

TOPICAL REVIEW • OPEN ACCESS

Spike-based local synaptic plasticity: a survey of computational models and neuromorphic circuits

To cite this article: Lyes Khacef *et al* 2023 *Neuromorph. Comput. Eng.* **3** 042001

View the [article online](#) for updates and enhancements.

You may also like

- [Brain-inspired nanophotonic spike computing: challenges and prospects](#)
Bruno Romeira, Ricardo Adão, Jana B Nieder et al.
- [Emerging memory technologies for neuromorphic computing](#)
Chul-Heung Kim, Suhwan Lim, Sung Yun Woo et al.
- [CMOS-compatible neuromorphic devices for neuromorphic perception and computing: a review](#)
Yixin Zhu, Huiwu Mao, Ying Zhu et al.



TOPICAL REVIEW

OPEN ACCESS

RECEIVED
30 September 2022REVISED
25 August 2023ACCEPTED FOR PUBLICATION
23 October 2023PUBLISHED
17 November 2023

Original Content from
this work may be used
under the terms of the
[Creative Commons
Attribution 4.0 licence](#).

Any further distribution
of this work must
maintain attribution to
the author(s) and the title
of the work, journal
citation and DOI.



Spike-based local synaptic plasticity: a survey of computational models and neuromorphic circuits

Lyes Khacef^{1,2} , Philipp Klein^{1,2,3} , Matteo Cartiglia⁴ , Arianna Rubino⁴ , Giacomo Indiveri⁴ and Elisabetta Chicca^{1,2,*} ¹ Bio-Inspired Circuits and Systems (BICS) Lab, Zernike Institute for Advanced Materials, University of Groningen, Groningen, The Netherlands² Groningen Cognitive Systems and Materials Center (CogniGron), University of Groningen, Groningen, The Netherlands³ Cluster of Excellence Cognitive Interaction Technology (CITEC), Bielefeld University, Bielefeld, Germany⁴ Institute of Neuroinformatics, University of Zurich and ETH Zurich, Zurich, Switzerland

* Author to whom any correspondence should be addressed.

E-mail: e.chicca@rug.nl**Keywords:** brain-inspired computing, neuromorphic CMOS circuits, spiking neural networks, local synaptic plasticity, online learning
Supplementary material for this article is available [online](#)

Abstract

Understanding how biological neural networks carry out learning using spike-based local plasticity mechanisms can lead to the development of real-time, energy-efficient, and adaptive neuromorphic processing systems. A large number of spike-based learning models have recently been proposed following different approaches. However, it is difficult to assess if these models can be easily implemented in neuromorphic hardware, and to compare their features and ease of implementation. To this end, in this survey, we provide an overview of representative brain-inspired synaptic plasticity models and mixed-signal complementary metal–oxide–semiconductor neuromorphic circuits within a unified framework. We review historical, experimental, and theoretical approaches to modeling synaptic plasticity, and we identify computational primitives that can support low-latency and low-power hardware implementations of spike-based learning rules. We provide a common definition of a locality principle based on pre- and postsynaptic neural signals, which we propose as an important requirement for physical implementations of synaptic plasticity circuits. Based on this principle, we compare the properties of these models within the same framework, and describe a set of mixed-signal electronic circuits that can be used to implement their computing principles, and to build efficient on-chip and online learning in neuromorphic processing systems.

1. Introduction

The ability of biological systems to learn and adapt to changes in their environment is the key to survival. This learning ability is expressed mainly as the change in strength of the synapses that connect neurons, to adapt the structure and function of the underlying network. The neural substrate of this ability has been studied and modeled intensively, and many brain-inspired learning rules have been proposed [1–8]. The vast majority, if not all, of these biologically plausible learning models rely on local plasticity mechanisms, where locality is considered as a computational principle, naturally emerging from the physical constraints of the system. The principle of locality in synaptic plasticity presupposes that all the information a synapse needs to update its state (e.g. its synaptic weight) is directly accessible in space and immediately accessible in time. This information is typically based on the activity of the pre- and postsynaptic neurons to which the synapse is connected, and not on the activity of other neurons to which the synapse is not physically connected [6].

From a biological perspective, locality is a key paradigm of cortical plasticity that supports self-organization, which in turn enables the emergence of consistent representations of the world [9]. From the hardware development perspective, the principle of locality is a key requirement for the design of

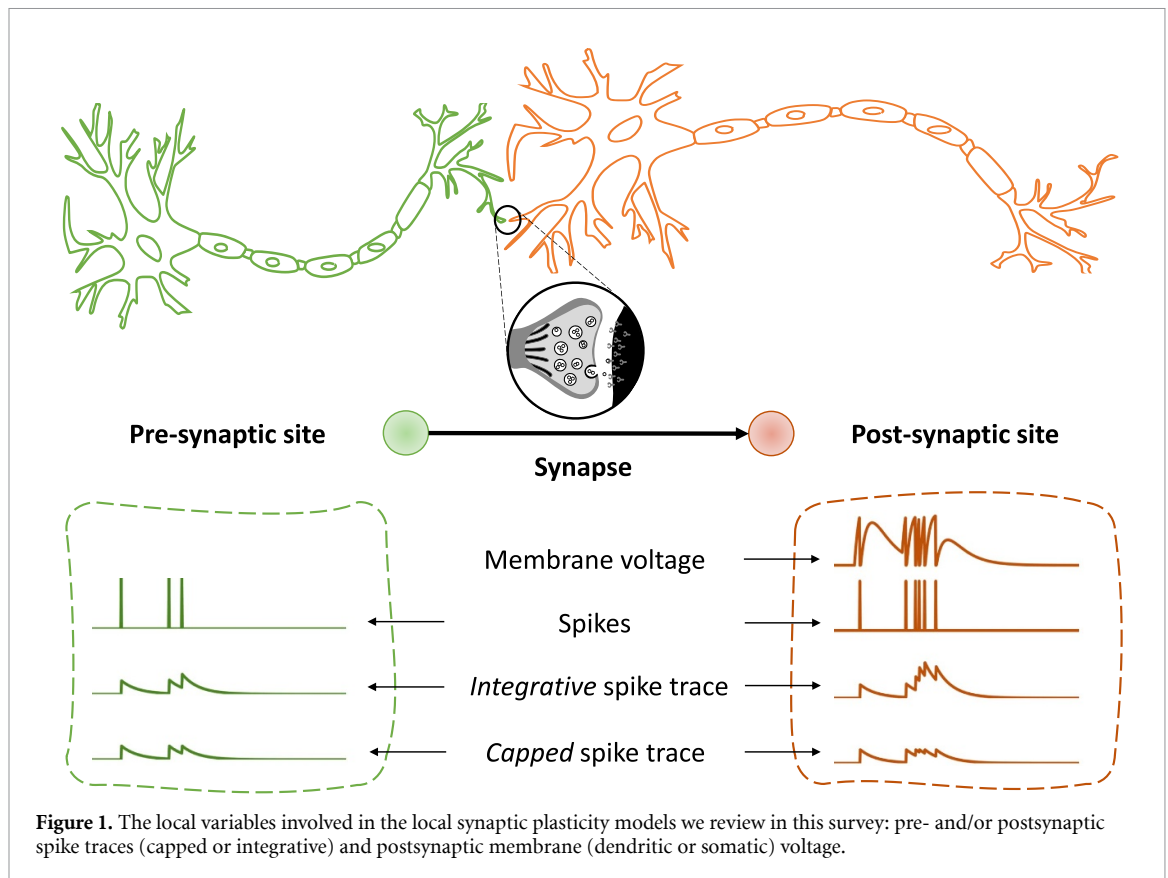
low-latency and low-power spike-based plasticity circuits integrated in embedded systems, and for enabling them to learn online, efficiently and without supervision. This is particularly important in recent times, as the rapid growth of application specific, compact, and autonomous sensory-processing devices brings new challenges in analysis and classification of sensory signals and streamed data at the edge. Consequently, there is an increasing need for online learning circuits that have low-latency, are low-power, and do not need to be trained in a supervised way with large labeled data-sets. As standard von Neumann computing architectures have separated processing and memory elements, they are not well suited for simulating parallel neural networks, they are incompatible with the locality principle, and they require a large amount of power compared to in-memory computing architectures. In contrast, neuromorphic architectures typically comprise parallel and distributed arrays of synapses and neurons that can perform computation using only local variables, and can achieve extremely low-energy consumption figures. In particular, analog neuromorphic circuits which operate the transistors in the weak inversion regime use extremely low currents (ranging from pico-Amperes to micro-Amperes), small voltages (in the range of a few hundreds of milli-Volts), and use the physics of their devices to directly emulate neural dynamics [10]. The spike-based learning circuits implemented in these architectures can exploit the precise timing of spikes and consequently take advantage of the high temporal resolutions of event-based sensors. Furthermore, the sparse and asynchronous nature of the spike patterns produced by neuromorphic sensors and processors can give these devices even higher gains in terms of energy-efficiency.

Given the requirements to implement learning mechanisms using limited resources and local signals, animal brains still remain one of our best sources of inspiration, as they have evolved to solve similar problems under similar constraints, adapting to changes in the environment and improving their survival chances [11]. Bottom-up, brain-inspired approaches to implement learning with local plasticity can be very challenging for solving real-world problems, because of the lack of a clear methodology for choosing specific plasticity rules, and the inability to perform global function optimization (as in gradient back-propagation (BP)) [12]. However, these approaches have the potential to support massively parallel and distributed computations and can be used for adaptive online systems at a minimum energy cost [13]. Recent work has explored the potential of brain-inspired self-organizing neural networks with local plasticity mechanisms for spatio-temporal feature extraction [14], unsupervised learning [15–19], multi-modal association [20, 21], adaptive control [22], and sensory-motor interaction [23, 24]. Some of the recently proposed models of plasticity have introduced the notion of a ‘third factor’, in addition to the two factors used in Hebbian learning rules that were derived from local information present at the pre- and postsynaptic site. In these three-factor learning rules, the local pre- and postsynaptic variables are used to determine the change in the weight, and the third factor is used to trigger or modulate it. This third factor could be implemented, for example, by a feedback signal representing reward, punishment, or novelty, transmitted by spikes from nearby processing areas or by diffusion of neuromodulators, such as dopamine [25, 26]. Similarly, recent works have combined local plasticity learning rules with non-local homeostatic stabilizing mechanisms, such as synaptic scaling or intrinsic plasticity [27–30], to add robustness and computational power to the networks they are embedded in. Three-factor learning and homeostatic plasticity circuits, such as the one presented in [31], could then be added as additional components to improve the learning performance of the system and increase its computational power.

In the next section we define the local variables that we take into consideration for analyzing the principle of locality in synaptic plasticity and the basic mechanisms that they have in common. In section 3 we provide an overview of a selection of representative spike-based synaptic plasticity models that adhere to the principle of locality and which can be easily mapped to neuromorphic electronic circuits. To derive common principles of computation, we review their operation mode using a common refactored notation. In section 4 we present the neuromorphic analog circuits that have been proposed in the literature implement the principles of computation derived. As different implementations have different characteristics that impact the type and number of elements that use local signals, for each target implementation, we assess the principle of locality taking into account the circuits’ physical constraints. Section 5 concludes with a discussion on synaptic plasticity frameworks for implementing on-line learning in neuromorphic systems, and presenting the challenges that still remain open in the field. To complete this work, we provide also a comprehensive overview on synaptic plasticity from a historical, an experimental, and a theoretical perspective (see supplementary material at page 1).

2. Computational primitives of synaptic plasticity

In this work, we refer to ‘computational primitives of synaptic plasticity’ as those basic plasticity mechanisms that make use of local variables.



2.1. Local variables

In addition to the spike trains produced by the neuron at the presynaptic site and the one at the postsynaptic site (as in figure 1), the signals that we consider as local variables are the following:

Pre- and postsynaptic spike traces: these are the traces generated at the pre- and postsynaptic site triggered by the spikes of the corresponding pre- or postsynaptic neurons. They can be computed by either integrating the spikes using a linear kernel, or by using non-linear operators/circuits. Figure 1 shows examples both linear (denoted as ‘integrative’) and non-linear (denoted as ‘capped’) spike traces. In general, these traces represent the recent average level of activation of the pre- and postsynaptic neurons. Depending on the learning rule, there might be one or more spike traces per neuron with different decay rates. The biophysical substrates of these traces can be diverse [32, 33], for example reflecting the amount of bound glutamate [34] or the number of N-methyl-D-aspartate (NMDA) receptors in an activated state [35]. The postsynaptic spike traces could reflect the calcium concentration mediated through voltage-gated calcium channels and NMDA channels [34], the number of secondary messengers in a deactivated state of the NMDA receptor [35] or the voltage trace of a back-propagating action potential [36].

Postsynaptic membrane voltage: the postsynaptic neuron’s membrane potential is also a local variable, as it is accessible to all of the neuron’s synapses.

These local variables are the basic elements that can be used to induce a change in the synaptic weight, which is reflected in the change of the postsynaptic membrane voltage that a presynaptic spike induces.

2.2. Spikes interaction

We refer to spike interactions as the number of spikes from past activity of neurons that are taken into account for weight update. In particular, we distinguish two spikes interaction schemes:

All spikes: in this scheme, the spike trace is ‘integrative’ and influenced, asymptotically, by the whole previous spiking history of the presynaptic neuron. The contribution of each spike is expressed in the form of a Dirac delta function which should be integrated. If spikes are considered to be point processes

for which their spike width is zero in the limit, the contribution of all spikes in equation (1) can be approximated as follows as described by [37–39]:

$$\tau \frac{dX}{dt} = -X + \sum_i A \delta(t - t_i) \quad (1)$$

where $\delta(t - t_i)$ is a spike occurring at time t_i , τ is the exponential decay time constant and A determines the jump height. In addition to being a good first-order model of synaptic transmission, this transfer function can be easily implemented in electronic hardware using integrator circuits. In fact, the trace $X(t)$ represents the online estimate of mean firing rate of the neuron [40].

Nearest spike: this is a non-linear mode in which the spike trace is only influenced by the most recent presynaptic spike. It is implemented by means of a hard bound that is limiting the maximum value of the trace, such that if the jumps reach it, the trace is ‘capped’ at that bound value. It is expressed in equation (2):

$$\tau \frac{dX}{dt} = -X + \sum_i (A - X(t - \epsilon)) \delta(t - t_i) \quad (2)$$

where A determines both the jump height and bound of X . It means that the spike trace gives an online estimate of the time since the last spike. It should be noted that $X(t - \epsilon)$ denotes the value of $X(t)$ just before the update.

Therefore, the jump and bound parameters control the sensitivity of the learning rule to the spike timing and rate combined (all spikes) or to the spike timing alone (nearest spike), while the decay time constant controls how fast the synapse forgets about these activities. Further spike interaction schemes are possible, for example by adapting the nearest spike interaction so that spike interactions producing long-term potentiation (LTP) would dominate over those producing long-term depression (LTD).

2.3. Update trigger

In most synaptic plasticity rules, the weights update is event-based and happens at the moment of a presynaptic spike (e.g. [41]), postsynaptic spike (e.g. [15]) or both pre- and postsynaptic spikes (e.g. [42]). These triggers are instantaneous events and mathematically correspond to Dirac delta functions (e.g. for a presynaptic spike: $\delta(t - t_{\text{pre}})$) [43, 44]. This event-based paradigm is particularly interesting for hardware implementations, as it exploits the spatio-temporal sparsity of the spiking activity to reduce the energy consumption with less updates. On the other hand, some rules use a continuous update (e.g. [45]) arguing for more biological plausibility, or a mixture of both with e.g. depression at the moment of a presynaptic spike and continuous potentiation (e.g. [46]). In case of continuous updates, instantaneous pre- or postsynaptic spikes are converted into traces by applying a kernel function (e.g. [45]) or by using a spike response model (e.g. [29, 37]).

2.4. Synaptic weights

The synaptic weight determines the strength of a connection between two neurons. It is here defined as the amplitude of the postsynaptic current generated by a presynaptic spike. Synaptic weights have three main characteristics:

1. Type: synaptic weights can be continuous, with full floating-point resolution in software, or with fixed/limited resolution (binary in the extreme case). Both cases can be combined by using fixed resolution synapses (e.g. binary synapses), which however have a continuous internal variable that determines if and when the synapse undergoes a low-to-high (LTP) or high-to-low (LTD) transition, depending on the learning rule.
2. Bistability: in parallel to the plastic changes that update the weights, on their weight update trigger conditions, synaptic weights can be continuously driven to one of two stable states, depending on additional conditions on the weight itself and on its recent history. These bistability mechanisms have been shown to protect memories against unwanted modifications induced by ongoing spontaneous activity [41] and provide a way to implement stochastic selection mechanisms.
3. Bounds: in any physical neural processing system, whether biological or artificial, synaptic weights have bounds: they cannot grow to infinity. While these bounds arise in artificial systems from software limitations (i.e. integer or floating resolution) or hardware limitations (i.e. maximum supply voltage or conductance of circuit elements), the synaptic weights in biology are bounded by constraints imposed by the biological substrate (see experimental perspective in the supplementary material at page 2, i.e. the

number of docked vesicles in the presynaptic terminal, the amount of released transmitters, the membrane potential threshold, etc). Two types of bounds can be imposed on the weights: (1) hard bounds, in rules with additive updates independent of the weight, or (2) soft bounds, in weight-dependent updates (for example multiplicative) rules that drive the weights toward the bounds asymptotically [47].

