

Emergence of stimulus-specific synchronous response through STDP in recurrent neural networks

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Abstract.

This paper presents learning simulation results on a balanced recurrent neural network of spiking neurons with a simple implementation of the STDP plasticity rule, whose potentiation and depression effects compensate. The synaptic weights and delays are randomly set and the network activity, which is a combination of an input signal and a recurrent feedback, is initially strong and irregular. Under a static stimulation, the learning process shapes the initial activity toward a more regular and synchronous response. The response is specific to this particular stimulus: the network has learned to select by synchrony one arbitrary stimulus from a set of random static stimuli.

1 Introduction: the STDP framework

Biological evidence of long-term plasticity [1], where a synapse is potentiated when the presynaptic neuron fires shortly before the postsynaptic one and depressed in the opposite case in a nearly anti-symmetrical way [2, 3, 4] gave rise to the Spike-Timing Dependent Plasticity (STDP) rule, which has inspired various studies these last years. An important effect of STDP is that it reduces the latency of a neuron's response to a given input [5, 6]; the behaviour of STDP has also been studied on larger, recurrent networks, but the results are more ambiguous: while it has been shown that in some conditions it can lead to the emergence of neuronal groups [7, 8], these results seem to depend on the precise implementation, since a slightly different rule on a different neuron model gives different results: there is no structure development, strong synapses remaining unstable [9].

We present here a series of simulations where connection strength between neurons is modified by a simple implementation of STDP. We show that in our model, such a learning process allows to distinguish by synchrony an arbitrary stimulus from a set of static stimuli associated to strong and irregular self-driving activity. The section 2 presents our model (an integrate-and-fire neural network model under the influence of static stimuli). The sections 3 and 4 illustrate how a particular stimulus may be learned from a set of arbitrary stimuli.

2 Model: heterogeneous weights and delays

The neural networks we simulate are random and recurrent, implemented with discrete leaky integrate-and-fire neurons¹. The individual weights and delays are independent and strongly heterogeneous². The synaptic weights are set according to a Gaussian draw $\mathcal{N}\left(\frac{\mu_J}{N}, \frac{\sigma_J^2}{N}\right)$, while the axonal transmission delays are set according to a Poisson draw of expected value $\lambda_\tau = 10$ ms. The simulations take place on rather small neural networks composed of $N = 100$ neurons (but could be extended with the same global parameters to larger sizes).

The inputs sent to the network are distributed among every neuron. We define a set of P static stimuli $(\mathbf{I}^{(p)})_{p=1..P}$ which are random vectors of size N and whose values are randomly set according to a gaussian draw $\mathcal{N}(0, \sigma_I^2)$ where $\sigma_I = 1$ ³.

The activity of such networks when fed with a stimulus looks very irregular at first glance. First, the *asynchrony* of the activity directly results from the balance between the excitatory and inhibitory influences [11]. Second, the irregularity of the activity is a well-known feature of recurrent heterogeneous networks [12, 13]. In order to characterise this irregularity, we use an estimation of the effective number of Degrees of Freedom (#DOF) based on a Principal Components Analysis⁴ [14, 15].

¹Consider a set of neurons labelled by indexes $i \in \{1, \dots, N\}$. The neuron activity $\{S_i(s)\}_{s < t}$ is defined as a sum of Diracs corresponding to the series of spikes emitted up to the t instant (see [10]). Taking into account the absolute refractory period τ_r , the firing threshold θ and the external signal $I_i(t)$, the current activity $S_i(t)$ is defined the following way:

$$\text{if } \max_{s \in [t-\tau_r, t]} (S_i(s)) = 0 \text{ and } V_i(t) \geq \theta - I_i(t) \text{ then } S_i(t) = \delta(0) \text{ else } S_i(t) = 0$$

where $\delta(0)$ is a Dirac impulse and $V_i(t)$ is the neuron's membrane potential, defined according to the Leaky Integrate-and-Fire (LIF) differential scheme:

$$\frac{dV_i}{dt} = -\frac{V_i(t) - V_0}{\tau_m} - S_i(t)(V_i(t) - V_S) + \sum_{j=1}^N J_{ij} S_j(t - \tau_{ij})$$

where V_0 is the resting potential, V_S is the refractory potential, τ_{ij} and J_{ij} are respectively the transmission delay and synaptic weight from neuron j to neuron i and τ_m is the membrane time constant. We set $\tau_r = 2$ ms, $\tau_m = 10$ ms, $V_0 = 0$, $V_S = 0$ and $\theta = 1$. In the simulations, we use a simple first order integration with resolution $\delta t = 1$ ms.

