Spike timing dependent plasticity - STDP

Markram et. al. 1997

Post before Pre: LTD
Pre before Post: LTP

EPSP amplitude (% of control)

Time (min)

Markram et. al. 1997
Spike Timing Dependent Plasticity: Temporal Hebbian Learning

Pre follows Post: Long-term Depression

Pre precedes Post: Long-term Potentiation

Weight-change curve (Bi&Poo, 2001)
Overview over different methods

**Machine Learning**
- Dynamic Prog. (Bellman Eq.)
- Monte Carlo Control
- SARSA
- Q-Learning
- SARSA
- Actor/Critic (technical & Basal Gangl.)
- Correlation based Control (non-evaluative)
- ISO-Control

**Classical Conditioning**
- Delta Rule
- Eligibility Traces
  - TD(λ)
  - TD(1)
  - TD(0)
  - often λ = 0

**Synaptic Plasticity**
- Hebb-Rule
- LTP (LTD = anti)
- STDP-Models
- Biophys. of Syn. Plasticity
  - Dopamine
  - Glutamate
- ISO-Control
- ISO-Model of STDP
- ISO-Learning
- Biophys. of Syn. Plasticity
  - Dopamine
  - Glutamate

**Evaluative Feedback (Rewards)**
- Neuronal Reward Systems (Basal Ganglia)
- Actor/Critic technical & Basal Gangl.
  - "Critic"

**Non-Evaluative Feedback (Correlations)**
- Neur. TD-formalism
- Neur. TD-Models
  - "fast"
  - "slow"
- Differential Hebb-Rule
- TD(1)
- TD(0)
- δ-Rule
- Rescorla/Wagner
- SARSA
- Correlation based Control (non-evaluative)
- ISO-Model
- Biophys. of Syn. Plasticity

**Un-Supervised Learning**
- correlation based

**Reinforcement Learning**
- example based
- supervised L.
History of the Concept of Temporally Asymmetrical Learning: Classical Conditioning

I. Pavlov
Pavlov Dog Labs

Please don't ring bell
Correlating two stimuli which are shifted with respect to each other in time.

Pavlov’s Dog: “Bell comes earlier than Food”

This requires to remember the stimuli in the system.

Eligibility Trace: A synapse remains “eligible” for modification for some time after it was active (Hull 1938, then a still abstract concept).
The first stimulus needs to be “remembered” in the system.
History of the Concept of Temporally Asymmetrical Learning: Classical Conditioning

Eligibility Traces

Note: There are vastly different time-scales for (Pavlov’s) behavioural experiments:
Typically up to 4 seconds

as compared to STDP at neurons:
Typically 40-60 milliseconds (max.)

I. Pavlow
Overview over different methods

**Machine Learning**
- Dynamic Prog. (Bellman Eq.)
- Monte Carlo Control
- SARSA
- Q-Learning

**Classical Learning**
- REINFORCEMENT LEARNING
  - example based
  - supervised L.
  - Rescorla/Wagner

**Mathematical formulation of learning rules is similar but time-scales are much different.**

- Differential Hebb-Rule ("slow")
- Differential Hebb-Rule ("fast")

**Eligibility Traces**
- TD(λ)
  - often λ=0
- TD(1)
- TD(0)

**ISO-Learning**
- STDP-Models
  - biophysical & network
- ISO-Model of STDP

**Neuronal Reward Systems (Basal Ganglia)**
- Biophys. of Syn. Plasticity
  - Dopamine
  - Glutamate

**Actor/Critic**
- technical & Basal Gangl.

**Correlation based Control**
- (non-evaluative)
- ISO-Control

**Evaluation over different methods**
- Mathematical formulation of learning rules is similar but time-scales are much different.
Differential Hebb Learning Rule

\[
\frac{d}{dt} \omega_i(t) = \mu \ u_i(t) \ V'(t)
\]

Simpler Notation

\(x = \text{Input}\)
\(u = \text{Traced Input}\)

Early: "Bell"
Late: "Food"
Defining the Trace

In general there are many ways to do this, but usually one chooses a trace that looks biologically realistic and allows for some analytical calculations, too.

\[ h(t) = \begin{cases} h_k(t) & t \geq 0 \\ 0 & t < 0 \end{cases} \]

**EPSP-like functions:**

**α-function:**  
\[ h_k(t) = te^{-at} \]

**Dampened Sine wave:**  
\[ h_k(t) = \frac{1}{b} \sin(bt) \ e^{-at} \]

**Double exp.:**  
\[ h_k(t) = \frac{1}{\delta} (e^{-at} - e^{-bt}) \]

This one is most easy to handle analytically and, thus, often used.
Defining the Traced Input $u$