2.5. Stop-learning

An intrinsic mechanism to modulate learning and automatically switch from training mode to inference mode is important, especially in an online learning context. This ‘stop-learning’ mechanism can be either implemented with a global signal related to the performance of the system, as in reinforcement learning or in three-factor learning rules, or with a local signal produced in the synapses or in the soma. For example, a local variable that can be used to implement stop-learning could be derived from the postsynaptic neuron’s membrane voltage [29, 46] or spiking activity [41, 45].

3. Models of synaptic plasticity

We present a representative set of spike-based synaptic plasticity models, summarize their main features, and explain their working principles. We reformulated the original equations and definitions of the rules to fit the unified notation given in table 1. The resulting weight is indicated by the variable $w(t)$ and traces are highlighted by the notation $T(t)$, fitting to the definition of traces and spike interactions given in sections 2.1 and 2.2, representing spike response kernels or filtered versions of state variables of the models. Some of the rules show a bistable behavior (B) of the weight with given rates (α, β) following the description given in section 2.4. The plastic updates can be triggered by either pre- or postsynaptic activity or are applied continuously as described in section 2.3. Through the model section $\sum_{\text{spikes } k} \delta(t - t_k)$ refers to the sum of Dirac delta functions of neuron spikes. We indicate in the rules tables the assumed units for the various variables. To keep the models general, we opted for choosing arbitrary units (a.u.) for the weight $w(t)$.

The presented rules are mostly, with the exception of the homeostatic membrane potential dependent plasticity (H-MPDP) rule, defined for the potentiation and depression of excitatory synapses. Nevertheless, plasticity is also observed in inhibitory synapses [48, 49] and plays an important role for network stability [50–53] and function [54, 55]. In contrast to excitatory plasticity, inhibitory plasticity shows a larger variance in the observed set of rules [55] and similar rules to excitatory plasticity have been found in the form of e.g. inhibitory spike-timing dependent plasticity (STDP) behavior [5, 56–58] and Hebbian plasticity [50]. These behaviors can be replicated by a selection of the presented rules (e.g. STDP see section 3.1 and calcium-based STDP (C-STDP) see section 3.5). Indeed, also inhibitory plasticity phenomena can be realized in neuromorphic hardware (e.g. by modifying circuit details, or trigger conditions). However, given that the modeling studies of inhibitory plasticity are relatively recent compared to those on excitatory plasticity, there are very few complementary metal–oxide–semiconductor (CMOS) circuits and systems that explicitly implement those models [59, 60]. Table 14 shows a direct comparison of the computational primitives used by the relevant models.

3.1. Song et al (2000): STDP

STDP [42] was proposed to model how pairs of pre–post spikes interact based solely on their timing. It is one of the most widely used synaptic plasticity algorithms in the literature and has been used as a benchmark to fit experimental data [61]

$$\frac{dw}{dt} = -A_- T_{\text{post}}(t) \sum_{\text{pre spikes } k} \delta(t - t_k) + A_+ T_{\text{pre}}(t) \sum_{\text{post spikes } l} \delta(t - t_l). \quad (3)$$

The synaptic weight is updated according to equation (3), whose variables are described in table 2. The traces $T_{\text{pre}}(t)$ and $T_{\text{post}}(t)$ are variables generated by pre- and postsynaptic spikes, respectively and contain information about the recent pre- and post-synaptic spiking activity. If a postsynaptic spike occurs after a presynaptic one ($\Delta t < 0$), potentiation is induced (triggered by the postsynaptic spike). In contrast, if a presynaptic spike occurs after a postsynaptic spike ($\Delta t \geq 0$), depression occurs (triggered by the presynaptic spike). The traces $T_{\text{pre}}(t)$ and $T_{\text{post}}(t)$ include separate time constants, originally τ_+ and τ_- , which determine the time window in which the spike interaction leads to changes in the synaptic weight. As shown in table 14, STDP is based on local pre- and post-spike traces. Depending on the chosen spike trace dynamics (see sections 2.1 and 2.2) the rule can implement different spike-pairing schemes [47]. Figure 2 illustrates how STDP is implemented using capped spike traces for a nearest spike interaction scheme.

Table 1. Unified notation list used to describe all the models.

Variables	Notation
Weights	$w(t)$
Traces	$T(t)$
Potentials	V
Scalars (thresholds/targets)	θ
Amplitude	A
Bistability	B
Bistability rates	α, β
Presynaptic	pre
Postsynaptic	$post$
Membrane/dendritic/somatic	mem/den/som
Long term depression/potential	LTD/LTP
Max/min/positive/negative	max/min/+/-

Table 2. Variables of the STDP rule.

Refactored	Unit	Description	Original
$w(t)$	a.u.	Synaptic weight	w
$T_{pre}(t), T_{post}(t)$	1	Pre- and postsynaptic spike traces	$\exp(\frac{\Delta t}{\tau_+}), \exp(\frac{-\Delta t}{\tau_-})$
A_+, A_-	$[w]$	Weight change amplitude	A_+, A_-

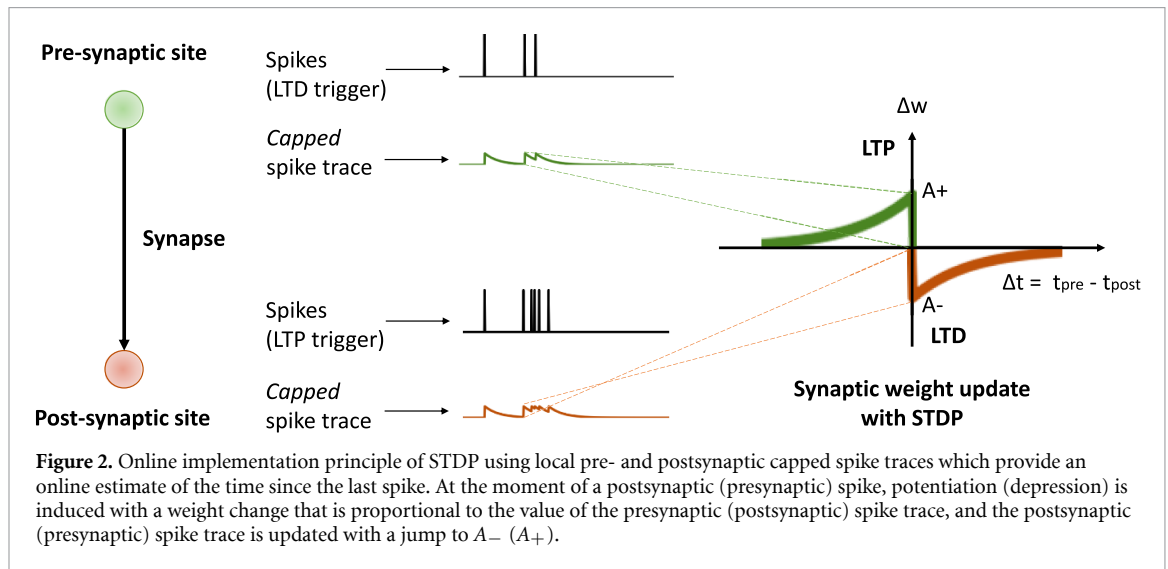


Table 3. Variables of the T-STDP rule.

Refactored	Unit	Description	Original
w	a.u.	Synaptic weight	w
$T_{\text{pre}_1}(t), T_{\text{pre}_2}(t)$	1	Presynaptic spike traces - integrative	$r_1(t), r_2(t)$
$T_{\text{post}_1}(t), T_{\text{post}_2}(t)$	1	Postsynaptic spike traces - integrative	$o_1(t), o_2(t)$
A_2^+, A_2^-	$[w]$	Weight change amplitude whenever there is a pair event	A_2^+, A_2^-
A_3^+, A_3^-	$[w]$	Weight change amplitude whenever there is triplet event	A_3^+, A_3^-

Table 4. Variables of the SDSP rule.

Refactored	Unit	Description	Original
$w(t)$	a.u.	Synaptic weight	X
w_{max}	$[w]$	Maximum synaptic weight	X_{max}
$T_{\text{post}}(t)$	1	Postsynaptic spike trace - integrative	$C(t)$
$\theta_{\text{up}}^l, \theta_{\text{up}}^h, \theta_{\text{down}}^l, \theta_{\text{down}}^h$	1	Thresholds on the trace $T_{\text{post}}(t)$	$\theta_{\text{up}}^l, \theta_{\text{up}}^h, \theta_{\text{down}}^l, \theta_{\text{down}}^h$
$V_{\text{post}_{\text{mem}}}(t)$	V	Post synaptic membrane potential	$V(t)$
θ_V	V	Membrane potential threshold	θ_V
A_1, A_2	$[w]$	Potential and depression amplitude	a, b
α, β	$[w] \cdot s^{-1}$	Bistability rates, $\in \mathbb{R}^+$	α, β
θ_{w_B}	$[w]$	Bistability threshold on the synaptic weight	θ_X
w_{eff}	$[w]$	Synapse efficacy	
$w_{\text{pot}}, w_{\text{dep}}$	$[w]$	Binary synaptic efficacies	J_+, J_-

While in classical STDP, potentiation takes place shortly after a presynaptic spike and upon the occurrence of a postsynaptic spike, in the current framework, several conditions need to be considered. Potentiation is triggered at every postsynaptic spike where the weight change is gated by the $T_{\text{pre}_1}(t)$ detector and modulated by the $T_{\text{post}_2}(t)$ detector. If there are no postsynaptic spikes shortly before the current one ($T_{\text{post}_2}(t)$ is zero) the degree of potentiation is determined by A_2^+ only, just like in the pair-based STDP. If however, a triplet of spikes occurs (in this case one-pre and two-post) $T_{\text{post}_2}(t)$ is non-zero and an additional potentiation term $A_3^+ T_{\text{post}_2}(t)$ contributes to the weight change. Analogously, $T_{\text{pre}_2}(t)$, $T_{\text{post}_1}(t)$, A_2^- and A_3^- operate for the case of synaptic depression which is triggered at every presynaptic spike. It should be noted that all the traces are computed at $(t - \epsilon)$ by subtracting a small positive constant from the exact time of the spike.

3.3. Brader *et al* (2007): spike-driven synaptic plasticity

The spike-driven synaptic plasticity (SDSP) learning rule addresses in particular the problem of memory maintenance and catastrophic forgetting: the presentation of new experiences continuously generates new memories that will eventually lead to saturation of the limited storage capacity and hence forgetting (see section stability of synaptic memory in the supplementary material at page 4). SDSP attempts to solve it by slowing the learning process in an unbiased way. The model randomly selects the synaptic changes that will be consolidated among those triggered by the input, therefore learning to represent the statistics of the incoming stimuli.

The SDSP model proposed by Brader *et al* [41] is demonstrated in a feed-forward neural network used for supervised learning in the context of pattern classification. Nevertheless, the model is also well suited for unsupervised learning of patterns of activation in attractor neural networks [41, 62]. It does not rely on the precise timing difference between pre- and postsynaptic spikes, instead the weight update is triggered by single presynaptic spikes. The sign of the weight update is determined by the postsynaptic neuron's membrane voltage $V_{\text{post}_{\text{mem}}}(t)$.

A spike trace $T_{\text{post}}(t)$ is used to represent the average postsynaptic activity. It is used to determine if synaptic updates should occur (stop-learning mechanism). The spike trace dynamics is described in equation (1).

The internal variable $w(t)$ is updated according to equation (5) with the variables described in table 4

$$\frac{dw}{dt} = A \sum_{\substack{\text{pre spikes} \\ k}} \delta(t - t_k) \quad (5)$$

Table 5. Variables of the V-STDP rule.

Refactored	Unit	Description	Original
$w(t)$	a.u.	Synaptic weight	w
w_{\max}	$[w]$	Maximum synaptic weight	w_{\max}
$T_{\text{pre}}(t)$	1	Presynaptic spike trace - integrative	$\bar{x}(t)$
$\bar{V}_{-\text{post_mem}}(t), \bar{V}_{+\text{post_mem}}(t)$	V	Low-pass filtered $V_{\text{post_mem}}(t)$ with different time constants for depression and potentiation	$\bar{u}_-(t), \bar{u}_+(t)$
$V_{\text{post_mem}}(t)$	V	Postsynaptic membrane voltage	$u(t)$
θ_-, θ_+	V	Thresholds	θ_-, θ_+
A_{LTD}	$[w] \cdot V^{-1}$	Amplitude for depression	A_{LTD}
A_{LTP}	$[w] \cdot V^{-2} \text{s}^{-1}$	Amplitude for potentiation	A_{LTP}

$$A = \begin{cases} A_1 & \text{if } V_{\text{post_mem}}(t) > \theta_V \text{ and } \theta_{\text{up}}^l < T_{\text{post}}(t) < \theta_{\text{up}}^h \\ -A_2 & \text{if } V_{\text{post_mem}}(t) \leq \theta_V \text{ and } \theta_{\text{down}}^l < T_{\text{post}}(t) < \theta_{\text{down}}^h \\ 0 & \text{otherwise} \end{cases} \quad (6)$$

The weight update depends on the instantaneous values of $V_{\text{post_mem}}(t)$ and $T_{\text{post}}(t)$ at the arrival of a presynaptic spike. A change of the synaptic weight is triggered by the presynaptic spike if $V_{\text{post_mem}}(t)$ is above a threshold θ_V , provided that the postsynaptic trace $T_{\text{post}}(t)$ is between the potentiation thresholds θ_{up}^l and θ_{up}^h . An analogous but flipped mechanism induces a decrease in the weights.

The synaptic weight is restricted to the interval $0 \leq w \leq w_{\max}$. The bistability on the synaptic weight implies that the internal variable $w(t)$ drifts (and is bounded) to either a low state or a high state, depending on whether $w(t)$ is below or above a threshold θ_{w_B} respectively. This is shown in equation (7). The rule uses the thresholded version of the internal variable w as synaptic efficacy w_{eff} as described in equation (8)

$$\frac{dw}{dt} = \begin{cases} \alpha & \text{if } w > \theta_{w_B} \\ -\beta & \text{if } w \leq \theta_{w_B} \end{cases} \quad (7)$$

$$w_{\text{eff}} = \begin{cases} w_{\text{pot}} & \text{if } w > \theta_{w_B} \\ w_{\text{dep}} & \text{if } w \leq \theta_{w_B} \end{cases} \quad (8)$$

3.4. Clopath *et al* (2010): voltage-based STDP

The voltage-based STDP (V-STDP) rule has been introduced to unify several experimental observations, such as postsynaptic membrane voltage dependence, pre-post spike timing dependence and postsynaptic rate dependence [63], but also to explain the emergence of some connectivity patterns in the cerebral cortex [46]. In this model, depression and potentiation are two independent mechanisms whose sum produces the total synaptic change. Variables of the equations are described in table 5.

Depression is triggered by the arrival of a presynaptic spike and is induced if the voltage trace $\bar{V}_{-\text{post_mem}}(t)$ of the postsynaptic membrane voltage $V_{\text{post_mem}}(t)$ is above the threshold θ_- .

On the other hand, potentiation is continuous and occurs if the following conditions are met at the same time:

- The instantaneous postsynaptic membrane voltage $V_{\text{post_mem}}(t)$ is above the threshold θ_+ , with $\theta_+ > \theta_-$;
- The postsynaptic membrane voltage trace $\bar{V}_{+\text{post_mem}}(t)$ is above θ_- ;
- A presynaptic spike occurred a few milliseconds earlier and has left a trace $T_{\text{pre}}(t)$.

$$\frac{dw}{dt} = A_{\text{LTP}} T_{\text{pre}}(t) [V_{\text{post_mem}}(t) - \theta_+]_+ [\bar{V}_{+\text{post_mem}}(t) - \theta_-]_+ - A_{\text{LTD}} [\bar{V}_{-\text{post_mem}}(t) - \theta_-]_+ \sum_{\text{pre spikes } k} \delta(t - t_k). \quad (9)$$

The total synaptic change is the sum of depression and potentiation expressed in equation (9), within the hard bounds of the weights 0 and w_{\max} . It should be noted that all brackets of the equations ($[\cdot]_+$) are rectifying brackets, making the result ≥ 0 .

