to the cycle[1,3,8,16].

We analyze the ability of the STDP-bases pruning strategy to memorize multiple phase-coded pattern, such that the spontaneous dynamics of the network selectively gives sustained activity which match one of the stored phase-coded patterns, depending on the initialization of the network.

We prune both negative and positive synapses that have low absolute values of synaptic efficacy in the STDP prescription. We eliminate a fixed percentage of positive weaker connections, so that each unit has exactly z positive outgoing connections. We then prune a number of the weakest negative connections, chosen to ensure that sum of negative outgoing connections is equal to the sum of positive outgoing connections.

We study the storage capacity for different degrees of pruning. The effect of spiking threshold on storage capacity have been studied previously [19,18,20]. Here we compute the storage capacity, as a function of connectivity z, at the optimal value of spiking threshold. We see that capacity of a pruned network with z = 200 = 0.02 N positive connections, already has 25% of the capacity of of the fully connected network, that is about $P_{\text{max}} \simeq 90$ for N = 10000.

The task of storing and recalling phase-coded memories with sparse connectivity has been also investigated in [27] in the framework of probabilistic inference and in [24,25,13] in the framework of networks with binary units. In [24,25,27], the case of limited connectivity is studied, showing how recall performance depends to the degree of connectivity when connections are cut randomly, and how inhibition may enhance memory capacity[25]. In our work connections are not cutted randomly, but only the ones which are weaker after the learning strategy Eq. (4) are eliminated. The pruning is guided from the STDP learning, the balance between excitation and inhibition is keeped, and therefore very good capacity is achieved even at small z. In [13] it has been shown that storage capacity of spatiotemporal patterns in the binary network also depends from the topology of the connectivity, and capacity depends not only from the number of connections but also from the fraction of long range versus short range connections. While in [13] we fixed the topology of the network, and then on the survided connections we applied the learning rule Eq. (4) for synaptic efficacies, here we first apply the learning rule for synaptic efficacies and then we eliminate the weaker synapses, in a sort of learning-guided competitive pruning. So the topology of the pruned network here is determined by the patterns to be stored.

References

- Siegel, M., Warden, M.R., Miller, E.K.: Phase-dependent neuronal coding of objects in short-term memory. PNAS 106, 21341–21346 (2009)
- Buzsaki, G., Draguhn, A.: Neuronal Oscillations in Cortical Networks. Science 304, 1926–1929 (2004)
- Kayser, C., Montemurro, M.A., Logothetis, N.K., Panzeri, S.: Spike-phase coding boosts and stabilizes information carried by spatial and temporal spike patterns. Neuron. 61, 597–608 (2009)
- Gerstner, W., Ritz, R., van Hemmen, J.L.: Why spikes? Hebbian learning and retrieval of time-resolved excitation patterns. Biological Cybernetics 69(5-6), 503– 515 (1993)
- Markram, H., Lubke, J., Frotscher, M., Sakmann, B.: Regulation of synaptic efficacy by coincidence of postsynaptic APs and EPSPs. Science 275, 213–215 (1997)
- Bi, G.Q., Poo, M.M.: Precise spike timing determines the direction and extent of synaptic modifications in cultured hippocampal neurons. J. Neurosci. 18, 10464– 10472 (1998)
- Scarpetta, S., Zhaoping, L., Hertz, J.: Hebbian Imprinting and Retrieval in Oscillatory Neural Networks. Neural Computation 14(10), 2371–2396 (2002)
- Scarpetta, S., Marinaro, M.: A learning rule for place fields in a cortical model: Theta phase precession as a network effect. Hippocampus 15(7), 979–989 (2005)
- Zhaoping, L., Lewis, A., Scarpetta, S.: Mathematical analysis and simulations of the neural circuit for locomotion in lampreys. Physical Review Letters 92(19), 198106 (2004)
- Yoshioka, M., Scarpetta, S., Marinaro, M.: Spatiotemporal learning in analog neural networks using spike-timing-dependent synaptic plasticity. Phys. Rev. E 75, 051917 (2007)
- Scarpetta, S., De Candia, A., Giacco, F.: Storage of phase-coded patterns via STDP in fully-connected and sparse network: a study of the network capacity. Frontiers in Synaptic Neuroscience 2 (2010)
- Marinaro, M., Scarpetta, S., Yoshioka, M.: Learning of oscillatory correlated patterns in a cortical network by a STDP-based learning rule. Mathematical Biosciences 207(2), 322–335 (2007)
- Scarpetta, S., Giacco, F., de Candia, A.: Storage capacity of phase-coded patterns in sparse neural networks. EPL (Europhysics Letters) 95(2), 28006 (2011)
- Scarpetta, S., De Candia, A., Giacco, F.: Dynamics and storage capacity of neural networks with small-world topology. In: Proceedings of the 2011 Conference on Neural Nets WIRN10. Frontiers in Artificial Intelligence and Applications, vol. 226 (2011) ISBN: 978-1-60750-691-1
- Yoshioka, M., Scarpetta, S., Marinaro, M.: Spike-Timing-Dependent Synaptic Plasticity to Learn Spatiotemporal Patterns in Recurrent Neural Networks. In: de Sá, J.M., Alexandre, L.A., Duch, W., Mandic, D.P. (eds.) ICANN 2007, Part I. LNCS, vol. 4668, pp. 757–766. Springer, Heidelberg (2007)

