Optimality Model of Unsupervised Spike-Timing Dependent Plasticity: Synaptic Memory and Weight Distribution

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  - Stable unimodal and bimodal weight distributions
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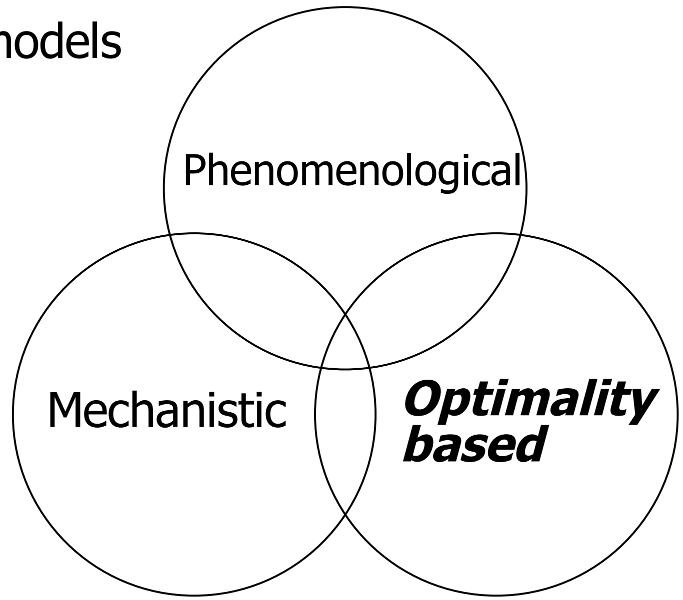
Motivation

- Synaptic plasticity models



- Optimality based plasticity models
  - Bridge between electrophysiological properties of neurons and synapses and their functional and computational roles
  - Reproduce several features of synaptic plasticity by introducing a small set of basic principles (postulates), thus
  - bring seemingly distinct experimental and theoretical results under a coherent framework

Synaptic Plasticity: features

i. Sensitive to pre-synaptic and postsynaptic firing rates (Dudek and Bear, 1992)

iii. Depend on exact timing of pre- and postsynaptic spikes (Markram et al. 1997, Bi and Poo 2001)

v. Sensitive to correlations between activity of pre- and postsynaptic neurons (Hebb 1949, Oja 1982)

vii. Unimodal weight distribution in case of absent or weak input features (Gutig et al. 2003)

ix. Neurons develop input selectivity only in presence of strong input features (Bienenstock et al. 1982, Miller et al. 1989)

xi. Produce stable synaptic memories (Fusi et al. 2005)

Postulates

A. Synaptic plasticity changes towards enabling neurons to maximize **information transmission**
  - Mutual information between presynaptic spike trains and postsynaptic firing is maximized

B. **Homeostasis**: synapses adapt such as to ensure that average firing rate of neuron stays close to some **target rate** specific to each neuron
  - Sustained high firing rates are energetically costly

D. **Maintenance cost** and weak synapses
  1) Maintenance of strong synapses is costly in terms of biophysical machinery

  2) Synaptic plasticity is slowed down for weak synapses

Neuron Model

- Stochastic rate point neuron model with 100 input synapses
- Membrane potential

$$u(t) = u_r + \sum_{j=1}^{N} w_j \sum_{t_j^f < t} \exp\left(-\frac{t - t_j^f}{t_m} \right) a\left(t_j^f - t\right) \qquad a(t_j^f - t) = 1 - \exp\left[-(t_j^f - t)/\tau_a\right]$$

$$u_r = -70mV, \tau_m = 20ms, \tau_a = 50ms$$

- EPSP suppression after an action potential included through the factor $a\left(t_j^f - t\right)$

