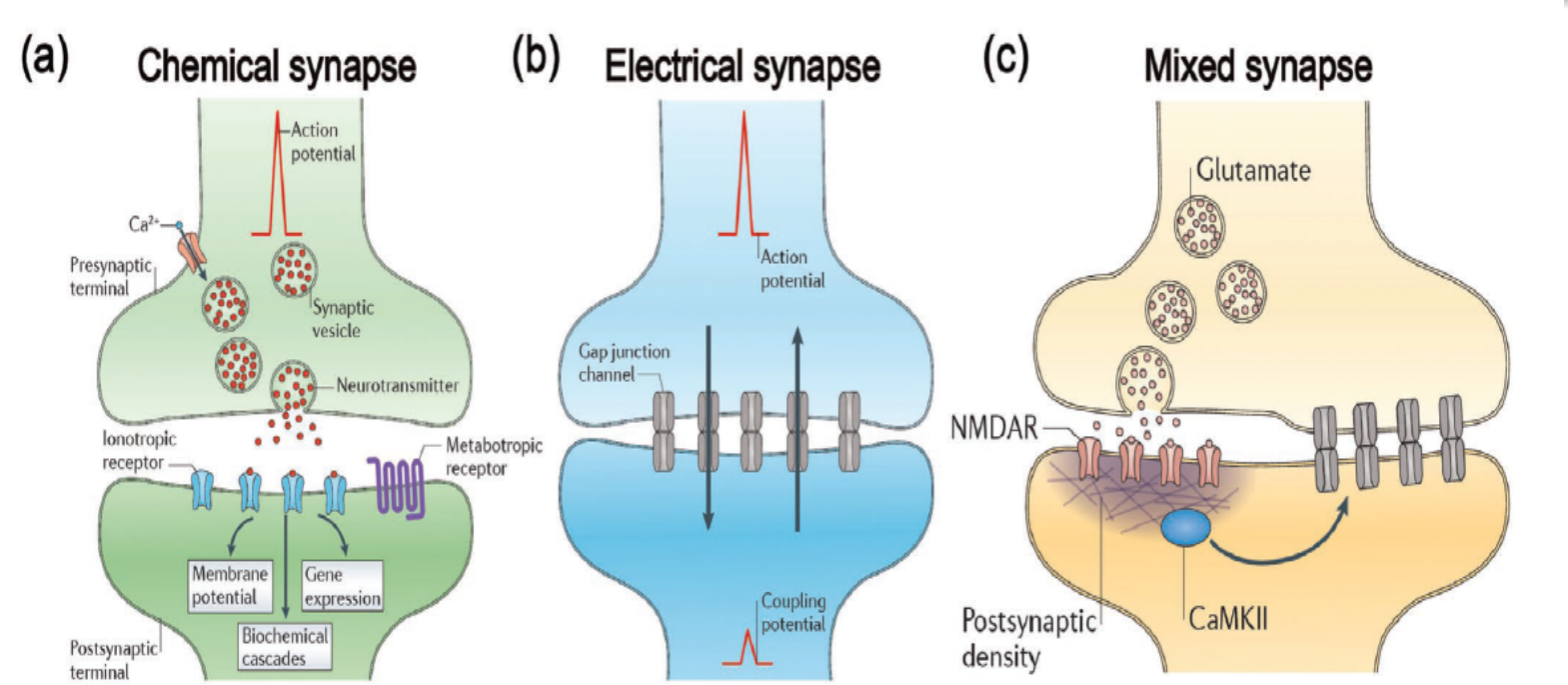
Lecture 14: Connectivity in static and adaptive neural networks.

Objectives

1. Understand how neurons connect with each other.
2. Understand the difference between static and adaptive neural networks
3. Learn about biological learning algorithms.
4. Simulate static and adaptive neural networks with and without noise.