Table 6. Variables of the C-STDP rule.

Refactored	Unit	Description	Original
$w(t)$	1	Synaptic weight	ρ
$T_{p-p}(t)$	1	Pre- and postsynaptic spike trace (calcium) - integrative	$c(t)$
θ_+, θ_-	1	Thresholds on $T_{p-p}(t)$ for potentiation and depression	θ_p, θ_d
A_{LTP}, A_{LTD}	1	Amplitudes of synaptic potentiation and depression	γ_p, γ_d
A_{pre}, A_{post}	1	Amplitudes of pre- and postsynaptic calcium trace jumps	C_{pre}, C_{post}
τ	s	Time constant of synaptic efficacy changes	τ
θ_{w_B}	1	Bistability threshold	ρ_*
$N(t)$	1	Activity-dependent noise	Noise(t)
$\Theta(\cdot)$	1	Heaviside function: $\Theta(x) = 1$ if $x > 0$, $\Theta(x) = 0$ otherwise	$\Theta(\cdot)$

3.5. Graupner and Brunel (2012): C-STDP

Founded on molecular studies, Graupner and Brunel [45] proposed a plasticity model (C-STDP) based on a transient calcium signal. They model a single calcium trace variable $T_{p-p}(t)$ which represents the linear sum of individual calcium transients elicited by pre- and postsynaptic spikes. The amplitudes of the transients elicited by pre- and postsynaptic spikes are given by A_{pre} and A_{post} , respectively, and $T_{p-p}(t)$ decays constantly toward 0.

In the proposed model, the synaptic strength is described by the synaptic efficacy, for the sake of this review, we consider the synaptic efficacy as the actual synaptic weight $w(t) \in [0, 1]$. The weight update is continuous, according to equation (10), whose variables are described in table 6. Changes on the synaptic weight are continuous and depend on the relative times in which the calcium trace $T_{p-p}(t)$ is above the potentiation (θ_+) and depression (θ_-) thresholds [45]

$$\tau \frac{dw}{dt} = -w(1-w)(\theta_{w_B} - w) + A_{LTP}(1-w)\Theta(T_{p-p}(t) - \theta_+) - A_{LTD}w\Theta(T_{p-p}(t) - \theta_-) + N(t). \quad (10)$$

If the calcium variable is above the threshold for potentiation ($\Theta(T_{p-p}(t) - \theta_+) = 1$) the synaptic weight is continuously increased by $\tau dw/dt = A_{LTP}(1-w)$ and as long as the calcium variable is above the threshold for depression $\Theta(T_{p-p}(t) - \theta_-) = 1$ the synaptic weight is continuously decreased by $\tau dw/dt = -A_{LTD}w$. Eventually, the weight updates induced by the calcium concentration are in direct competition with each other as long as $T_{p-p}(t)$ is above both thresholds [45]. In addition to constant potentiation or depression updates, the bistability mechanism $\tau dw/dt = -w(1-w)(\theta_{w_B} - w)$ drives the synaptic weight toward 0 or 1, depending on whether the instantaneous value of $w(t)$ is below or above the bistability threshold θ_{w_B} . Graupner and Brunel [45] show that their rule replicates a plethora of dynamics found in numerous experiments, including pair-based STDP behavior with different STDP curves, synaptic dynamics found in CA3–CA1 slices for postsynaptic neuron spikes and dynamics based on spike triplets or quadruplets. However, the rule contains only a single calcium trace variable $T_{p-p}(t)$ per synapse, which is updated by both pre- and postsynaptic spikes. Since the synaptic weight update only depends on this variable and not on the individual or paired spike events of the pre- and postsynaptic neuron, the system can get into a state in which isolated presynaptic or isolated postsynaptic activity can lead to synaptic weight changes. In extreme cases, isolated pre(post)synaptic spikes could drive a highly depressed ($w(t) = 0$) synapse into the potentiated state ($w(t) = 1$), without the occurrence of any post(pre)synaptic action potential. In a recent work, Chindemi *et al* [7] use a modified version of the C-STDP rule based on data-constrained postsynaptic calcium dynamics according to experimental data. They show that the rule is able to replicate the connectivity of pyramidal cells in the neocortex, by adapting the probabilistic and limited release of calcium during pre- and postsynaptic activity.

3.6. Bekolay *et al* (2013): spiking Bienenstock Cooper Munro

The spiking Bienenstock Cooper Munro (SBCM) learning rule [64] has been proposed as another spike-based formulation of the Bienenstock Cooper Munro (BCM) learning rule [65], after the T-STDP rule. The weight update of the SBCM learning rule is continuous and is expressed in equation (11). The variables of this equation are described in table 7. Note that the modification threshold equation in table 7 has been reformulated, compared to the original version presented in [64], to account for the continuous-time nature of the rule

$$\frac{dw}{dt} = A A_{post} T_{pre}(t) T_{post}(t) (T_{post}(t) - \theta_T(t)). \quad (11)$$

Table 7. Variables of the SBCM rule.

Refactored	Unit	Description	Original
$w(t)$	a.u.	Synaptic weight	w_{ij}
$T_{\text{pre}}(t), T_{\text{post}}(t)$	1	Pre- and postsynaptic spike traces	a_i, a_j
$\theta_T(t)$	1	Modification threshold (filtered version of $T_{\text{post}}(t)$): $\tau_\theta \frac{d\theta_T}{dt} = -\theta_T + A_\theta T_{\text{post}}(t)$	$\theta(t)$
τ_θ	s	Time constant of modification threshold	τ
A	1	Learning rate	κ
A_θ	1	Scaling factor of the postsynaptic trace	
A_{post}	$[w] \cdot s^{-1}$	Scaling factor (gain) associated with the postsynaptic neuron	α_j

Table 8. Variables of the MPDP rule.

Refactored	Unit	Description	Original
$w(t)$	a.u.	Synaptic weight	w
$T_{\text{syn}}(t)$	1	Synaptic eligibility trace	Ψ
$T_{\text{pre}}(t)$	1	Sum of presynaptic spike responses	$\sum_{i=1}^{N_s} K(t - t_i)$
$\eta_{\text{post}}(t)$	1	Function of the postsynaptic membrane voltage	$F'(V(\tau))$
θ_+, θ_-	1	Thresholds for potentiation and depression	$\theta_{\text{pot}}, \theta_{\text{dep}}$
τ_{syn}	s	Decay time constant	T
A	$[w] \cdot s^{-1}$	Learning rate	

The properties of the SBCM rule are closer to the BCM rule [65], with the activities of the neurons expressed as spike activity traces and a filtered modification threshold. The modification threshold θ_T represents a moving average (expectation) of the postsynaptic spiking activity and activity higher than this average ($T_{\text{post}}(t) > \theta_T(t)$) results in potentiation, while activity lower than this average results in depression of the afferent synapses [64]. Nevertheless, the SBCM exhibits both the timing dependence of STDP and the frequency dependence of the T-STDP rule.

3.7. Yger and Harris (2013): MPDP

The MPDP rule, also called the ‘Convallis’ rule [66] aims to approximate the coincidence detector mechanism of the neocortex and is derived from principles of unsupervised learning algorithms. The main assumption of the rule is that feature extraction with non-Gaussian distributions is more likely to identify useful information in real-world patterns [67]. Therefore, synaptic changes should tend to increase the skewness of a neuron’s sub-threshold membrane potential distribution. The rule is therefore derived from an objective function that measures how non-Gaussian the membrane potential distribution is, such that the postsynaptic neuron is often close to either its resting potential or spiking threshold (and not in between).

The resulting plasticity rule reinforces synapses that are active during postsynaptic depolarization and weakens those active during hyper-polarization. It is expressed in equation (12), where changes are continuously made on an internal update trace $T_{\text{syn}}(t)$, and are then applied on the synaptic weight w as expressed in equation (13). The variables of the equations are explained in table 8. The rule was used for unsupervised learning of speech data, where an additional mechanism was implemented to maintain a constant average firing rate

$$\tau_{\text{syn}} \frac{dT_{\text{syn}}(t)}{dt} = -T_{\text{syn}} + \eta_{\text{post}}(t) T_{\text{pre}}(t) \quad (12)$$

$$\frac{dw}{dt} = \begin{cases} A(T_{\text{syn}}(t) - \theta_+) & \text{if } \theta_+ < T_{\text{syn}}(t) \\ 0 & \text{if } \theta_- < T_{\text{syn}}(t) \leq \theta_+ \\ A(T_{\text{syn}}(t) - \theta_-) & \text{if } T_{\text{syn}}(t) \leq \theta_- \end{cases} \quad (13)$$

3.8. Urbanczik and Senn (2014): dendritic prediction of somatic spiking

Urbanczik and Senn [68] proposed a new learning model based on the dendritic prediction of somatic spiking (DPSS), which aims to implement a biologically plausible non-Hebbian learning rule. In their rule, they rely on the presynaptic spike trace, the postsynaptic spike event and the postsynaptic dendritic voltage of a multi-compartment neuron model. Plasticity in dendritic synapses is the realization of a predictive coding scheme that matches the dendritic potential with the somatic potential.

The somatic potential $V_{\text{som}}(t)$ is influenced by both a scaled version of the dendritic compartment potential $V_{\text{den}}(t)$ and the teaching inputs from excitatory or inhibitory proximal synapses.

Table 9. Variables of the DPSS rule.

Refactored	Unit	Description	Original
$w(t)$	a.u.	Synaptic weight	w_i
A	$[w]$	Learning rate	η
$\eta(t)$	s^{-1}	Plasticity induction variable	$PI_i(t)$
$T_{pre}(t)$	1	Sum of presynaptic spike responses $PSP_i(t) = \sum_{s \in X_i^{dnd}} \kappa(t-s)$	$PSP_i(t)$
$V_{som}(t)$	V	Somatic potential	U
$V_{den}(t)$	V	Scaled dendritic potential	V_w^*
$\phi(V_{den})$	s^{-1}	(Sigmoidal) rate prediction function	$\phi(V_w^*)$
$f(V_{den})$	1	Positive weighting function $h(x) = d/dx \ln \phi(x)$	$h(V_w^*)$

In their proposed learning rule (see equation (14)), the aim is to minimize the error between the predicted somatic spiking activity based on the dendritic potential $\phi(V_{den}(t))$ and the real somatic spiking activity represented by back-propagated spikes $\sum_{\text{soma spikes } l} \delta(t - t_l)$. The equation's variables are described in table 9. The error $\sum_{\text{soma spikes } l} \delta(t - t_l) - \phi(V_{den}(t))$ is assigned to individual dendritic synapses based on their recent activation represented by $T_{pre}(t)$, similar to Yger and Harris [66] and Albers *et al* [29] and a positive weighting function $f(V_{den}(t))$

$$\tau \frac{d\eta}{dt} = -\eta + \left[\sum_{\text{soma spikes } l} \delta(t - t_l) - \phi(V_{den}(t)) \right] f(V_{den}(t)) T_{pre}(t). \quad (14)$$

Since the back-propagated spikes $\sum_{\text{soma spikes } l} \delta(t - t_l)$ are only 0 or 1, but the predicted rate $\phi(V_{den}(t))$ based on a sigmoidal function is never 0 or 1, $\eta(t)$ will never be 0. In this case, there is never a zero weight change [68]. The plasticity induction variable $\eta(t)$ is continuously updated and used as an intermediate variable before it is applied to induce a scaled persistent synaptic change, as expressed in equation (15)

$$\frac{dw}{dt} = A \eta(t). \quad (15)$$

Sacramento *et al* [69] showed later analytically that the DPSS learning rule combined with similar dendritic predictive plasticity mechanisms approximate the error BP algorithm, and demonstrated the capabilities of such a learning framework to solve regression and classification tasks.

3.9. Diehl and Cook (2015): rate dependent synaptic plasticity

Diehl and Cook [15] proposed the rate dependent synaptic plasticity (RDSP) rule as a local credit assignment mechanism for unsupervised learning in self-organizing spiking neural networks (SNNs). The idea is to potentiate or depress the synapses for which the presynaptic neuron activity was high or low at the moment of a postsynaptic spike, respectively. The RDSP weight change amplitude depends solely on the presynaptic information and it is triggered by postsynaptic spikes. The latter mechanism is instrumental for unsupervised competitive learning in winner-take-all (WTA) networks. The competition ensures that only the neurons already suited for representing the current input are active, and therefore can further tune the weights of their synapses by triggering weight updates with their spikes. The weight update is shown in equation (16), whose variables are described in table 10

$$\frac{dw}{dt} = A (T_{pre}(t) - \theta_{tar}) (w_{max} - w(t))^\mu \sum_{\text{post spikes } l} \delta(t - t_l). \quad (16)$$

u determines the weight dependence of the update for implementing a soft bound, while the target value of the presynaptic spike trace θ_{tar} is crucial in this learning rule because it acts as a threshold between depression and potentiation. If it is set to 0, then only potentiation is observed. It is hence important to set it to a non-zero value to ensure that presynaptic neurons that rarely lead to the firing of the postsynaptic neuron will become more and more disconnected. More generally, the higher the value of θ_{tar} value, the more depression occurs and the lower the synaptic weights will be [15].

This rule was first proposed as a more biologically plausible version of a previously proposed rule for memristive implementations by Querlioz *et al* [70]. The main difference between the two models is that the

Table 10. Variables of the RDSP rule.

Refactored	Original	Unit	Description
$w(t)$	w	a.u.	Synaptic weight
w_{\max}	w_{\max}	$[w]$	Maximum weight
μ	μ	1	Weight dependence - soft bound
$T_{\text{pre}}(t)$	x_{pre}	1	Presynaptic spike trace - integrative
θ_{tar}	x_{tar}	1	Target value of the presynaptic spike trace
A	η	$[w]^{1-\mu}$	Learning rate

Table 11. Variables of the H-MPDP rule.

Refactored	Unit	Description	Original
$w(t)$	a.u.	Synaptic weight	w_i
$T_{\text{pre}}(t)$	1	Presynaptic spike trace - integrative	$\sum_k \epsilon(t - t_i^k)$
$V_{\text{post}_{\text{mem}}}(t)$	V	Instantaneous membrane potential	$V(t)$
θ_+, θ_-	V	Thresholds for plasticity induction	ϑ_P, ϑ_D
A_-	1	Scaling factor for LTD/LTP	γ
A	$[w] \cdot V^{-1} \text{ s}^{-1}$	Learning rate	η

RDSP rule uses an exponential time dependence for the weight change which is more biologically plausible [71] than a time-independent weight change. This can also be more useful for pattern recognition depending on the temporal dynamics of the task to solve. A recent development by Paredes-Vallés *et al* [72] uses the presynaptic spike trace to generate two non-mutually exclusive processes LTP and LTD processes that are then linearly combined to update the synaptic weight. The authors show that this learning rule is inherently stable and can be used in hierarchical SNNs with a layer-wise training for feature extraction and local/global motion perception.

3.10. Albers *et al* (2016): H-MPDP

The H-MPDP learning rule proposed by Albers *et al* [29] is derived from an objective function similar to that of the membrane potential dependent plasticity (MPDP) rule but with opposite sign, as it aims to balance the membrane potential of the postsynaptic neuron between two fixed thresholds; the resting potential and the spiking threshold of the neuron. Hence, the MPDP and the H-MPDP implement a Hebbian or homeostatic mechanism, respectively. In addition, the H-MPDP differs from the other described models by inducing plasticity only to inhibitory synapses.

Albers *et al* [29] use a conductance based neuron and synapse model, similar to the C-MPDP and the DPSS rules. The continuous weight updates of the H-MPDP rule depend on the instantaneous membrane potential $V_{\text{post}_{\text{mem}}}(t)$ and the presynaptic spike trace $T_{\text{pre}}(t)$ as expressed in equation (17) whose variables are described in table 11

$$\frac{dw}{dt} = A \left(-A_- [V_{\text{post}_{\text{mem}}}(t) - \theta_-]_+ + [\theta_+ - V_{\text{post}_{\text{mem}}}(t)]_+ \right) T_{\text{pre}}(t). \quad (17)$$

The authors claim that their model is able to learn precise spike times by keeping a homeostatic membrane potential between two thresholds. This definition differs from the homeostatic spike rate definition of the C-MPDP rule by Sheik *et al* [43].

It should be noted that, as in the V-STDP rule [63], brackets of the equations $([\cdot]_+)$ are rectifying brackets, making the result ≥ 0 .

3.11. Sheik *et al* (2016): C-MPDP

The C-MPDP learning rule [43] was proposed with the explicit intention to have a local spike-timing based rule that would be sensitive to the order of spikes arriving at different synapses and that could be ported onto neuromorphic hardware.