- Spike generation: Inhomogenous Poisson Process

$$\rho(t) = \rho_r + \left[u(t) - u_r\right] \cdot g$$

$$\rho_r = 1Hz, g = 12.5Hz/mV$$

Plasticity Rule: Objective Function

$$L = I - \gamma D - \lambda \Psi$$

- Maximizing information transmission

$$I = \left\langle \log \frac{P(Y \mid X)}{P(Y)} \right\rangle_{Y,X}$$

Mutual information between the input X from all 100 synapses and output Y

- Homeostasis

$$D = \left\langle \log \frac{P(Y)}{\widetilde{P}(Y)} \right\rangle_{Y}$$

Difference between the actual output distribution and output distribution generated by constant target rate

- Synaptic maintenance cost

$$\Psi = \frac{1}{2} \sum_j w_j^2 \left\langle n_j \right\rangle_X$$

Having strong synapses decrease the objective function. Only synapses that are activated in the past contribute to the cost.

Plasticity Rule

- Weights are updated in the direction of the gradient ascent of the objective function

$$\Delta w_j = \alpha(w_j)\frac{\partial L}{\partial w_j} \qquad \alpha(w_j) = 4\cdot 10^{-2}\frac{w_j^4}{w_j^4 + w_s^4}$$

- Plasticity is reduced for weak synapses through α(w_j) term

$$\frac{dw_j}{dt} = \alpha(w_j)\left[C_j(t)B_{post}(t) - \lambda w_j x_j(t)\right] \qquad C_j(t) = \lim_{\varepsilon\to+0}\int_0^{t+\varepsilon} c_j(t')e^{-(t-t')/\tau_C}\,dt'$$

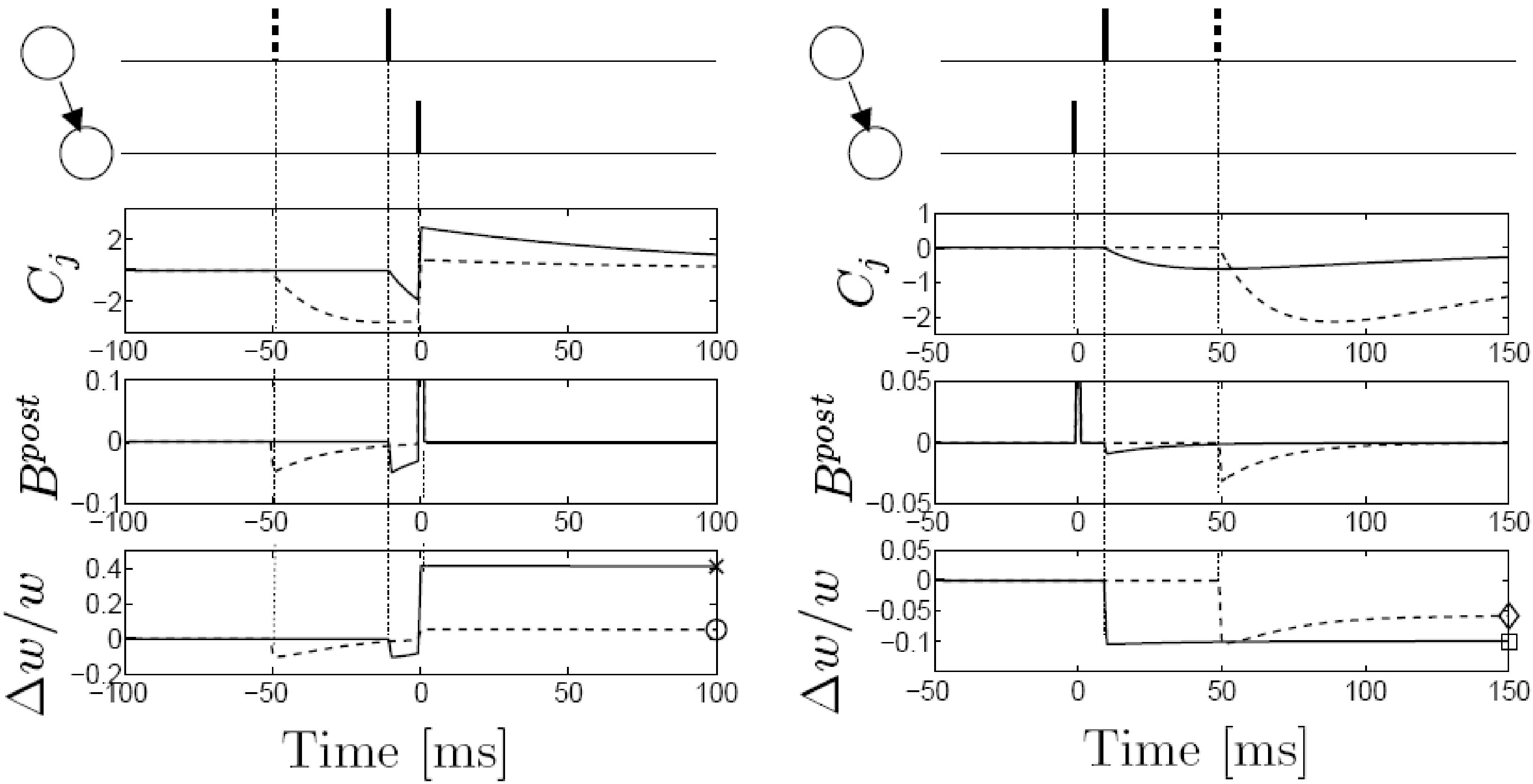
- Depends on
  - instantaneous postsynaptic firing rate
  - Expected postsynaptic firing rate
  - presynaptic spike times
  - postsynaptic spike times