Mathematical modeling of (non)adaptive neural networks



A. E. Pereda, Nat. Rev. Neurosci. 2014, 15, 250..

- a) Chemical synapses are by far the most prevalent and are the main players involved in excitatory synapses. The transfer of neurotransmitters from a presynaptic axon to a postsynaptic dendrite. Unlike an electrical synapse, chemical synapses are separated by a space called the synaptic cleft, typically measured between 15 and 25 nm. In the figure, the arrival of action potential results in the activation of voltage-gated Ca+ channels, promoting the probabilistic release of neurotransmitters by exocytosis from the presynaptic membrane. The ionotropic and metabotropic receptors on the postsynaptic membrane can detect and translate the information carried by neurotransmitters into different postsynaptic behaviors, varying from changes in membrane potential to gene expression.
- b) Electrical synapses allow direct, virtually instantaneous, and passive flow of electric current through special intercellular connections called gap junctions. Electrical transmission is conducted by gap junctions (some clusters of intercellular channels) between two adjacent cells. The transmission is bidirectional: when an action potential is transmitted from pre-synapse to postsynapse, the postsynaptic resting potential propagates concurrently to the pre-synapse.

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- Some common network architectures (topology) include small-world, random, and scale-free networks, which are encoded by a connectivity matrix.

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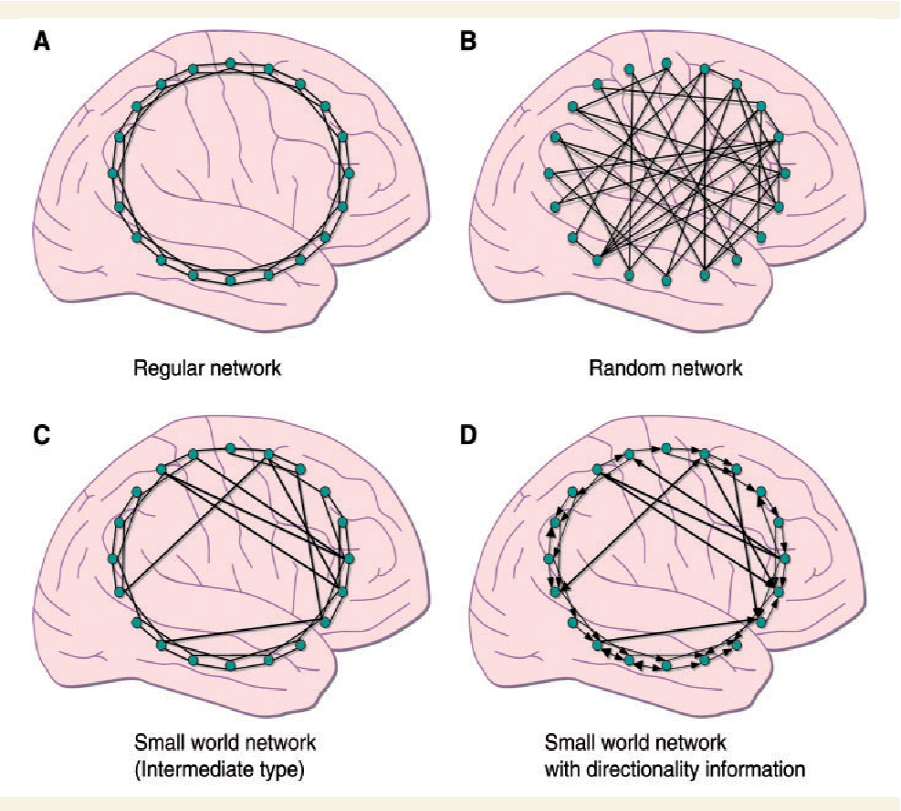

