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Spike-Rate Neural Networks

▶ Large-Scale Neural Networks: Vision

Spike-Timing Dependent Plasticity, Learning Rules

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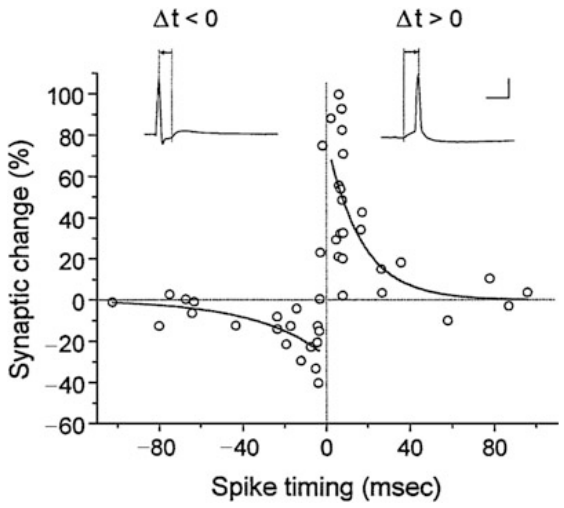
Synonyms

Spike-dependent synaptic learning rules; Spike-timing dependent synaptic plasticity; STDP

Definition

Biological phenomenon. Spike-timing-dependent plasticity (STDP) in its narrow sense refers to the change in the synaptic strength as a result of repeatedly triggering pairs of action potentials ("spikes") with a fixed time difference between the pre- and postsynaptic action potentials (Markram et al. 1997; Bi and Poo 1998; Sjostrom et al. 2001). STDP is typically observed for synapses between hippocampal or cortical pyramidal neurons in slices of juvenile rodents, and the spike pairings are repeated 50–100 times with various frequencies, e.g. 1 or 10 Hz. This protocol induces a change in the amplitude of a single excitatory postsynaptic potential (EPSP) which is plotted against the spike time difference $\Delta t = t_{post} - t_{pre}$ between the postsynaptic spike and the presynaptic spike (Fig. 1). The change takes in many cases a few minutes to be expressed and lasts at least for the duration of the experiment. Typically, when the presynaptic spike precedes the postsynaptic spike by roughly 10 ms, the synapse is potentiated; if the presynaptic spike follows the postsynaptic spike, the synapse is depressed (for reviews, see Bi and Poo (2001); Senn (2002); Sjostrom et al. (2008); Sjöström and Gerstner (2010)).



Spike-Timing Dependent Plasticity, Learning Rules, Fig. 1 Change of the EPSP amplitudes as a function of the time difference $\Delta t = t_{post} - t_{pre}$ between the post- and presynaptic spike. Time constants for LTP and LTD fits are $\tau_{pre} \approx 17$ ms and $\tau_{post} \approx 34$ ms, respectively (for an interpretation, see Fig. 2). Pairing protocol: 60 spike pairs at 1 Hz. Inset: postsynaptic action potential, relative to the time of the presynaptic spike (*vertical line*). Scale bars: 10 ms, 50 mV (Figure from Bi and Poo (2001))

Learning rules. In a computational context, STDP refers to plasticity rules that depend on the timing of pre- and postsynaptic spikes and that are involved in various learning scenarios for neuronal networks. These learning rules either emphasize the link to the biophysics underlying the synaptic modification (Senn et al. 2001; Shouval et al. 2002; Karmarkar and Buonomano 2002; Rubin et al. 2005; Graupner and Brunel 2012), or are minimalistic with respect to a biological implementation (Kempter et al. 2001; Song and Abbott 2001), or are derived from the maximization of a utility function (Pfister et al. 2006; Toyoizumi et al. 2007; Florian 2007; Urbanczik and Senn 2009; Friedrich et al. 2011). The learning rules are studied in the context of supervised, unsupervised, or reinforcement learning. When evaluated from the performance point of view, learning rules that are mathematically derived from an optimization principle are superior over STDP rules designed to fit a given set of experimental data (Frémaux et al. 2010). Interestingly, biological plausibility and computational relevance may go together when considering 2-compartment neurons with synapses on a dendritic tree (Urbanczik and Senn 2014).

