[Re] Connectivity reflects coding: a model of voltage-based STDP with homeostasis

René Larisch[1]

1 Professorship for Artificial Intelligence, Department of Computer Science, Chemnitz University of Technology, D-09107 Chemnitz, Germany

rene.larisch@informatik.tu-chemnitz.de

Editor
Name Surname

Reviewers
Name Surname
Name Surname

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Code repository

A reference implementation of

→ Connectivity reflects coding: a model of voltage-based STDP with homeostasis, C. Clopath, L. Büsing, E. Vasilaki and W. Gerstner, In: Nature Neuroscience 13.3 (2010), pp. 344–352, doi= 10.1038/nn.2479

Introduction

Since the first description of spike timing-dependent plasticity (STDP) [1], different models of STDP are published to reproduce different experimental findings. The early implementations, so called pair-based STDP learning rules, failed on reproducing some experimental observations, like from triplet or quadruplets experiments [3].

Here, we introduce a reimplementation of the Clopath et al. [2] STDP model, what is able to reproduce experimental findings of triplet studies. They propose a biological motivated model with a voltage based learning rule. This means, that the occurrence of long term depression (LTD) or long term potentiation (LTP) depends on the postsynaptic membrane voltage. Clopath and colleagues could reproduce different STDP experiments. Further, they were able to show that their learning rule can develop stable weights, as it is necessary for learning receptive fields of V1 simple cells. Therefore, they implemented a homeostatic mechanism to adjust the amount of generated LTD. This based on the relation between the average postsynaptic membrane potential and a reference value. Furthermore, their model led to two different connection structures, depending on the spiking behavior of the neurons [2]. If neurons fire high at the same time, they build strong bidirectional connections (rate code). If neurons fire in a specific temporary order, they connection structure follows that order (temporal code). To simulate the membrane potential, Clopath et al. [2] used a adaptive exponential integrate-and-fire (AdEx) model.

Methods

Overview

The original model was implemented in matlab (http://modeldb.yale.edu/144566) demonstrating the stable learning of weights. This model reimplementation is written in Python (v2.7) and with help of the neuronal simulator ANNarchy [5] (v4.6). For the analysis and the figures we used numpy (v1.11.0) and matplotlib (v1.5.1). Not only the voltage based STDP learning rule is reimplemented, even the AdEx neuron model. In the supplementary material of the original publication, the matlab source code for a simple example is published.

The reimplementation is mainly orientated on the description of neuron model and learning rule in the original publication [2]. Because of the lack on a further description of the homeostatic mechanism and a more precise description of the neuron after a emitted spike, the available matlab code is the second reference for this reimplementation.

Model description

$$C\frac{du}{dt} = -g_L(u - E_L) + g_L\Delta_T e^{\frac{u-V_T}{\Delta_T}} - w_{ad} + z + I \tag{1}$$

The neuron model is mainly borrowed from the description in the matlab source code (see **Eq.** 1). Therefore, u is the membrane potential, C the membrane capacitance, the leak conductance is g_L and E_L is the resting potential. The slope factor (Δ_T) and the spiking threshold (V_T) are describing the behavior of the exponential term. If the membrane potential (u) is above V_T, the neuron spikes and the membrane potential increases exponentially. To simulate the spike upswing for $2ms$ after a spike is emitted, they used the so called 'resolution trick'.
The membrane potential is set to $29.4mV$, one millisecond later to $29.4mV + 3.462mV$ and another millisecond later to $E_L + 15mV + 6.0984mV$. The depolarizing spike afterpotential is z and the hyperpolarization current described by w_{ad}. Together with the adaptive spiking threshold (V_T), they are changing over the time. There descriptions are equal to those in the original paper. Further, values of the parameters in the neuron model are equal to the description in the original paper and will not be presented here.

Here, only a short description about the learning dynamic is given. For further information read the original publication by Clopath et al. [2]. The discussed learning rule consists of a term for long term depression (LTD) (**Eq.** 3) and long term potentiation (LTP) (**Eq.** 2).

$$LTP_{Term} = A_{LTP}\bar{x}_i(u - \theta_+)_+(\bar{u}_+ - \theta_-)_+ \tag{2}$$

LTP occurs if the presynaptic spike trace ($\bar{x}_i$) is above zero, the membrane potential u over the threshold θ_+ and the membrane potential trace $\bar{u}_-$ is above θ_- (**Eq.** 2). This happens if the postsynaptic neuron spikes shortly after the presynaptic neuron or if the membrane potential is high long enough, so that $\bar{u}_-$ exceeds θ_-.

$$LTD_{Term} = A_{LTD}(\frac{\bar{\bar{u}}}{u^2_{ref}})X_i(\bar{u}_- - \theta_-)_+ \tag{3}$$

