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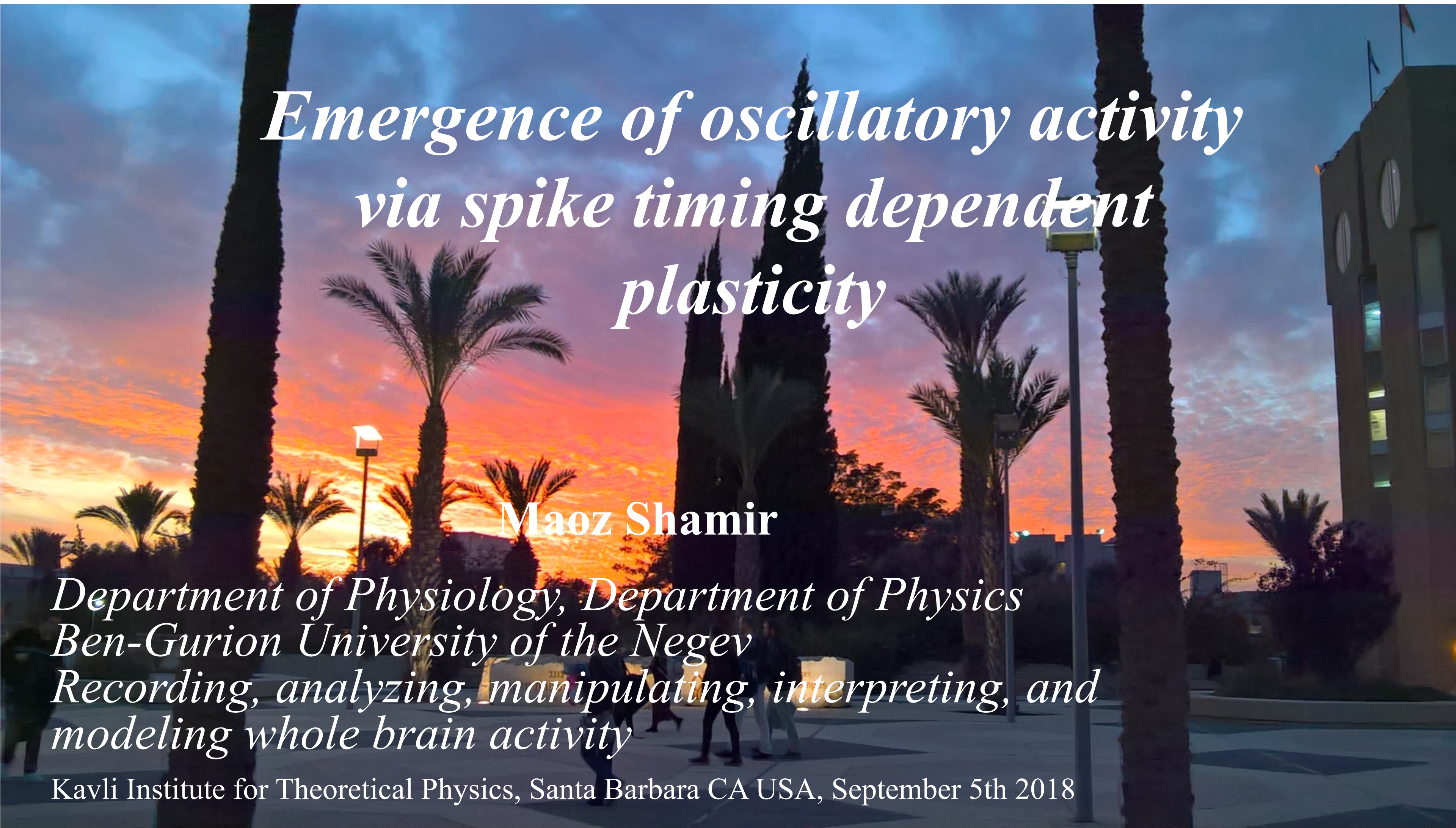
מרכז זלוטובסקי למדעי העצב
Zlotowski Center for Neuroscience



Emergence of oscillatory activity via spike timing dependent plasticity

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Recording, analyzing, manipulating, interpreting, and modeling whole brain activity

Kavli Institute for Theoretical Physics, Santa Barbara CA USA, September 5th 2018

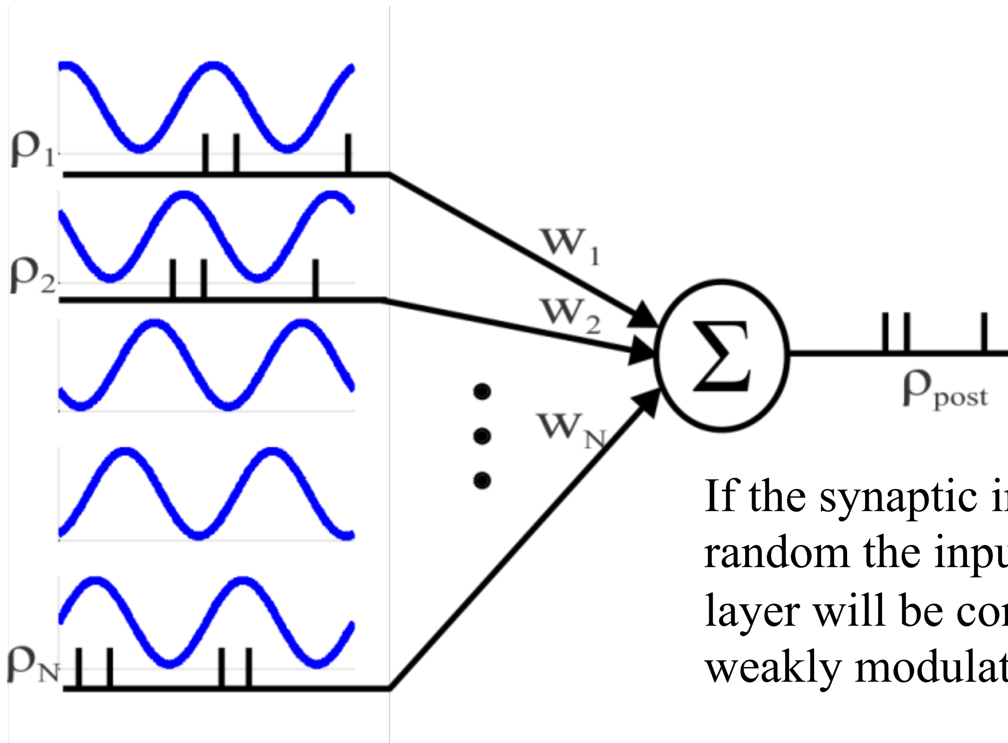
Outline of the talk

- Introduction:
  - The question: transmission of oscillations downstream
  - Plasticity & learning
- The transfer of oscillatory information
  - Effect of oscillations on learning dynamics of single synapse
  - Learning dynamics of oscillating synaptic population
- Emergence of oscillations via learning

How can information about oscillatory activity be transmitted downstream?

Assume simple feed-forward architecture

Input layer neurons oscillate at frequency *f* with uniformly distributed phases.



If the synaptic inputs are uniform or random the input to the downstream layer will be constant in time or very weakly modulated.

