

STDP Learning Under Variable Noise Levels

Dalius Krunglevicius

Faculty of Mathematics and Informatics, Vilnius University, Naugarduko st 24, Vilnius, Lithuania

Keywords: Artificial Neural Networks, Spike-Timing-Dependent Plasticity, STDP, Hebbian Learning, Unsupervised Learning, Temporal Coding, Neuroscience.

Abstract: Spike-timing-dependent plasticity (STDP) is a set of Hebbian learning rules which are firmly based on biological evidence. It has been demonstrated that one of the STDP learning rules is suited for learning spatiotemporal patterns in a very noisy environment. Parameters of the neuron are only optimal, however, for a certain range of quantity of injected noise. This means the level of noise must be known beforehand so that the parameters can be set accordingly. That could be a real problem when noise levels vary over time. We found that the model of a leaky-integrate-and-fire inhibitory neuron with an inverted STDP learning rule is capable of adjusting its response rate to a particular level of noise. In this paper we suggest a method that uses an inverted SDTP learning rule to modulate spiking rate of the trained neuron. This method is adaptive to noise levels; subsequently spiking neuron can be trained to learn the same spatiotemporal pattern with a wide range of background noise injected during the learning process.

1 INTRODUCTION

Spiking neural networks (SNNs) are third generation artificial neural networks (Maas, 1997). Compared to previous generations, SNNs are more biologically based than their predecessors. Because of large computational costs, the applications of SNNs in machine learning or pattern recognition is problematic for the moment. It is reasonable to expect, however, that growing computer power will make SNNs practical in the near future. The main motivation behind this paper is research on how SNNs can be applied to pattern recognition in particular. In this paper we address the problems associated with training SNNs for spatiotemporal pattern recognition.

Neurons of most animal species communicate by releasing chemical messengers called neurotransmitters during an atomic event called a spike. There are two major approaches to interpret neural spikes as data. One is rate coding, where data are encoded in an averaged count of spikes over a specific time window. The other is temporal coding, where data are encoded within the precise timing of an individual spike.

In this paper we address temporal coding only.

Findings from biological research suggest that rate coding alone cannot account for the speed of

data transfer in living organisms (Gerstner et al., 1996; VanRullen and Thorpe, 2001). Temporal coding, on the other hand, can, because it requires very minimal time for the neuron to respond. It is debatable if temporal coding does take place in living neural systems (Rolls et al., 2004), however there is experimental evidence to support the concept of temporal coding (Gerstner and Kistler, 2002; Fellous et al., 2004; VanRullen et al., 2005, Kayser et al., 2009). Moreover, the discovery of spike-timing-dependent plasticity (STDP) suggests that the timing of the spikes is what matters. STDP is a function of time difference between presynaptic and postsynaptic spikes that guards the amount of change of synaptic strength. Persistent increases of synaptic strength are referred as long-term potentiation (LTP), while persistent decreases are referred as long-term depression (LTD). There are a few distinct STDP rules of different types of synapses known at the moment (Caporale and Dan, 2008). STDP is often referred to as a form of Hebbian learning.

One of the possible interpretations of temporal coding is as a spatiotemporal pattern. The simplest example of a spatiotemporal pattern is a binary on/off map of spikes in a short temporal window, where the probability of the spike at the “on” synapse is significantly larger than at the “off” synapses and “on” spikes are largely correlated in

time, while “off” spikes are not and produce only noise. In the case of STDP learning, under a certain range of parameters, the strengths of the synapses associated with the pattern grow, while the strengths of other synapses which receive only noise decay. In other words, the individual neuron acts as coincidence detector (Abbott and Nelson, 2000). In the simplest case possible, when the pattern is static and background noise is absent, such training can be reduced to supervised learning as a simple assignment operation: set strength to 1 if input is in the pattern, set to 0 otherwise.

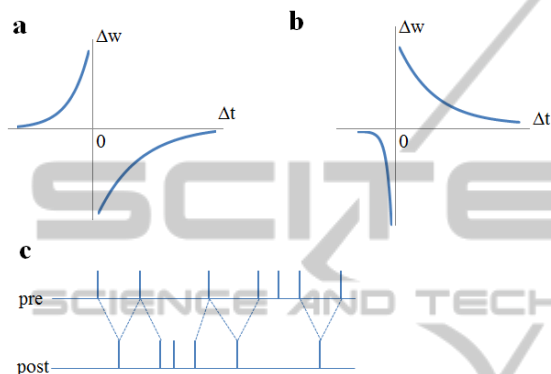


Figure 1: STDP training rules addressed in this paper. Δw is the amount of change in synaptic strength; Δt is time difference between postsynaptic and presynaptic spikes. a) STDP rule of excitatory-to-excitatory synapses. b) STDP rule of excitatory-to-inhibitory synapses. c) Update is guarded by the nearest-neighbour rule with immediate pairings only (Burkitt et al. 2004: Model IV).