$$c_j(t) = \frac{d\rho/du\big|_{u=u(t)}}{\rho(t)}\left[y(t)-\rho(t)\right]\int_0^{\infty} ds'\,\varepsilon(s')x_j(t-s')$$

$$B^{post}(t) = \left[y(t)\log\frac{\rho(t)}{\bar\rho(t)} - (\rho(t)-\bar\rho(t))\right] - \gamma\left[y(t)\log\frac{\bar\rho(t)}{\tilde\rho} - (\bar\rho(t)-\tilde\rho)\right]$$

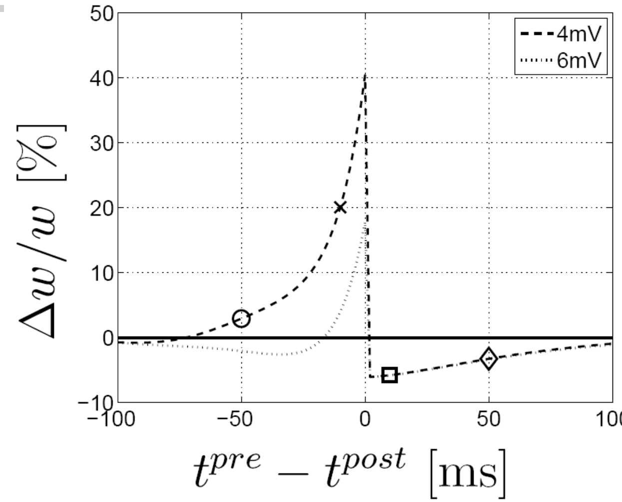
$$\bar\rho(t) = \left\langle \rho(t)\right\rangle_{X(t)|Y(t)} \qquad \tau_{\bar\rho}\frac{d\bar\rho^{est}}{dt} = -\bar\rho^{est}(t) + y(t)$$