Similarly to the DPSS rule, the C-MPDP rule uses a conductance-based neuron model. However, instead of relying on mean rates, it relies on the exact timing of the spikes. Furthermore, as for the H-MPDP rule, Sheik *et al* [43] propose to add a homeostatic element to the rule that targets a desired output firing rate. This learning rule is very hardware efficient because it depends only on the presynaptic spike time and not on the postsynaptic one. The equation that governs its behavior is equation (18). The weight update, triggered

Table 12. Variables of the C-MPDP rule.

Refactored	Unit	Description	Original
$w(t)$	a.u.	Synaptic weight	W
$T_{\text{post}}(t)$	1	Postsynaptic spike trace (calcium) - integrative	Ca
θ_{tar}	1	Calcium target concentration	Ca_t
$V_{\text{post_mem}}(t)$	V	Membrane potential	V_m
θ_V	V	Threshold on membrane potential	V_{th}
A_+, A_-, A_h	$[w]$	Magnitude of LTP/LTD/homeostasis	η_+, η_-, η_h

by the presynaptic spike, depends on a membrane voltage component (A_v) and on a homeostatic one ($A_h (\theta_{\text{tar}} - T_{\text{post}}(t))$). All equation variables are described in table 12

$$\frac{dw}{dt} = [A_v + A_h (\theta_{\text{tar}} - T_{\text{post}}(t))] \sum_{\substack{\text{pre spikes} \\ k}} \delta(t - t_k) \quad (18)$$

$$A_v = \begin{cases} A_+ & \text{if } V_{\text{post_mem}}(t) > \theta_V \\ A_- & \text{if } V_{\text{post_mem}}(t) \leq \theta_V \end{cases}. \quad (19)$$

The postsynaptic membrane voltage dependent weight update A_v depends on the values of the membrane voltage $V_{\text{post_mem}}(t)$ and an externally set threshold θ_V , which determines the switch between LTP and LTD. The homeostatic weight update $A_h (\theta_{\text{tar}} - T_{\text{post}}(t))$ is proportional to the difference in postsynaptic activity represented by the postsynaptic spike trace $T_{\text{post}}(t)$ and an externally set threshold θ_{tar} .

The authors show that this learning rule, using the spike timing together with conductance-based neurons, is able to learn spatio-temporal patterns in noisy data and differentiate between inputs that have the same 1st-moment statistics but different higher moment ones. Although they gear the rule toward neuromorphic hardware implementations, they do not propose circuits for the learning rule.

3.12. Payeur et al (2021): burst-dependent synaptic plasticity

The burst-dependent synaptic plasticity (BDSP) learning rule [44] has been proposed to enable spike-based local solutions to the credit assignment problem in hierarchical networks [6] for online learning. It aims to find a local mechanism so that neurons high up in a hierarchy can signal to other neurons, sometimes multiple synapses apart, whether to engage in LTP or LTD to improve behavior. The BDSP learning rule is formulated in equation (20) whose variables are described in table 13

$$\frac{dw}{dt} = A T_{\text{pre}}(t) \left[\sum_{\substack{\text{post burst} \\ \text{spikes } k}} \delta(t - t_k) - \frac{T_{\text{post_burst}}(t)}{T_{\text{post_event}}(t)} \sum_{\substack{\text{post event} \\ \text{spikes } l}} \delta(t - t_l) \right]. \quad (20)$$

Here, the authors introduce the notion of a burst which is defined as any occurrence of at least two spikes with an inter-spike interval which is less than 16 ms. Any additional spike within this time threshold belongs to the same burst. Then, they differentiate between two types of spiking events: single events or bursting events. Single events are isolated spikes and the two first spikes of a burst, while a bursting event is the second spike of a burst. Hence, LTP and LTD are triggered by a burst and an event, respectively. Since a burst is always preceded by an event, every potentiation is preceded by a depression. However, the potentiation through the burst is larger than the previous depression, which results in an overall potentiation.

The ratio between averaged postsynaptic burst and event traces ($T_{\text{post_burst}}(t)/T_{\text{post_event}}(t)$) regulates the relative strength of burst-triggered potentiation and event-triggered depression. It has been established that such a moving average exists in biological neurons [73]. The authors show that manipulating this ratio (i.e. the probability that an event becomes a burst) controls the occurrence of LTP and LTD, while changing the pre- and postsynaptic event rates simply modifies the rate of change of the weight while keeping the same transition point between LTP and LTD. Hence, the BDSP rule paired with the control of bursting provided by apical dendrites enables a form of top-down steering of synaptic plasticity in an online, local and spike-based manner.

Moreover, the authors show that this dendrite-dependent bursting combined with short-term plasticity supports multiplexing of feed-forward and feedback signals, which means that the feedback signals can steer plasticity without affecting the communication of bottom-up signals. Taken together, these observations

Table 13. Variables of the BDSP rule.

Refactored	Unit	Description	Original
$w(t)$	a.u.	Synaptic weight between pre- and postsynaptic neurons j and i	w_{ij}
A	$[w]$	Learning rate	η
$T_{\text{pre}}(t)$	1	Presynaptic spike trace	$\tilde{E}_j(t)$
$T_{\text{post}_{\text{burst}}}(t)$	1	Postsynaptic burst trace	$\tilde{B}_i(t)$
$T_{\text{post}_{\text{event}}}(t)$	1	Postsynaptic event trace	$\tilde{E}_i(t)$

show that combining the BDSP rule with short-term plasticity and apical dendrites can provide a local approximation of the credit assignment problem. In fact, the learning rule has been shown to implement an approximation of gradient descent for hierarchical circuits and achieve good performance on standard machine learning benchmarks.

4. Neuromorphic electronic circuits for implementing synaptic plasticity

Our comparison of plasticity models has highlighted many common functional primitives that are shared among the rules. These primitives can be grouped according to their function into the following blocks: integrator circuits, eligibility traces, and weight updates. These blocks can be readily implemented in CMOS technology, and they can be combined to implement different learning circuits. An overview of the proposed real-time CMOS learning circuits (as opposed to accelerated-time like in BrainScaleS [74]) that implement some of the models discussed is shown in table 15. To better link the CMOS implementations with the models presented, we named all the current and voltage variables of our circuits to match those in the original model equations.

The basic building blocks found required for building neuromorphic learning circuits can be grouped in four different families.

Eligibility trace blocks these are implemented using either a current-mode integrator circuit, such as the differential pair integrator (DPI), or other non-linear circuits that produce slowly decaying signals.

Input spikes can either increase the trace amplitude, decrease it, or completely reset it. The rate at which the trace decays back to its resting state can be typically modulated with externally controllable parameters. Circuit blocks implementing eligibility traces are highlighted in green in the schematics.

Comparator blocks they are typically implemented using WTA current mode circuits, or voltage mode transconductance or operational amplifiers. The comparator block changes its output based on which input is greater. Circuit blocks implementing comparators are highlighted in yellow in the schematics.

Weight update blocks they typically comprise a capacitor that stores a voltage related to the amplitude of the weight. The synaptic weight is thus emulated by the voltage across this capacitor in all the circuits that are presented in this section. Charging and discharging pathways connected to the capacitor enable potentiation and depression of the weight depending on the status of other signals.

These blocks are similar to the eligibility trace ones, except for the fact that they can produce both positive and negative changes. Circuit blocks implementing weight updates are highlighted in violet in the schematics.

Bistability blocks these are typically implemented using a transconductance amplifier (TA) connected in feedback operation which compares the weight voltage to a reference voltage.

Depending on the value of the weight voltage the bistability circuit will push the weight to the closest stable state. In its simplest form they have one single reference voltage, but they could be expanded to produce multiple stable states. Circuit blocks implementing bistability are highlighted in red in the schematics.

4.1. STDP

Following the formalization of the STDP model in 2000 (see equation (3)), many CMOS implementations have been proposed. Most implement the model as explained in section 3.1 [75, 77, 79, 80, 84]. However, some exploit the physics of single transistors to propose a floating gate implementation [82, 85, 86].

Indiveri *et al* [79] presented the implementation in figure 3. This circuit increases or decreases the analog voltage V_w across the capacitor C_w depending on the relative timing of the pulses *pre* and *post*. Upon arrival of a presynaptic pulse (*pre*), a waveform $V_{T_{\text{pre}}}$ is generated within the p-channel metal-oxide-semiconductor (pMOS) based trace block (see figure 3). $V_{T_{\text{pre}}}$ has a sharp onset and decays linearly with an adjustable slope set by $V_{\tau+}$. $V_{T_{\text{pre}}}$ serves to keep track of the most recent presynaptic spike. Analogously, when a postsynaptic

Table 14. Spike-based local synaptic plasticity rules: comparative table.

Plasticity rule	Local variables	Spikes interaction	Update trigger (spike)		Synaptic weights			Stop-learning
			LTD	LTP	Type	Bistability	Bounds	
STDP [42]	Pre- and postsynaptic spike traces	All spikes	Pre	Post	Analog	No	Hard	No
T-STDP [32]	Presynaptic spike trace + two postsynaptic spike traces (different time constants)	Nearest spike/all spikes	Pre	Post	Analog	No	Hard	No
SDSP [41]	Postsynaptic membrane voltage + postsynaptic spike trace	All spikes	Pre		Binary*	Yes	Hard	Yes ^a
V-STDP [46]	Presynaptic spike trace + postsynaptic membrane voltage + two postsynaptic membrane voltage traces	All spikes	Pre	Continuous	Analog	No	Hard	Yes ^b
C-STDP [45]	One synaptic spike trace updated by both pre- and postsynaptic spikes	All spikes	Continuous		Analog	Yes	Soft	Yes ^c
SBCM [64]	Pre- and postsynaptic spike traces	All spikes	Continuous		Analog	No	Hard	No
MPDP [66]	Presynaptic spike trace + postsynaptic membrane voltage	All spikes	Continuous		Analog	No	Hard	Yes ^d
DPSS [68]	Presynaptic spike trace + postsynaptic dendritic voltage + postsynaptic somatic spike	All spikes	Continuous		Analog	No	Hard	No
RDSP [15]	Presynaptic spike trace	All spikes	Post		Analog	No	Soft	No
H-MPDP [29]	Presynaptic spike trace + postsynaptic membrane voltage	All spikes	Continuous		Analog	No	Hard	Yes ^e
C-MPDP [43]	Postsynaptic membrane voltage + postsynaptic spike trace	All spikes	Pre		Analog	No	Hard	No
BDSP [44]	Presynaptic spike trace + postsynaptic event trace + postsynaptic burst trace	All spikes	Post (event)	Post (burst)	Analog	No	Hard	No

* Binary with analog internal variable.

^a At low and high activities of post-neuron (postsynaptic spike trace).^b At low postsynaptic membrane voltage trace.^c At low activity of pre- and post-neurons merged (synaptic spike trace).^d At medium (between two thresholds) internal update trace.^e At medium (between two thresholds) postsynaptic membrane voltage.

Table 15. Neuromorphic circuits for spike-based local synaptic plasticity models.

Rule	Paper	Difference with the model	Implementation
STDP [42]	Bofill-i-Petit <i>et al</i> [75] ^a	/	0.6 μm fabricated
	Indiveri [76]	Bistable weights	1.5 μm fabricated
	Bofill-i-Petit and Murray [77]	/	0.6 μm fabricated
	Cameron <i>et al</i> [78]	Anti-STDP + non-exponential spike trace	0.35 μm fabricated
	Indiveri <i>et al</i> [79]	Bistable weights	1.6 μm fabricated
	Arthur and Boahen [80] ^b	Binary weights	0.25 μm fabricated
	Koickal <i>et al</i> [81]	Soft bounds	0.6 μm fabricated
	Liu and Mockel [82]	Asymmetric bounds (soft lower bound + hard upper bound)	0.35 μm fabricated
	Tanaka <i>et al</i> [83]	/	0.25 μm fabricated
	Bamford <i>et al</i> [84]	/	0.35 μm fabricated
	Gopalakrishnan and Basu [85]	Asymmetric bounds (soft lower bound + hard upper bound)	0.35 μm fabricated
T-STDP [32]	Polidori <i>et al</i> [86]	/	0.15 μm fabricated
	Rachmuth <i>et al</i> [59]	Iono-neuromorphic model + NMDAR-mediated plasticity + digital storage of synaptic weights	1.5 μm fabricated
	Mayr <i>et al</i> [87]	/	Simulated
	Azghadi <i>et al</i> [88]	/	0.35 μm simulated
	Gopalakrishnan and Basu [89]	/	0.35 μm fabricated
SDSP [41]	Meng <i>et al</i> [90]	Iono-neuromorphic model	0.15 μm fabricated
	Fusi <i>et al</i> [91]	No postsynaptic spike trace + no stop-learning mechanism	1.2 μm fabricated
	Chicca and Fusi [92]	No postsynaptic spike trace + no stop-learning mechanism	0.6 μm fabricated
	Chicca <i>et al</i> [93]	No postsynaptic spike trace + no stop-learning mechanism	0.6 μm fabricated
	Giulioni <i>et al</i> [94]	Analog weights	0.35 μm fabricated
	Mitra <i>et al</i> [95]	Analog weights	0.35 μm fabricated
C-STDP [45]	Chicca <i>et al</i> [96]	Analog weights	0.35 μm fabricated
	Maldonado Huayaney <i>et al</i> [97]	Hard bounds	0.18 μm fabricated
RDSP [15]	Häfliger <i>et al</i> [98]	Nearest spike interaction + reset of presynaptic spike trace at post-spike + very small soft bounds	2 μm fabricated
	Ramakrishnan <i>et al</i> [99]	Nearest spike interaction + asymmetric bounds (soft lower bound + hard upper bound)	0.35 μm fabricated

^a Potentiation and depression triggers done with digital logic gates.

^b Weight storage in digital SRAM.

spike (*post*) occurs, $V_{T\text{post}}$ and V_{T-} create a trace of postsynaptic activity. By ensuring that $V_{T\text{pre}}$ and $V_{T\text{post}}$ remain below the threshold of the transistors they are connected to and the exponential current–voltage relation in the sub-threshold regime, the exponential relationship to the spike time difference Δt of the model is achieved. While V_{A+} and V_{A-} set the upper-bounds of the amount of current that can be injected or removed from C_w , the decaying traces $V_{T\text{pre}}$ and $V_{T\text{post}}$ determine the value of I_{A+} or I_{A-} and ultimately the weight increase or decrease on the capacitor C_w within the weight update block (see figure 3).

4.2. T-STDP

Similarly, as for the pair-based STDP, there are many implementations of the T-STDP rule. While some are successful in implementing the equations in the model [59, 87, 88, 90], others exploit the properties of floating gates [89].

Specifically, Mayr *et al* [87] as well as Rachmuth *et al* [59] and Meng *et al* [90] implement learning rules that model the conventional pair-based STDP together with the BCM rule. Azghadi *et al* [88] is the first, to our knowledge, to not only model the function but also model the equations presented in Pfister *et al* [100] (see equation (4)). Figure 4 shows the circuit proposed by Azghadi *et al* [88] in 2013 to model the T-STDP rule. It faithfully implements the equations by having independent circuits and biases, for the model

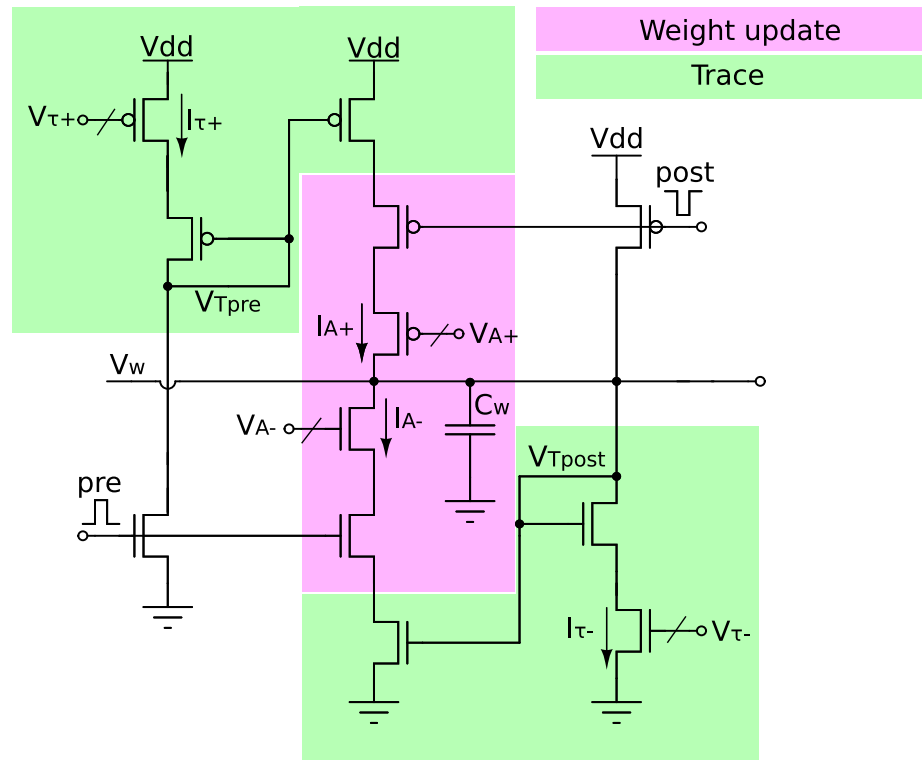


Figure 3. STDP circuit with highlighted the CMOS building blocks used: eligibility traces (in green) and weight updates (in violet). The voltage and current variables reflect the model equation. Adapted from [79].