Detailed Description

STDP models come in different flavors, emphasizing more the phenomenology, the biophysics, or the computational aspects. As learning rules, their primary focus is on doing computations rather than on reproducing synaptic plasticity data. An excellent and comprehensive review to STDP models, starting with the basic pair-based STDP models (Fig. 2A) and including also functional consequences, is found in the Scholarpedia article by Sjöström and Gerstner (2010). Here we highlight the properties of third-order STDP models and focus on gradient rules.

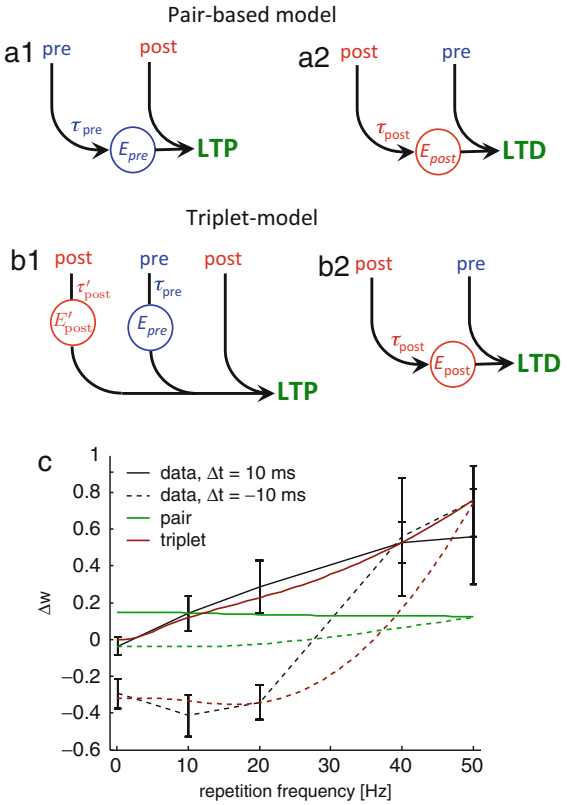
Phenomenological STDP Models

The simplest online model that phenomenologically reproduces the basic STDP curve (Fig. 1) separately induces long-term potentiation (LTP) or long-term depression (LTD), by either a pre-post or post-pre-coincidence detector, respectively. The key feature is that pre- and postsynaptic spikings are each tracked by leaky integrators, the so-called synaptic eligibility traces, while LTP and LTD are triggered proportionally to these traces at the times of the post- and presynaptic spikes, respectively (Fig. 2a, see also Sjöström and Gerstner (2010)).

The triplet model The simple STDP model which depends on pairs of spikes (pre-post and post-pre) correctly predicts the weight change only for a restricted number of protocols. If potentiation is assumed to be governed by triplets of spikes (pre-post-post) instead of pairs of spikes, a much broader class of experimental data can be captured (Pfister and Gerstner 2006). This so-called triplet model can be expressed as a sum of a depression term (Fig. 2B2) and a triplet term where at the time of the postsynaptic spike the weight change is proportional to the product of a postsynaptic and a presynaptic eligibility trace (Fig. 2B1).

The triplet model becomes especially relevant when the repetition frequency of the pre-post pairs increases. The pair-based model predicts a decrease of potentiation as a function of the pairing frequency. But in the visual cortex (L5 → L5 pyramidal neurons, Sjostrom et al. (2001)), potentiation increases with increasing repetition frequency, and this is well reproduced by the triplet model (Fig. 2c; it is also qualitatively captured by the Senn-Markram-Tsodyks model; see Senn (2002)).

This triplet model has also interesting computational properties. Under the assumption of independent pre- and postsynaptic Poisson firing rate (Pfister and Gerstner 2006), the expected weight change predicted by the triplet model is consistent with the Bienenstock-Cooper-Munro (BCM) learning rule (Bienenstock et al. 1982) which elicits input selectivity, i.e., the output neuron becomes strongly responsive to one given (rate-based) input pattern and much less to all the other ones. Furthermore, if the independent Poisson assumption is relaxed such that output firing rate depends on the presynaptic spike timings, the triplet rule becomes sensitive to third-order spiking correlations in the input, thereby generalizing the BCM learning rule to spiking-correlated patterns (Gjorgjieva et al. 2011).