To transmit information about oscillatory activity we need a mechanism that will shape feed-forward synaptic connections according to their phases

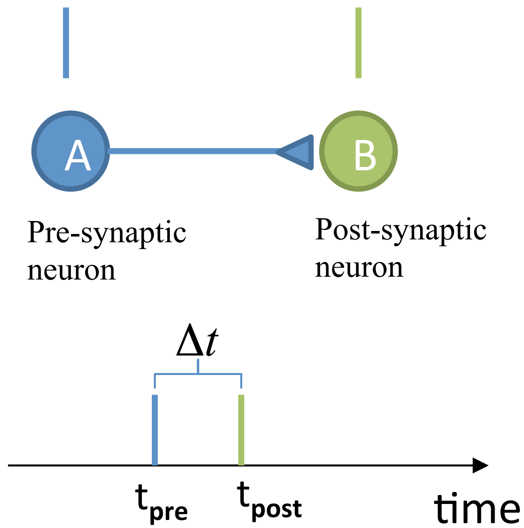
What mechanism facilitates the transmission of oscillatory activity downstream?

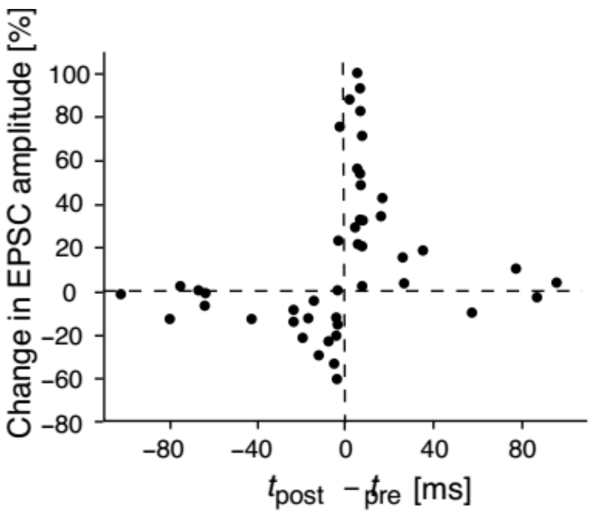
Is this mechanism genetically hard wired?

OR

Can it be acquired via a process of learning?

Spike Timing Dependent Plasticity

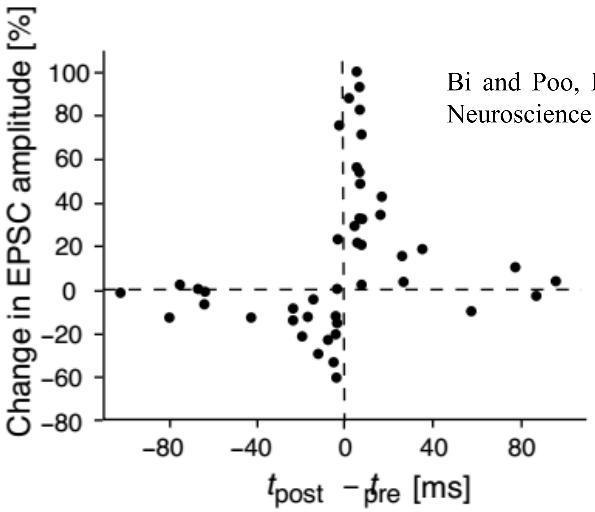




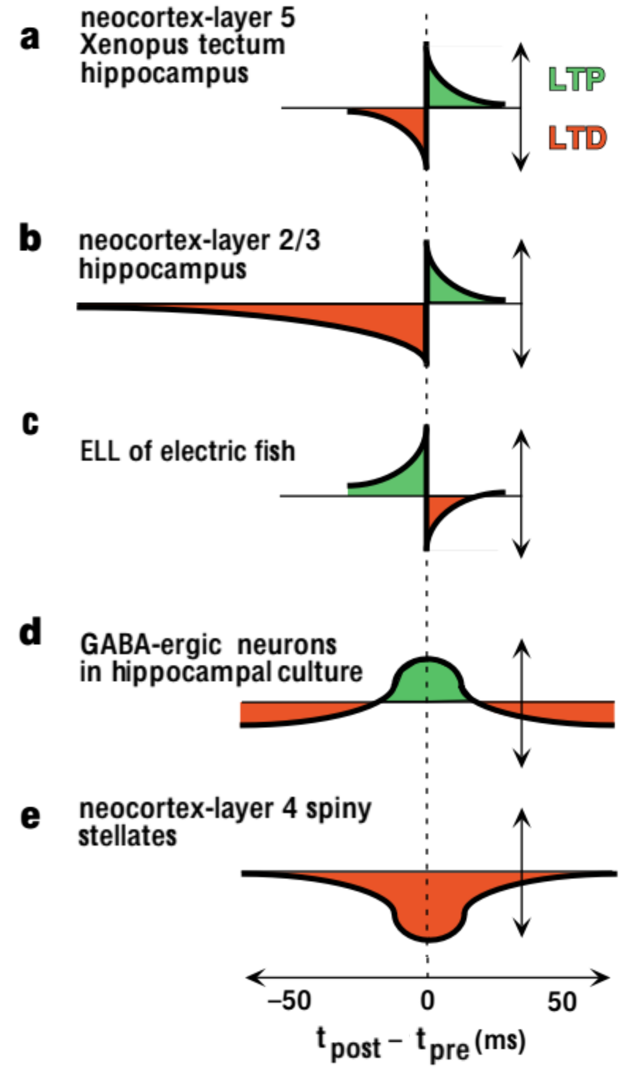
Adopted from Bi and Poo, Dec. 1998; The Journal of Neuroscience 18(24): 10464-10472

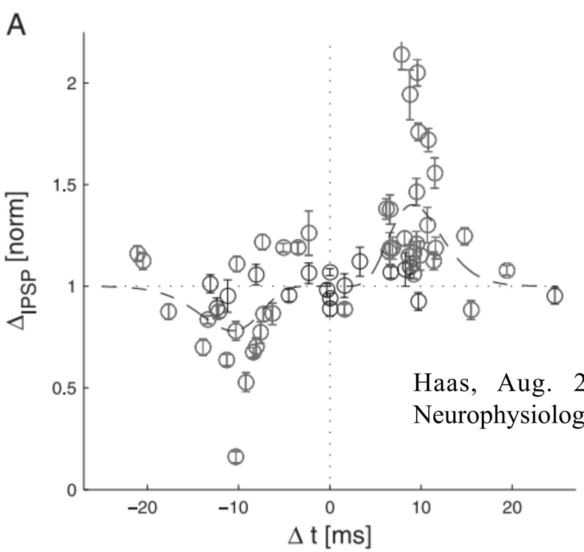
Bi and Poo JNS (1998)

