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

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Supplementary material: A broad perspective on synaptic plasticity

A brief history of plasticity

The quest for understanding learning in human beings is a very old one, as the process of acquiring new skills and knowledge was already a subject of debate among philosophers back in Ancient Greece where Aristotle introduced the notion of the mind as a blank state (or *tabula rasa*) at birth that was then developed through education [1]. It was in contrast to the idea of Plato, his teacher, who believed the mind was pre-formed in the "heavens" then sent to earth to join the body. In modern times, the question of nature versus nurture is still being debated, with the view that we are born without preconceptions and our brain is molded by experience proposed by modern philosophers such as Locke [2], and the studies that emphasize the importance of pre-defined structure in the nervous system and in neural networks, to guide and facilitate the learning process [3–5].

In the later half of the nineteenth century, learning and memory were linked for the first time to "junctions between cells" by Bain [6], even before the discovery of the synapse. In 1890, the psychologist William James postulated a mechanism for associative learning in the brain: "When two elementary brain-processes have been active together or in immediate succession, one of them, on reoccurring, tends to propagate its excitement into the other" [7]. In the same period, neuroanatomists discovered the two main components of the brain: neurons and synapses. They postulated that the brain is composed of separate neurons [8], and that long-term memory requires the growth of new connections between existing neurons [9]. These connections became known then as "synapses" [10]. At the end of the nineteenth century, synapses were already thought to control and change the flow of information in the brain, thus being the substrate of learning and memory [1].

The first half of the twentieth century confirmed this hypothesis by various studies on the chemical synapses and the direction of information flow among neurons, going from the pre-synaptic axons to the post-synaptic dendrites. Neural processing was associated to the integration of synaptic inputs in the soma, and the emission of an output spike once a certain threshold was reached, propagating along the axon. Donald Hebb combined earlier ideas and recent discoveries on learning and memory in his book "The Organization of Behavior". Similarly to the ideas of James 60 years earlier, Hebb published, in 1949, his formal postulates for the neural mechanisms of learning and memory: "When an axon of cell A is near enough to excite a cell B and repeatedly or persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells such that A's efficiency, as one of the cells firing B, is increased" [11]. Although Hebb stated that this idea is old, strengthening synapses (that is, increasing synaptic efficacy or weight) connecting co-active neurons has since been called "Hebbian plasticity". It is also called Long-Term Potentiation (LTP).

Even though Hebb wrote that "less strongly established memories would gradually disappear unless reinforced through a slow "synaptic decay" [11], he did not provide an active mechanism for weakening synapses. Hence,

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the synaptic strengths or "weights" are unbounded and it is not possible to forget previously learned patterns to learn new ones. The first solution proposed a few years later was to maintain the sum of synaptic weights in a neuron constant [12]. In 1982, Oja proposed a Hebbian-like rule [13] that adds a "forgetting" parameter and solves the stability problem with a form of local multiplicative normalization for synaptic weights. In the same year, Bienenstock, Cooper, and Munro [14] proposed the Bienenstock Cooper Munro (BCM) learning rule where during pre-synaptic stimulation, low-frequency activity of the post-synaptic neuron leads to Long-Term Depression (LTD) while high-frequency activity would lead to LTP. This model was an important shift as it introduced the so-called homo-synaptic LTD, where the plasticity was determined by the post-synaptic spike rate with no requirement on the temporal order of spikes. The importance of the post-synaptic neuron in synaptic plasticity was further demonstrated by showing how post-synaptic sub-threshold depolarization can determine whether LTP or LTD occurs [15, 16].