Spike-Timing Dependent Plasticity, Learning Rules, Fig. 2 Phenomenological STDP models. (**a**) Simplest model reproducing Fig. 1. (**A1**) Each presynaptic spike stepwise increases a presynaptic eligibility trace E_{pre} that otherwise exponentially decays to 0 with time constant τ_{pre} (Eq. 1). LTP is induced by each postsynaptic spike proportionally to the amount of E_{pre} available at that time. (**A2**) LTD is induced by each presynaptic spike proportionally to E_{post} that low-pass filters the postsynaptic spiking. Note that the post-pre-chain is itself acausal and does not appear in the gradient-based learning schemes represented in the subsequent figures. (**b**) Triplet rule. (**B1**) In the triplet model, LTP is induced at the time of the postsynaptic spike and is proportional to the product $E_{\text{pre}}E'_{\text{post}}$ (**B2**). In the triplet model, LTD is induced by pairs of spikes as in B1. (**c**) Weight change as a function of the repetition frequency of the pre-post pairs (*solid lines*, $t_{\text{post}} - t_{\text{pre}} = 10$ ms) and the post-pre pairs (*dashed lines*, $t_{\text{post}} - t_{\text{pre}} = -10$ ms). The triplet model (*brown*) fits well the data from (Sjostrom et al. 2001) (*black*) while the pair-based model (*green*) cannot

Extended models A next important extension of STDP models takes account of the modulation of plasticity by the postsynaptic voltage (Clopath et al. 2010; Clopath and Gerstner 2010). This unifying model is formulated in terms of the postsynaptic voltage time course and presynaptic spikes. It can explain the widest set of STDP experiments, including burst-induced synaptic plasticity and those experiments that reveal the dependence on the postsynaptic voltage, as e.g. in Artola et al. (1990) and Sjostrom et al. (2001). This voltage-dependent model can also be seen as an extension of the triplet model where the postsynaptic eligibility trace in the potentiation term is replaced by a low-pass filter of the postsynaptic voltage. The triplet model, in turn, can be seen as a simplified version of the model by Senn et al. (2001). This latter model also depends on triple events (pre-post-post) for the induction of long-term plotentiation, but the pre-post-post ordering is important while in the triplet model both pre-post-post as well as post-pre-post events lead to potentiation.

Biophysical STDP models Another class of STDP models explains the synaptic modifications as a nonlinear function of the postsynaptic calcium concentration. The question whether the postsynaptic calcium alone can capture the characteristical STDP curve of Fig. 1 (see Shouval et al. (2002) versus Karmarkar and Buonomano (2002)) has been affirmed by taking into account the calcium dynamics (Rubin et al. 2005) or additional nonlinearities (Graupner and Brunel 2012). Functionally, these threshold nonlinearities are very similar to the ones imposed on the pre- and postsynaptic eligibility traces introduced in the phenomenological models (Senn et al. 2001; Clopath et al. 2010). Yet, by starting with individual protein kinetics, a biophysical model may explain how these nonlinearities arise (Rubin et al. 2005), see also "▶ Spike-Timing Dependent Plasticity (STDP), Biophysical Models."

Gradient-Based STDP Learning Rules

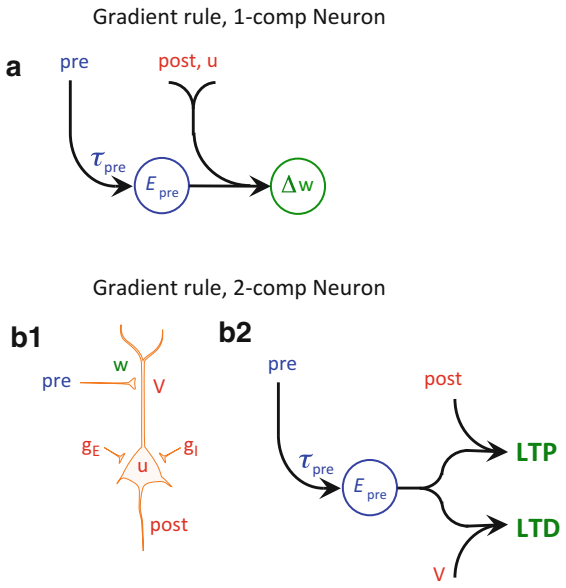
By their nature, the phenomenological and biophysical STDP models are not directly designed as synaptic learning rules that solve an explicit learning task. When canonical target functions for the learning can be defined, such as in the supervised and reinforcement learning scenario, spike-timing-dependent learning rules can be derived from gradient procedures that maximize/minimize these functions. A very convenient neuron model suited for a theory of learning is the escape rate neuron. Indeed since it allows to explicitly quantify the probability for a given postsynaptic spike train as a function of the afferent synaptic strengths w_j, the likelihood of a given spike train is differentiable (w.r.t to w_j) (Pfister et al. 2006). This neuron stochastically emits spikes with instantaneous firing rate $\rho(u)$ that is an increasing function of the instantaneous membrane potential $u(t)$. The latter is itself a sum of the postsynaptic potentials (PSPs) weighted by the synaptic strengths, $u(t) = \sum_j w_j \mathrm{PSP}_j(t)$, optionally subtracted with a reset kernel after a postsynaptic spike.