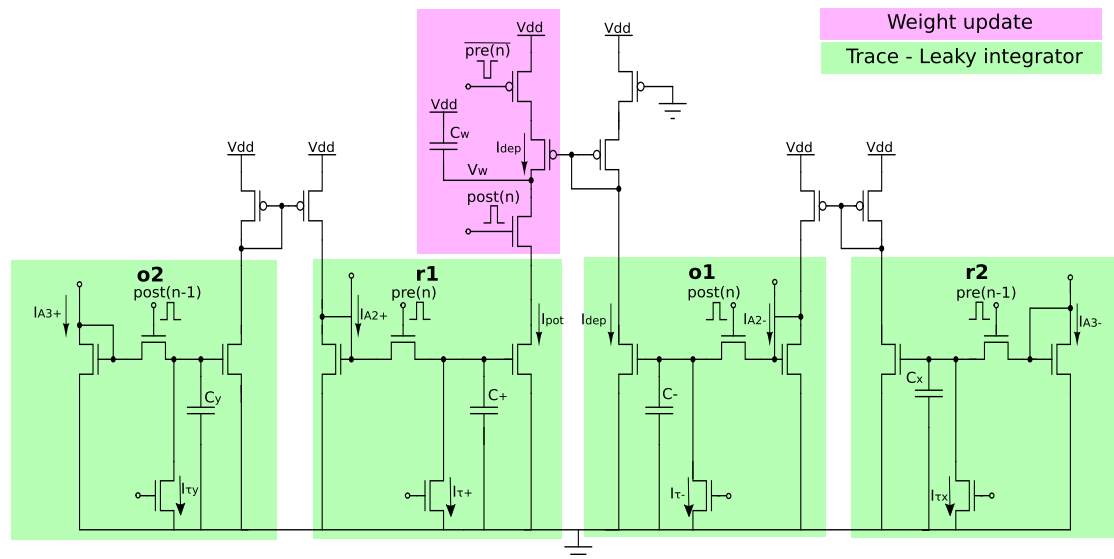
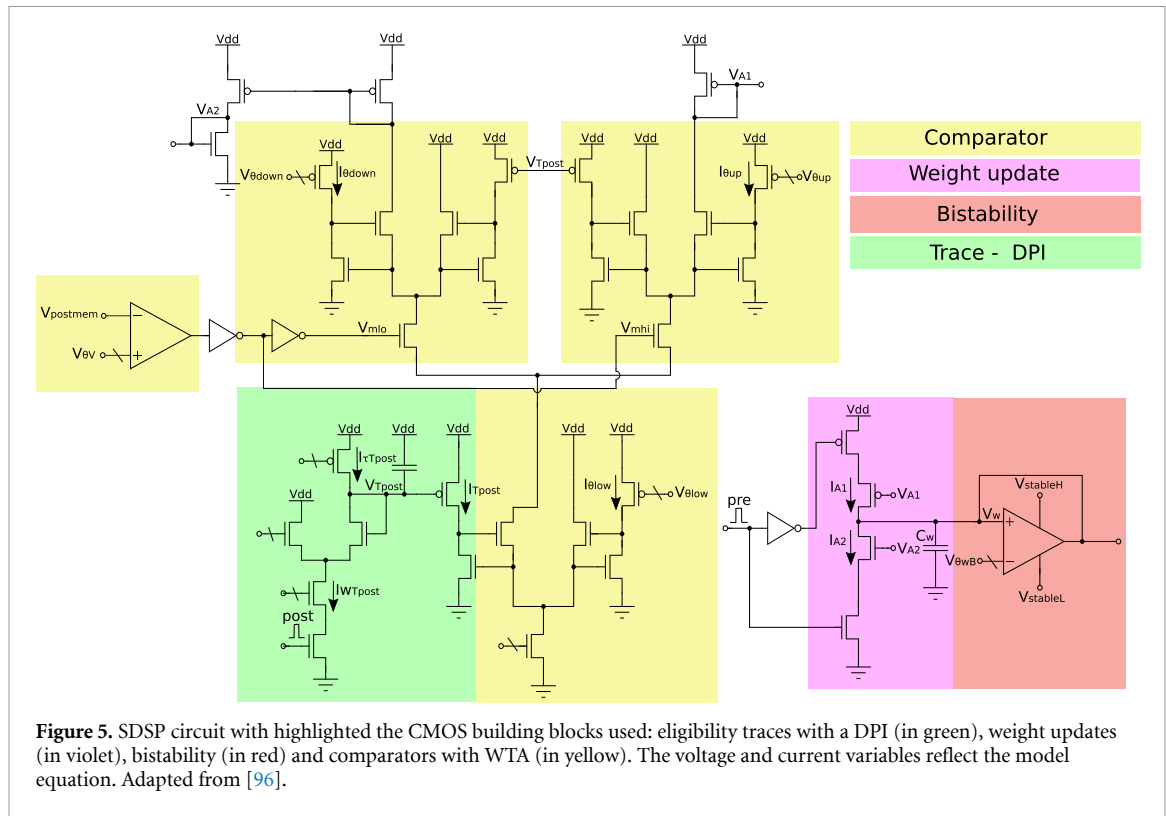


Figure 4. T-STDP circuit with highlighted CMOS building blocks used: eligibility traces with leaky integrators (in green) and weight updates (in violet). The voltage and current variables reflect the model equation. The r and o detectors of the model are also reported in this circuit figure. Adapted from [88].

parameters A_2^- , A_2^+ , A_3^- , and A_3^+ . These parameters correspond to spike-pairs or spike-triplets: post-pre, pre-post, pre-post-pre, and post-pre-post, respectively.

In this implementation, the voltage across the capacitor C_w determines the weight of the specific synapse. Here, a high potential of the voltage V_w indicates a low synaptic weight, resulting in a depressed synapse. In the same way, a low potential at this node resembles a strong synaptic weight, and in turn a potentiated synapse. The capacitor is charged and discharged by the two currents I_{pot} and I_{dep} respectively. These two



currents are gated by the most recent pre- and postsynaptic spikes through the transistors controlled by $\overline{pre(n)}$ and $post(n)$ within the weight update block (see figure 4)

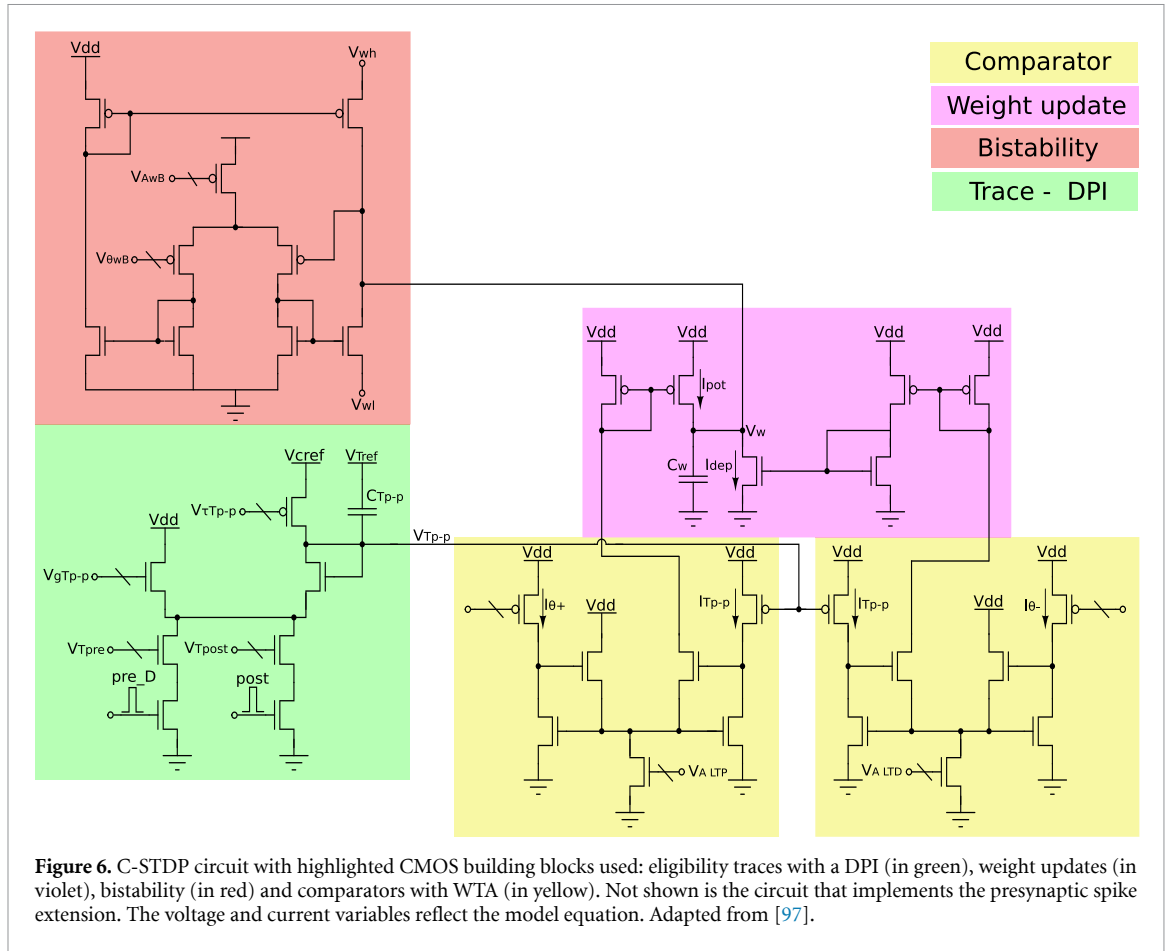
The amplitude of the depression current I_{dep} and the potentiation current I_{pot} is given by the recent spiking activity of the pre- and postsynaptic neurons. On the arrival of a presynaptic spike, the capacitors C_+ and C_x (in the trace - leaky integrator blocks r1 and r2 in figure 4) are charged by the currents I_{A2+} and I_{A3-} implementing the traces T_{pre_1} and T_{pre_2} of the model (see equation (4)). Analogously, the capacitors C_- and C_y (in the trace - leaky integrator blocks o1 and o2 in figure 4) are charged at the arrival of a postsynaptic spike by the currents I_{A2-} and I_{A3+} and implement the traces T_{post_1} and T_{post_2} of the model (see equation (4)). Here, both currents I_{A2+} and I_{A2-} depend on an externally set constant input current plus the currents generated by the o2 and r2 blocks, respectively. These additional blocks o2 and r2 activated by previous spiking activity, realize the triplet-sensitive behavior of the rule. All capacitors within the trace - leaky integrator blocks (C_+ , C_- , C_x , C_y) constantly discharge with individual rates given by $I_{\tau+}$, $I_{\tau-}$, $I_{\tau x}$, $I_{\tau y}$, respectively.

4.3. SDSP

The SDSP formalization by Brader *et al* [41] was preceded by several spike based learning rules designed in the theoretical frameworks of attractor neural network and mean field theory accompanied by several hardware implementations by Badoni *et al* [101], Fusi *et al* [91] and Chicca *et al* [93]. Following formalization by Brader *et al* [41] and with the desire of building smarter, larger and more autonomous networks, several implementations of the SDSP rule were proposed. The implementations by Chicca *et al* [93], Mitra *et al* [95], Giulioni *et al* [94] and Chicca *et al* [96] share similar building blocks: trace generators, comparators, circuits implementing the weight update and bistability mechanism. Here, we present the most complete design by Chicca *et al* [96], shown in figure 5, which replicates more closely the model equations (see equations (5) and (7)).

At each presynaptic spike pre , the weight update block (see figure 5) charges or discharges the capacitor C_w altering the voltage V_w depending on the values of V_{A1} and V_{A2} . Here, V_w represents the synaptic weight. If $I_{A1} > I_{A2}$, V_w increases, while in the opposite case V_w decreases. Moreover, over long time scales, in the absence of presynaptic spikes, V_w is slowly driven toward the bistable states $V_{stableH}$ or $V_{stableL}$ depending on whether V_w is higher or lower than V_{wB0} respectively (see bistability block in figure 5).

V_{A1} and V_{A2} are continuously calculated in the learning block, which compares the membrane potential of the neuron ($V_{postmem}$) to the threshold $V_{\theta V}$ and evaluates in which region the postsynaptic spike trace



V_{Tpost} lies. The neuron's membrane potential is compared to the threshold $V_{\theta V}$ by a transconductance amplifier. If $V_{postmem} > V_{\theta V}$, V_{mhi} is high and V_{mlo} is low, while if $V_{postmem} < V_{\theta V}$, V_{mhi} is low and V_{mlo} is high. At the same time, the postsynaptic neuron spikes (*post*) are integrated by a DPI to produce the postsynaptic spike trace V_{Tpost} (see trace - DPI block in figure 5), which is then compared with three thresholds by three WTA circuits (see comparator circuits in figure 5). In the lower comparator, I_{Tpost} is compared to $I_{\theta low}$ and if $I_{Tpost} < I_{\theta low}$ no learning conditions of the SDSP rule is satisfied and there is no weight update (assuming $\theta_{low} = \theta_{up}^l = \theta_{down}^l$ in the model equation (6)). For $I_{Tpost} > I_{\theta low}$, the two upper comparators set the signals V_{A1} and V_{A2} . If V_{mlo} is high and $I_{Tpost} < I_{\theta down}$, V_{A2} is increasing, setting the strength of the n-channel metal-oxide-semiconductor (nMOS) based pull-down branch in the weight update block. If V_{mhi} is high and $I_{Tpost} < I_{\theta up}$, V_{A1} is decreasing, setting the strength of the pMOS-based pull-up branch of the weight update block. These two branches in the weight update block are activated by the *pre* input spike.

4.4. C-STDP

The C-STDP rule proposed by Graupner and Brunel [45] (see equation (10)) attracted the attention of circuit designer thanks to its claim to closely replicate biological findings and explain synaptic plasticity in relation to both spike timing and rate. To implement the C-STDP rule, Maldonado Huayaney *et al* [97] adapted the original model by converting the soft bounds of the efficacy update to hard bounds (see equation (21)). The circuit is shown in figure 6. Specifically, they proposed to convert the soft bounds of the efficacy update to hard bounds, resulting in the following model for the update of the synaptic efficacy (adapted to our notation):

$$\tau \frac{dw}{dt} = -A_{wB} w (1 - w) (\theta_{wB} - w) + A_{LTP} \Theta(T_{p-p}(t) - \theta_+) - A_{LTD} w \Theta(T_{p-p}(t) - \theta_-) \quad (21)$$

$$w > 1 \rightarrow w = 1$$

$$w < 0 \rightarrow w = 0.$$

Here A_{wB} is acting as a constant which scales the bistability dynamics and the hard-bounds implemented by the Heaviside function Θ . The building blocks implemented in this work are shown in figure 6. The trace block implements the local spike trace T_{p-p} represented by the voltage V_{Tp-p} . It consists of a DPI with two input branches. On the arrival of either a postsynaptic spike (*post*) or the delayed presynaptic spike (*pre_D*) the capacitor C_{Tp-p} is charged by a current defined by the gain of the DPI (V_{gTp-p}) and V_{Tpost} or V_{Tpre} , respectively. Charging the capacitor decreases the voltage V_{Tp-p} . In the absence of input pulses, the capacitor discharges at a rate controlled by $V_{\tau Tp-p}$ toward its resting voltage V_{Tref} . The voltage V_{Tp-p} of the trace block sets the amplitude of the current I_{Tp-p} within the comparator blocks (see figure 6). The current I_{Tp-p} is compared with the potentiation and depression thresholds defined by the currents $I_{\theta+}$ and $I_{\theta-}$, respectively. The WTA functionality of the comparator circuits implements the Heaviside functionality of the comparison of the local spike trace T_{p-p} with the thresholds for potentiation (θ_+) and depression (θ_-) in the model (see equation (21)).