The STDP rule of excitatory-to-excitatory synapses (Figure 1a) is the most widely researched one. In this paper we will refer to this rule as STDP rule A. When using this rule, and organizing multiple neurons in a competitive network, that is, connecting neurons with lateral inhibitory synapses, it is possible to train that network for multiple distinct spatiotemporal patterns, where individual neuron becomes selective for only one of the patterns. This has been demonstrated by many authors (Masquelier et al., 2009; Song et al., 2000; Guyonneau et al., 2005; Gerstner and Kistler, 2002). Such a network is capable of learning even if the pattern is highly obscured by noise (Masquelier et al., 2008, 2009). STDP learning of spatiotemporal patterns holds potential for practical pattern recognition, something explored by other authors (Gupta and Long, 2007; Nessler et al., 2009; Hu et al., 2013; Kasabov et al., 2013).

In this paper we address the problem associated with levels of noise injected during the training of a neuron. Values of the neuron threshold, amplitude of

relative refraction and initial synaptic strengths might be optimal only for a certain range of amounts of injected noise. These parameters define the initial spiking rate of the neuron (See Methods and Parameters for further details). This means the level of noise must be known beforehand, so the parameters can be set accordingly. It could be a real problem if the level of noise changes over time. To overcome this problem, we introduced inhibitory neurons which received excitatory input from the same neurons as the training neuron. We used an inverted STDP rule for excitatory-to-inhibitory synapses (Figure 1b). In this paper we refer to this rule as STDP rule B.

A similar rule of excitatory-to-inhibitory synapses has been discovered in a cerebellum-like structure of an electric fish (Bell et al., 1997) and in mice (Tzounopoulos et al. 2004, 2007). The rule in Figure 1b is not precisely the same: in the electric fish LTD gradually becomes LTP, while in mice there was zero LTP.

We found the model of an inhibitory neuron with the inverted STDP learning rule is capable of adjusting its response rate to a particular level of noise. In this paper we suggest a method that uses an inverted STDP learning rule to modulate spiking rate of the trained neuron. This method is adaptive to noise levels; subsequently spiking neuron can be trained to learn the same spatiotemporal pattern with a wide range of background noise injected during the learning process.

2 SOME PROPERTIES OF THE INVERTED STDP RULE

2.1 Training for Poisson Noise

We exposed neurons with the different threshold values to Poisson noise. Each trained neuron received input from 4,096 input neurons which produced Poisson noise by producing an input spike with a probability of 0.02 at each discrete step in the simulation. STDP rules A and B were compared. Results are represented in Figure 2. See Methods and Parameters for further details.

When exposed to Poisson noise only, STDP rule A, as expected, leads to two possible outcomes: either synaptic strengths decay until the neuron is not capable of firing, or all synaptic strengths grow and the neuron is activated by any random spike from the input.

The behavior of inverted rule B is far more

interesting: the neuron tends to stabilize its firing rate at a certain point. The point of stable firing rate depends on more than just threshold variables and the level of noise: the training step and initial values of synaptic strengths are very important as well. It seems that in case of rule B capping of synaptic strengths to some maximal value is not required.