Supervised learning In the supervised learning scenario, the target function can be defined as a distance between the desired postsynaptic spike train, $S^{\mathrm{cl}}_{\mathrm{post}}(t) = \sum_i \delta(t - t_i^{\mathrm{post}})$, that is clamped as an output to the neuron and the spike trains that would be generated by the neuron itself. If we pick out a specific synapse, the presynaptic eligibility trace $E_{\mathrm{pre}}(t)$ is again obtained by the leaky integration of the presynaptic spike train $S_{\mathrm{pre}}(t) = \sum_i \delta(t - t_i^{\mathrm{pre}})$. Typically, the integration time constant τ_{pre} is equal to the membrane time constant, and hence this trace can also be identified with the postsynaptic potential induced by that synapse, $E_{\mathrm{pre}}(t) = \mathrm{PSP}(t)$. The gradient rule that maximizes the log-likelihood of reproducing the clamped target spike trains is then obtained as (Pfister et al. (2006); see Fig. 3a)

$$E_{\mathrm{pre}}(t) = \int_{-\infty}^{t} S_{\mathrm{pre}}(\tilde{t}) e^{-\frac{t-\tilde{t}}{\tau_{\mathrm{pre}}}} d\tilde{t} \qquad (1)$$

$$\dot{w}(t) = \eta \frac{\rho'}{\rho} \left(S^{\mathrm{cl}}_{\mathrm{post}}(t) - \rho(u(t)) \right) E_{\mathrm{pre}}(t), \qquad (2)$$

where η is some small learning rate. Here, $\rho' = \rho'(u(t))$ is the derivative of the escape rate ρ with respect to u, evaluated at t. Interestingly,



Spike-Timing Dependent Plasticity, Learning Rules, Fig. 3 Gradient-based SDTP for supervised learning (**a**, **b**) and unsupervised learning (**b**). (**a**) An optimal learning rule that reproduces the timing of a given ("clamped") output spike needs to take account of the postsynaptic membrane potential u beside the pre- *and* postsynaptic spikes (Eqs. 1 and 2). (**B1**) In a biological version, u is only slightly "nudged" by excitatory and inhibitory conductances g_E and g_I. The strength of synapses on the dendrites is adapted such that the dendritic potential V converges to the nudged somatic potential u. (**B2**) The corresponding gradient rule yields LTP that does only depend on the pre-post spike timings and LTD that depends only on the presynaptic spike time (captured by E_{pre}) and the local dendritic voltage (V; see Eqs. 1 and 3)

by expressing Eq. 2 as a sum of a potentiation and a depression term, we note that potentiation depends on three factors (the postsynaptic spike, the presynaptic eligibility trace, and a nonlinear function of the postsynaptic membrane potential $\rho'(u)/\rho(u)$) and depression on two factors (the presynaptic eligibility trace and $\rho'(u)$). This learning rule is reminiscent of the voltage-triplet rule discussed above (Clopath and Gerstner (2010); see also Brea et al. (2013) for a detailed discussion of the mapping between those two learning rules).

Arguably, clamping the postsynaptic spike train $S^{\text{cl}}_{\text{post}}$ is biologically unfeasible as it would require that the membrane potential u is ∞ at the time of a target spike and $-\infty$ else, conflicting with the evaluation of ρ and ρ' at the synaptically generated value of u. An alternative is to separate the spike-generating voltage from the synaptically induced voltage and consider a somatic and dendritic membrane potential, u and V, that are interpreted as a "teacher" (u) and "student" (V) potential, respectively (Fig. 2B1; Urbanczik and Senn (2014)). The soma receives conductance-based synaptic input that represents a teaching signal, and the postsynaptic spike train S_{post} is stochastically generated in the "free" run, i.e., according to a firing intensity $\rho(u)$ that is affected by this teaching input. Without teaching input, the somatic membrane potential is just the attenuated dendritic voltage, $u = \alpha V$, where α represents some dendritic attenuation factor and the instantaneous somatic firing is therefore $\rho(\alpha V)$. But if the somatic teaching input is turned on, the somatic voltage typically differs from the "dendritic prediction," $u \neq \alpha V$. Learning is driven by the "prediction error" measured in terms of the firing rates, $\rho(u) - \rho(\alpha V)$. It reduces this error by adapting the synaptic strengths of the dendritic "student inputs." At the synaptic location on the dendrite, the somatic rate $\rho(u)$ can be sampled by the backpropagating spikes S_{post}. The learning rule (Eq. 2) now translates to the biological version