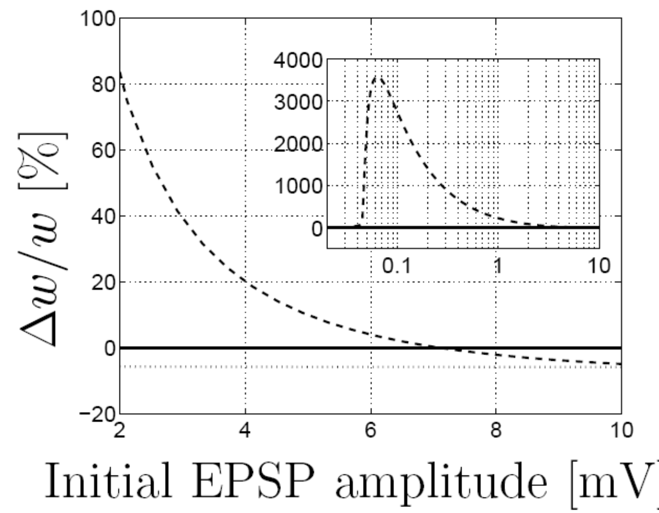
Plasticity Rule: Dynamics



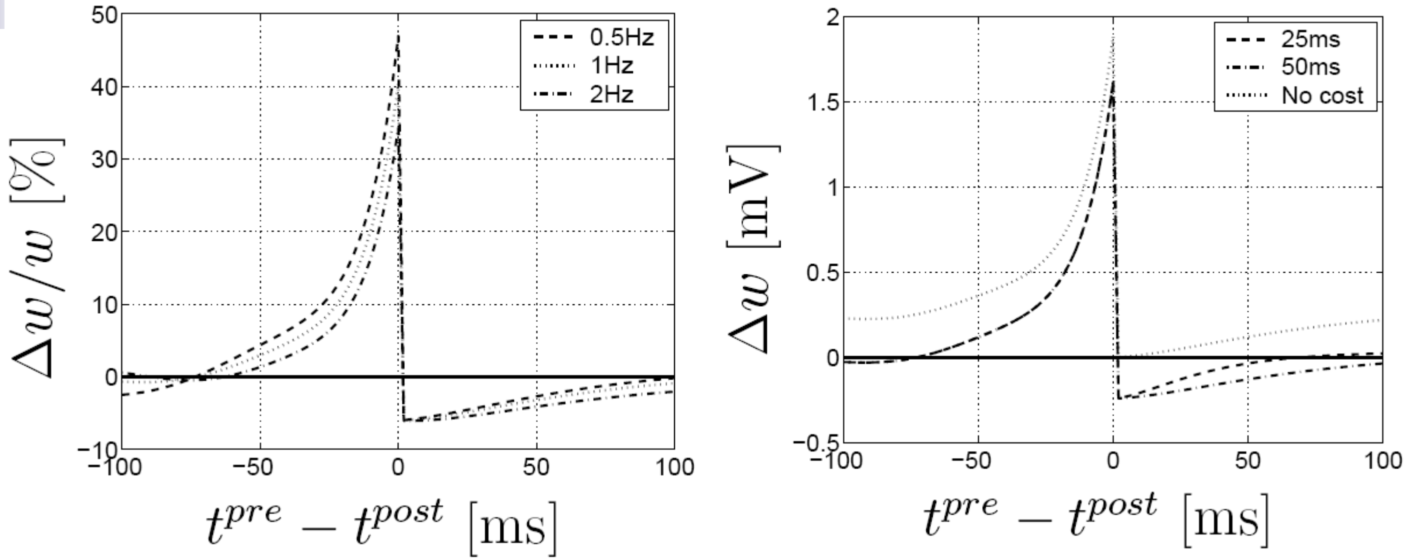
STDP (1)

- 60 pairs of pre- and postsynaptic spikes are applied at a frequency of 1Hz
- The rule exhibits STDP, with LTP on pre-before-post spike firing and DTP on reversed spiking
- Relative update of the weights decreases for strong synapses