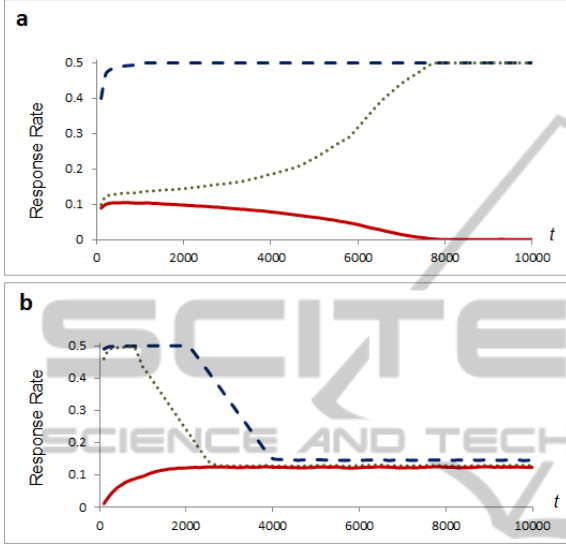


Figure 2: Comparison of STDP rules A and B, response rates to the same level of Poisson noise and different neuron thresholds. Vertical axis represents the response rate; horizontal axis represents the simulation time. a) STDP rule A, dashed line denotes a threshold value $\Theta=100$, dotted line $\Theta=340$, solid line $\Theta=900$. b) STDP rule B, dashed line at threshold value $\Theta=100$, dotted line $\Theta=160$, solid line $\Theta=170$.

In this case, if noise is mixed with a recurring spatiotemporal pattern of sufficient size, STDP rule B also leads to remembering the pattern in synaptic strengths, but in an inverted manner: synapses which are associated to the pattern are weaker than those not associated. When compared with rule A, the variance of synaptic strengths after training is significantly larger.

2.2 Stability of Response Rate at Different Noise Levels

To illustrate the dependency of stable rate points on the noise level of STDP rule B, we repeated the experiment described in the previous section over a range of Poisson noise. The results are presented in Figure 3.

While noise levels increase, depending on a neuron threshold value, firing rate slowly approaches the maximum value, which is 0.5, since

the neuron has a period of absolute refraction equal to one step of the simulation in our model.

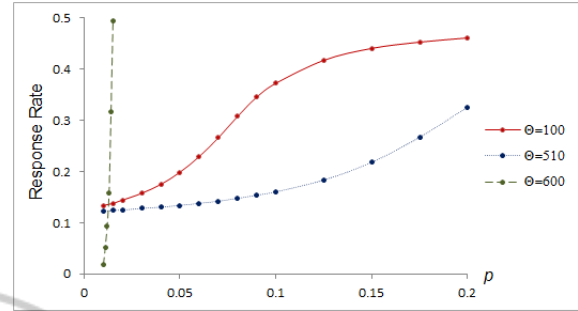


Figure 3: Points of stability in STDP rule B. Vertical axis represents the spiking rate; horizontal axis represents the probability of a spike of an individual input neuron at each discrete step of the simulation. Solid red line denotes a threshold value $\Theta=100$; solid blue line $\Theta=510$; dashed green line denotes response rates when synaptic strengths are static, at $\Theta=600$.

The neuron with static synapses approaches maximal response rate very rapidly in a narrow range of stimulation (Figure 3, dashed green line). Our goal was to get a neuron to provide inhibition in proportion to the amount of background noise. Therefore, we preferred STDP rule B instead of static synapses.

3 METHODS AND PARAMETERS

3.1 Leaky Integrate-and-Fire Neuron

Neurons were modelled on a simplified version of the Spike Response Model (SRM) (Gerstner and Kistler, 2002). The original SRM model has a smoothly decaying hyperpolarization function during the refractory period, but has little or no influence when the simulation time step and the absolute refractory period combined are sufficiently high to overstep the smooth curve, and this was the case in our simulations. In the model potential P at the time t of the neuron membrane is given by:

$$P(t) = \begin{cases} -W_r e^{-\Delta t/T_r} + \sum P_{sp}(t) & \text{if } t <> t_{spike} \\ P_{spike} = const & \text{otherwise} \end{cases} \quad (1)$$

where W_r and T_r are the parameters that define the amplitude and duration of relative refraction. Since at the time of the spike the neuron is in the phase of absolute refraction, the value of the membrane potential plays no role in training. Therefore this value is set to a constant just for ease of visualization and convenience. The value of

postsynaptic potential coming in from an individual synapse $PSP(t)$ is given by:

$$PSP_j(t) = \phi_j w_j \left(e^{-\frac{\Delta t}{T_m}} (1 + \kappa_{m_j}(t)) - e^{-\frac{\Delta t}{T_s}} (1 + \kappa_{s_j}(t)) \right) \quad (2)$$

where $\Delta t = t - t_{pre}$; w_j is the strength of the synapse, ϕ_j is the factor assigned to each individual synapse, it can be 1 or -1 depending on synapse type; T_s and T_m are the time constants.