The presynaptic spike counter (X_i) is set to one at a spike, or zero otherwise. The $\bar{u}_-$ is a second trace of the postsynaptic membrane potential. If this exceeds the θ_- threshold, and a presynaptic spike is emitted, LTD occurs (**Eq.** 3). Therefore, this can happen when the presynaptic neurons spikes after the postsynaptic. The strength of the LTD term, and with that the balance between LTP and LTD, is adjusted with respect to the ratio between $\bar{\bar{u}}$ and the reference value (u^2_{ref}), hence implementing a homeostatic mechanism.

$$\tau_{\bar{\bar{u}}}\frac{d\bar{\bar{u}}}{dt} = [(u - E_L)^2] - \bar{\bar{u}} \tag{4}$$

These mechanism are computed over the quadratic distance of the membrane potential and the resting potential E_L (**Eq.** 4). With a higher activity, the $\bar{\bar{u}}$ increases. This leads to a higher amount of LTD and the weights decreases. In contrast, a lower activity decreases the amount of LTD and the weights can increase. Through the ratio of $\bar{\bar{u}}$ with u^2_{ref}, this mechanism can enforce the connections to decrease down to the minimum weight bound or increase to the maximum weight bound. This requires a hard upper and lower bound for the weights and leads to a binomial distribution of the weights. The changing in the weight over time depends on the positive LTP and the negative LTD term (**Eq.** 5).

$$\frac{dw}{dt} = -LTD_{Term} + LTP_{Term} \tag{5}$$

All parameters of the neuron model and the basis set of parameters for the learning rule are taken from the original publication. Unfortunately, some parameters of the learning rule differ from experiment to experiment. Mainly the value of the homeostatic mechanism and the maximum weight are different. A table with the different parameters for the different task is presented in **Tab.** 2 and **Tab.** 1.

Reimplemented Analysis

In the original publication, the authors mentioned the possibility to reproduce spike timing triplet experiments, made in the visual cortex of rats [4]. Further, they investigated the emerged structure of the connectivity depending on the spiking behavior.

To validate the reimplementation, we reproduce the classical spike timing-dependent learning window (**Fig.** 2a in [2]), the frequency repetition task to reproduce a triplet experiment (**Fig.** 2b in [2]) and the influence of spiking order to connectivity (**Fig.** 4a, down and **Fig.** 4b, down in [2]). In the available matlab source code, they present the stable learning of weights by 500 input neurons and one postsynaptic neuron. The firing rate of these neurons follow a Gaussian distribution and the spike timing a Poisson process (similar to **Fig.** 5a in [2]). This task is reimplemented as well. With this analysis, the functionality of the reimplementation is shown on the main feature of this learning rule. The reproduced pair based and triplet STDP data, and the analysis of connection patterns, depending on the neuronal spiking behavior.

The experiment protocols are based on the description on the publication of Clopath et al. [2]. The implementation of the learning rule was mainly made according to the available matlab source code. Despite the effort to be as close as possible to the original implementation and description, the internal processing of the equations by ANNarchy can leads to a different execution order. Therefore, differing results occurred. Further, the chosen integration time step can have an influence of the computation result. On all reimplemented analysis, a time step of $dt = 1ms$ is chosen. Because of that, adaption on some parameters was necessary to reproduce the original results. For the connectivity experiments, the homeostatic mechanism follow **Eq.** 4.

To reproduce the STDP learning window, we create a list of discrete time points, where the pre- or postsynaptic neuron is active. The presynaptic neuron spikes every $50ms$. The postsynaptic neurons spikes in a range from $1ms$ to $15ms$ before or after the presynaptic neuron. For the repetition frequency experiment, or the triplet experiment, the number of pre- and postsynaptic spike pairs increases from a pair frequency of $0.1Hz$ to $50Hz$. The time between a pre- and postsynaptic spike of a pair is $10ms$. To reproduce this experiments, it was necessary to set $\bar{\bar{u}}$ to a fix value. The parameter changes are shown in **Tab.** 2.

To evaluate the connectivity over the number of spikes, a small network with ten neurons connected to each other was build. Every neuron receives input from one additional neuron, with Poisson distributed spike timing. Therefore, the *PoissonPopulation* population type of ANNarchy is used. The firing rate of every Poisson neuron is increased from two to twenty and with that, the firing rate of the ten corresponding neurons in the network.

For temporal order of spiking, the Poisson neurons were replaced with the *SpikeSourceArray* population type from ANNarchy. With a given list of time steps it is possible to determine the exact spiking time point of the corresponding neuron.

