1 Microscopic Foundation: Neural Dynamics

Before deriving the macroscopic plasticity rules, we must first establish the microscopic dynamics of the individual neurons comprising the network. We employ the Leaky Integrate-and-Fire (LIF) model, a standard reduction of the Hodgkin-Huxley formalism that captures the essential subthreshold integration and thresholding behavior of cortical neurons [**gerstner_neuronal_2014**].

1.1 Membrane Potential Dynamics

The state of a postsynaptic neuron i is described by its membrane potential $V_i(t)$. In the absence of input, the membrane potential relaxes to a resting potential E_L. The evolution of $V_i(t)$ is governed by the conservation of current across the cell membrane, modeled as an RC circuit consisting of a leakage resistor R_m and a membrane capacitor C_m in parallel:

$$\tau_m \frac{dV_i(t)}{dt} = -(V_i(t) - E_L) + R_m I_{syn,i}(t) + R_m I_{ext,i}(t), \tag{1}$$

where $\tau_m = R_m C_m$ represents the membrane time constant, typically in the range of 10–20 ms [1]. The term $I_{syn,i}(t)$ represents the total synaptic current received from presynaptic neurons, and $I_{ext,i}(t)$ accounts for any external background currents or noise.

1.2 Synaptic Interaction

The synaptic current $I_{syn,i}(t)$ is determined by the activity of the presynaptic population. Let the spike train of a presynaptic neuron j be denoted by a sum of Dirac delta functions, $\rho_j(t) = \sum_k \delta(t - t_j^k)$.

The arrival of a spike from neuron j induces a transient change in the conductance or current of neuron i. In the current-based approximation, appropriate for this level of reduction, the total synaptic current is the linear sum of filtered presynaptic spikes weighted by the synaptic efficacy w_{ij}:

$$I_{syn,i}(t) = \sum_j w_{ij} \int_{-\infty}^{t} \alpha(t-s)\rho_j(s)\, ds, \tag{2}$$

where $\alpha(t)$ is the postsynaptic current (PSC) kernel, typically modeled as an exponential decay $\alpha(t) = \frac{1}{\tau_s} e^{-t/\tau_s}\Theta(t)$, with synaptic time constant τ_s.

1.3 Spike Generation Mechanism

The continuous voltage dynamics defined above give rise to discrete events. A spike is generated at time t_i^k when the membrane potential crosses a fixed threshold ϑ from below:

$$t_i^k : V_i(t_i^k) = \vartheta \quad \text{and} \quad \left.\frac{dV_i}{dt}\right|_{t=t_i^k} > 0. \tag{3}$$

Immediately following a spike, the potential is reset to a value $V_{reset} < \vartheta$ and held constant for a refractory period τ_{ref}, simulating the temporary inactivation of Na^+ channels.

This mechanism defines the postsynaptic spike train $\rho_i(t) = \sum_k \delta(t - t_i^k)$, which serves as the input to the plasticity equations in the following section.

2 Mathematical Formulation of the Three-Factor Plasticity Model

Having defined the generation of spike times $\mathcal{T}_j$ and $\mathcal{T}_i$ via the LIF dynamics, we now analyze the evolution of the synaptic weights w_{ij}. We focus on a plasticity rule belonging to the class of *three-factor learning rules*, as reviewed by Frémaux and Gerstner [2]. In this framework, synaptic updates are gated by a global neuromodulatory signal (factor three) rather than relying solely on the pairwise correlation of presynaptic and postsynaptic activity (factors one and two).

2.1 Neural Activity and Notation

Following the framework established in the previous section, the neural response functions are formally treated as sums of Dirac distributions:

$$\rho_j(t) = \sum_{k=1}^{N_j} \delta(t - t_j^k) \quad \text{and} \quad \rho_i(t) = \sum_{k=1}^{N_i} \delta(t - t_i^k). \tag{4}$$

Here, N_j and N_i denote the total number of spikes fired by each neuron over the interval $t \in [0, T]$, determined stochastically by the interaction of the membrane potential equation (Eq. 1) and the threshold condition (Eq. 3).

To prevent unbounded growth, we constrain the weight to a closed interval $w_{ij} \in [0, w_{\max}]$, where $w_{\max} \in \mathbb{R}^+$ is a constant parameter representing the maximum possible synaptic efficacy [2].