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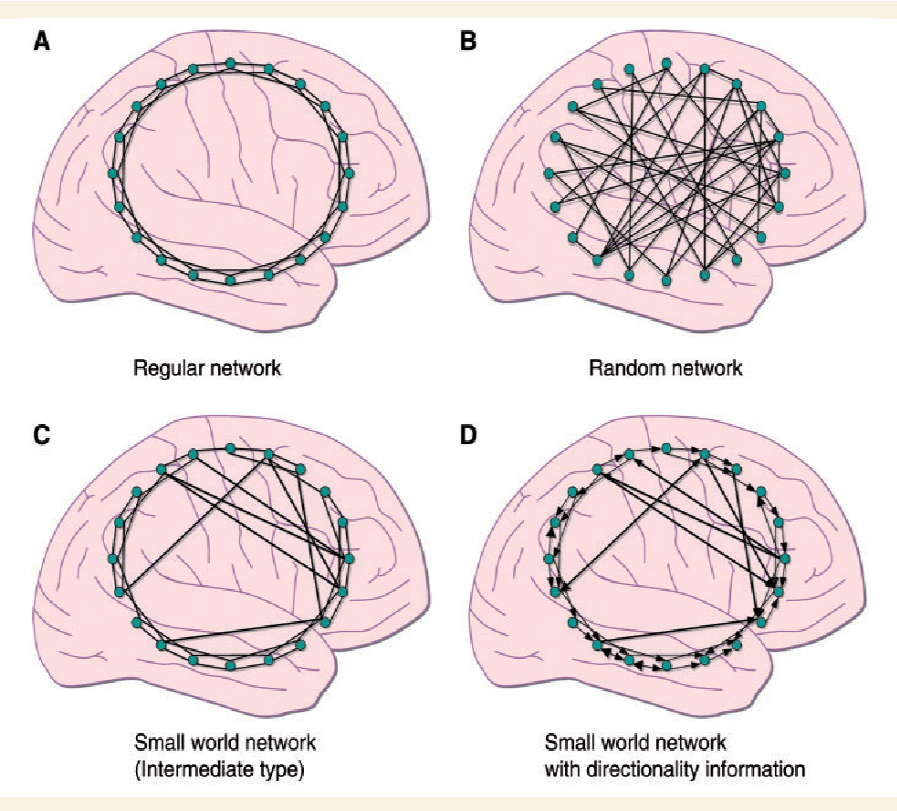