Because the reimplementation of the model based mainly on the matlab source code from modelDB, the emergence of stable weights was achieved by presenting a Gaussian input over 500 presynaptic neurons and one postsynaptic neuron. For every epoch ten Gaussian patterns are created to determine the activity of the 500 input neurons. One epoch has a duration of $125ms$. The presynaptic population is implemented with the *PoissonPopulation* from ANNarchy to achieve a Poisson distributed spiking behavior, as mentioned in the original matlab implementation. Equal to the matlab source code, the learning rates (A_{LTP} and A_{LTD}) are increased by the factor ten to speed up the learning.

The experiments for stable weight learning, to show a specific connectivity pattern, require the original homeostatic mechanism. Changes to the default parameters for this tasks are shown in **Tab.** 1.

Table 1: Changed parameters for connectivity experiments.

Task	Parameter	Value
Rate based connectivity	w_{max}	$0.25nA$
Temporal based connectivity	w_{max}	$0.30nA$
Stable weight by Gaussian input	w_{max}	$3.0nA$
Stable weight by Gaussian input	A_{LTD}	$1.4 * 10^{-3}$
Stable weight by Gaussian input	A_{LTP}	$0.8 * 10^{-3}$

Table 2: Changed parameters for weight change experiments.

Task	Parameter	Value
STDP learning window	$\bar{\bar{u}}$	$80mV^2$
STDP learning window	θ_-	$-60.0mV$
triplet experiment	$\bar{\bar{u}}$	$120mV^2$

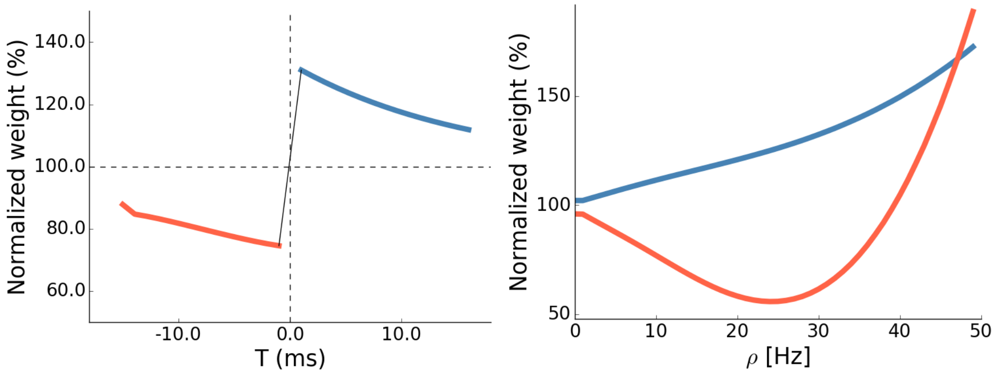

Figure 1: Replication of experimental findings. Left, the classic STDP learning window. On the x-axis is the time of a postsynaptic spike in relation to the presynaptic spike presented. **Right**, weight changes as a function of pair frequency repetition. Pre-post pairs are the blue line and post-pre pairs the red line.

Results

The classic pair based spike timing learning window is presented in **Fig. 1 left**. If the postsynaptic neuron spikes before the presynaptic one, LTD occurs (red line). If the postsynaptic neuron spikes after the presynaptic one, LTP occurs (blue line). Therefore, on the x-axis is the time difference between a pre- and postsynaptic spike indicated, with reference to the postsynaptic spike. The resulting graph is similar to the presented one in the original publication. A small difference can be seen in the highest positive and negative change. This could be caused by a different internal processing of ANNarchy.

The analysis of the pairing repetition frequency task is seen in **Fig. 1 right**. With lower repetition frequency, post-pre pairs (red line) lead to LTD. At a repetition frequency around $30Hz$, the post-pre pairs are under the influence of the next post-pre pair and the post-pre-post triplets lead to LTP. If the repetition frequency of post-pre pairs around $50Hz$, the same amount of LTP emerges as in pre-post pairs. The same results were shown in the original paper.

Besides the replication of experimental findings of pair based and triplet STDP experiments, Clopath et al. [2] presented how the connectivity, they emerging from the proposed learning rule, is influenced by the spiking behavior of the neurons. Therefore, **Fig. 2 left** shows the connection structure, if neurons fire with different frequencies. Here, the color scheme is different from the original publication. Weak connections (above $\frac{3}{4}$ of the maximum activity) are yellow. Light green are strong unidirectional and dark green are strong bidirectional connections. Neurons with similarly high firing rates develop strong bidirectional connections, because they are often active at the same time point. This suggest, that the learning is based on correlation between the neuronal activities. This corresponds with the connection pattern in the original paper.

If the neurons fire in a specific temporal order, this sequence is reflected in the connection pattern (**Fig. 2 left**). The connections are weak to neurons they firing a long time after or before the neuron. Meanwhile, the connections are strong to neurons they fired a short time after the neurons. This is similar to the analysis in the original paper.