2.2 Local Dynamics: The Eligibility Trace

A central feature of this model is that the coincidence of spikes does not immediately change the synaptic weight. Instead, it creates a temporary memory trace, $E_{ij}(t)$, known as the *eligibility trace* [**gerstner_neuronal_2014**, 2]. This trace allows the synapse to bridge the temporal delay—often termed the "distal reward problem"—between millisecond-scale neural activity and second-scale reward signals. The eligibility trace evolves according to:

$$\tau_e \frac{dE_{ij}(t)}{dt} = -E_{ij}(t) + S_{ij}(t), \tag{5}$$

where $\tau_e \in \mathbb{R}^+$ is the decay time constant of the trace.

The driving term $S_{ij}(t)$ represents the instantaneous induction of Spike-Timing-Dependent Plasticity (STDP). To define $S_{ij}(t)$, we use variables $x_j(t)$ and $y_i(t)$ that track the recent history of presynaptic and postsynaptic activity, respectively:

$$\tau_+ \frac{dx_j(t)}{dt} = -x_j(t) + \rho_j(t), \tag{6}$$

$$\tau_- \frac{dy_i(t)}{dt} = -y_i(t) + \rho_i(t), \tag{7}$$

where $\tau_+, \tau_- \in \mathbb{R}^+$ are the time constants for the potentiation and depression windows. These constants are derived from experimental data and define the temporal window of sensitivity for plasticity [1].

The STDP induction term $S_{ij}(t)$ combines Long-Term Potentiation (LTP) and Long-Term

Depression (LTD):

$$S_{ij}(t) = \underbrace{A_+(w_{ij})x_j(t)\rho_i(t)}_{\text{LTP contribution}} - \underbrace{A_-(w_{ij})y_i(t)\rho_j(t)}_{\text{LTD contribution}}. \tag{8}$$

The LTP term is active only when a postsynaptic spike occurs ($\rho_i(t) \neq 0$), and its magnitude depends on the accumulated presynaptic activity $x_j(t)$. Similarly, the LTD term is active when a presynaptic spike occurs, depending on the postsynaptic activity.

2.3 Weight Dependence and Stability

To ensure the weight w_{ij} stays within the bounds $[0, w_{\max}]$, the scaling functions $A_+(w_{ij})$ and $A_-(w_{ij})$ include a "soft bound" dependence on the current weight:

$$A_+(w_{ij}) = \eta_+(w_{\max} - w_{ij}) \quad \text{and} \quad A_-(w_{ij}) = \eta_- w_{ij}, \tag{9}$$

where $\eta_+, \eta_- \in \mathbb{R}^+$ are the learning rates. This formulation ensures that the rate of weight change drops to zero as the weight approaches either limit.

2.4 Global Dynamics: Neuromodulated Update

The actual change in synaptic weight is governed by a global neuromodulatory signal $M(t)$. The differential equation for the weight is the product of this global signal and the local eligibility trace:

$$\frac{dw_{ij}(t)}{dt} = M(t)E_{ij}(t). \tag{10}$$

The signal $M(t)$ is modeled as a Reward Prediction Error (RPE), calculated as the difference between the instantaneous reward $R(t)$ and a baseline expectation $\bar{R}(t)$:

$$M(t) = R(t) - \bar{R}(t). \tag{11}$$

Here, $\bar{R}(t)$ serves as a reference point. It ensures that the neuromodulatory signal can be positive (indicating better-than-expected outcomes) or negative (indicating worse-than-expected outcomes), allowing for bidirectional regulation of synaptic weights [2].

References

[1] Peter Dayan and L. F. Abbott. *Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems*. Cambridge, MA: MIT Press, 2001. ISBN: 0-262-04199-5.

[2] Nicolas Frémaux and Wulfram Gerstner. "Neuromodulated Spike-Timing-Dependent Plasticity, and Theory of Three-Factor Learning Rules". In: *Frontiers in Neural Circuits* 9 (2016), p. 85. ISSN: 1662-5110. DOI: 10.3389/fncir.2015.00085. URL: https://www.frontiersin.org/articles/10.3389/fncir.2015.00085/full.