Introduction – STDP



Bi and Poo, Dec. 1998; The Journal of Neuroscience 18(24):10464-10472

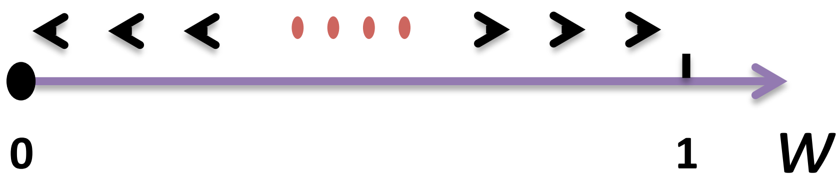




Haas, Aug. 2006; The Journal of Neurophysiology Vol.96 no.6:3305-3313

STDP as unsupervised learning process

Positive feedback of "canonical" excitatory STDP



Weak synapse

⇩

Post spike uncorrelated with pre spike

⇩

Learning dynamics will sample randomly both branches

⇩

Synapse will weaken if α>1

Strong synapse

⇩

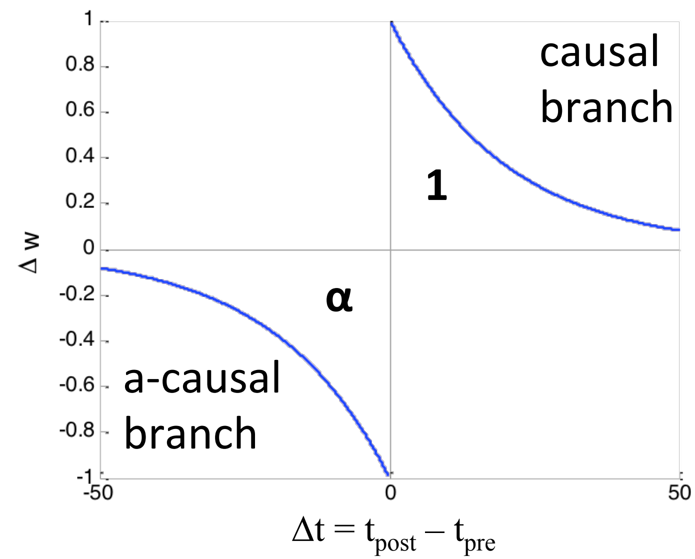
Post spike more likely to follow pre

⇩

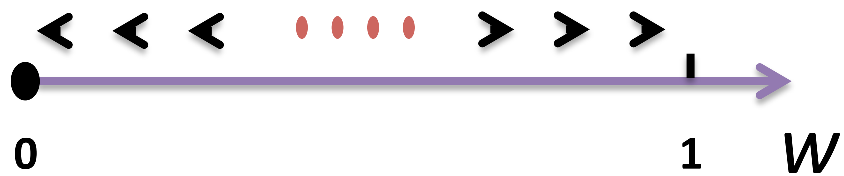
Learning dynamics will sample more causal branch

⇩

Synapse will strengthen



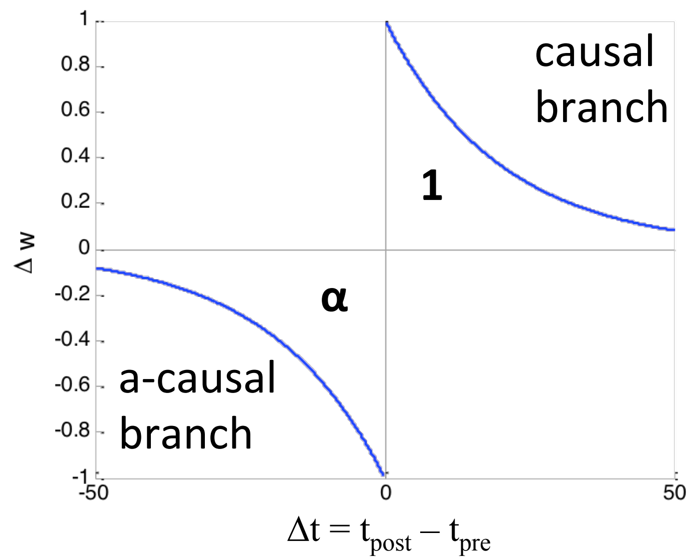
Positive feedback can by weakened by Scaling the learning with the synaptic weight



$$\Delta w = \pm \lambda f_{\pm}(w) K(t_{pre} - t_{post})$$

$$f_{+}(w) = (1 - w)^{\mu}$$

$$f_{-}(w) = \alpha w^{\mu}$$



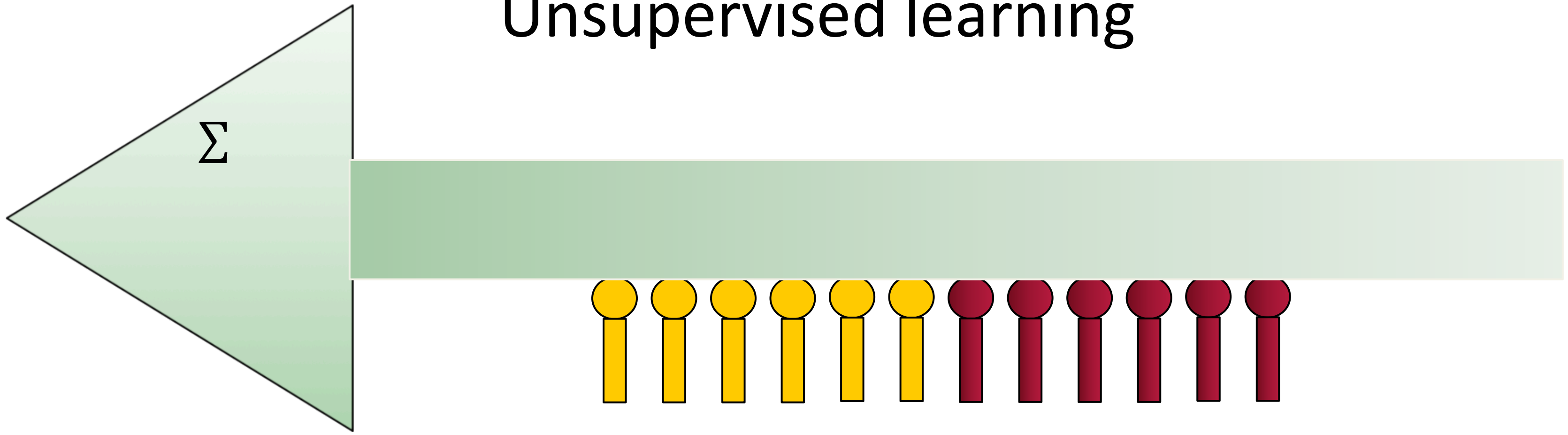
Gütig et al JNS (2003)

Correlations can strengthen the positive feedback

Red group is strong → A spike from a Red cell will be more likely to be followed by post spike → Red synaptic weight will potentiate

Yellow group is weak → A spike from a Yellow cell is less correlated with post spike → Yellow synaptic weights will depress

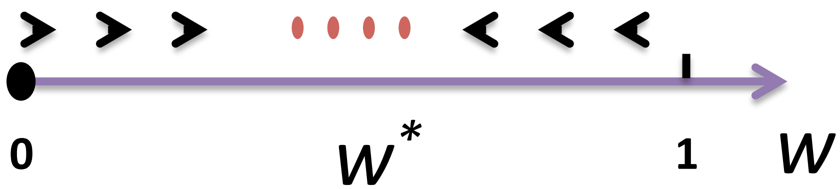
Unsupervised learning



Gütig et al JNS (2003)