$$\dot{w}(t) = \eta \frac{\rho'}{\rho} \big(S_{\text{post}}(t) - \rho(\alpha V(t))\big) E_{\text{pre}}(t), \quad (3)$$

that can operate all the time, without need for clamping (Fig. 2B2).

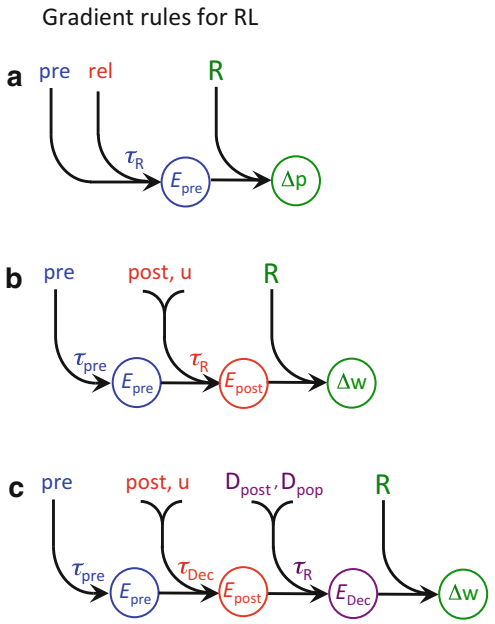
Crucially, after learning the teaching input driving, the synaptic plasticity (Eq. 3) can be turned off or on, without affecting the somatic voltage and hence without inducing additional weight changes. This is a consequence of the conductance-based teacher input that itself only changes the membrane potential if it deviates from the reversal potential defined that teaching input (Urbanczik and Senn 2014). The rule shares other interesting biological features. When the backpropagation is hampered, say due to insufficient dendritic depolarization, S_{post} is thinned out at the synaptic site and a putative LTP turns

into LTD, as observed for synapses on the distal apical tree of cortical pyramidal neurons (Sjostrom and Hausser 2006). Similarly, when the dendritic depolarization V is enhanced without additional postsynaptic spikes, LTD dominates as observed for these same cells (Sjostrom et al. 2004).

Unsupervised learning The learning rule (Eq. 2) in the free run is itself not suited for unsupervised learning since averaging $\dot{w}$ across trials cancels out to 0 at each point in time. However, if we consider a 2-dimensional sheet of 2-compartmental neurons as described in Fig. 2b, with Mexican-hat shaped somato-somatic connections, the somatic potential u is nudged away from V^* and the somatic firing in average does not anymore reflect the dendritic drive, $\langle S_{\text{post}} \rangle \neq \rho(V^*)$. In this case, the lateral connectivity induces a soft winner-take-all dynamics in the network that becomes a spike-based self-organizing feature map (Urbanczik and Senn 2014). When the dendrites of these neurons are supplied by spatiotemporal spike patterns via plastic synapses governed by the rule (Eq. 3), the feature map learns to cluster the spike patterns according to their similarity.

Another form of a gradient-based unsupervised learning that maximizes the mutual information between the pre- and postsynaptic spike trains was also shown to share classical STDP features while being able to develop receptive field properties (Toyoizumi et al. 2007). In the unsupervised setting, functional properties have also been shown for phenomenological STDP models in forming auditory maps (Gerstner et al. 1996), cortical columns (Song and Abbott 2001), direction-selective neurons in the visual cortex (Buchs and Senn 2002), or receptive fields similarly as described in the BCM theory (Gjorgjieva et al. 2011).