While the current I_{Tp-p} is greater than the potentiation threshold current $I_{\theta+}$, the synapse efficacy capacitor C_w within the weight update block (see figure 6) is continuously charged by a current defined by the parameter $V_{A_{LTP}}$. Similarly, as long as I_{Tp-p} is greater than the depression threshold current $I_{\theta-}$, C_w is constantly discharged with a current controlled by $V_{A_{LTD}}$. The voltage across the synapse capacitor V_w resembles the efficacy w of the synapse. To implement the bistability behavior of the synaptic efficacy, Maldonado Huayaney *et al* [97] use an TA in positive feedback configuration with a very small gain defined by $V_{A_{wB}}$ (see figure 6). As long as the synaptic efficacy voltage V_w is above the bistability threshold $V_{\theta_{wB}}$ the positive feedback constantly charges the capacitor C_w and drives V_w toward the upper limit defined by V_{wh} . In the case that V_w is below $V_{\theta_{wB}}$, the TA discharges the capacitor and drives V_w toward the lower limit defined by V_{wl} .

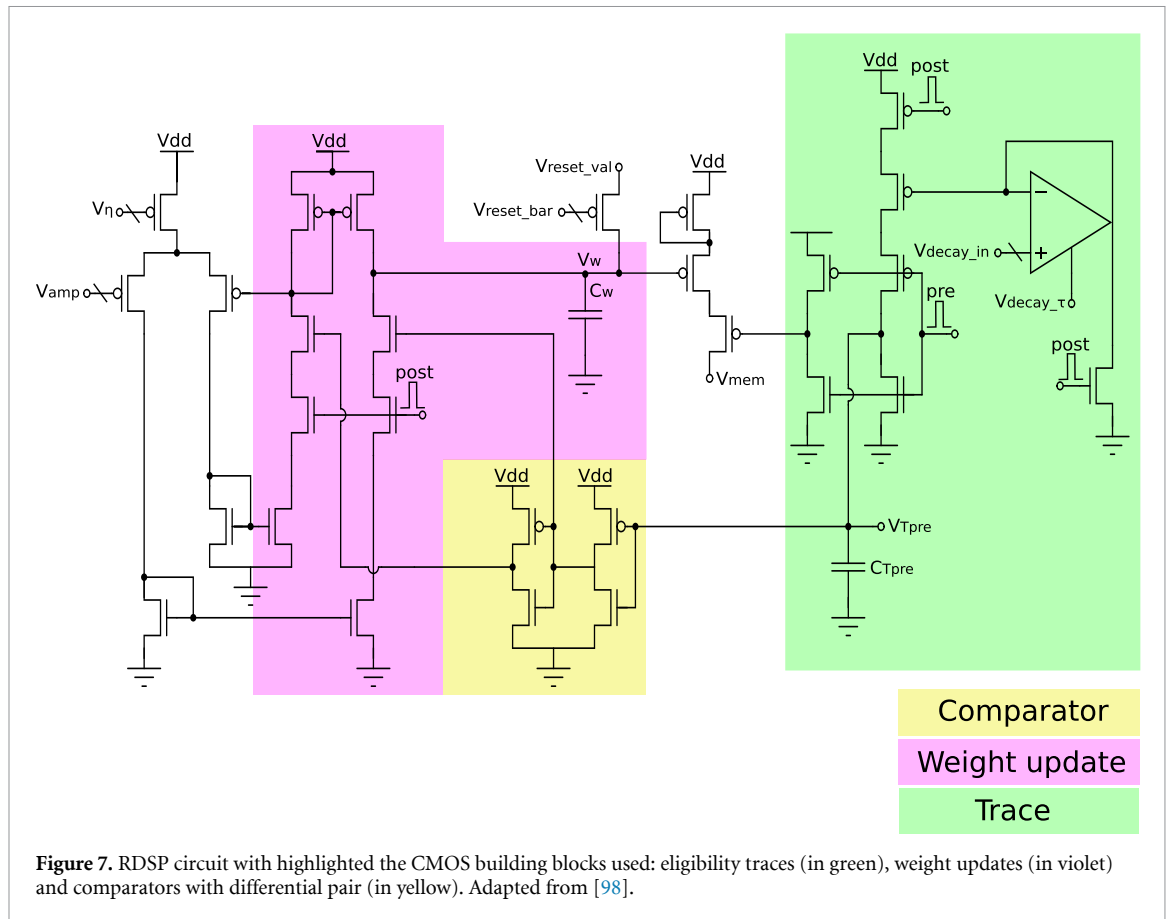
4.5. RDSP

The first CMOS implementation of a spike-based learning rule done by Häfliger *et al* [98] pre-dates the formalization of the RDSP model, which happened almost 20 years later [15]. It is one of the most obvious cases of how building electronic circuits that mimic biological behavior leads to the discovery of useful mechanisms to solve real-world problems.

The algorithmic definition of their learning rule is based on a correlation signal, local to each synapse, which keeps track of the presynaptic spike activity. The correlation signal is refreshed at each presynaptic event and decays over time. When a post-signal arrives, depending on the value of the correlation, the weight is either increased or decreased, while the correlation signal is reset. Similarly, the RDSP rule relies on the presynaptic spike time information and is triggered when a post synaptic spike arrives. The direction of weight update depends on a target value θ_{tar} , which determines the threshold between depression and potentiation.

The two main differences between the circuit by Häfliger *et al* [98] (see figure 7) and the RDSP rule (see equation (16)) is that the correlation signal in Häfliger *et al* [98] is binary and is compared to a fixed threshold voltage (the switching threshold of the first inverter), which resembles a fixed θ_{tar} . In the Häfliger *et al* [98] implementation, the voltage V_w across the capacitor C_w represents the synaptic weight and the voltage V_{Tpre} at the capacitor C_{Tpre} represents the correlation signal. At the arrival of a presynaptic input spike (*pre*), the voltage V_w determines the amplitude of the current toward the soma (V_{mem}) of the postsynaptic neuron. At the same time, the capacitor C_{Tpre} is fully discharged and V_{Tpre} is low. In the absence of presynaptic and postsynaptic spikes (*pre* and *post* are low), C_{Tpre} is slowly charged toward V_{dd} by the pMOS branch in the trace block (see figure 7).

The voltage V_{Tpre} is constantly compared to the threshold voltage (resembling θ_{tar}) of the first inverter it is connected to. At the arrival of a postsynaptic spike (*post* is high) the weight capacitor C_w is either charged (depressed) or discharged (potentiated) depending on the momentary level of V_{Tpre} . If V_{Tpre} is above the inverter threshold voltage, the right branch of the weight update block (see figure 7) is inactive, while the left branch is active and the pMOS-based current mirror charges the capacitor C_w . In the opposite case, where V_{Tpre} is below the inverter threshold voltage, the right branch is active while the output of the second inverter disables the left branch of the weight update block. This results in a discharge of the capacitor C_w controlled by the nMOS-based current mirror. The amplitude for potentiation and depression is set by the two biases V_{η} and V_{amp} . At the end of a postsynaptic spike the correlation signal V_{Tpre} is reset to V_{dd} . A similar approach implementing a nearest-spike interaction scheme and a fixed θ_{tar} was implemented by Ramakrishnan *et al* [99] exploiting the properties of floating gates.



4.6. Additional models

In this work we covered a large fraction of (if not all) the spike-based learning models implemented using analog neuromorphic electronic circuits presented in the literature to date. The overview and comparison of the theoretical models should therefore enable the implementation of additional models using the principles and circuits presented. For example, novel models that require to keep track of pre- or postsynaptic spiking activity for extended periods of time could make use of circuits such as those described for the SDSP and C-STDP models. Models that require both postsynaptic traces (for potentiation and depression) and a presynaptic trace (for potentiation) could employ the circuits used to describe the V-STDP rule. In general, slowly decaying traces can be implemented with the DPI block present in many of the learning circuits described. To compare signals (e.g. to determine the sign of an error signal), one could use the WTA current mode circuit, used in the SDSP model. To increase or decrease synaptic weight values, one could use the weight update block presented in figure 3, which makes use of a capacitor. To store the value of the learned weight, one would need to digitize and memorize the voltage across the weight capacitance (e.g. using four bits, which have been shown to be sufficient for a wide variety of problems [102]).

Therefore, to implement local spike-based learning models not covered in this survey, one could re-use many of the circuits presented here. However, additional innovation and design efforts might be required for more elaborate learning rules. For instance, the DPSS learning rule requires a multi-compartment neuron circuit, while the H-MPDP and C-MPDP rules require conductance-based neuron and synapse circuits. Similarly, although the V-STDP rule [46, 63] shares similarities with the T-STDP one, and the main building blocks introduced in the previous section can be used to implement it with analog CMOS neuromorphic circuits, its complexity comes from its multiple transient signals on different timescales. To this end, emerging novel technologies, such as memristors [103–107] and neuristors [108] offer promising solutions to implement different timescales in a compact and efficient manner. Also implementations for the DPSS rule [68] are difficult to implement due to the increased complexity of the required multi-compartment neuron models. Recently, implementations based on hybrid memristor–CMOS systems [109, 110] or using existing neuromorphic processors to exploit neuron structures to replicate the multi-compartment model [111, 112] have been proposed.

5. Discussion and conclusion

5.1. Toward a unified synaptic plasticity framework

In this survey, we highlighted the similarities and differences of representative models of synaptic plasticity and provided examples of neuromorphic CMOS circuits that can be used to implement their principles of computation. We highlighted how the principle of locality in learning and neural computation in general is essential and enables the development of fast, efficient and scalable neuromorphic processing systems. We highlighted how the different features of the plasticity models can be summarized in (1) synaptic weights properties, (2) plasticity update triggers and (3) local variables that can be exploited to modify the synaptic weight (see also table 14). Although all local variables of these rules are similar in nature, the plasticity rules can be subdivided as follows:

- Presynaptic spike trace: RDSP.
- Pre- and postsynaptic spike traces: STDP, T-STDP, C-STDP, SBCM, BDSP.
- Presynaptic spike trace + postsynaptic membrane voltage: V-STDP, DPSS, MPDP, H-MPDP.
- Postsynaptic membrane voltage + postsynaptic spike trace: SDSP, C-MPDP.

Many possibilities arise when exploring how the local variables used by these rules interact (e.g. comparison, addition, multiplication, etc). The heterogeneity of the rules reviewed in this work arises by the dual nature of bottom-up approaches (e.g. driven by biological experiments to assess the spike-time or spike-frequency dependence in learning) and top-down approaches driven by theoretical requirements for solving specific problems (e.g. local approximation of the credit assignment problem in BDSP).

It is difficult to predict whether a unified rule of synaptic plasticity can be formulated, based on the observation that several plasticity mechanisms coexist in the brain [5], and that different problems may require different plasticity mechanisms. However, we provided here a single unified framework that allowed us to systematically overview the features of many representative models of synaptic plasticity developed following experiment-driven bottom-up approaches and/or application-driven top-down approaches [113].

5.2. Overcoming BP limits for online learning

Local synaptic plasticity in neuromorphic circuits offers a promising solution for online learning in embedded systems. However, due to the very local nature of this approach, there is no direct way of implementing global learning rules in multi-layer neural networks, such as the gradient-based BP algorithm [114, 115]. This algorithm has been the work horse of artificial neural networks training in deep learning over the last decade. Gradient-based learning has recently been applied for offline training of SNNs, where the BP algorithm coupled with surrogate gradients is used to solve two critical problems: first, the temporal credit assignment problem which arises due to the temporal inter-dependencies of the SNN activity. It is solved offline with BP through time (BPTT) by unrolling the SNN like standard recurrent neural networks [13]. Second, the spatial credit assignment problem, where the credit or 'blame' with respect to the objective function is assigned to each neuron across the layers. However, BPTT is not biologically plausible [116, 117] and not practical for on-chip and online learning due to the non-local learning paradigm. On one hand, BPTT is not local in time as it requires keeping all the network activities for the duration of the trial. On the other hand, BPTT is not local in space as it requires information to be transferred across multiple layers. Indeed, synaptic weights can only be updated after complete forward propagation, loss evaluation, and BP of error signals, which lead to the so-called 'locking effect' [118]. Furthermore, software implementations of BP and of spike-based learning rules in general, often use learning-rate optimizers such as Adam [119], which requires additional synaptic traces and memory resources which would significantly increase the hardware cost of the plasticity circuits.

Recently, intensive research in neuromorphic computing has been dedicated to bridge the gap between BP and local synaptic plasticity rules [12, 120] by reducing the non-local information requirements, at a cost of accuracy in complex problems [12]. Relaxing BP constraints for neuromorphic hardware often results in three-factor learning rules, where the temporal credit assignment can be handled using eligibility traces [121, 122] that can, for example, solve the distal reward problem by bridging the delay between the network output and the feedback signal that may arrive later in time [123]. Similarly, inspired by recent progress in deep learning, several strategies have been explored to solve the spatial credit assignment problem in three-factor learning rules using feedback alignment [124], direct feedback alignment [125, 126], random error BP [127] or by replacing the backward pass with an additional forward pass whose input is modulated with error information [128–130]. However, these approaches only partially solve the problem [12], since they still suffer from the locking effect, which can nevertheless be tackled by replacing the global loss by a number of

local loss functions [13, 131–133] or by using direct random target projection [113, 134]. The assignment of credit locally, especially within recurrent SNNs, is still an open question and an active field of research [135].

The local synaptic plasticity models and circuits presented in this survey do not require the presence of a teacher signal in the form of a third factor and contrast with supervised learning using labeled data which is neither biologically plausible [133] nor practical in most online scenarios [136]. Nevertheless, the main limit of spike-based local learning is the diminished performance on complex pattern recognition problems. Different approaches have been explored to bridge this gap, for example using multi-compartment neurons to approximate BP with local mechanisms as in the DPSS [68, 69] and BDSP [44] learning rules, developing global gradient-based approaches to train offline the local plasticity mechanisms that will be used online [137–140], or exploring multimodal association to improve the self-organizing system's performance [20, 21, 141] since in contrast to labeled data, multiple sensory modalities (e.g. sight, sound, touch) are freely available in the real-world environment.

5.3. Challenges of three-factor local plasticity

In three-factor learning rules, in addition to depending on state-variables present at the pre- and postsynaptic terminals, the weight update depends also on a third signal, which can come from a phasic increase of neuromodulators such as dopamine and serotonin, or from an additional spiking input [26]. From a top-down approach, these types of learning rules have been used to approximate the BP learning algorithm, and have been used to solve practical real-world problems with very promising results (e.g. see the e-prop rule [122], the deep continuous local learning (DECOLLE) rule [132], or the event-based three-factor local plasticity (ETLP) rule [134]). From a bottom-up approach, these types of rules can be implemented using biologically plausible mechanisms and signals in neuromorphic hardware. However the extra flexibility and computational power offered by these rules comes at a cost of additional resources. For example, many of these rules require additional synaptic traces or eligibility traces with very long decay rates (e.g. at behavioral time scales of seconds to minutes). This would require circuits with very long time constants at each synapse, achievable with either very large capacitors or very large resistors or both. This would in turn require large area overhead (e.g. in case of large capacitors for each synapse), or large power consumption (e.g. in case of having to operate circuits with very large impedance values). In addition, the signals that represent the third factor are typically non-local, and require dedicated means of transmission (e.g. via broadcast routing schemes, or global bias values that need to be modulated hardwired in need to be broadcast to large populations). These limitations and challenges need to be addressed both at the algorithmic level and at the hardware level, following a tightly integrated co-design approach, that has only been used in rare cases so far [113].

5.4. Structural plasticity and network topology

Exploring local synaptic plasticity rules could provide valuable information on how plasticity results in learning and memory in the brain. However, in bringing the plasticity of single synapses to the function of entire networks, many more factors come into play. Functionality at a network level is determined by the interplay between the synaptic learning rules, the spatial location of the synapse, and the neural network topology. Furthermore, the brain network topology is itself plastic [142]. Le Bé and Markram [143] provided the first direct demonstration of induced rewiring (i.e. sprouting and pruning) of a functional circuit in the neocortex [144], which requires hours of general stimulation. Some studies suggest that glutamate release is a key determinant in synapse formation [145, 146], but additional investigations are needed to better understand the computational foundations of structural plasticity and how it is linked to the synaptic plasticity models we reviewed in this survey. Together, structural and synaptic plasticity are the local mechanisms that lead to the emergence of the global structure and function of the brain. Understanding, modeling, and implementing the interplay between these two forms of plasticity is a key challenge for the design of self-organizing systems that can come closer to the unique efficiency and adaptation capabilities of the brain.