Inhibitory STDP

Negative feedback of “canonical” inhibitory STDP



Weak synapse

⇓

Post spike uncorrelated with pre spike

⇓

Learning dynamics will sample randomly both branches

⇓

Synapse will strengthen if α<1

Strong synapse

⇓

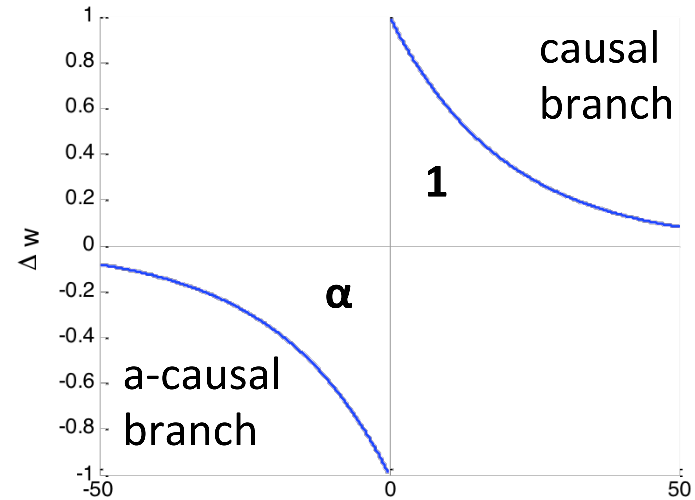
Post spike less likely to follow pre

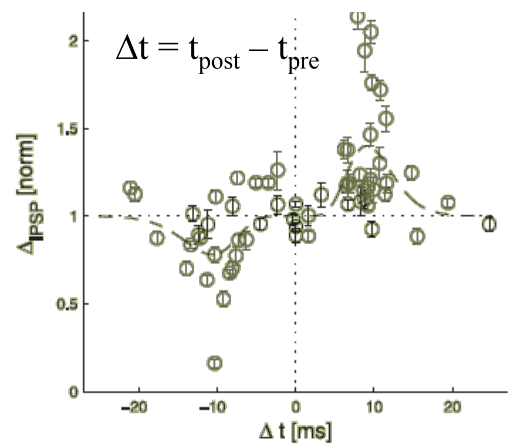
⇓

Learning dynamics will sample more the a-causal branch

⇓

Synapse will weaken





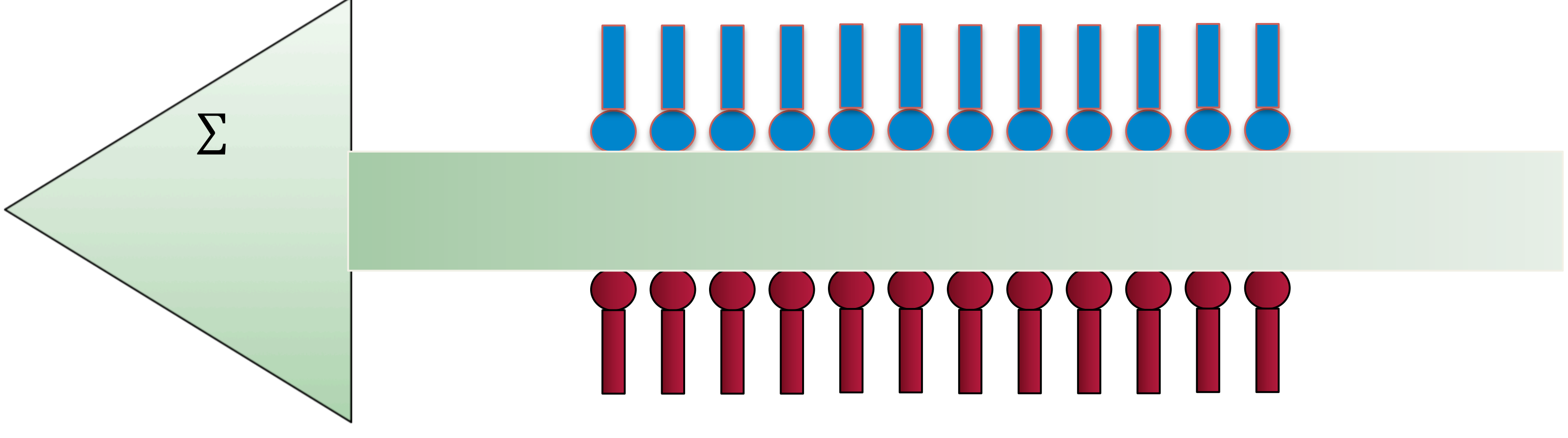
Haas et al JNP (2006)

Balance of excitation and inhibition

Excitation increases → A spike from an inhibitory cell will be less correlated with post spike → Inhibitory synaptic weights will potentiate

Excitation decreases → A spike from an inhibitory cell is less likely to be followed by a post spike → Inhibitory synaptic weights will depress

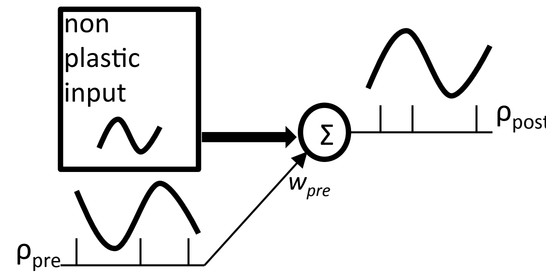
Homeostatic mechanism

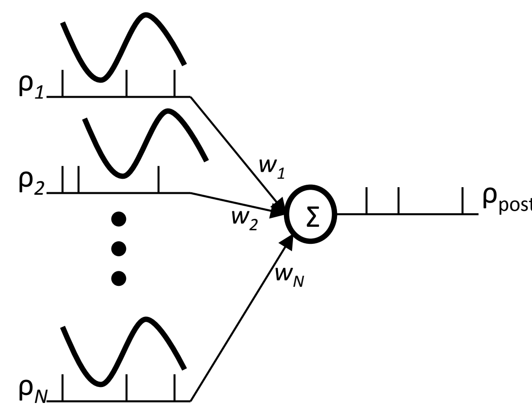


Can STDP facilitate the transmission of oscillatory activity?

Study the effect of oscillatory activity on STDP of a purely feed-forward architecture in two stages:

A. STDP of a single synapse
B. STDP of a 'synaptic population'

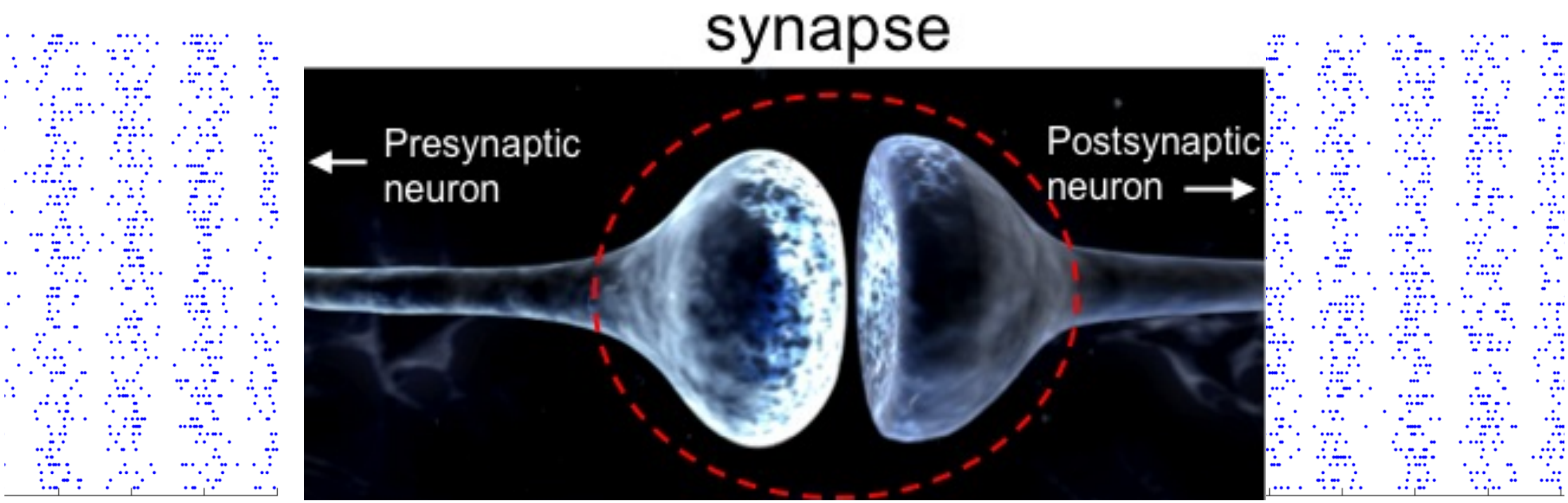




Luz and Shamir (2016)