The development of the weights over time, by presenting Gaussian shaped input, is presented in **Fig. 3**, Around 500 epochs, stable weights begin to emerge, similar to the original matlab source code.

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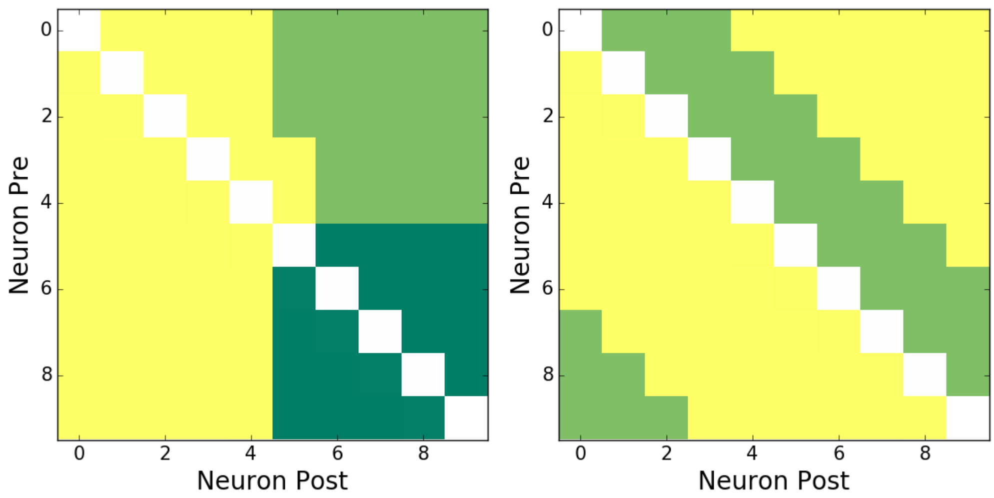

Figure 2: Different connectivity patterns. Depending on the activity different connectivity patterns emerge between the neurons. The color scheme is different from the original publication. Weak connections are yellow, strong unidirectional connections are light green and dark green are strong bidirectional connections. **Left**, Neurons with similar high firing rates develop strong bidirectional connections. **Right**, connection pattern follows the temporal order of the occurred spikes.

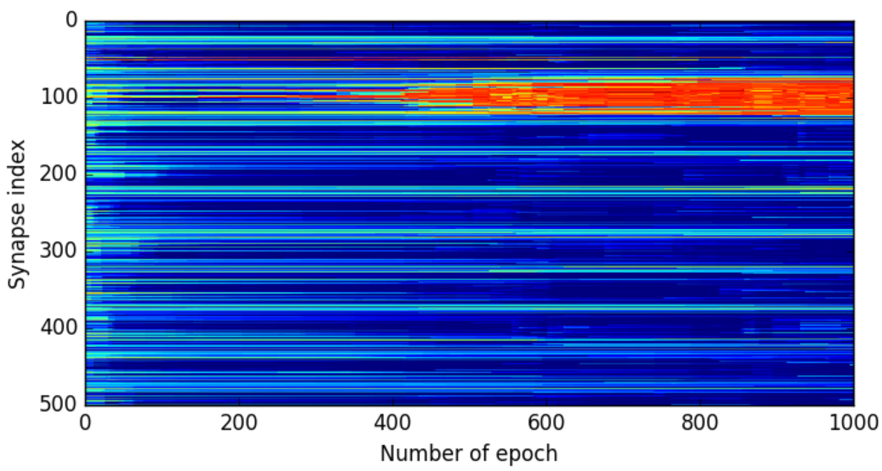

Figure 3: Stable weights on Poisson distributed Input. Colors show the weight value at the end of the current epoch from the presynaptic neuron to a single postsynaptic neuron. On the y-Axis is the presynaptic index indicated and the x-axis shows the number of epoch.

Conclusion

The here proposed reimplementation of voltage based STDP learning rule from Clopath et al. [2], is able to reproduce the experimental data and the emergent connectivity structures as proposed in the original paper.

The description of the learning rule in the original publication consists of enough details , to understand the different components and the collaboration of them. Certainly, two main components are described inadequate to facilitate a reimplementation. On one site, the 'resolution trick' of the membrane potential . And on the other site, the equation for the homeostatic mechanism ($\bar{\bar{u}}$).
Stable learning is only accessible with a working homeostasis mechanism, that regulates the LTD amount. The dependence of $\bar{\bar{u}}$ on the homeostatic mechanism makes it necessary to implement the right behavior of the membrane potential. Therefore, it requires the 'resolution trick'. The reimplementation benefits from the release of the source code on modelDB. Nonetheless, the reimplementation with the ANNarchy frame work was successful.

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