²Our parameters are chosen in order to allow the internal self-sustained activity to compete with the external stimulation. The expected value of the weights sum is $\mu_J = 0$ so that the excitatory influences compensate the inhibitory ones (balanced networks configuration). The weights sum standard deviation is $\sigma_J = 2$. This value corresponds to a strong internal influence (which is typically the case when the weights sum overtakes the threshold - here $\theta = 1$).

³Each stimulus is presented to the network for a duration which is greater than the mixing time of the system in order to converge to a stationary response.

⁴Our data set is composed of the membrane potentials of all the neurons over sliding windows of 100 ms. A Principal Components Analysis is first applied to the data set, followed by a calculation of the entropy of the normalised principal values p_i of the transformation matrix: $S = -\sum_{i=1}^N p_i \ln(p_i)$. This value is considered as an approximate log count of significant principal components weighted by their respective size, so that $\#DOF = e^S$ is an approximation of the effective number of degrees of freedom.

3 Weight adaptation: emergence of synchrony

Several implementations of the STDP update mechanism have been proposed in the literature. Our implementation is all-to-all [16] and additive: the weight update depends on every previous synaptic event (the influence of the less recent events fading with time) and doesn't take into account the current weight of the synapse. Concretely:

$$\frac{dJ_{ij}(t)}{dt} = \alpha [S_i(t)\varepsilon_j(t - \tau_{ij}) - \varepsilon_i(t)S_j(t - \tau_{ij})]$$

where the trace $\tau_m \frac{d\varepsilon_i}{dt} = -\varepsilon_i + S_i(t)$ can be considered as a short-term estimation of the firing rate of the i^{th} neuron. This update scheme divides in two terms. The first term corresponds to the synaptic potentiation: a significant weight increment takes place when a post-synaptic spike is associated with a strong pre-synaptic trace (recent pre-synaptic excitations). The second term corresponds to the synaptic depression: the weight significantly decreases when a pre-synaptic pulse is associated with a strong post-synaptic trace (i.e. after post-synaptic excitation). The result is a global facilitation of pre-post sequences of excitation and a depression of post-pre sequences of excitation. This rule is strictly antisymmetrical, i.e. the potentiation compensates the depression, so it can be considered as "balanced". From a computational point of view, the storage of a trace is not very expensive. It is moreover strictly local and as such biologically implementable.

In a first simulation, the learning process lasts between $t = 5$ s and $t = 25$ s on a network under a static input. The value of the learning parameter is $\alpha = 0.005$. We present in figure 1 some aspects of the activity evolution during the learning process. Figure 1A presents a sliding autocovariogram of the average membrane potential. It offers a synthetic view of the ongoing transformation taking place in the activity. Figure 1C shows a raster plot of the activity on the time window between 5 s and 15 s, which corresponds to the core of learning.

The initial activity is rather unstructured and irregular; when submitted to STDP it becomes simpler, which is testified by a decrease in the #DOF measure (see figure 1B). The activity eventually becomes periodic and synchronised, which manifests in the form of a series of red stripes in the autocovariogram and is also directly visible on the activity plot. The transition from irregular activity to synchrony isn't necessarily straightforward: there is a period (around $t = 10$ s) where the two regimes "coexist", causing multiple transitions and an occasional burst of complexity.

4 Specificity of the learned response

We address here the question of input selectivity after learning. Is the network response specific to the learned stimulus or would it respond in the same way to other stimuli? We tested the network response to 4 arbitrary stimuli before and