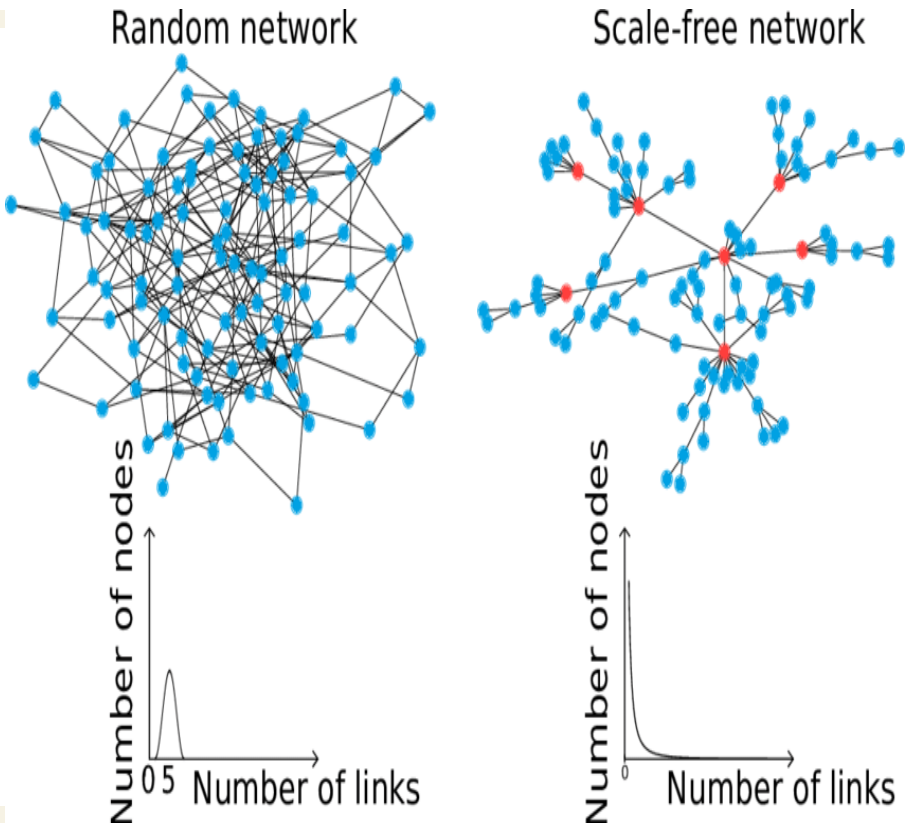

Mathematical modeling of adaptive neural networks

Mathematically, a network of coupled neurons (e.g., the FitzHugh-Nagumo neuron) can be modeled as follows:

$$\begin{cases} \dfrac{dv_i}{dt} &= \left(v_i - \dfrac{v_i^3}{3} - w_i + I + E_s^i + C_s^i \right) + \sigma_i^s \dfrac{dB_i^s}{dt}, \\ \dfrac{dw_i}{dt} &= \varepsilon(v_i + \alpha - \beta w_i) + \sigma_i^c \dfrac{dB_i^c}{dt}, \end{cases} \tag{1}$$

where each neuron is represented by a node $i = 1, ..., N$, and the functional dependencies E_s^i and C_i represent the electrical and chemical synapses, respectively, and are given by:

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where each neuron is represented by a node $i = 1, ..., N$, and the functional dependencies E_s^i and C_i represent the electrical and chemical synapses, respectively, and are given by:

$$\begin{cases} E_s^i = \displaystyle\sum_{j=1(\neq i)}^{N} A_{ij}^E \, G_{ij}^E \left[v_j(t - \tau_e) - v_i(t) \right], \\ C_s^i = \displaystyle\sum_{j=1(\neq i)}^{N} A_{ij}^C \; G_{ij}^C(t) \, \Gamma_j(t) \left[v_i(t) - V_{syn} \right], \\ \Gamma_j(t) = \dfrac{1}{1 + \exp\left[-\lambda \left(v_j(t - \tau_c) - \Theta_{syn} \right) \right]}, \end{cases} \tag{2}$$

Mathematical modeling of adaptive neural networks

- The membrane potential and the recovery current variables of neuron i are given by $v_i \in \mathbb{R}$ and $w_i \in \mathbb{R}$, respectively.
- $0 < \varepsilon \ll 1$ sets the timescale separation between the fast v_i and the slow w_i.
- The excitability threshold $\beta > 0$ of this version of the FHN neurons is a codimension-one Hopf bifurcation parameter.
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- I is an input current.
- $\alpha \in (0, 1)$ is a constant parameter.
- The Wiener processes modeling the synaptic noise term B_i^s represents mean-centered Gaussian white noise with $\langle B_i^s(t)\, B_i^s(t')\rangle_t = \delta(t - t')$ and variance (amplitude) σ_i^s, and represents the synaptic fluctuations observed in neural networks. And similarly, for channel noise B_i^c is given by a mean-centered Gaussian white noise with $\langle B_i^c(t)\, B_i^c(t')\rangle_t = \delta(t - t')$ and variance (amplitude) σ_i^c represents the random opening and closing of channel ion.

Mathematical modeling of adaptive neural networks

- E_s^i represent the electrical synaptic interactions between connected neurons, with strength G_{ij}^E and time delay τ_e, respectively. Since electrical synapses interact only locally, the coupling mediated by electrical synapses is of diffusive type, i.e., the electrical coupling term vanishes if v_i and v_j are equal and if the time delay is zero, i.e., $\tau_e = 0$.

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- C_s^i represent chemical synaptic interactions between connected neurons. The chemical synaptic time delay is given by τ_c. The chemical synaptic function is modeled by a sigmoidal input-output function, $\Gamma(v_i) = \dfrac{1}{1 + e^{-\lambda(v_i - \Theta_{\text{syn}})}}$, see Eq. (2), where parameter $\lambda = 10.0$ determines the slope of the function and $\Theta_{\text{syn}} = -0.25$ the synaptic firing threshold. Note there are other mathematical forms of chemical synapses as you shall see in Exercise 5.