Reinforcement learning In reinforcement learning (RL), the putative synaptic weight changes induced by the pre- and postsynaptic activities are first low-pass filtered, and when a binary reward signal $R = \pm 1$ is applied, the changes accumulated until this time are multiplicatively modulated by R and turned into a real synaptic weight change. The phenomenological STDP model shown in Fig. 2 has also been adapted to this reinforcement learning scenario where it is referred to as R-STDP (Izhikevich 2007; Legenstein et al. 2008). However, R-STDP is shown to be problematic since for each stimulus class the expected reward must be 0 (Frémaux et al. 2010). This is because the integral over the STDP curve (Fig. 1) in general deviates from 0, and hence learning with $\langle R \rangle \neq 0$ would cause a weight drift. This is not the case for Eq. 2 in the free run, nor for Eq. 3 without somatic teaching conductances. These latter rules translate to the RL rule schematized in Fig. 4b:



Spike-Timing Dependent Plasticity, Learning Rules, Fig. 4 Gradient-based SDTP for reinforcement learning (*RL*). With incorporating downstream quantities into the synaptic plasticity, learning becomes faster. (**a**) The simplest spike-based *RL* rule changes the presynaptic release probability p (a proxy for the synaptic strength w) as a function of the presynaptic spike and the release, low-pass filtered with a time constant $\boldsymbol{\tau_R}$ corresponding to the typical reward delay (Seung 2003). (**b**) The same synaptic modifications for supervised learning (Fig. 3) yields *RL* when low-pass filtered with $\tau_{\mathbf{R}}$ and modulated with the delayed reward R (Eqs. 1, *4*, and 5). (**c**) As a decision is made by a population of neurons, synaptic updates should take account of the population decision signal D_{pop}, compare it with the single neuron decision D_{post}, low-pass filter the correlation between the two decision signals with $\tau_{\mathbf{R}}$, and only then implement the resulting weight change modulated by R (Eqs. 1, 6, 7, and 8)

$$E_{\text{post}}(t) = \int_{-\infty}^{t} \frac{\rho'}{\rho}\left(S_{\text{post}}(\tilde{t}) - \rho(u(\tilde{t}))\right) E_{\text{pre}}(\tilde{t}) e^{-\frac{t-\tilde{t}}{\tau_R}} d\tilde{t} \tag{4}$$

$$\Delta w(T) = \eta R E_{post}(T), \tag{5}$$

where E_{pre} is given in (Eq. 1) and for the 2-compartmental model, the argument u of ρ and ρ' is replaced by V^*. The rule is shown to perform stochastic gradient ascent on the expected reward and has been studied in different applications (Xie and Seung 2004; Pfister et al. 2006; Florian 2007; Frémaux et al. 2010).

Stochastic gradient rules are not unique since the same gradient can be obtained from different estimators. The rule in Eq. 5, for instance, represents an estimator of the gradient of the expected reward, $\frac{\partial}{\partial w}\langle R\rangle = \left\langle R \frac{\partial}{\partial} \log P_w(y|x)\right\rangle$, averaged across stimuli x, network activity y, time and reward. The reward R may depend on quantities downstream of x and y like the decision (or action) D that itself may stochastically depend on y. The reward R(x, y) therefore is a stochastic function of (x, y) with conditional expectation $\langle R|x, y\rangle = \sum_D R(x, D)P(D|x, y)$. For a synapse that has only access to the pre- and postsynaptic activities (components of x and y), the samples R(x, y) have a large variance and so will the samples $R(x,y)\frac{\partial}{\partial w}\log P_w(y|x)$ of the gradient estimate have. In contrast, R(x, D) may be a deterministic function (or again a stochastic function with smaller variance) and the samples $R(x,D)\frac{\partial}{\partial w}\log P_w(D|x)$ of the same reward gradient $\frac{\partial}{\partial w}\langle R\rangle$ show a smaller variance. To calculate $\frac{\partial}{\partial w}\log P_w(D|w)$, however, a synapse needs to have access to D (beside the pre- and postsynaptic activities).