Time is inherently present in any associative learning since it only relies on co-occurring events. McNaughton, Douglas, and Goddard [17] were the first to experimentally explore the importance of the pre- and post-synaptic spike timing in plasticity. Fifteen years later, Gerstner, Ritz, and van Hemmen [18] hypothesized that these pre/post spike times contain more information for plasticity compared to spike rates. Their hypothesis would be confirmed by experiments conducted by Stuart and Sakmann [19] who discovered that the post-synaptic spike is back-propagating into the dendrites, as well as by Markram, Helm, and Sakmann [20] who showed that a single spike leaves behind a Calcium trace of about 100 ms which is propagated back into the dendrites. These findings were highly influential in the field because they provided evidence that synapses have local access to the timings of pre-synaptic and postsynaptic neurons spikes. In their subsequent experiments, Markram, Helm, and Sakmann [20] provided additional evidence that precise timing is important in neocortical neurons: They showed that using a pre/post pairing with a time difference of 10 ms led to LTP, while using the same time difference of 10 ms in an inverted post/pre pairing led to LTD [21]. Larger time differences of 100 ms did not lead to any change in the synaptic weights. Almost concurrently, Bi and Poo [22] performed similar experiments and found a 40 ms coincidence time window using paired recordings. These experiments proved that in addition to mean rates, also spike-timing matters. This phenomenon was later formulated in a learning rule named Spike-Timing Dependent Plasticity (STDP) [23].

In this respect, the Hebbian learning formula proposed by Shatz [24] that "cells that fire together wire together" could be misleading, as Hebb [11] postulate is directional: "axon of cell A is near enough to excite a cell B", which may be interpreted as implicitly time-dependent since cell A has to fire before cell B. On the other hand, STDP had been later found to only partially explain more elaborate learning protocols, which showed that while both LTP and LTD are compatible STDP at low frequencies, only LTP occurs at high frequencies regardless of the temporal order of spikes [16]. As pair-based STDP models do not reproduce the frequency dependence of synaptic plasticity, Pfister and Gerstner [25] proposed Triplet-based STDP (T-STDP) rule where LTP and LTD depend on a combination of three pre- and post-synaptic spikes (either two pre- and one post or one pre- and two post). Both pair-based and triplet-based STDP were then shown to be capable of reproducing the BCM like behavior [26]. Furthermore, the same frequency dependent experiments [16] showed that the state of the post-synaptic membrane voltage is important for driving LTP or LTD under the same pre/post timing conditions, confirming previous studies on the role of the neuron membrane voltage in plasticity [15]. Therefore, these recent findings supported computational plasticity models that depend on the arrival of the pre-synaptic spike and the voltage of the postsynaptic membrane [27–29], and which were also compatible with the STDP model. The more recent three-factor learning rules aim at bridging the gap between the different time scales of learning, specifically from pre-post spike timings (milliseconds) to behavioral time scales (seconds) [30].

Today, after more than two millennia of questioning, experimenting and more recently modeling, synaptic plasticity is still not fully understood and many questions remain unanswered. However, it is clear that multiple forms of plasticity and time scales coexist in the synapse and in the whole brain [31]. They link to each other by sharing locality as an essential computational principle.

Experimental perspective

Synaptic weights are correlated with various elements in biological synapses [32] such as the number of docked vesicles in the pre-synaptic terminal [33], the area of the pre-synaptic active zone [34], the dendritic spine head size [35, 36], the amount of released transmitters [37–39], the area of the post-synaptic density [40], and

the number of AMPA receptors [41]. Synaptic plasticity is known to be heterogeneous in different types of synapses [42, 43], and there is no unified experimental protocol to confront the different observations. Here we present the experimental results that led to the bottom-up definition of multiple plasticity rules.

Spike-timing dependence. Multiple experiments have been performed to demonstrate the dependence of plasticity on the exact pre- and post-synaptic neurons spike times [16, 21, 22]. From a computational point of view, these experiments led to the proposal of the STDP learning rule [1, 42], and its variants, such as T-STDP [25]. Typically in these experiments, a pre-synaptic neuron is driven to fire shortly before or shortly after a postsynaptic one, by injecting a current pulse to the specific soma at the desired time. Specifically, these pre-post and post-pre pairings are repeated for 50 to 100 times at a relatively low frequency of about 1 Hz to 10 Hz [44]. Experimental results reveal synaptic plasticity mechanisms that are sensitive to the difference in spike times at the time scale of milliseconds [18]. LTP is observed when the pre-synaptic spike occurs within 10 ms before the post-synaptic spike is produced, while LTD is observed when the order is reversed [21, 22]. In biology, this precise spike timing dependence could be supported by local processes in the synapses that have access to both the timing information of pre-synaptic spikes and to the postsynaptic spike times, either by sensing their local membrane voltage changes or by receiving large depolarizations caused by output spikes that are back-propagated into the dendrite [19].