5.5. CMOS neuromorphic circuits

The computational primitives that are shared by the different plasticity models were grouped together in corresponding functional primitives and circuit blocks that can be combined to map multiple plasticity models into corresponding spike-based learning circuits. Many of the models considered rely on exponentially decaying traces. By operating the CMOS circuits in the sub-threshold regime, this exponential dependency is given by the physical substrate of transistors showing an exponential relationship between current and voltage [10, 147].

The circuits presented make use of both analog computation (e.g. analog weight updates) and digital communication (e.g. pre- and postsynaptic spike events). This mixed-signal analog/digital approach aligns

with the observations that biological neural systems can be considered as hybrid analog and digital processing systems [148]. Due to the digital nature of spike transmission in these neuromorphic systems, plasticity circuits that require the use of presynaptic traces need extra overhead to generate this information directly at the postsynaptic side. The emergence of novel nanoscale memristive devices has high potential for allowing the implementation of such circuits at a low overhead cost, in terms of space and power [149]. In addition, these emerging memory technologies have the potential of allowing long-term storage of the synaptic weights in a non-volatile way, that would allow these neuromorphic systems to operate continuously, without having to upload the neural network parameters at boot time. This will be a significant advantage in large-scale systems, as input/output operations required to load network parameters can take a significant amount of power and time. In addition, the properties of emerging memristive devices could be exploited to implement different features of the plasticity models proposed [107].

Overall, the number of proposed CMOS-based analog or mixed-signal neuromorphic circuits over the past 25 years was mainly driven by fundamental academic research taking place in a handful of laboratories. However, with the increasing need for low-power neural processing systems at the edge, the increasing maturity of novel technologies, and the rising interest in brain-inspired neural networks and learning for data processing, we can expect an increasing number of new mixed signal analog/digital circuits implementing new plasticity rules also for commercial exploitation. In this sense, this review can provide valuable information to make informed decisions about circuit design and modeling in developing novel spike-based neuromorphic processing systems for online learning.

Data availability statement

No new data were created or analyzed in this study.

Acknowledgments

We would like to thank the BICS group at the University of Groningen, and the NCS group at the Institute of Neuroinformatics of the University of Zurich and ETH Zurich for fruitful discussions. We would also like to thank Hugh Grotto, Maxime Fabre, Jannes Jegminat, Samuel R Schmidgall, Ali Safa, Sebastian Schmitt, Adam Kohan and Carver Mead for providing valuable feedback on the first revisions of the manuscript, Madison Cotteret for the helpful comments on the equations details and Michele Mastella and Wouter Serdijn for the fruitful discussions on circuit details. We want to acknowledge the financial support of the CogniGron research center and the Ubbo Emmius Funds (University of Groningen), the European Union's H2020 research and innovation programme under the H2020 'BeFerroSynaptic' Project (No. 871737), the MSCA ITN 'MANIC' Project (No. 861153), the EU ERC 'NeuroAgents' Project (No. 724295), the Swiss National Science Foundation 'Sinergia' Project (CRSII5-18O316).

ORCID iDs

Lyes Khacef  <https://orcid.org/0000-0002-4009-174X>
Philipp Klein  <https://orcid.org/0000-0003-4266-2590>
Matteo Cartiglia  <https://orcid.org/0000-0001-8936-6727>
Arianna Rubino  <https://orcid.org/0000-0002-5036-1969>
Giacomo Indiveri  <https://orcid.org/0000-0002-7109-1689>
Elisabetta Chicca  <https://orcid.org/0000-0002-5518-8990>

References

- [1] McNaughton B L, Douglas R M and Goddard G V 1978 Synaptic enhancement in fascia dentata: cooperativity among coactive afferents *Brain Res.* **157** 277–93
- [2] Gerstner W, Ritz R and van Hemmen J L 1993 Why spikes? Hebbian learning and retrieval of time-resolved excitation patterns *Biol. Cybern.* **69** 503–15
- [3] Stuart G and Sakmann B 1994 Active propagation of somatic action potentials into neocortical pyramidal cell dendrites *Nature* **367** 69–72
- [4] Fusi S 2002 Hebbian spike-driven synaptic plasticity for learning patterns of mean firing rates *Biol. Cybern.* **87** 459–70
- [5] Caporale N and Dan Y 2008 Spike timing-dependent plasticity: a Hebbian learning rule *Annu. Rev. Neurosci.* **31** 25–46
- [6] Zenke F and Nefzger E O 2021 Brain-inspired learning on neuromorphic substrates *Proc. IEEE* **109** 935–50
- [7] Chindemi G et al 2022 A calcium-based plasticity model for predicting long-term potentiation and depression in the neocortex *Nat. Commun.* **13** 1–19
- [8] Jegminat J, Surace S C, Pfister J-P and Richards B A 2022 Learning as filtering: implications for spike-based plasticity *PLoS Comput. Biol.* **18** 1–23
- [9] Varela F J, Rosch E and Thompson E 1991 *The Embodied Mind: Cognitive Science and Human Experience* (MIT Press)

- [10] Mead C 1990 Neuromorphic electronic systems *Proc. IEEE* **78** 1629–36
- [11] Hofman M A 2015 *Evolution of the Human Brain: From Matter to Mind* (Springer) pp 65–82
- [12] Eshraghian J K, Ward M, Neftci E, Wang X, Lenz G, Dwivedi G, Bennamoun M, Jeong D S and Lu W D 2021 Training spiking neural networks using lessons from deep learning (arXiv:2109.12894)
- [13] Neftci E O, Mostafa H and Zenke F 2019 Surrogate gradient learning in spiking neural networks: bringing the power of gradient-based optimization to spiking neural networks *IEEE Signal Process. Mag.* **36** 51–63
- [14] Bichler O, Querlioz D, Thorpe S J, Bourgoin J-P and Gamrat C 2012 Extraction of temporally correlated features from dynamic vision sensors with spike-timing-dependent plasticity *Neural Netw.* **32** 339–48
- [15] Diehl P and Cook M 2015 Unsupervised learning of digit recognition using spike-timing-dependent plasticity *Front. Comput. Neurosci.* **9** 99
- [16] Iyer L R and Basu A 2017 Unsupervised learning of event-based image recordings using spike-timing-dependent plasticity 2017 *Int. Joint Conf. on Neural Networks (IJCNN)* pp 1840–6
- [17] Hazan H, Saunders D, Sanghavi D T, Siegelmann H and Kozma R 2018 Unsupervised learning with self-organizing spiking neural networks 2018 *Int. Joint Conf. on Neural Networks (IJCNN)* pp 1–6
- [18] Kheradpisheh S R, Ganjtabesh M, Thorpe S J and Masquelier T 2018 STDP-based spiking deep convolutional neural networks for object recognition *Neural Netw.* **99** 56–67
- [19] Khacef L, Rodriguez L and Miramond B 2020 Improving self-organizing maps with unsupervised feature extraction *Int. Conf. on Neural Information Processing* vol 12533 (Springer) pp 474–86
- [20] Khacef L, Rodriguez L and Miramond B 2020 Brain-inspired self-organization with cellular neuromorphic computing for multimodal unsupervised learning *Electronics* **9** 1605
- [21] Rath N and Roy K 2021 STDP based unsupervised multimodal learning with cross-modal processing in spiking neural networks *IEEE Trans. Emerg. Top. Comput. Intell.* **5** 143–53
- [22] DeWolf T, Jaworski P and Eliasmith C 2020 Nengo and low-power AI hardware for robust, embedded neurorobotics *Front. Neurobot.* **14** 73
- [23] Lalle S and Dominey P F 2013 Multi-modal convergence maps: from body schema and self-representation to mental imagery *Adapt. Behav.* **21** 274–85
- [24] Zahra O and Navarro-Alarcon D 2019 A self-organizing network with varying density structure for characterizing sensorimotor transformations in robotic systems *Towards Autonomous Robotic Systems* (Springer) pp 167–78
- [25] Kuśmierz L, Isomura T and Toyozumi T 2017 Learning with three factors: modulating Hebbian plasticity with errors *Curr. Opin. Neurobiol.* **46** 170–7
- [26] Gerstner W, Lehmann M, Liakoni V, Corneil D and Brea J 2018 Eligibility traces and plasticity on behavioral time scales: experimental support of neoHebbian three-factor learning rules *Front. Neural Circuits* **12** 53
- [27] Renart A, Song P and Wang X-J 2003 Robust spatial working memory through homeostatic synaptic scaling in heterogeneous cortical networks *Neuron* **38** 473–85
- [28] Lazar A, Pipa G and Triesch J 2009 SORN: a self-organizing recurrent neural network *Front. Comput. Neurosci.* **3** 23
- [29] Albers C, Westkott M and Pawelzik K 2016 Learning of precise spike times with homeostatic membrane potential dependent synaptic plasticity *PLoS One* **11** 1–28
- [30] Keck T et al 2017 Integrating Hebbian and homeostatic plasticity: the current state of the field and future research directions *Phil. Trans. R. Soc. B* **372** 1–9
- [31] Qiao N, Bartolozzi C and Indiveri G 2017 An ultralow leakage synaptic scaling homeostatic plasticity circuit with configurable time scales up to 100 ks *IEEE Trans. Biomed. Circuits Syst.* **11** 1271–7
- [32] Pfister J-P and Gerstner W 2006 Triplets of spikes in a model of spike timing-dependent plasticity *J. Neurosci.* **26** 9673–82
- [33] Graupner M and Brunel N 2010 Mechanisms of induction and maintenance of spike-timing dependent plasticity in biophysical synapse models *Front. Comput. Neurosci.* **4** 1–19
- [34] Karmarkar U R and Buonomano D V 2002 A model of spike-timing dependent plasticity: one or two coincidence detectors? *J. Neurophysiol.* **88** 507–13
- [35] Senn W, Markram H and Tsodyks M 2001 An algorithm for modifying neurotransmitter release probability based on pre- and postsynaptic spike timing *Neural Comput.* **13** 35–67
- [36] Shouval H Z, Bear M F and Cooper L N 2002 A unified model of NMDA receptor-dependent bidirectional synaptic plasticity *Proc. Natl Acad. Sci.* **99** 10831–6
- [37] Gerstner W and Kistler W 2002 *Spiking Neuron Models: Single Neurons, Populations, Plasticity* (Cambridge University Press) (<https://doi.org/10.1017/CBO9780511815706>)
- [38] Sterratt D, Graham B, Gillies A and Willshaw D 2011 *Principles of Computational Modeling in Neuroscience* (Cambridge University Press) (<https://doi.org/10.1017/CBO9780511975899>)
- [39] Gerstner W, Kistler W, Naud R and Paninski L 2014 *Neuronal Dynamics. From Single Neurons to Networks and Models of Cognition* (Cambridge University Press)
- [40] Dayan P and Abbott L 2001 *Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems* (MIT Press)
- [41] Brader J, Senn W and Fusi S 2007 Learning real world stimuli in a neural network with spike-driven synaptic dynamics *Neural Comput.* **19** 2881–912
- [42] Song S, Miller K and Abbot L 2000 Competitive Hebbian learning through spike-timing-dependent plasticity *Nat. Neurosci.* **3** 919–26
- [43] Sheik S, Paul S, Augustine C and Cauwenberghs G 2016 Membrane-dependent neuromorphic learning rule for unsupervised spike pattern detection 2016 IEEE Biomedical Circuits and Systems Conf. (BioCAS) pp 164–7
- [44] Payeur A, Guerguiev J, Zenke F, Richards B A and Naud R 2021 Burst-dependent synaptic plasticity can coordinate learning in hierarchical circuits *Nat. Neurosci.* **24** 1010–9
- [45] Graupner M and Brunel N 2012 Calcium-based plasticity model explains sensitivity of synaptic changes to spike pattern, rate and dendritic location *Proc. Natl Acad. Sci.* **109** 3991–6
- [46] Clopath C, Büsing L, Vasilaki E and Gerstner W 2010 Connectivity reflects coding: a model of voltage-based STDP with homeostasis *Nat. Neurosci.* **13** 344–52
- [47] Morrison A, Diesmann M and Gerstner W 2008 Phenomenological models of synaptic plasticity based on spike timing *Biol. Cybern.* **98** 459–78
- [48] Maffei A 2011 The many forms and functions of long term plasticity at GABAergic synapses *Neural Plast.* **2011** 254724

- [49] Capogna M, Castillo P E and Maffei A 2021 The ins and outs of inhibitory synaptic plasticity: neuron types, molecular mechanisms and functional roles *Eur. J. Neurosci.* **54** 6882–901
- [50] Wu Y K, Miehl C and Gjorgjieva J 2022 Regulation of circuit organization and function through inhibitory synaptic plasticity *Trends Neurosci.* **45** 884–98
- [51] Froemke R C 2015 Plasticity of cortical excitatory-inhibitory balance *Annu. Rev. Neurosci.* **38** 195–219
- [52] Hennequin G, Agnes E J and Vogels T P 2017 Inhibitory plasticity: balance, control and codependence *Annu. Rev. Neurosci.* **40** 557–79
- [53] Chiu C Q, Barberis A and Higley M J 2017 Preserving the balance: diverse forms of long-term GABAergic synaptic plasticity *Nat. Rev. Neurosci.* **20** 272–81
- [54] Schulz A, Miehl C, Berry M J I and Gjorgjieva J 2021 The generation of cortical novelty responses through inhibitory plasticity *eLife* **10** e65309
- [55] Vogels T P et al 2013 Inhibitory synaptic plasticity: spike timing-dependence and putative network function *Front. Neural Circuits* **7** 1–11
- [56] Haas J S, Nowotny T and Abarbanel H D I 2006 Spike-timing-dependent plasticity of inhibitory synapses in the entorhinal cortex *J. Neurophysiol.* **96** 3305–13
- [57] Vogels T P, Sprekeler H, Zenke F, Clopath C and Gerstner W 2011 Inhibitory plasticity balances excitation and inhibition in sensory pathways and memory networks *Science* **334** 1569–73
- [58] Luz Y, Shamir M and Latham P E 2012 Balancing feed-forward excitation and inhibition via Hebbian inhibitory synaptic plasticity *PLoS Comput. Biol.* **8** 1–12
- [59] Rachmuth G, Shouval H Z, Bear M F and Poon C-S 2011 A biophysically-based neuromorphic model of spike rate- and timing-dependent plasticity *Proc. Natl Acad. Sci.* **108** E1266–74
- [60] Ma G, Man M, Zhang Y and Liu S 2023 A fast homeostatic inhibitory plasticity rule circuit with a memristive synapse *Electronics* **12** 490
- [61] Abarbanel H D I, Huerta R and Rabinovich M I 2002 Dynamical model of long-term synaptic plasticity *Proc. Natl Acad. Sci.* **99** 10132–7
- [62] Del Giudice P, Fusi S and Mattia M 2003 Modeling the formation of working memory with networks of integrate-and-fire neurons connected by plastic synapses *J. Physiol. Paris* **97** 659–81
- [63] Clopath C and Gerstner W 2010 Voltage and spike timing interact in STDP—a unified model *Front. Synaptic Neurosci.* **2** 25
- [64] Bekolay T, Kolbeck C and Eliasmith C 2013 Simultaneous unsupervised and supervised learning of cognitive functions in biologically plausible spiking neural networks *35th Annual Conf. of the Cognitive Science Society* pp 169–74
- [65] Bienenstock E L, Cooper L N and Munro P W 1982 Theory for the development of neuron selectivity: orientation specificity and binocular interaction in visual cortex *J. Neurosci.* **2** 32–48
- [66] Yger P, Harris K and Behrens T 2013 The Convallis rule for unsupervised learning in cortical networks *PLoS Comput. Biol.* **9** e1003272
- [67] Hyvärinen A and Oja E 2000 Independent component analysis: algorithms and applications *Neural Netw.* **13** 411–30
- [68] Urbanczik R and Senn W 2014 Learning by the dendritic prediction of somatic spiking *Neuron* **81** 521–8
- [69] Sacramento J, Ponte Costa R, Bengio Y and Senn W 2018 Dendritic cortical microcircuits approximate the backpropagation algorithm *32nd International Conf. on Neural Information Processing Systems* pp 8735–46
- [70] Querlioz D, Bichler O, Dollfus P and Gamrat C 2013 Immunity to device variations in a spiking neural network with memristive nanodevices *IEEE Trans. Nanotechnol.* **12** 288–95
- [71] Abbott L F and Song S 1998 Temporally asymmetric Hebbian learning, spike timing and neural response variability *Advances in Neural Information Processing Systems* vol 11 pp 69–75 (available at: https://proceedings.neurips.cc/paper_files/paper/1998/file/806beafe154032a5b81e97b4420ad98-Paper.pdf)
- [72] Paredes-Vallés F, Scheper K Y W and De Croon G C H E 2019 Unsupervised learning of a hierarchical spiking neural network for optical flow estimation: from events to global motion perception *IEEE Trans. Pattern Anal. Mach. Intell.* **42** 2051–64
- [73] Mäki-Marttunen T, Iannella N, Edwards A G, Einevoll G T and Blackwell K T 2020 A unified computational model for cortical post-synaptic plasticity *eLife* **9** e55714
- [74] Pehle C, Billaudelle S, Cramer B, Kaiser J, Schreiber K, Stradmann Y, Weis J, Leibfried A, Müller E and Schemmel J 2022 The BrainScaleS-2 accelerated neuromorphic system with hybrid plasticity *Front. Neurosci.* **16** 795876
- [75] Bofill-i-Petit A, Thompson D and Murray A 2001 Circuits for VLSI implementation of temporally asymmetric Hebbian learning *Advances in Neural Information Processing Systems* vol 14 (MIT Press) pp 1091–8
- [76] Indiveri G 2002 Neuromorphic bistable VLSI synapses with spike-timing-dependent plasticity *Advances in Neural Information Processing Systems* vol 15 (MIT Press) pp 1115–22
- [77] Bofill-i-Petit A and Murray A 2004 Synchrony detection and amplification by silicon neurons with STDP synapses *IEEE Trans. Neural Netw.* **15** 1296–304
- [78] Cameron K, Boonsobhak V, Murray A and Renshaw D 2005 Spike timing dependent plasticity (STDP) can ameliorate process variations in neuromorphic VLSI *IEEE Trans. Neural Netw.* **16** 1626–37
- [79] Indiveri G, Chicca E and Douglas R J 2006 A VLSI array of low-power spiking neurons and bistable synapses with spike-timing dependent plasticity *IEEE Trans. Neural Netw.* **17** 211–21
- [80] Arthur J and Boahen K 2006 Learning in silicon: timing is everything *Advances in Neural Information Processing Systems* vol 18, ed Y Weiss, B Schölkopf and J Platt (MIT Press)
- [81] Koickal T, Hamilton A, Tan S, Covington J, Gardner J and Pearce T 2007 Analog VLSI circuit implementation of an adaptive neuromorphic olfaction chip *IEEE Trans. Circuits Syst. I* **54** 60–73
- [82] Liu S C and Mockel R 2008 Temporally learning floating-gate VLSI synapses *2008 IEEE Int. Symp. on Circuits and Systems* pp 2154–7
- [83] Tanaka H, Morie T and Aihara K 2009 A CMOS spiking neural network circuit with symmetric/asymmetric STDP function *IEICE Trans. Fundam. Electron. Commun. Comput. Sci.* **E92-A** 1690–8
- [84] Bamford S A, Murray A F and Willshaw D J 2012 Spike-timing-dependent plasticity with weight dependence evoked from physical constraints *IEEE Trans. Biomed. Circuits Syst.* **6** 385–98
- [85] Gopalakrishnan R and Basu A 2014 Robust doublet STDP in a floating-gate synapse *2014 Int. Joint Conf. on Neural Networks (IJCNN)* pp 4296–301
- [86] Polidori E, Camisa G, Mesri A, Ferrari G, Polidori C, Mastella M and Prati E 2022 Experimental validation of an analog spiking neural network with STDP learning rule in CMOS technology *2022 IEEE Int. Conf. on Metrology for Extended Reality, Artificial*