Single synapse STDP dynamics

$$r_{pre/post}(t) = D_{pre/post} + A_{pre/post}\cos\left(\nu t - \varphi_{pre/post}\right)$$



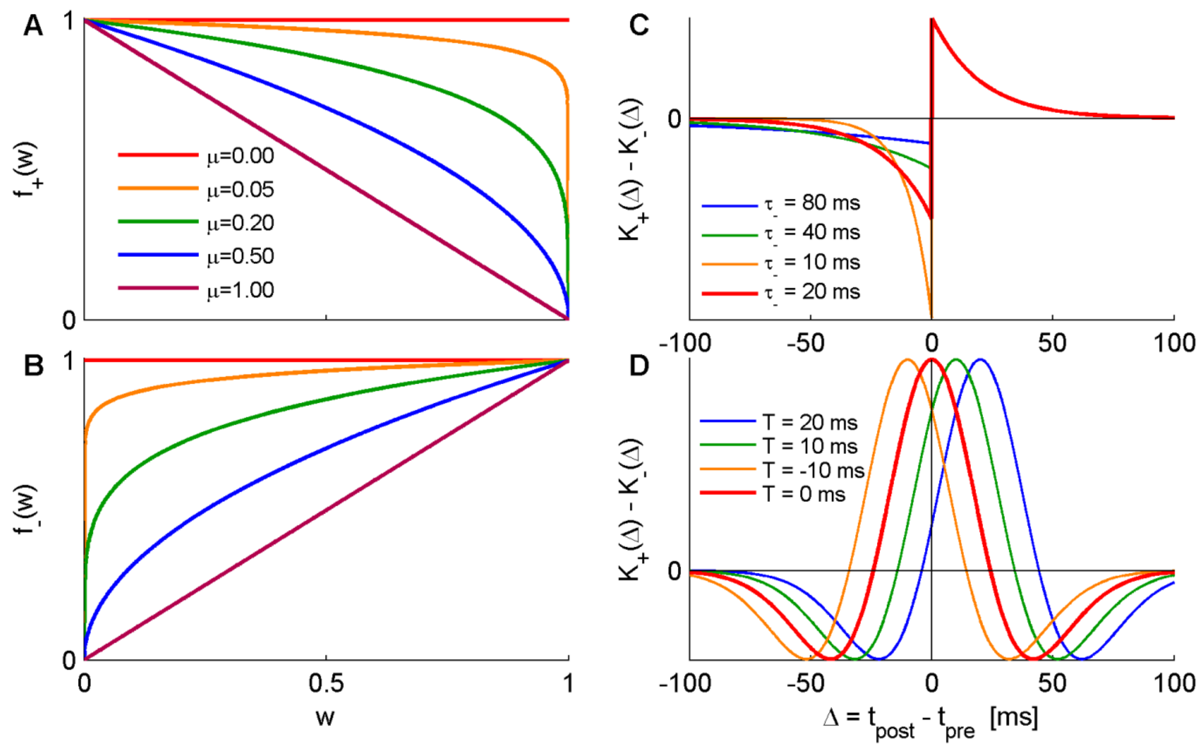
The STDP learning rule

$$\Delta w = \lambda\left(f_+(w)K_+(\Delta t) - f_-(w)K_-(\Delta t)\right)$$

We assumed a separation of variables: $f_\pm (w)K(\Delta t)$.
The learning rate: λ. We will be interested in the limit of slow learning rate, $\lambda \to 0$.
Our interest results from the fact that this is what we can solve.

$$f_+(w) = (1-w)^\mu$$

$$f_-(w) = \alpha w^\mu$$



Gütig et al JNS (2003)

Mean-field Fokker Planck Theory

$$\Delta w = \begin{cases} +\lambda f_{+}(w) K(\Delta t) & \text{Potentiation term} \\ -\lambda f_{-}(w) K(\Delta t) & \text{Depression term} \end{cases}$$

$$w(t+\delta t) - w(t) = \pm\lambda f_{\pm}(w) X(\hat{spike}^{post} \in [t, t+\delta t]) \int_{-\infty}^{t} dt' \rho_{pre}(t') K_{\pm}(t-t') \pm \lambda f_{\pm}(w) X(\hat{spike}^{pre} \in [t, t+\delta t]) \int_{-\infty}^{t} dt' \rho_{post}(t') K_{\pm}(t'-t)$$

Taking the short times limit $\delta t \rightarrow 0$,

$$\dot{w}(t) = \lambda f_{+}(w) \mathcal{L}^{C}(t) - \lambda f_{-}(w) \mathcal{L}^{A}(t)$$

$$\mathcal{L}^{C}(t) = \int_{-\infty}^{t} \rho_{pre}(t') \rho_{post}(t) K_{+}(t-t') dt'$$

Mean-field Fokker Planck Theory

In the limit of slow learning rate, $\lambda \rightarrow 0$, the STDP dynamics samples the pre-post correlations over long periods in which the synaptic weight is relatively fixed.

$$\langle w \rangle (w) = \lambda f_{+}(w) \int_{-\infty}^{\infty} \Gamma(\Delta) K_{+}(\Delta) d\Delta - \lambda f_{-}(w) \int_{-\infty}^{\infty} \Gamma(\Delta) K_{-}(\Delta) d\Delta$$

$$\Gamma(\Delta) \equiv \langle \rho_{pre}(0) \rho_{post}(\Delta) \rangle$$

STDP dynamics is governed by the pre-post correlations.

Single synapse STDP dynamics: Analytical results

- The "Mean field" Fokker–Planck of the learning dynamics:

$$\frac{1}{\lambda}\frac{d}{dt}w = f_+(w)\int_{-\infty}^{\infty}\Gamma(\Delta)K_+(\Delta)d\Delta - f_-(w)\int_{-\infty}^{\infty}\Gamma(\Delta)K_-(\Delta)d\Delta$$

- The pre-post correlation structure:

$$\Gamma(\Delta)=\Gamma_D+\Gamma_A\cos(\nu\Delta+\varphi);\quad \Gamma_D=D_{pre}D_{post},\quad \Gamma_A=\frac{1}{2}A_{pre}A_{post},\quad \varphi=\varphi_{pre}-\varphi_{post}$$