- Scarpetta, S., Giacco, F.: Associative memory of phase-coded spatiotemporal patterns in leaky Integrate and Fire networks. Journal of Computational Neuroscience. J Comput Neurosci. 34(2), 319–336 (2013), doi:10.1007/s10827-012-0423-7; Epub (October 4, 2012)
- Giacco, F., Scarpetta, S.: Attractor networks and memory replay of phase coded spike patterns. In: Frontiers in Artificial Intelligence and Applications, vol. 234, pp. 265–274 (2011)
- Scarpetta, S., Giacco, F., Lombardi, F., de Candia, A.: Effects of Poisson noise in a IF model with STDP and spontaneous replay of periodic spatiotemporal patterns, in absence of cue stimulation. Biosystems 112(3), 303–2647 (2013), doi:10.1016/j.biosystems.2013.03.017, ISSN 0303-2647
- Scarpetta, S., de Candia, A.: Critical behavior near a phase transition between retrieval and non-retrieval regimes in a LIF network with spatiotemporal patterns. AIP Conf. Proc, vol. 1510, pp. 36–43 (2013), doi:http://dx.doi.org/10.1063/1.4776499
- Scarpetta, S., de Candia, A.: Neural avalanches at the critical point between replay and non-replay of spatiotemporal patterns. Plos One (accepted May 11) (in press, 2013), doi:10.1371/journal.pone.0064162, PONE-D-13-11021R1
- Scarpetta, S., Yoshioka, M., Marinaro, M.: Encoding and Replay of Dynamic Attractors with Multiple Frequencies: Analysis of a STDP Based Learning Rule. In: Marinaro, M., Scarpetta, S., Yamaguchi, Y. (eds.) Dynamic Brain. LNCS, vol. 5286, pp. 38–60. Springer, Heidelberg (2008)
- Gerstner, W., Kempter, R., van Hemmen, L., Wagner, H.: A neuronal learning rule for sub-millisecond temporal coding. Nature 383, 76–78 (1996)
- Abarbanel, H., Huerta, R., Rabinovich, M.I.: Dynamical model of long-term synaptic plasticity. Proc. Nas. Acad. Sci. 99(15), 10132–10137 (2002)
- Leibold, C., Kempter, R.: Memory Capacity for Sequences in a Recurrent Network with Biological Constraints. Neural Computation 18(4), 904–941 (2007)
- Kammerer, A.A., Tejero-Cantero, A.A., Leibold Inhibition, C.C.: enhances memory capacity: optimal feedback, transient replay and oscillations. J. Comput. Neurosci. 34(1), 125–136 (2013)
- Lengyel, M., Dayan, P.: Uncertainty, phase, and oscillatory hippocampal recall. Advances in Neural Information Processing Systems 19, 833–840 (2007)
- Lengyel, M., Kwag, J., Paulsen, O., Dayan, P.: Matching storage and recall: hippocampal spike timing-dependent plasticity and phase response curves. Nat. Neurosci. 8, 1677–1683 (2005)
- Thurley, K., Leibold, C., Gundlfinger, A., Schmitz, D., Kempter, R.: Phase precession through synaptic facilitation. Neural Computation 20(5), 1285–1324 (2008)
- Latham, P.E., Lengyel, M.: Phase Coding: Spikes Get a Boost from Local Fields. Curr. Biology 18(8), R349–R351 (2008)