Variables κ_m and κ_s are given by:

$$\kappa_{m_j}(t) = \begin{cases} \frac{w_j(t-1)}{w_j(t)} e^{-\frac{\Delta t}{T_m}} (1 + \kappa_{m_j}(t-1)) & \text{if } t = t_{pre} \\ \kappa_{m_j}(t-1) & \text{otherwise} \end{cases} \quad (3)$$

$$\kappa_{s_j}(t) = \begin{cases} \frac{w_j(t-1)}{w_j(t)} e^{-\frac{\Delta t}{T_s}} (1 + \kappa_{s_j}(t-1)) & \text{if } t = t_{pre} \\ \kappa_{s_j}(t-1) & \text{otherwise} \end{cases} \quad (4)$$

Initial values of κ_m and κ_s are zero. Equations 3 and 4 were derived in the following way: the summed values of individual PSPs of a single synapse at the moment t can be expressed as a finite series:

$$PSP_j(t) = w_0 e^{-\frac{(t-t_0)}{T_m}} - w_0 e^{-\frac{(t-t_0)}{T_s}} + \dots + w_n e^{-\frac{(t-t_n)}{T_m}} - w_n e^{-\frac{(t-t_n)}{T_s}} \quad (5)$$

where w_j is the set of strengths at the moment of each spike and t_j is the set of times of spikes. The expression is valid assuming that all $t_j < t$. Treating the positive and negative parts of the series separately, the first two members of the series could be expressed as the equation:

$$(1 + \kappa_0) w_0 e^{-\frac{(t-t_0)}{T}} + w_1 e^{-\frac{(t-t_1)}{T}} = (1 + \kappa_1) w_1 e^{-\frac{(t-t_1)}{T}} \quad (6)$$

where $\kappa_0 = 0$ at the beginning of the simulation. Algebraically solving equation 6 gives the equations 3 and 4. Since in the discrete-time simulation, exponentials functions can be pre-calculated, and κ computed only at the time of the spike, this allows minimizing computational costs.

Constants during the simulations were set to values: $T_m = 10$; $T_r = 10$; $T_s = 0.5$; $W_r = 2\Theta$; $P_{spike} = 300$. Θ is the neuron threshold value. The threshold value of inhibitory neurons was fixed such that $\Theta_{inh} = 1835$.

3.2 Plasticity

The STDP window for excitatory-to-excitatory synapses:

$$\Delta w_j = \begin{cases} A_{LTP} \cdot e^{-\frac{\Delta t}{T_{LTP}}} & \text{if } \Delta t < 0 \\ -A_{LTD} \cdot e^{-\frac{\Delta t}{T_{LTD}}} & \text{if } \Delta t > 0 \\ 0 & \text{if } \Delta t = 0 \end{cases} \quad (7)$$

The STDP window for excitatory-to-inhibitory synapses:

$$\Delta w_j = \begin{cases} -A_{LTD} \cdot e^{-\frac{\Delta t}{T_{LTD}}} & \text{if } \Delta t < 0 \\ A_{LTP} \cdot e^{-\frac{\Delta t}{T_{LTP}}} & \text{if } \Delta t > 0 \\ 0 & \text{if } \Delta t = 0 \end{cases} \quad (8)$$

There Δw_j is a change in synaptic strength, Δt is time difference between presynaptic and postsynaptic spikes, A_{LTP} , A_{LTD} , T_{LTP} and T_{LTD} are the constants. Synaptic strengths were confined in $w_{min} \leq w \leq w_{max}$.

Simulation constants for excitatory-to-excitatory synapses were:

$A_{LTP} = 0.75$; $A_{LTD} = 0.63$; $T_{LTP} = 16$; $T_{LTD} = 35$; $w_{min} = 0.5$; $w_{max} = 30$. Initial synaptic strengths were uniformly distributed between 4.5 and 5.5.

Simulation constants for excitatory-to-inhibitory synapses were:

$A_{LTP} = 6.048$; $A_{LTD} = 7.2$; $T_{LTP} = 4$; $T_{LTD} = 16$; $w_{min} = 10^6$; $w_{max} = 1.0$. Initial synaptic strengths were uniformly distributed between 0.9 and 1.0.

Synaptic strengths of static inhibitory synapses was $w = 7.3$ in the case of STDP rule B, and $w = 2.0$ otherwise.