- W converges to this steady state solution:

$$w^{*}(\varphi)=1/(\alpha Q(\varphi))^{1/\mu}+1 \qquad Q(\varphi)=1+\Gamma_r K_{-}^{\nu}\cos(\Omega_{-}^{\nu}+\varphi)/1+\Gamma_r K_{+}^{}$$

$$\Gamma_r \equiv \Gamma_A/\Gamma_D = A_{pre}A_{post}/2 D_{pre}D_{post}$$

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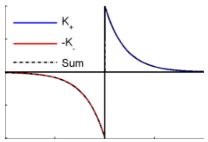
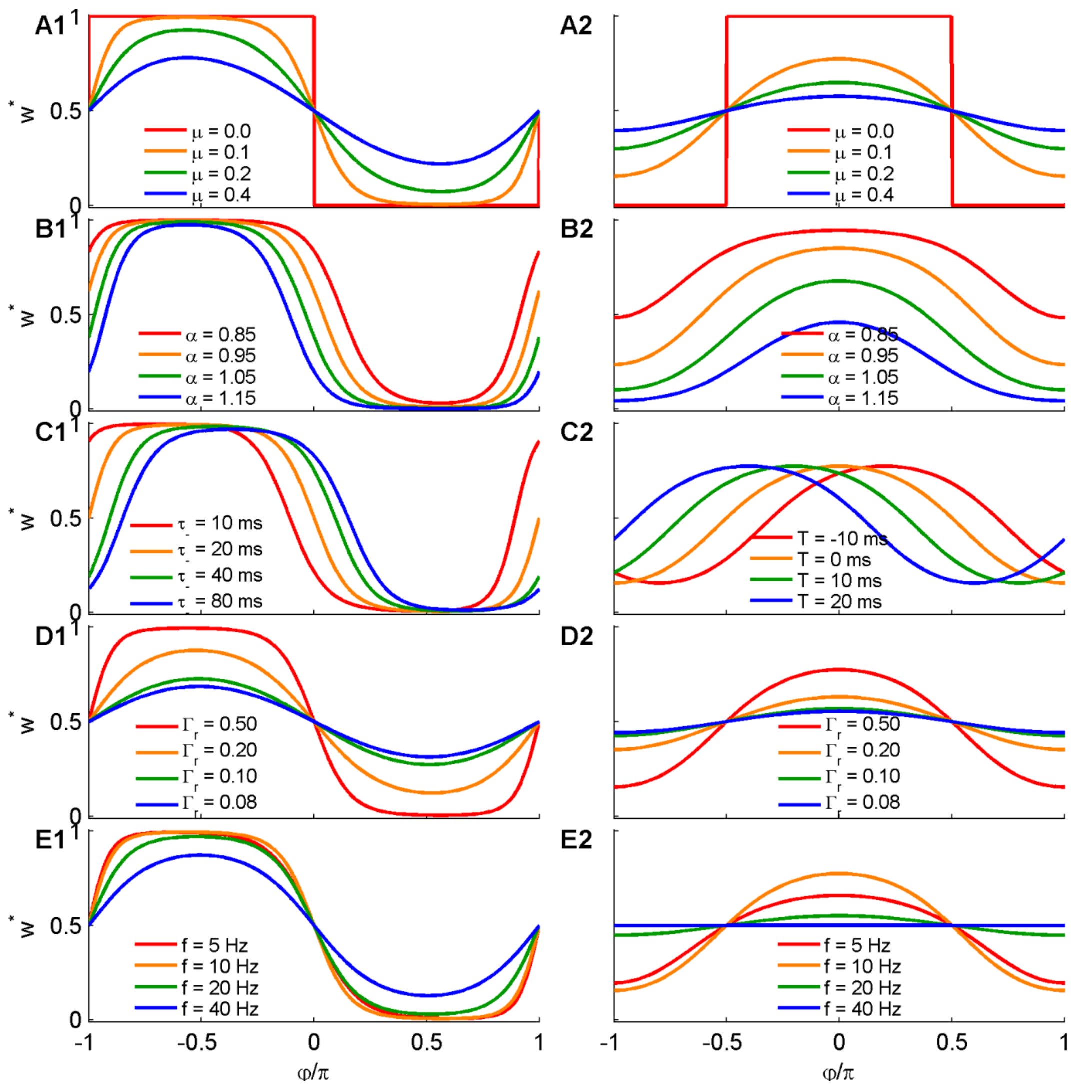
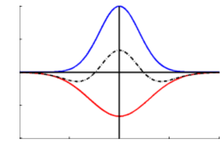
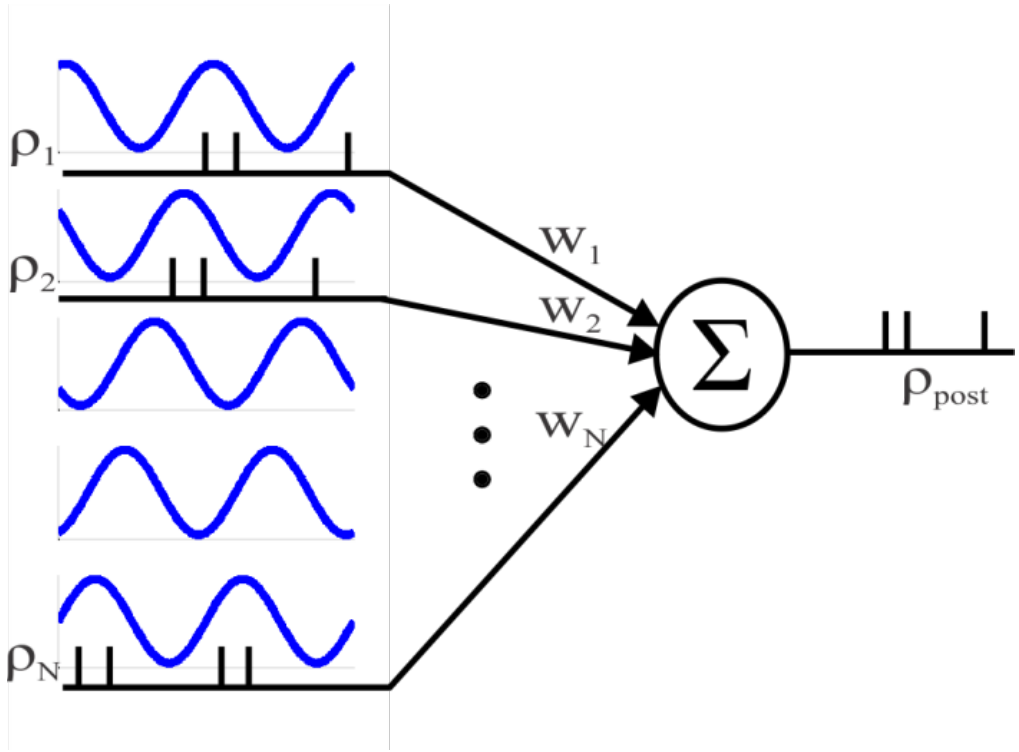
Single synapse STDP – useful model







How can information about oscillatory activity be transmitted downstream?



Luz and Shamir (2016)

The mean-field Fokker Planck Theory

N non-linear equations

$$\dot{w}(\varphi,t)/\lambda = f_+(w(\varphi,t))\int_{-\infty}^{\infty}\Gamma(\varphi,\Delta)K_+(\Delta)d\Delta - f_-(w(\varphi,t))\int_{-\infty}^{\infty}\Gamma(\varphi,\Delta)K_-(\Delta)d\Delta$$

The delayed linear-Poisson neuron

$$\langle\rho_{post}(t)\rangle = \frac{1}{N}\sum_{j=1}^{N} w_j\rho_j(t-d)$$

Luz and Shamir (2016)

The mean-field Fokker Planck Theory

The STDP dynamics is dominated by order parameters

$$\dot{w}(\varphi, t)/\lambda = \bar{w}(t)F_0(\varphi, t) + \tilde{w}(t)F_1(\varphi, t)$$

$$\bar{w} := \int_{-\pi}^{\pi} w(\phi)\,\frac{d\phi}{2\pi},$$

$$\tilde{w}e^{i\psi} := \int_{-\pi}^{\pi} e^{i\phi} w(\phi)\,\frac{d\phi}{2\pi}.$$

$$F_0(\varphi, t) := D^2(\bar{K}_+ f_+(w(\varphi, t)) - \bar{K}_- f_-(w(\varphi, t))),$$

$$F_1(\varphi, t) := \frac{A^2}{2}\{\tilde{K}^v_+ f_+(w(\varphi, t))\cos(\varphi - \Omega^v_+ - vd - \psi(t)) - \tilde{K}^v_- f_-(w(\varphi, t))\cos(\varphi - \Omega^v_- - vd - \psi(t))\}$$