- Intelligence and Neural Engineering (MetroXRaine) 2022 IEEE Int. Conf. on Metrology for Extended Reality, Artificial Intelligence and Neural Engineering (MetroXRaine) pp 187–92
- [87] Mayr C, Noack M, Partzsch J and Schüffny R 2010 Replicating experimental spike and rate based neural learning in CMOS 2010 IEEE Int. Symp. on Circuits and Systems pp 105–8
- [88] Azghadi M R, Al-Sarawi S, Abbott D and Iannella N 2013 A neuromorphic VLSI design for spike timing and rate based synaptic plasticity *Neural Netw.* **45** 70–82
- [89] Gopalakrishnan R and Basu A 2017 Triplet spike time-dependent plasticity in a floating-gate synapse *IEEE Trans. Neural Netw. Learn. Syst.* **28** 778–90
- [90] Meng Y, Zhou K, Monzon J J C and Poon C S 2011 Iono-neuromorphic implementation of spike-timing-dependent synaptic plasticity 2011 Annual Int. Conf. of the IEEE Engineering in Medicine and Biology Society pp 7274–7
- [91] Fusi S, Annunziato M, Badoni D, Salamon A and Amit D J 2000 Spike-driven synaptic plasticity: theory, simulation, VLSI implementation *Neural Comput.* **12** 2227–58
- [92] Chicca E and Fusi S 2001 Stochastic synaptic plasticity in deterministic a VLSI networks of spiking neurons *World Congress on Neuroinformatics* (ARGESIM/ASIM Verlag) pp 468–77
- [93] Chicca E, Badoni D, Dante V, D'Andreagiovanni M, Salina G, Carota L, Fusi S and Del Giudice P 2003 A VLSI recurrent network of integrate-and-fire neurons connected by plastic synapses with long-term memory *IEEE Trans. Neural Netw.* **14** 1297–307
- [94] Giulioni M, Camilleri P, Dante V, Badoni D, Indiveri G, Braun J and Del Giudice P 2008 A VLSI network of spiking neurons with plastic fully configurable “stop-learning” synapses 15th IEEE Int. Conf. on Electronics, Circuits and Systems (IEEE) pp 678–81
- [95] Mitra S, Fusi S and Indiveri G 2009 Real-time classification of complex patterns using spike-based learning in neuromorphic VLSI *IEEE Trans. Biomed. Circuits Syst.* **3** 32–42
- [96] Chicca E, Stefanini F, Bartolozzi C and Indiveri G 2014 Neuromorphic electronic circuits for building autonomous cognitive systems *Proc. IEEE* **102** 1367–88
- [97] Maldonado Huayaney F L, Nease S and Chicca E 2016 Learning in silicon beyond STDP: a neuromorphic implementation of multi-factor synaptic plasticity with calcium-based dynamics *IEEE Trans. Circuits Syst. I* **63** 2189–99
- [98] Häfliger P, Mahowald M and Watts L 1996 A spike based learning neuron in analog VLSI *Advances in Neural Information Processing Systems* vol 9, ed M Mozer, M Jordan and T Petsche (MIT Press) pp 692–8
- [99] Ramakrishnan S, Hasler P E and Gordon C 2011 Floating gate synapses with spike-time-dependent plasticity *IEEE Trans. Biomed. Circuits Syst.* **5** 244–52
- [100] Pfister J-P, Toyozumi T, Barber D and Gerstner W 2006 Optimal spike-timing dependent plasticity for precise action potential firing in supervised learning *Neural Comput.* **18** 1309–39
- [101] Badoni D, Bertazzoni S, Buglioni S, Salina G, Amit D and Fusi S 1995 Electronic implementation of an analogue attractor neural network with stochastic learning *Netw. Comput. Neural Syst.* **6** 125
- [102] Pfeil T, Potjans T C, Schrader S, Potjans W, Schemmel J, Diesmann M and Meier K 2012 Is a 4-bit synaptic weight resolution enough? - constraints on enabling spike-timing dependent plasticity in neuromorphic hardware *Front. Neurosci.* **6** 90
- [103] Cantley K D, Subramaniam A, Stiegler H J, Chapman R A and Vogel E M 2011 Spike timing-dependent synaptic plasticity using memristors and nano-crystalline silicon TFT memories 11th IEEE Int. Conf. on Nanotechnology pp 421–5
- [104] Li Y, Zhong Y, Xu L, Zhang J, Xu X, Sun H and Miao X 2013 Ultrafast synaptic events in a chalcogenide memristor *Sci. Rep.* **3** 1619
- [105] Li Y, Zhong Y, Zhang J, Xu L, Wang Q, Sun H, Tong H, Cheng X and Miao X 2014 Activity-dependent synaptic plasticity of a chalcogenide electronic synapse for neuromorphic systems *Sci. Rep.* **4** 4906
- [106] Ziegler M, Riggert C, Hansen M, Bartsch T and Kohlstedt H 2015 Memristive Hebbian plasticity model: device requirements for the emulation of Hebbian plasticity based on memristive devices *IEEE Trans. Biomed. Circuits Syst.* **9** 197–206
- [107] Diederich N, Bartsch T, Kohlstedt H and Ziegler M 2018 A memristive plasticity model of voltage-based STDP suitable for recurrent bidirectional neural networks in the hippocampus *Sci. Rep.* **8** 9367
- [108] John R A, Liu F, Chien N A, Kulkarni M R, Zhu C, Fu Q, Basu A, Liu Z and Mathews N 2018 Synergistic gating of electro-iono-photoactive 2D chalcogenide neuristors: coexistence of Hebbian and homeostatic synaptic metaplasticity *Adv. Mater.* **30** 1800220
- [109] Nair M V, Muller L K and Indiveri G 2017 A differential memristive synapse circuit for on-line learning in neuromorphic computing systems *Nano Futures* **1** 035003
- [110] Payvand M, Fouda M E, Kurdahi F, Eltawil A and Neftci E O 2020 Error-triggered three-factor learning dynamics for crossbar arrays 2nd IEEE Int. Conf. on Artificial Intelligence Circuits and Systems (AICAS) pp 218–22
- [111] Cartiglia M, Haessig G and Indiveri G 2020 An error-propagation spiking neural network compatible with neuromorphic processors 2nd IEEE Int. Conf. on Artificial Intelligence Circuits and Systems (AICAS) pp 84–88
- [112] Cartiglia M, Rubino A, Narayanan S, Frenkel C, Haessig G, Indiveri G and Payvand M 2022 Stochastic dendrites enable online learning in mixed-signal neuromorphic processing systems *IEEE Int. Symp. on Circuits and Systems (ISCAS)* pp 476–80
- [113] Frenkel C, Bol D and Indiveri G 2023 Bottom-up and top-down approaches for the design of neuromorphic processing systems: tradeoffs and synergies between natural and artificial intelligence *Proc. IEEE* **111** 623–52
- [114] LeCun Y, Bottou L, Bengio Y and Haffner P 1998 Gradient-based learning applied to document recognition *Proc. IEEE* **86** 2278–324
- [115] Schmidhuber J, Wierstra D, Gagliolo M and Gomez F 2007 Training recurrent networks by EVOLINO *Neural Comput.* **19** 757–79
- [116] Bengio Y, Lee D H, Bornschein J and Lin Z 2015 Towards biologically plausible deep learning (arXiv:1502.04156)
- [117] Lillicrap T P, Santoro A, Marris L, Akerman C J and Hinton G 2020 Backpropagation and the brain *Nat. Rev. Neurosci.* **21** 335–46
- [118] Czarnecki W M, Swirszcz G, Jaderberg M, Osindero S, Vinyals O and Kavukcuoglu K 2017 Understanding synthetic gradients and decoupled neural interfaces 34th Int. Conf. on Machine Learning vol 70 (JMLR.org) pp 904–12
- [119] Kingma D and Ba J 2014 Adam: a method for stochastic optimization *Int. Conf. on Learning Representations (ICLR)*
- [120] Richards B and Kording K 2023 The study of plasticity has always been about gradients *J. Physiol.* **601** 3141–9
- [121] Zenke F and Ganguli S 2018 Superspike: supervised learning in multilayer spiking neural networks *Neural Comput.* **30** 1514–41
- [122] Bellec G, Scherr F, Subramoney A, Hajek E, Salaj D, Legenstein R and Maass W 2020 A solution to the learning dilemma for recurrent networks of spiking neurons *Nat. Commun.* **11** 3625
- [123] Izhikevich E M 2007 Solving the distal reward problem through linkage of STDP and dopamine signaling *Cereb. Cortex* **17** 2443–52
- [124] Lillicrap T P, Cownden D, Tweed D B and Akerman C 2016 Random synaptic feedback weights support error backpropagation for deep learning *Nat. Commun.* **7** 1–10

- [125] Nøkland A 2016 Direct feedback alignment provides learning in deep neural networks *Advances in Neural Information Processing Systems* vol 29 (Curran Associates, Inc.)
- [126] Wolters C, Taylor B, Hanson E, Yang X, Schlichtmann U and Chen Y 2022 Biologically plausible learning on neuromorphic hardware architectures (arXiv:2212.14337)
- [127] Neftci E O, Augustine C, Paul S and Deterakis G 2017 Event-driven random back-propagation: enabling neuromorphic deep learning machines *Front. Neurosci.* **11** 324
- [128] Kohan A A, Rietman E A and Siegelmann H T 2018 Error forward-propagation: reusing feedforward connections to propagate errors in deep learning (arXiv:1808.03357)
- [129] Kohan A, Rietman E A and Siegelmann H T 2022 Signal propagation: a framework for learning and inference in a forward pass (arXiv:2204.01723)
- [130] Dellaferrera G and Kreiman G 2022 Error-driven input modulation: solving the credit assignment problem without a backward pass *39th Int. Conf. on Machine Learning* vol 162 pp 937–4955 (available at: <https://proceedings.mlr.press/v162/dellaferrera22a.html>)
- [131] Mostafa H, Ramesh V and Cauwenberghs G 2018 Deep supervised learning using local errors *Front. Neurosci.* **12** 608
- [132] Kaiser J, Mostafa H and Neftci E 2020 Synaptic plasticity dynamics for deep continuous local learning (DECOLLE) *Front. Neurosci.* **14** 424
- [133] Halvagal M S and Zenke F 2023 The combination of Hebbian and predictive plasticity learns invariant object representations in deep sensory networks *Nat. Neurosci.* **26** 1906–15
- [134] Quintana F M, Perez-Peña F, Galindo P L, Neftci E O, Chicca E and Khacef L 2023 ETLP: event-based three-factor local plasticity for online learning with neuromorphic hardware (arXiv:2301.08281)
- [135] Christensen D V et al 2022 Roadmap on neuromorphic computing and engineering *Neuromorphic Comput. Eng.* **2** 022501
- [136] Muliukov A R, Rodriguez L, Miramond B, Khacef L, Schmidt J, Berthet Q and Upegui A 2022 A unified software/hardware scalable architecture for brain-inspired computing based on self-organizing neural models *Front. Neurosci.* **16** 825879
- [137] Schmidgall S, Ashkanazy J, Lawson W and Hays J 2021 Spikepropamine: differentiable plasticity in spiking neural networks *Front. Neurobot.* **15** 629210
- [138] Schmidgall S and Hays J 2022 Learning to learn online with neuromodulated synaptic plasticity in spiking neural networks (arXiv:2206.12520)
- [139] Safa A, Ocket I, Bourdoux A, Sahli H, Catthoor F and Gielen G G E 2022 Event camera data classification using spiking networks with spike-timing-dependent plasticity *2022 Int. Joint Conf. on Neural Networks (IJCNN)* pp 1–8
- [140] Stewart K M and Neftci E O 2022 Meta-learning spiking neural networks with surrogate gradient descent *Neuromorphic Comput. Eng.* **2** 044002
- [141] Gilra A and Gerstner W 2017 Predicting non-linear dynamics by stable local learning in a recurrent spiking neural network *eLife* **6** 1–43
- [142] Holtmaat A and Svoboda K 2009 Experience-dependent structural synaptic plasticity in the mammalian brain *Nat. Rev. Neurosci.* **10** 647–58
- [143] Le Bé J-V and Markram H 2006 Spontaneous and evoked synaptic rewiring in the neonatal neocortex *Proc. Natl Acad. Sci. USA* **103** 13214–9
- [144] Markram H, Gerstner W and Sjöström P J 2011 A history of spike-timing-dependent plasticity *Front. Synaptic Neurosci.* **3** 1–24
- [145] Engert F and Bonhoeffer T 1999 Dendritic spine changes associated with hippocampal long-term synaptic plasticity *Nature* **399** 66–70
- [146] Kwon H-B and Sabatini B L 2011 Glutamate induces *de novo* growth of functional spines in developing cortex *Nature* **474** 100–4
- [147] Zendrikov D, Solinas S and Indiveri G 2022 Brain-inspired methods for achieving robust computation in heterogeneous mixed-signal neuromorphic processing systems *Neuromorph. Comput. Eng.* **3** 034002
- [148] Sarpeshkar R 1998 Analog versus digital: extrapolating from electronics to neurobiology *Neural Comput.* **10** 1601–38
- [149] Demirag Y, Moro F, Dalgaty T, Navarro G, Frenkel C, Indiveri G, Vianello E and Payvand M 2021 PCM-trace: scalable synaptic eligibility traces with resistivity drift of phase-change materials *2021 IEEE Int. Symp. on Circuits and Systems (ISCAS)* (IEEE) pp 1–5