Instead of considering *R(x,y)*, the reward can even be seen as a stochastic function of only the presynaptic spikes and the synaptic releases, *R(x, rel)*. This leads to a learning rule where synaptic releases that are correlated with subsequent rewards are made more likely by enhancing the corresponding release probability (Seung, 2003). But the variance of this reward gradient estimator can be reduced by taking account of the postsynaptic activity. In this way, more and more downstream information can be taken into account in the synaptic update, leading to learning rules that consider (A) only presynaptic spikes/releases and reward, (B) presynaptic spikes/releases, postsynaptic activity and reward, and (C) presynaptic spikes/releases, postsynaptic activities, single neuron and network decisions, and reward (Fig. 4). In these gradient estimators, the correlation between the synaptic parameter change and reward is progressively increased the more reward-relevant information the synapse exploits. In the case of only evaluating presynaptic spikes and releases, learning was claimed to mimic song acquisition in the zebra finch (Seung, 2003). When additionally evaluating the postsynaptic spikes and the membrane potential, the rule was shown to learn motor trajectories (Frémaux et al. 2010). When further evaluating the population decision the rule was shown to be successful in a complex sequential association task with delayed and scrambled rewards that is even hard to be learned by humans (Friedrich et al. 2011).

In population RL, the synaptic plasticity is modulated by the population decision that ultimately leads to the reward signal (Urbanczik and Senn 2009). The sign of the weight change should depend on whether the decision of the individual postsynaptic neuron D_{post} coincides with population decision D_{pop} formed by the majority of population neurons. These signals intrinsically depend on the neuronal code with which neurons and populations represent the possibly multivalued decisions and actions (Friedrich et al. 2014). In the simplest case of binary decisions, these signals may be set to 1 or −1, depending on whether the neuronal or population activity, low-pass filtered by τ_{Dec}, is above or below the corresponding decision threshold (Friedrich et al. 2011). The gradient rule emerging from this reasoning reads as (cf. Fig. 4c)

$$E_{\text{post}}(t) = \int_{-\infty}^{t} \frac{\rho'}{\rho}\left(S_{\text{post}}(\tilde{t}) - \rho(u(\tilde{t}))\right) E_{\text{pre}}(\tilde{t}) e^{-\frac{t-\tilde{t}}{\tau_{\text{Dec}}}} d\tilde{t} \tag{6}$$

$$E_{\text{Dec}}(t) = \int_{-\infty}^{t} D_{\text{post}}(\tilde{t}) D_{\text{pop}}(\tilde{t}) E_{\text{post}}(\tilde{t}) e^{-t-\tilde{t}^{\tau_R}} d\tilde{t} \tag{7}$$

$$\Delta w(T) = \eta R E_{\Delta\varepsilon\chi}(T). \quad (8)$$

Intracellular recordings from dendrites during plasticity induction protocols have shown that SDTP also depends on dendritic NMDA spikes (Gordon et al. 2006). This raises the question whether there are spike-timing-dependent plasticity rules that take account of such dendritic spikes as well. There is in fact a class of gradient-based RL rules that incorporate the "triple-spike timing" among the presynaptic, dendritic, and postsynaptic spike sequence, including the dendritic and somatic voltage and the reward modulation, analogously to the four-step cascade schematized in Fig. 4c (Schiess et al. 2012).

Cross-References

- ▶ Learning Rules: Overview
- ▶ Long Term Plasticity, Biophysical Models
- ▶ Reinforcement Learning in Cortical Networks
- ▶ Reward-Based Learning, Model-Based and Model-Free
- ▶ Spike-Timing Dependent Plasticity (STDP), Biophysical Models
- ▶ Tempotron Learning

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Spike-Timing Dependent Synaptic Plasticity

► Spike-Timing Dependent Plasticity, Learning Rules

Spike Triggered Average

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Synonyms

Reverse correlation; SFC; Spike-field coherence; STA

Definition

The spike-triggered average (STA) is a measure to relate a continuous signal and a simultaneously recorded spike train. It represents the average signal taken at the times of spike occurrences and with proper normalization is equivalent to the cross-correlation between the continuous signal and the spike train.

Detailed Description

The STA is widely used to study the temporal relationship between a spike train and a simultaneously recorded continuous signal, such as the local field potential (Eckhorn et al. 1988; Gray and Singer 1989; Murthy and Fetz 1996; Fries et al. 2001; Okun et al. 2010; Denker et al. 2011), membrane potential (Matsumura et al. 1996; Lampl et al. 1999; Poulet and Petersen 2008), synaptic conductance (under dynamic clamp, Gauck and Jaeger 2000) and electromyogram (McKiernan et al. 1998). Even non-physiological signals, such as electric stimulation to a single neuron (Mainen and Sejnowski 1995) or visual (Ringach and Shapley 2004) and auditory (Eggermont et al. 1983) stimulation, have been related to a spike train via the STA. In such cases the STA is commonly referred to as reverse correlation.