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The STDP dynamics is governed by three order parameters

- The dynamic equations for the order parameters $\bar{w}$, $\tilde{w}$ and ψ:

$$\frac{d}{dt}\bar{w}(t) = \lambda\left(\bar{w}(t)\overline{F_0} + \tilde{w}(t)\overline{F_1}(t)\right)$$

$$\frac{d}{dt}\tilde{w}(t) = \lambda\left(\bar{w}(t)\tilde{F}_0\cos\left(\Phi_0 - \psi(t)\right) + \tilde{w}(t)\tilde{F}_1\cos\left(\Phi_1 - \psi(t)\right)\right)$$

$$\tilde{w}(t)\frac{d}{dt}\psi(t) = \lambda\left(\bar{w}(t)\tilde{F}_0\sin\left(\Phi_0 - \psi(t)\right) + \tilde{w}(t)\tilde{F}_1\sin\left(\Phi_1 - \psi(t)\right)\right)$$

- Where:

$$F_0(\varphi) = \frac{D^2}{2\pi}\left(\overline{K_+}f_+\left(w(\varphi)\right) - \overline{K_-}f_-\left(w(\varphi)\right)\right)$$

$$F_1(\varphi,t) = \frac{A^2}{4\pi}\begin{pmatrix}\tilde{K}_+f_+\left(w(\varphi)\right)\cos\left(\Omega_+ + \psi(t) + \varphi\right) \\ -\tilde{K}_-f_-\left(w(\varphi)\right)\cos\left(\Omega_- + \psi(t) + \varphi\right)\end{pmatrix}$$

$$\overline{F_n} \equiv \int_{-\pi}^{\pi}F_n(\varphi)d\varphi \quad \tilde{F}_n e^{i\Phi_n} \equiv \int_{-\pi}^{\pi}e^{-i\theta}F_n(\varphi)d\varphi$$

$$\tilde{K}_{+/-} \equiv \tilde{K}^{\nu}_{+/-} \quad \Omega_{+/-} \equiv \nu d - \Omega^{\nu}_{+/-}$$

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Stability of the homogeneous solution

Aim: study development of non-trivial phase preference profile.

Problem: non-linear, coupled, high dimensional.

Strategy: study the homogeneous solution and investigate when it looses stability.

Stability of the homogeneous solution

The stability of the homogeneous solution is governed by the temporal structure of the STDP rule and the pre-post delay

$$\mu_c \geq \frac{A^2}{4D^2}\left(\frac{\tilde{K}_+^\nu}{\bar{K}}\cos(\Omega_+^\nu + \nu d) - \frac{\tilde{K}_-^\nu}{\bar{K}}\cos(\Omega_-^\nu + \nu d)\right)$$

Assumes $\alpha > 1$

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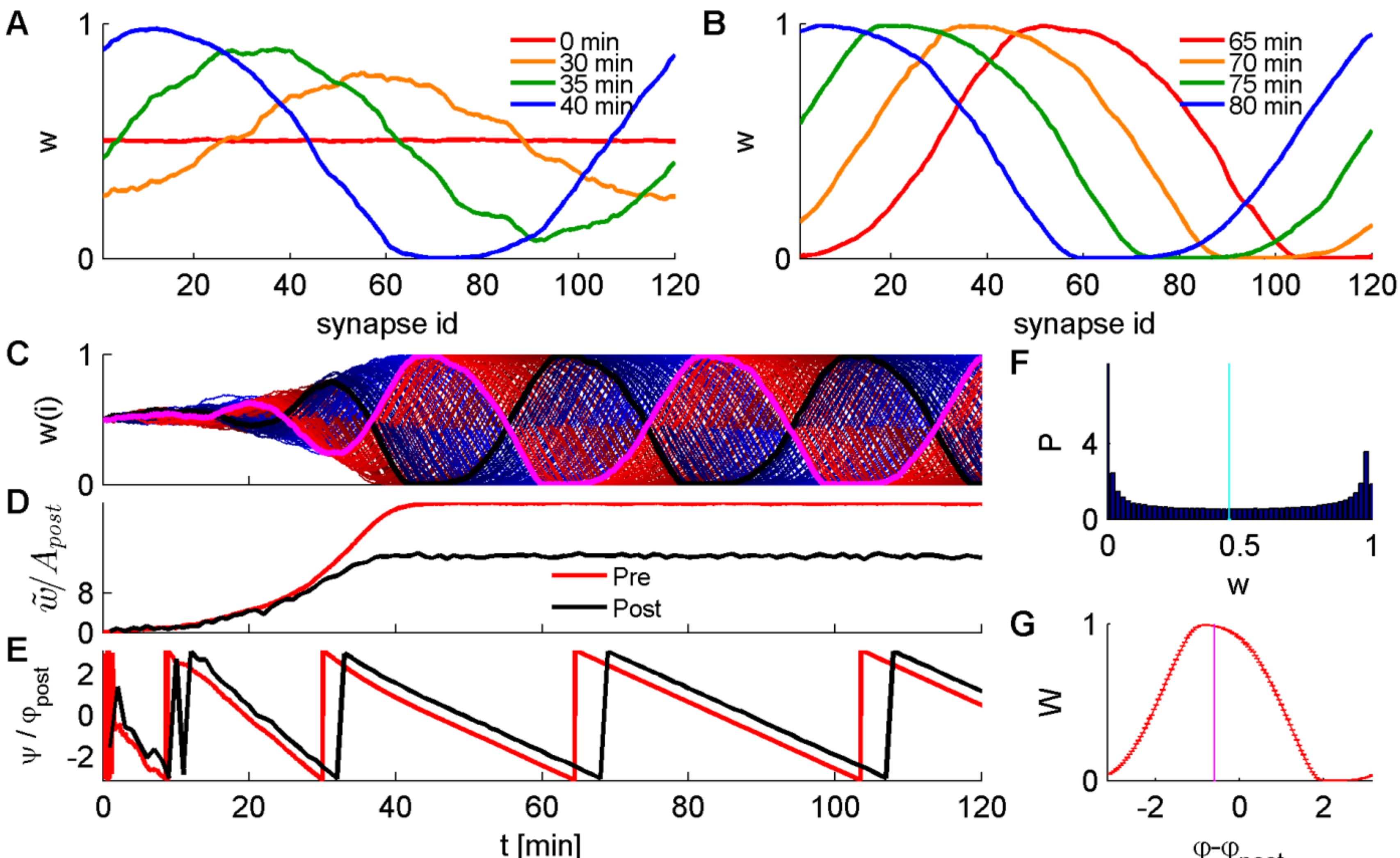
Unstable homogeneous solution



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The limit cycle solution

- Assuming a limit cycle solution
  - Ansatz converts our differential equations into algebraic equations:

$$\bar{w}(t) = w_0 \qquad\qquad 0 = w_0 \overline{F_0} + w_1 \overline{F_1}$$

$$\tilde{w}(t) = w_1 \quad \rightarrow \quad \overline{F_1}\tilde{F}_0 \cos(\Phi_0) = \overline{F_0}\tilde{F}_1 \cos(\Phi_1)$$

$$\psi(t) = \lambda V_d t + \psi^0 \qquad\qquad V_d = -\frac{\overline{F_1}}{\overline{F_0}} \tilde{F}_0 \sin(\Phi_0) + \tilde{F}_1 \sin(\Phi_1)$$