**Convolution:**

$$u(x) = \int_{-\infty}^{\infty} f(u)g(x-u)du = f(x) \circ g(x) = g(x) \circ f(x)$$

**Correlation:**

$$w(x) = \int_{-\infty}^{\infty} f(u)g(u-x)du = g(x) \ast f(x) \neq f(x) \ast g(x)$$

Convolution used to define the traced input,

Correlation used to calculate weight growth (see below).
Defining the Traced Input $u$

Convolution:

$$u(x) = \int_{-\infty}^{\infty} f(u)g(x-u)\,du = f(x) \circ g(x) = g(x) \circ f(x)$$

Specifically (we are dealing with causal functions!):

$$u(t) = \int_{0}^{\infty} x(\tau)h(t - \tau)\,d\tau$$

If $x$ is a spike train (using the $\delta$-function):

$$x(t) = \sum_{j=0}^{M} \delta(t_j)$$

Then:

$$u(t) = \sum_{j=0}^{M} h(t - t_j)$$

For example:

$$x(t) = \delta(0) \quad u(t) = h(t)$$

$$x(t) = \delta(T) \quad u(t) = h(t - T)$$
### Differential Hebb Rules – The Basic Rule

**General:**

Two inputs only. Thus we get for the output:

\[ v = w_0 u_0 + w_1 u_1 \]

One weight unchanging:

\[ w_0 = 1 = \text{const.} \]

Same \( h \) for all inputs.

**ISO rule**

\[ \frac{dw_1}{dt} = \mu u_1 v' \]

Isotropic Sequence Order Lng. (as we can also allow \( w_0 \) to change!)
Differential Hebb Rules – More rules (but why?)

**ICO - Learning**

\[ \frac{dw_1}{dt} = \mu \ u_1 \ u'_0 \]

Input correlation Learning
(as we take the derivative of the unchanging input \( u_0 \))

**ISO3 - Learning**

\[ \frac{dw_1}{dt} = \mu \ u_1 \ v' \ R' \]

Three factor learning

The \( \mid \) denotes that we are only using positive contributions
Stability Analysis

$$\frac{d\omega_1}{dt} = \mu u_1 v'$$

$$\Delta \omega_1(t) = \int_0^\infty \frac{d\omega_1(t)}{dt} dt$$

$$\Delta \omega_1(t) = \Delta \omega_1^{AC}(t) + \Delta \omega_1^{CC}(t)$$
Stability Analysis

\[ \Delta w_1(t) = \Delta w^{AC}_1(t) + \Delta w^{CC}_1(t) \]

**Desired contribution**

**Undesired contribution**

Some problems with these differential equations:

1) As we are integrating to $\infty$ strictly we need to assume that there is no second pulse pair coming in “ever”.

2) Furthermore we should assume that $w_1' \rightarrow 0$ (hence $\mu$ small) or we get second order influences, too.
Stability Analysis (ISO)

Under these assumptions we can calculate $\Delta w^{AC}$ and $\Delta w^{CC}$ to find out whether the rules are stable or not.

In general we assume two inputs:

\[ x_1(t) = \delta(t) \quad \text{and} \quad x_0(t) = \delta(t - T) \]

and get for ISO:

\[ \frac{dw_1}{dt} = \mu u_1 v' \]

\[ \Delta w^{CC}_1 = w_0 \int h(t)h'(t - T)dt = w_0 \frac{1}{2\sigma} \frac{a-b}{a+b} h(t) \]

\[ \Delta w^{AC}_1 = w_1 \left( e^{\int h(t)h'(t-T)dt} - 1 \right) = w_1 \left( e^{\frac{1}{2}h^2(\infty)} - 1 \right) = 0 \]

ISO is (only) asymptotically stable for $t \to \infty$
Stability Analysis for pulse pair inputs (ISO)

The remaining upward drift is only due to the AC term influence (Instable!)