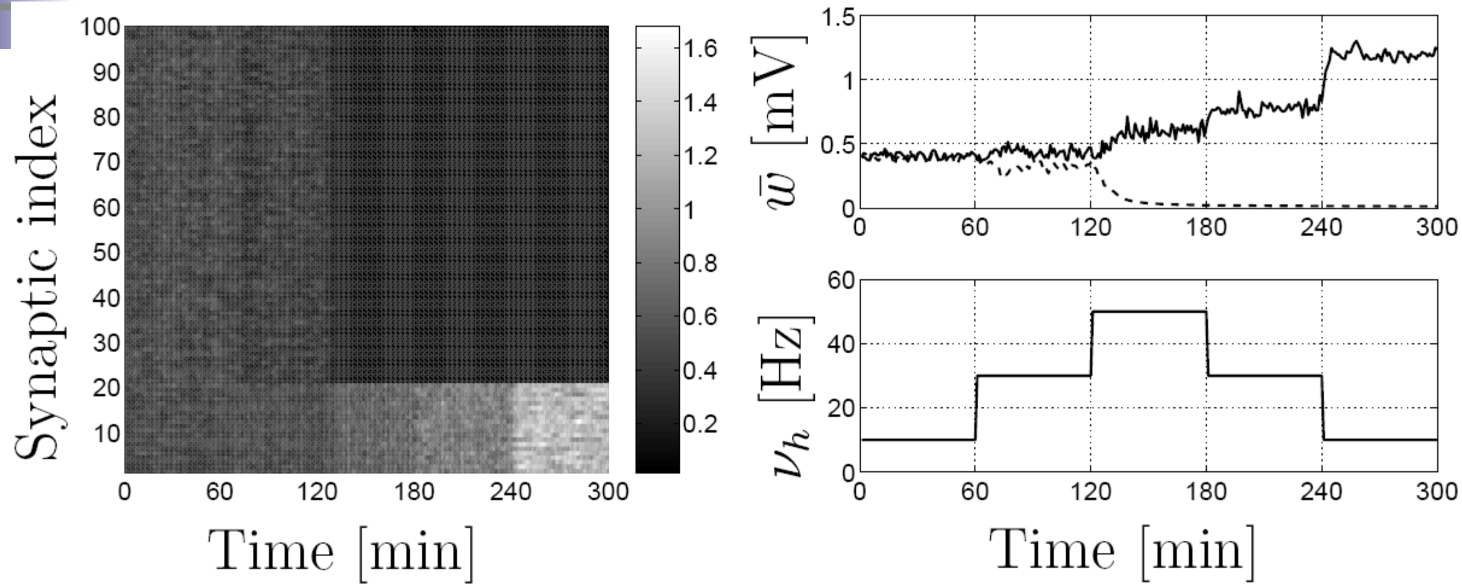


STDP (2)



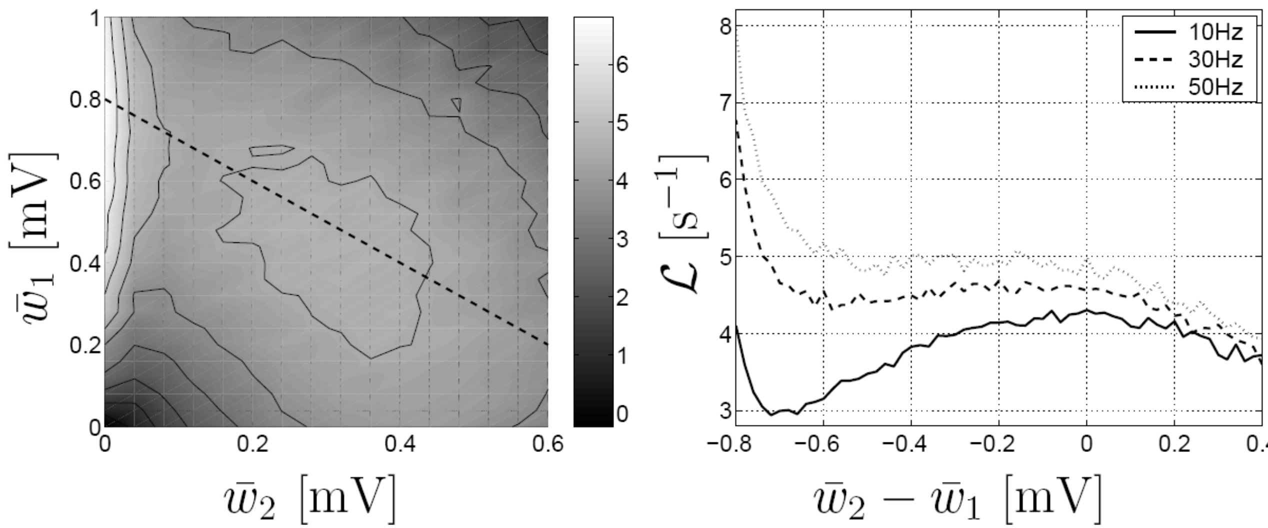
- The shape of STDP curve is weakly dependent on the frequency
- Time constant of EPSP suppression correlates with the shape of the LTD part of the function (Froemke et al, 2005)
- The cost term Ψ is required to lower the offset of the STDP function, and produce depression