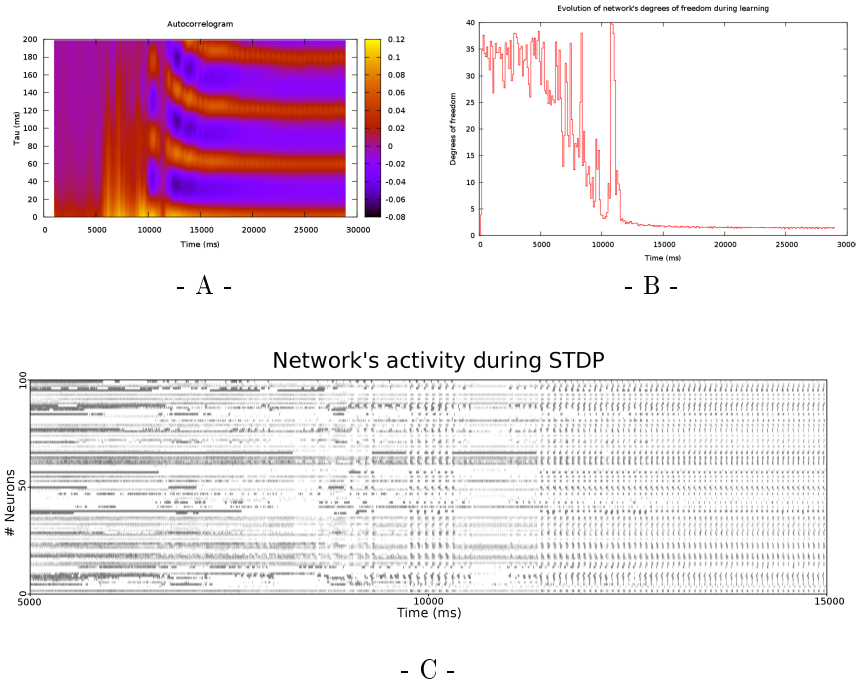


Fig. 1: - **A** - Evolution of the autocovariance of the average membrane potential during the learning process. At each time step t , the signal $\bar{V}(t)$ is covaried with $\bar{V}(t + \tau)$ for τ in $0..200$ ms, \bar{V} being the average of all neurons' membrane potentials. The red zones denotes a high covariance while the deep blue zones denote low covariance values. - **B** - Evolution of the #DOF measure across learning - **C** - Activity of the network in the first 10s of STDP.

after learning⁵. Before this learning session, all the stimuli trigger a response with the similar complexity. After learning, the pattern of activity for the first stimulus is significantly simplified, making it dissociable from the other patterns of activity. We tested the reproducibility of this experiment: the same simulation on 10 different networks⁶ gives a similar reduction of the #DOF measure (see figure 2).

In the given learning configuration (strong learning coefficient, short learning process), the response remains specific to the learned stimulus. We also verified that such a periodic shaping is systematically observed for other parameter configurations, but the activity simplification is not always synchronous. Moreover,

⁵In order to do so, the 4 different stimuli are presented sequentially on 1 second each. STDP is applied with a strong learning coefficient ($\alpha = 0.05$) on a short period of time (500 ms – between 12.5 s and 13 s) where only the stimulus #1 is presented.

⁶Identical parameters, but different initial random settings for the weights, delays and inputs.

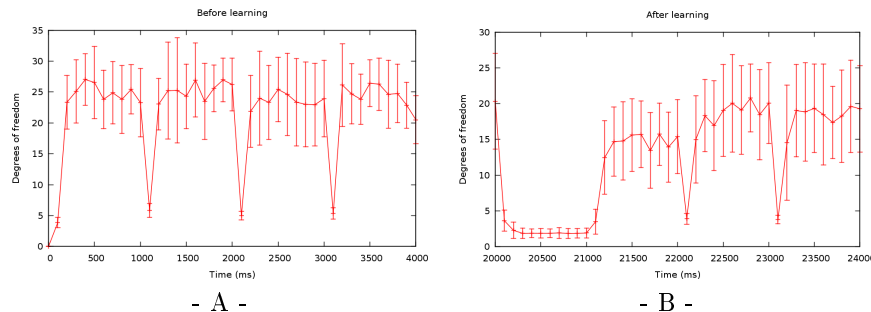


Fig. 2: Mean and variability over ten networks of the effective degrees of freedom for a similar sequential presentation of the four stimuli. - **A** - Before learning ($0 < t < 4$ s). - **B** - After learning the first stimulus (20 s $< t < 24$ s).

such a learning process relies on a fine tuning of both the learning coefficient value and the learning session duration. Some complexity decrease for the other stimuli, which is visible on the mean #DOF, may be amplified if the learning session lasts too long or if the learning parameter is too strong. A systematic study of our system's loading capacity is thus to be done, in order to estimate to the best how many different stimuli can be learned in the same way.

5 Discussion: which input selection in biological networks?

We have presented a neuronal model of perception which encompasses the effects of recurrent self-feeding activity⁷ and a simple, biologically-implementable, STDP mechanism which allows to learn to differentiate by phase transition one stimulus out of a set of several statistically equivalent stimuli. The learned stimulus is found to drive a regular and synchronous pattern of activity while the response remains unstructured for the other stimuli. While the synchronisation effect of STDP appears in other works [8, 9], albeit in different circumstances, its dependence to a particular stimulus is to our knowledge unheard of.

This study emphasises the role of qualitative transitions rather than mean activity changes, and may be considered as complementary to the classical feed-forward input selectivity mechanisms. It is highly probable that several extraction mechanisms combine in the real brain to produce appropriate responses. For instance, the presence of both synchronous activity and STDP may help to propagate the sensory signal to deeper layers by a synchrony consolidation effect, as proposed for instance for the olfactory bulb by [17, 18].

Some questions remain at the present stage, concerning an estimation of the loading capacity in multiple stimuli learning or the possible extensions of this learning scheme to dynamical/temporal input signals. This study would also

⁷Our recurrent neural networks can be seen as non-autonomous dynamical systems which undergo perturbations from the external world. The interesting regimes lie in the domain where the incoming signal is in concurrence with the internal self-sustained signal.

benefit a comparison with real data, in particular in the olfactory [17] or motor [19] systems.

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