Setting $x_0=0$

$\mu=0.001$

$\mu=0.002$

Magn. of one step

Notice the AC contribution

This shows that early arrival of a new pulse pair might easily fall into a not fully relaxed system. (Instable!)
The weight change curve plots $\Delta w$ in dependence on the pulse pairing distance $T$ in steps, where we define $T>0$ if the $x_1$ signal arrives before $x_0$ and $T<0$ else.
Stability Analysis: Compare ISO with ICO

The basic rule: ISO-Learning

ISO rule
\[ \frac{dw_1}{dt} = \mu u_1 v' \]

ICO - Learning

ICO rule
\[ \frac{dw_1}{dt} = \mu u_1 u'_0 \]

Input correlation Learning
(as we take the derivative of the unchanging input \( u_0 \))

Notice the difference
Stability Analysis: ICO

\[ \Delta w_1^{CC} = w_0 \int h(t) h'(t - T) dt = w_0 \frac{1}{2\sigma} \frac{a-b}{a+b} h(t) \]

\[ \Delta w_1^{AC} \equiv 0 \]

Fully stable!

No more drift!

x_0 = 0

\[ \mu = 0.001 \]

\[ \mu = 0.002 \]

ICO: Weight change curve (same as for ISO)

Single pulse pair (no more AC term in ICO).

ICO: Weight change curve

ISO: Weight change curve

Same as for ISO!
Stability Analysis: More comparisons

The basic rule: ISO-Learning

ISO rule
\[ \frac{d w_1}{d t} = \mu u_1 v' \]

Conjoint learning-control-signal (same for all inputs!)

ICO - Learning

ICO
\[ \frac{d w_1}{d t} = \mu u_1 u_0' \]

Single input as designated learning-control-signal.

Makes ICO a heterosynaptic rule of questionable biological realism.
Stability Analysis: More comparisons
This difference is especially visible when wanting to symmetrize the rules (both weights can change!).

ISO-Sym One control signal!

ICO-Sym Two control signals!
The Effects of Symmetry

Synapse $w_1$ grows because $x_1$ is before $x_0$.

Synapse $w_0$ shrinks because $x_0$ is after $x_1$.

ICO-sym is truly symmetrical, but needs two control signals.

ISO-sym behaves in a difficult and unstable oscillatory way.
ISO3: uses – like ISO – a single learning-control-signal

**ISO3 - Learning**

Idea: The system should learn ONLY at that *moment in time* when there was a “relevant” event r!

We use a shorter trace for r, as it should remain rather restricted in time.

Same filter function h but parameters $a_r$ and $b_r$.

We also define $T_r$ as the interval between $x_1$ and r. Many times $T_r=T$, hence r occurs together with $x_0$. 

$$\frac{dw_1}{dt} = \mu \; u_1 \; v' \; R'$$
\[ \Delta w_1^{CC} = w_0 \int h(t)h'(t - T)h'_r(t - T_r)\, dt \]

\[ \Delta w_1^{AC} = w_1 \int h(t)h'(t)h'_r(t - T_r)\, dt \]

Observations:
1) Cannot be solved anymore!
2) AC term is generally NOT equal to zero.
3) Not even asymptotic convergence can be generally assured.

So what have we gained?

One can show that for \( T_r = T \) the AC term vanishes if \( v \) has its maximum at \( T \).
If we restrict learning to the moment when $x_0$ occurs then we do not have any AC contribution.

!! A questionable assumption: $\text{argmax}(u_1) = T$ !!
Stability Analysis: ISO3

No more upwards drift for ISO3

$x_0 = 0$

ISO $\mu = 10^{-4}$

ISO3 $\mu = 7.25 \times 10^{-5}$

Single pulse pair (ISO3 is stable and relaxes instantaneously).

Weight change curve (no more STDP!)

$\Delta \omega$

$t$
A General Problem: $T$ is usually unknown and variable

Introducing a filter bank: (example ISO)

Spreading out the earlier input over time!

Remember: “A questionable assumption: $\arg\max(u_1) = T$”
Stability Analysis: ISO3 with a filter bank

With a filter bank we get for the output:

\[ v = w_0 u_0 + \sum_{j=0}^{N} w_j^j u_1^j \]

Original Rule was:

\[ \frac{dw_1}{dt} = \mu \ u_1 \ v' \ R' \]

Single weights develop now as:

\[ \frac{1}{\mu} \Delta w_1^k = \int w_0 \ u_1^k u_0' R' \] + \[ \int u_1^k \ \sum_{j=1}^{N} w_j^j (u_j^j)' R' \]

CC \hspace{2cm} AC

With delta-function inputs at t=0 and t=T we get:

\[ \frac{1}{\mu} \Delta w_1^k = w_0 u'(0) u_1^k(T) \] + \[ \left( \sum_{j} w_j^j u_j^j(T) \right)' u_1^k(T) \]

It is possible to prove that this term becomes zero as a consequence of the learning!