4 RESULTS

We measured the performance and success of the training of a neuron for a spatiotemporal pattern. The sample pattern was generated from 122 neurons firing at the same time. The sample pattern was demonstrated to the network periodically, in intervals of 40 iterations. We executed the experiment at a 1 ms scale, so that one iteration corresponded to one millisecond. Overall there were 4,096 neurons in the input layer. All neurons in the input layer produced noise except for the neurons associated to the pattern at the moment of exposure to the pattern (see Figure 6a).

The success of training was evaluated by measuring differences between means of synaptic strengths of synapses associated to the pattern and of those which were not: $\Delta \mu_w = \mu_{w_{in}} - \mu_{w_{out}}$. Mean values were scaled to range at the interval [0, 1] respectively to the minimal and maximal values of synaptic strengths. The criterion for successful training was $\Delta \mu_w > 0.85$ at the end of the simulation. Neurons which were unresponsive at the end of the simulation were counted as unsuccessful, despite possible large values for $\Delta \mu_w$. Performance of the training was evaluated by measuring the velocity of $\Delta \mu_w$.

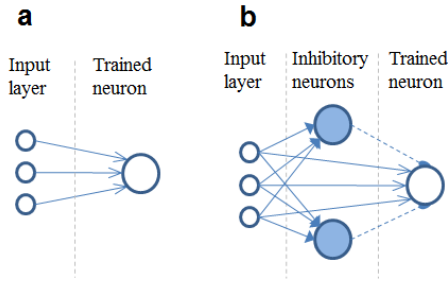


Figure 4: Neural network model. a) Simple network. b) Network with vertical inhibition.

We compared the performance of a simple neural network with that of a network with vertical inhibition (Figure 4).

The neural network with vertical inhibition consisted of an input layer, multiple inhibitory neurons and the trained neuron. The trained neuron received input from all neurons in the input layer, while each inhibitory neuron received input from a random fraction of an input layer (~10%). The trained neuron had synapses with STDP rule A, while inhibitory neurons had synapses with STDP rule B. In addition the trained neuron received inhibition from inhibitory neurons via static synapses (Figure 4b).

In order to reduce variance in inhibitory postsynaptic potentials (iPSP), we added multiple inhibitory neurons instead of a single such neuron. Variance of iPSPs reduces correlation between the presynaptic spike of the sample pattern and the postsynaptic spike; therefore, it has a negative influence on the training process. By selecting only a fraction of input neurons we ensured inhibitory neurons would not fire synchronously. The network contained 50 inhibitory neurons.

4.1 Training at Different Levels of Constant Noise

We conducted a number of experiments at different levels of Poisson noise mixed with a recurring spatiotemporal pattern. Poisson noise was generated by setting a fixed probability for an input spike at each iteration of the simulation. Success of the training was measured in a range of neuron threshold values Θ . Amplitude of relative refraction was set to $W_r=2\Theta$. (see Methods and Parameters for details).

In the case of a simple network (Figure 5a) we observed, as expected, that under a fixed threshold value, training is only possible within a narrow range of noise levels.

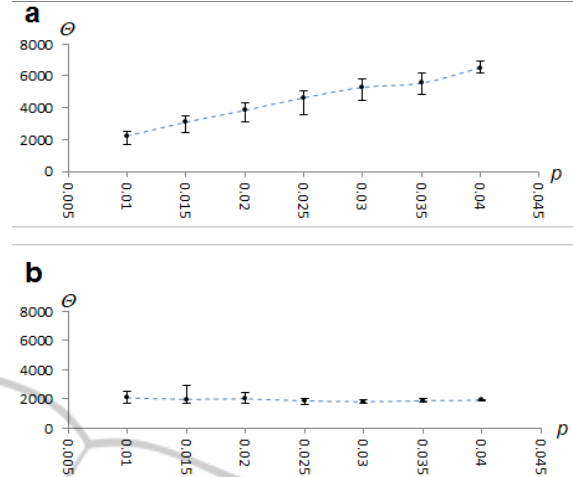


Figure 5: Dependency of training success on neuron threshold value and level of the injected Poisson noise. Vertical axis represents the neuron threshold value Θ ; horizontal axis represents the level of noise. a) Results from a simple network. Markers represent the point where training was most rapid; error bars represent the range of Θ when training was successful. b) Results from a network with vertical inhibition and STDP rule B.