Bimodal and Unimodal Weight Distribution



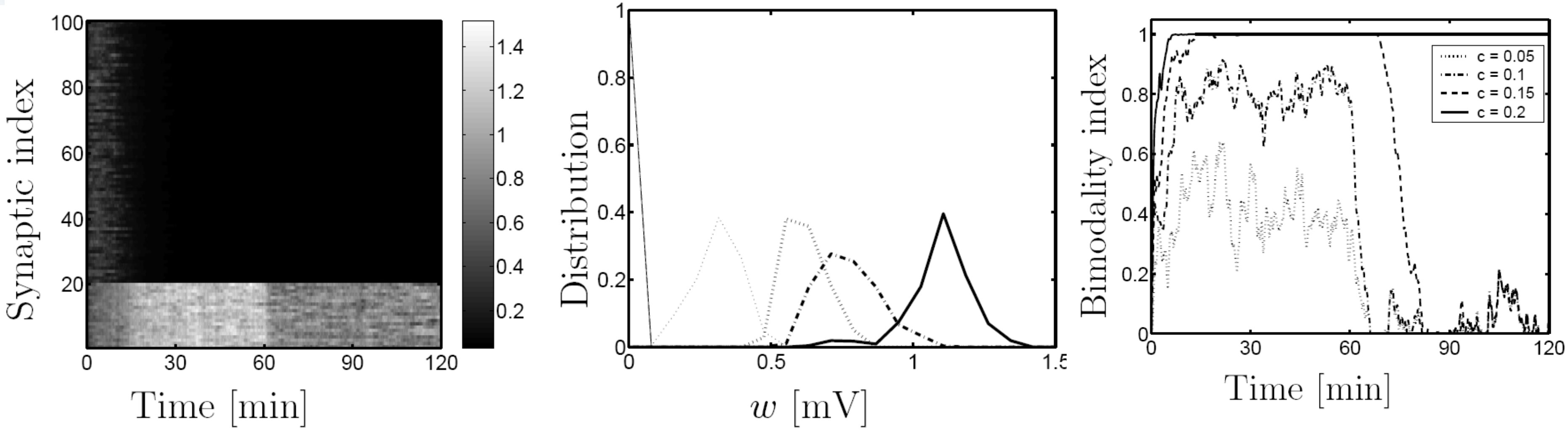
- Rate modulation between $v_l=1Hz$ *and* v_h is applied to first 20 synapses, and random spike train at constant rate of 10Hz to the other 80 synapses
- The unspecific (unimodal) weight distribution is stable for weak input features (low rate modulation)
- Bimodal weight distribution (synaptic specialization) develops under strong input features, and remains stable after these features are no longer present in the input

Bimodal and Unimodal Weight Distribution (2)