Post-synaptic membrane voltage dependence. Another feature of synaptic plasticity is its dependence on the post-synaptic neuron membrane voltage [15]. To study this dependence, the pre-synaptic neuron is driven to fire while the post-synaptic neuron is clamped to a fixed voltage. The clamped voltage level will determine the outcome of the synaptic changes: If the voltage is only slightly above the resting potential of the neuron, then LTD is observed while if it is higher, then LTP is observed [15, 45]. These experiments show that post-synaptic spikes are not strictly necessary to induce long-term plasticity [46, 47]. Moreover, even in the presence of a constant pre/post timing (10 ms) at low frequencies (0.1 Hz), the post-synaptic membrane voltage determines whether LTP or LTD can be induced [16, 44]. These findings suggest that the post-synaptic membrane voltage might be more important than the pre/post spike timing for synaptic plasticity.

Frequency dependence. While both spike-timing and post-synaptic membrane voltage dependence are observed in experimental protocols when relatively low spike frequencies are used, at high frequencies LTP tends to dominate over LTD regardless of precise spike timing [16]. This spike-rate dependence, which is correlated with the Calcium concentration of the postsynaptic neuron [16], is captured by multiple learning rules such as BCM [14] or the T-STDP [25] rule. In these rules, high spike rates produce a strong / rapid increase in Calcium concentration that leads to LTP, while low spike rates produce a modest / slow increase in Calcium concentration that decays over time and leads to LTD [48].

Theoretical perspective

Theoretical investigations of plasticity have yielded crucial insights in computational neuroscience. Here, we summarize the essential theoretical and practical requirements for long-term synaptic plasticity.

Sensitivity to pre-post spikes correlations. Synaptic plasticity must adjust synaptic weights depending on the correlation between pre- and post-synaptic neurons [11]. Depending on how information is encoded, this can be achieved using spike times, spike rates, or both [49]. It is important to note that the objective behind the detection of correlation is to detect causality which would ensure a better prediction [50]. Even if correlation does not imply causality [49], correlation can be considered as a tangible trace of causality in learning.

Selectivity to different patterns. By associating local plasticity with a Winner-Take-All (WTA) network, it is possible to create internal models of the probability distributions of the input patterns. This can be interpreted as an approximate Expectation-Maximization algorithm for modeling the input data [51]. Recently, the combination of STDP with WTA networks has been successfully used to solve a variety of pattern recognition problems in both supervised [52] and unsupervised scenarios [53–56].

Stability of synaptic memory. Long-term plasticity requires continuous adaptation to new patterns but it also requires the retention of previously learned patterns. As any physical system has limited storage capacity, the presentation of new experiences will continuously generate new memories that will eventually lead to saturation of the capacity. When presenting new experiences, the stability (and retrieval) of old memories is a major problem in Artificial Neural Networks (ANNs). When learning of new patterns leads to the complete corruption or destruction of previously learned ones, then the network undergoes *catastrophic forgetting* [57, 58]. Both catastrophic forgetting and continual learning are critical problems that need to be addresses for always-on neural processing systems, including artificial embedded processors applied to solving edge-computing tasks. The main challenge in always-on learning is not its resilience against time, but its resilience against ongoing activity [59].

Different strategies can be used to find a good balance between plasticity and stability. A first solution is to introduce stochasticity in the learning process, for example by using Poisson distributed spike trains to represent input signals to promote plasticity, while promoting stability using a bi-stable internal variable that slowly drives the weight between one of two possible stable states [28]. As a result, only a few synapses will undergo a LTP or LTD transition for a given input, to progressively learn new patterns without forgetting previously learned patterns. A second solution is to have an intrinsic stop-learning mechanism to modulate learning and not change synaptic weights if there is enough evidence that the current input pattern has already been learned.

Depending on the particular pattern recognition problem to be solved and the learning paradigm (offline/online), specific properties can be more or less important.

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