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- The connectivity matrices A_{ij}^E and A_{ij}^C (also known as the Adjacency matrix) encode the architecture (topology) of the electrically and chemically connected neurons, respectively. If neuron i is connected to neuron j, then the entries $\{a_{ij}^E\} = 1$ ($\{a_{ij}^c\} = 1$), if not $\{a_{ij}^E\} = 0$ ($\{a_{ij}^C = 0\}$). Recall that the adjacency matrices can be generated using *networkx* Python package.

- $V_{\text{syn}} < v_i(t)$ the chemical synaptic interaction has a depolarizing effect that makes the synapse inhibitory, and for $V_{\text{syn}} > v_i(t)$, the synaptic interaction has a hyper-polarizing effect making the synapse excitatory.

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- The version of the FHN neuron given in Eq.(1) above, if the membrane potentials $|v_i(t)| \leq 2.0$ $(i = 1, 2, ..., N)$ for all time t. Thus, if we for example, fix $V_{\text{syn}} = -3.0$, then the term $\left[v_i(t) - V_{\text{syn}}\right]$ in Eq. (2) is always positive. So, the inhibitory and excitatory natures of chemical synapses will depend only on the sign in front of the chemical synaptic interaction C_s^i.

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- While electrical synapses do not exhibit STDP, they contribute to various important functions in the nervous system, including the synchronization of neuronal activity, the spread of electrical signals, and the coordination of network activity.

Mathematical modeling of adaptive neural networks

- The weight of the synaptic connection from the pre-synaptic jth neuron to the post-synaptic ith neuron is represented by $G_{ij}^{C}(t)$. With increasing time t, the synaptic strength $G_{ij}^{C}(t)$ for each synapse is updated with a nearest-spike pair-based STDP rule.

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- In simulations, to prevent unbounded growth, negative conductances (i.e., negative coupling strength), and elimination of synapses (i.e., $G_{ij}^{C}(t) = 0$), we usually set a range with the lower and upper bounds, e.g., $G_{ij}^{C}(t) \in [G_{min}^{C}, G_{max}^{C}] = [0.0001, 1.0]$.

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- Then, the synapses are updated according to additive (state-independent) update rule, where the coupling weights are changed relative to their current values as:

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- Or the synapses are updated according to multiplicative (state-dependent) update rule, where the coupling weights are changed relative to their current values as:

$$G_{ij}^C(t) \to G_{ij}^C(t) + \lambda (G_0^C - G_{ij}^C(t)) |\Delta G_{ij}^C(\Delta t_{ij})|, \tag{4}$$

where $G_0^C = G_{max}^C$ or $G_0^C = G_{min}^C$ depending on whether the coupling update $\Delta G_{ij}^C(\Delta t_{ij})$ is positive (LTP) or negative (LTD), respectively.

Notice that in Eq.(4) we have absolute value on $\Delta G_{ij}^{C}(\Delta t_{ij})$. Hence, $\Delta G_{ij}^{C}(\Delta t_{ij})$ can be positive or negative. If $\Delta G_{ij}^{C}(\Delta t_{ij}) > 0 \Rightarrow G_0^C = G_{max}^C$ and if $\Delta G_{ij}^{C}(\Delta t_{ij}) < 0 \Rightarrow G_0^C = G_{min}^C$.

In the context of synaptic plasticity, one will investigate (and compare the effects) both multiplicative and additive STDP, where the coupling update either depends or not, respectively, on the current value of the synaptic weights $G_{ij}^{C}(t)$ and leads to "soft" or "hard" bounds, accordingly.

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  - **Meaning**: Soft bounds imply that the update to the synaptic weights is dependent on the current value of the weights. This typically results in more gradual changes as the weight approaches its maximum or minimum value.

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  - **Effect**: The synaptic weights tend to approach their bounds asymptotically, meaning they slow down as they get closer to the maximum or minimum allowed values.