- The objective function has two maxima, one at the unspecific synapse pattern $(\overline{w}_1 \approx \overline{w}_2 \approx 0.4mV)$ and one for the specialized synapse pattern $(\overline{w}_1 \approx 0.8mV, \overline{w}_2 \approx 0mV)$
- The maximum at the unspecific synapse pattern disappears with strong input features (v_h=50Hz), thus weights change with gradient ascent towards the other maximum

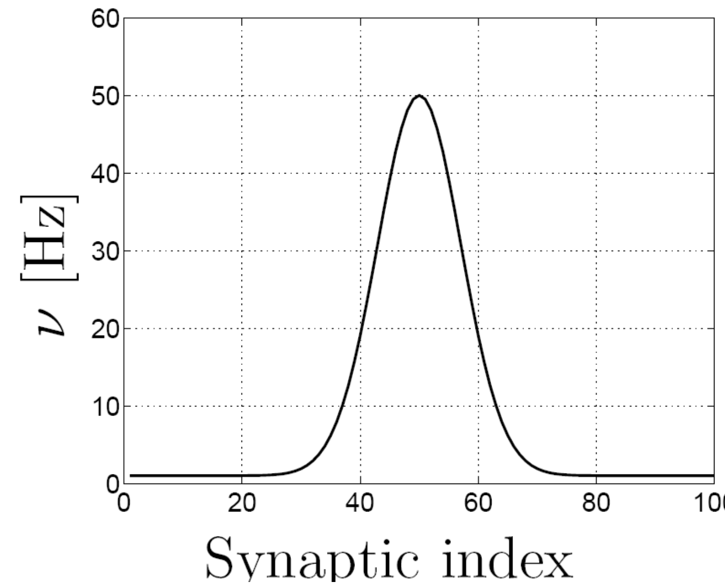
Memory retention



- Correlated input (*spike-spike correlations*) applied to 20 synapses, and independent poisson spikes is applied to other 80 synapses
- Correlation is active during first 60 min, then all inputs are uncorrelated
- Correlation index c: percentage of coincidental spike times between correlated inputs
- Bimodality index b: degree of separation of weight distributions of the two synaptic groups
- Memory is retained after memory induction process, but only for sufficiently high correlation index