In the case of the network with adaptive vertical inhibition (Figure 5b), the optimal value for a threshold was much less dependent on the level of noise, and remained more or less stable. The same neuron with a fixed threshold could be trained over the broad range of noise levels we used in our experiment (0.01 to 0.04). The range of possible threshold values narrows, however, as noise increases. This was due, most likely, to an increased variance of postsynaptic potentials, which reduces correlation between the spike from the input neuron (presynaptic spike) and the spike of the trained neuron (postsynaptic spike).

4.2 Training with Varying Noise Levels

In our next experiment we trained neurons with variable levels of noise injected. We used a sine function for setting the probability for the input neuron to fire: $p=0.01+0.015*(\sin(t/\lambda)+1)$. See Figure 6a. We evaluated training performance for λ values 50, 100 and 150.

We compared the performance of a simple network, the network with vertical inhibition and STDP rule B, and a network with static synapses of vertical inhibition. Results are presented in Figure 6b.

The training was executed over a range of a neuron threshold values and only the best results were taken into account.

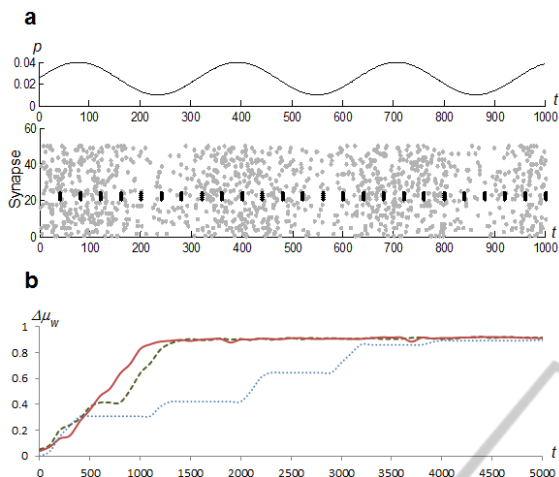


Figure 6: Training with varying noise level. a) Example of input spikes. Black dots represent fraction of a sample pattern, grey dots represent injected noise. b) Values of $\Delta\mu_w$ during the first 5,000 training iterations. Results are from an experiment where $\lambda=150$. Solid red line denotes a network with STDP rule B; dashed green line denotes a network with static synapses of inhibitory neurons; dotted blue line denotes a simple network.

In all cases of λ , the network with STP rule B performed best. The network with static inhibitory neurons performed only slightly worse, which was a somewhat surprising result. The simple network was the worst performer because the trained neuron was capable of firing only at peaks of stimulation from the input layer.

5 DISCUSSION

We suggested a method that uses an inverted SDTP learning rule to modulate spiking rate of the trained neuron. We have shown that this method can be applied to extend the range of noise levels under which a neuron is able to learn a spatiotemporal pattern. There are upper limits, however, for the level of noise under which a neuron can be successfully trained. By tuning the threshold value, the neuron can be trained under conditions of much more intense noise than we achieved in our experiments. This is likely caused by the increased variance introduced by vertical inhibition. This problem requires additional research.

In our experiments we used a sample pattern of a fixed size encoded as parallel singular spikes. This is not a necessary condition: the sample pattern can be encoded as parallel spike bursts or as parallel fixed temporal patterns (Masquelier et al., 2008) and the

sample patterns can vary in size. Plainly these factors influence the amount of stimulation received by the trained and inhibitory neurons, so that the effect of vertical inhibition could be very different. This is the subject of our continuing research.

The main motivation for this research was to explore prospects for building a practical machine based on STDP. We did not intend to simulate any particular biological neural system. It is difficult to determine to what extent the training model is possible biologically, and our model ignores the many non-linearities of STDP known from biological research (Caporale & Dan, 2008; Pfister & Gerstner, 2006; van Elburg & van Ooyen, 2010), nor does it take into account short-term plasticity, meta-plasticity and etc.

ACKNOWLEDGEMENTS

The author is thankful to Professor Sarunas Raudys for useful suggestions and valuable discussion.