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$$G_{ij}^{C}(t) \to G_{ij}^{C}(t) + \lambda(G_0^{C} - G_{ij}^{C}(t))|\Delta G_{ij}^{C}(\Delta t_{ij})|, \tag{5}$$

- G_0^C is either G_{max}^C or G_{min}^C, indicating the maximum or minimum bound.
- The term $\lambda(G_0^C - G_{ij}^C(t))$ suggests a dependency on the current value of G_{ij}^C, which is characteristic of a soft bound.

Conversely, if the update $\Delta G_{ij}^C(\Delta t_{ij})$ were independent of G_{ij}^C, it would be more indicative of hard bounds, where the changes are made directly and limits are imposed strictly when the bounds are reached.

Mathematical modeling of adaptive neural networks

- The parameter λ represents the learning rate. It was found experimentally that small learning rates led to more robust learning. Hence, in simulations, we usually choose a small learning rate (i.e., $\lambda = 0.0001$) which, by the way, also simulates the effect of STDP on the long-term evolution of the neural networks.

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- In simulations, we usually consider that the STDP update rules are not applied to connections that are initially non-existent, i.e., we do not consider the creation of synapses. Moreover, if neurons are disconnected, they will remain disconnected throughout the total simulation time (there is no rewiring of synapses). However, when the neural network topology becomes time-varying, these assumptions may no longer be true, in which case appropriate assumptions have to be considered.

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- The biological learning rule, i.e., the synaptic modification $\Delta G_{ij}^{C}(\Delta t_{ij})$ depends on the relative time difference $\Delta t_{ij} = (t_i^{(post)} - t_j^{(pre)})$ between the nearest-spike times of the post-synaptic neuron i and the pre-synaptic neuron j.

Mathematical modeling of adaptive neural networks

- The STDP learning rule can be excitatory (we talk of eSTDP) with an asymmetric Hebbian time window for the synaptic modification $\Delta G_{ij}^{C}(\Delta t_{ij})$ given by:

$$\Delta G_{ij}^{C}(\Delta t_{ij}) = \begin{cases} A_1 e^{-\Delta t_{ij}/\tau_1}, \text{ if } \Delta t_{ij} > 0 \\ -A_2 e^{\Delta t_{ij}/\tau_2}, \text{ if } \Delta t_{ij} < 0 \\ 0, \text{ if } \Delta t_{ij} = 0 \end{cases}, \tag{6}$$

- The STDP learning rule can be excitatory (we talk of eSTDP) with an asymmetric Hebbian time window for the synaptic modification $\Delta G_{ij}^{C}(\Delta t_{ij})$ given by:

$$\Delta G_{ij}^{C}(\Delta t_{ij}) = \begin{cases} A_1 e^{-\Delta t_{ij}/\tau_1}, \text{ if } \Delta t_{ij} > 0 \\ -A_2 e^{\Delta t_{ij}/\tau_2}, \text{ if } \Delta t_{ij} < 0 \\ 0, \text{ if } \Delta t_{ij} = 0 \end{cases}, \tag{6}$$

where long-term potentiation (LTP — strengthening of synapses) occurs for $\Delta t_{ij} > 0$ (i.e., a post-synaptic spike follows a pre-synaptic spike), long-term depression (LTD — weakening of synapses) occurs for $\Delta t_{ij} < 0$ (i.e., a post-synaptic spike precedes a pre-synaptic spike), and no synaptic modifications for $\Delta t_{ij} = 0$ (i.e., a post-synaptic spike coincides a pre-synaptic spike). The amount of synaptic modification (i.e., strengthening or weakening) is limited by the adjusting rate potentiation parameter A_1, adjusting rate depression parameter A_2, and their respective temporal window for synaptic modification τ_1 and τ_2.

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- The Figure below shows the asymmetric Hebbian time window of eSTDP for the synaptic modification $\Delta G_{ij}^{C}(\Delta t_{ij})$ given by Eq.(6). We see in both cases that ΔG_{ij}^{C} varies, depending on the relative time difference Δt_{ij} between the nearest spike times of the post-synaptic neuron i and the pre-synaptic neuron j.