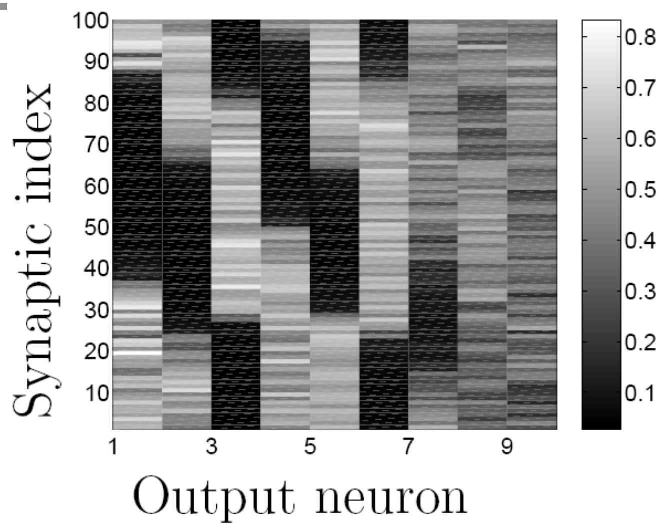
Receptive field development

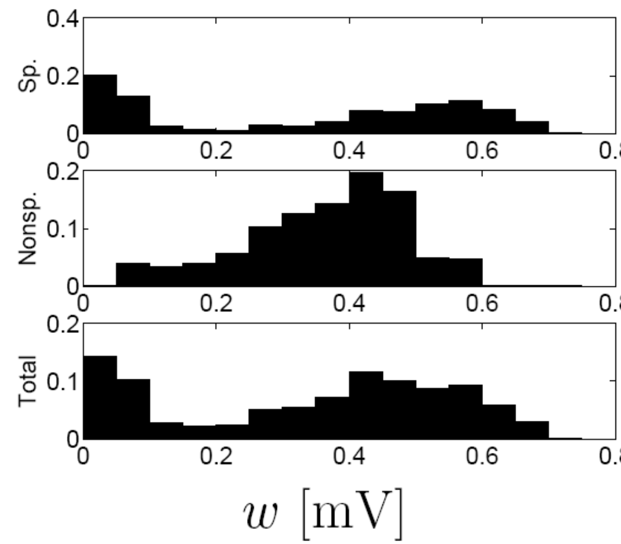
- Gaussian firing rate profile spanned across 100 synapses
- The center of the gaussian profile was shifted every 200 ms to a new presynaptic neuron
- Nine postsynaptic neurons with different initial weights received identical input



- During one hour of stimulus presentation 6 out of 9 developed synaptic specialization
- Specialized neurons developed different and slightly overlapping receptive fields

Receptive field development (2)





- Number of neurons developing synaptic specialization depends on
  - total stimulation time
  - strength of the stimulus
- Coexistence of unselective and selective neurons during development could explain broad distribution of EPSP amplitudes in experiments (Sjostrom)

Correlations, Memory Retention

- Sensitive to correlations

  As a by-product of maximizing information transmission, the weight update rule is sensitive to correlations between activity of pre- and postsynaptic neurons.

- Synaptic patterns (memories) are stable
  - Both unspecialized (unimodal) and specialized (bimodal) synaptic patterns are stable
  - Only highly strong correlations in the input can induce bimodal patterns
  - Bimodal patterns are preserved after their induction for a time period longer than the induction time
  - Slow update of weak synapses is important for stability of bimodal patterns and long term retention of memories

STDP Features

- Time-scale of LTP correlates with EPSP decay time constant
- Time-scale of LTD correlates with EPSP suppression time constant (Froemke et al, 2005)

- Complementary to other optimality models:
  - Chechik, 2003 – information maximisation with static input patterns
  - Bell and Para, 2005 – minimise output entropy
  - Bohte and Mozer, 2005 – maximise spike reliability

It combines homeostatic and maintenance cost constrains with statistical properties of input-output mapping

- The weight dependent cost term is indispensable, and must be fine tuned in order to achieve no weight change for large $| t_{pre} - t_{post} |$

Normalization and Input Selectivity

- Normalizes weights
  - Performs indirectly weight normalization by trying to keep postsynaptic activity close to some target firing rate
  - Similar to sliding threshold of the rate based Bienenstock-Cooper-Munro (BCM) rule
  - Weight normalization coupled with information maximization which favors increasing of weights, together create input selectivity in neurons

EPSP distributions during development

- Early in development all neurons have unspecialized unimodal synapse patterns, which produces broad weight distribution function

- Afterwards input selectivity forces forming two groups of synapses, silent and strong, which changes the shape of the distribution:
  - Sharp peak is formed for very weak synapses
  - The broad peak shifts towards large weights

- Both existence of unselective and selective neurons can explain broad EPSP distributions found in experiments (Sjostrom)

Scope of Utility and Significance

- Optimality models cannot explain the role of different molecular and physiological mechanisms within synaptic plasticity dynamics

- But, the functional role of synaptic dynamics can be independent of its underlying molecular implementation.

- There is evidence that different molecular mechanisms implement the same type of STDP and classical LTP.

- Hence, optimality models can serve as a good tool to understand common principles behind computational roles of synaptic plasticity, no matter how it’s implemented.

Conclusion

- Optimality models can help trace seemingly diverse experimental and theoretical results about plasticity to a small set of basic principles

- Information maximization, homeostasis and maintenance cost represent a sufficient set of computational and physiological, optimality based principles which can explain several experimentally found features of synaptic plasticity (STDP, input selectivity, stable synaptic patterns, memory retention)

Thank you for your attention.

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