REFERENCES

- Abbott L. F., Nelson S. B. (2000) Synaptic plasticity: taming the beast. *Nat. Neurosci.* 3:1178-1183.
- Bi G. Q. and Poo M. M. (1998). Synaptic modifications in cultured Hippocampal neurons: dependence on spike timing, synaptic strength, and postsynaptic cell type. *J Neurosci*, 18:10464-72.
- Bell C. C., Han V. Z., Sugawara Y., Grant K. (1997) Synaptic plasticity in a cerebellum-like structure depends on temporal order. *Nature* 387:278-81.
- Burkitt A. N., Meffin H., Grayden D. B. (2004) Spike-timing-dependent plasticity: the relationship to rate-based learning for models with weight dynamics determined by a stable fixed point. *Neural Comput* 16:885-940.
- Caporale N., Dan Y. (2008) Spike timing-dependent plasticity: a Hebbian learning rule. *Annu. Rev. Neurosci.* 31:25-46.
- Fellous J. M., Tiesinga P. H., Thomas P. J., Sejnowski T. J. (2004) Discovering spike patterns in neuronal responses. *J Neurosci* 24: 2989-3001.
- Gerstner W., Kempter R., van Hemmen J. L., Wagner H. (1996) A neuronal learning rule for sub-millisecond temporal coding. *Nature* 383: 76-81.
- Gerstner W., Kistler W. M. (2002) *Spiking neuron models*. Cambridge: Cambridge UP.
- Gupta A., Long L. N. (2007) Character recognition using spiking neural networks. *IJCNN*, pages 53-58.
- Guyonneau R., VanRullen R., Thorpe S. J. (2005) Neurons tune to the earliest spikes through STDP. *Neural Comput.* 17: 859-879.

- Hu J., Tang H., Tan K. C., Li H., Shi L. (2013) A spike-timing-based integrated model for pattern recognition. *Neural Computation* 25: 450–472.
- Kasabov N., Dhoble K., Nuntalid N., Indiveri G. (2013) Dynamic evolving spiking neural networks for on-line spatio- and spectro-temporal pattern recognition. *Neural Netw.* 41: 188–201.
- Kayser C., Montemurro M. A., Logothetis N. K., Panzeri S. (2009) Spike-phase coding boosts and stabilizes information carried by spatial and temporal spike patterns. *Neuron* 61:597–608.
- Maass W. (1997) Networks of spiking neurons: The third generation of neural network models. *Neural Networks*. 10, 1659–1671.
- Masquelier T., Guyonneau R., Thorpe S. J. (2008) Spike timing dependent plasticity finds the start of repeating patterns in continuous spike trains. *PLoS ONE*, 3(1), e1377.
- Masquelier T., Guyonneau R., Thorpe S. J. (2009) Competitive STDP-based spike pattern learning. *Neural Comput* 21:1259–1276.
- Morrison A., Diesmann M., Gerstner W. (2008). Phenomenological models of synaptic plasticity based on spike timing. *Biol. Cybern.* 98, 459–478. doi: 10.1007/s00422-008-0233-1
- Nessler B., Pfeiffer M., Maass M. (2009). STDP enables spiking neurons to detect hidden causes of their inputs. *Proceedings of NIPS Advances in Neural Information Processing Systems* (Vancouver: MIT Press).
- Pfister J. P., Gerstner W. (2006) Triplets of spikes in a model of spike timing-dependent plasticity. *J Neurosci.* 2006;26:9673–9682.
- Rolls E. T., Aggelopoulos N. C., Franco L., Treves A (2004) Information encoding in the inferior temporal cortex: contributions of the firing rates and correlations between the firing of neurons. *Biol Cybern.* 90:19–32.
- Song S., Miller K. D., Abbott L. F. (2000) Competitive hebbian learning through spike-timing-dependent synaptic plasticity. *Nat Neurosci.* 3: 919–926.
- Tzounopoulos T., Kim Y., Oertel D., Trussell L. O. (2004) Cell-specific, spike timing-dependent plasticities in the dorsal cochlear nucleus. *Nat. Neurosci.* 7:719–25.
- Tzounopoulos T., Rubio M. E., Keen J. E., Trussell L. O. (2007) Coactivation of pre- and postsynaptic signaling mechanisms determines cell-specific spike-timing-dependent plasticity. *Neuron*54:291–301.
- van Elburg R. A., van Ooyen A. (2010) Impact of dendritic size and dendritic topology on burst firing in pyramidal cells. *PLoS Comp Biol.* 2010;6:1000781.
- VanRullen R., Thorpe S. J. (2001) Rate coding versus temporal order coding: what the retinal ganglion cells tell the visual cortex. *Neural Comput.* 13: 1255–1283.
- VanRullen R., Guyonneau R., Thorpe S. J. (2005) Spike times make sense. *Trends Neurosci.* 28:1–4.