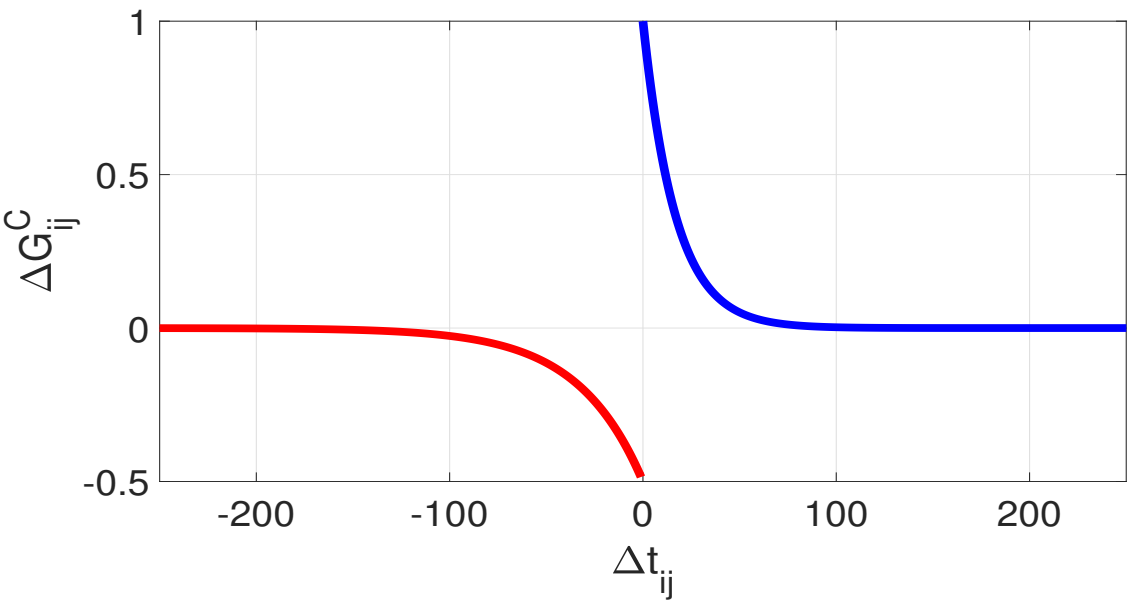

Figure: Plot of synaptic modification ΔG_{ij}^{C} versus Δt_{ij} for eSTDP. The blue and red curves represent LTP and LTD, respectively. $A_1 = 1.0$, $A_2 = 0.5$, $\tau_1 = 20.0$, $\tau_2 = 20.0$.

- The STDP learning rule can be inhibitory (we talk of iSTDP) with an asymmetric anti-Hebbian time window for the synaptic modification $\Delta G_{ij}^{C}(\Delta t_{ij})$ given by:

$$\Delta G_{ij}^{C}(\Delta t_{ij}) = \begin{cases} -A_1 e^{-\Delta t_{ij}/\tau_1}, \text{ if } \Delta t_{ij} > 0 \\ -A_2 \dfrac{\Delta t_{ij}}{\tau_2} e^{\Delta t_{ij}/\tau_2}, \text{ if } \Delta t_{ij} < 0, \\ 0, \text{ if } \Delta t_{ij} = 0 \end{cases} \tag{7}$$

in which, when $\Delta t_{ij} > 0$, LTD occurs, while LTP occurs in the case of $\Delta t_{ij} < 0$, in contrast to the Hebbian time window for the excitatory STDP (eSTDP) where LTP (LTD) occurs for $\Delta t_{ij} > (<) 0$. The amount of synaptic modification (i.e., strengthening or weakening) is limited by the adjusting rate potentiation parameter A_2, adjusting rate depression parameter A_1, and their respective temporal window for synaptic modification τ_2 and τ_1. Please make sure you get the differences between eSTDP and iSTDP.