- Retrieving the "weak coupling limit" to in the zero drift scenario
  - Assuming the drift V_d is zero.

$$D_{post} = D\bar{w} \qquad\qquad \Gamma_r \equiv \frac{A^2 \tilde{w}}{2D^2 \bar{w}}$$

$$A_{post} = A\tilde{w} \quad \rightarrow$$

$$\varphi_{post} = \psi + \nu d \qquad\qquad Q(\varphi) = \frac{1 + \Gamma_r \tilde{K}_-^{\nu} \cos\left(\Omega_-^{\nu} + \varphi - \psi - \nu d\right)}{1 + \Gamma_r \tilde{K}_+^{\nu} \cos\left(\Omega_+^{\nu} + \varphi - \psi - \nu d\right)}$$

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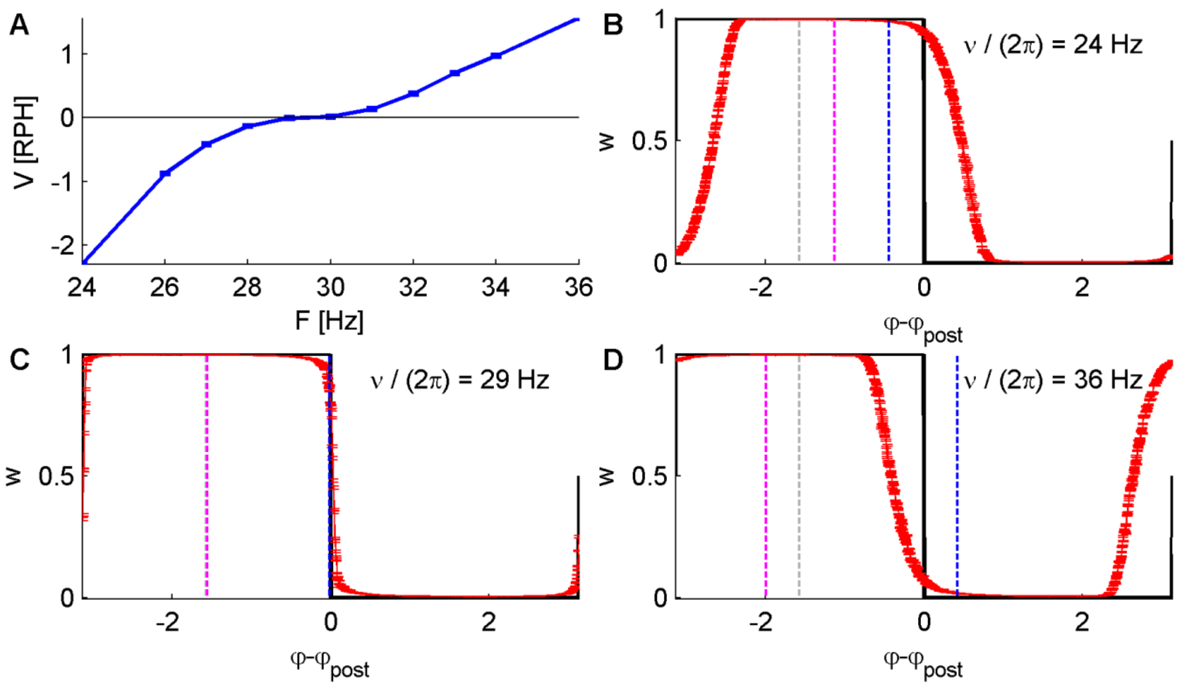
The zero drift solution



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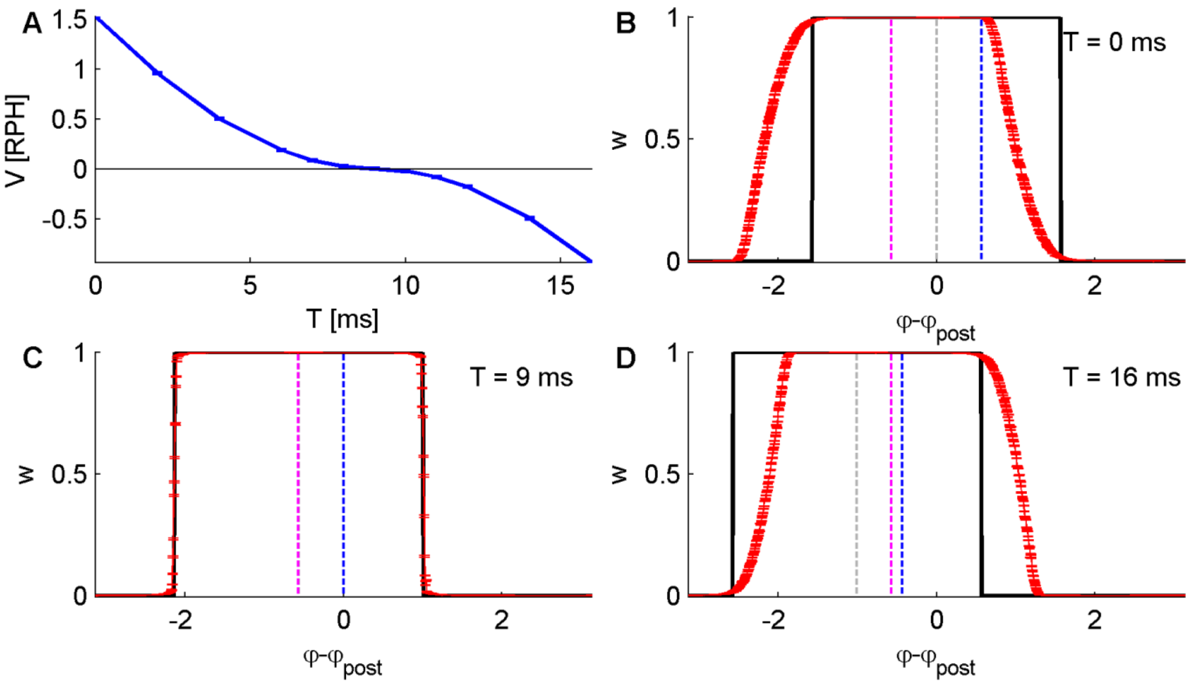
The zero drift solution



Luz and Shamir (2016)

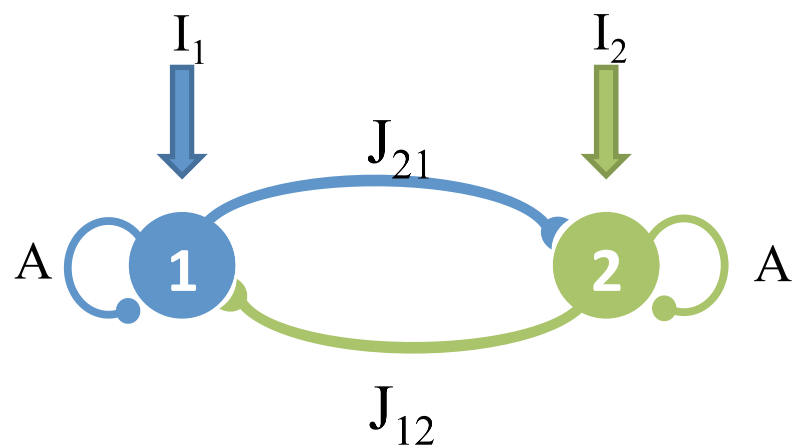
Interim Summary

- STDP can provide a mechanism for shaping synaptic weights to enable transmission of oscillatory activity.
- Typically, the weights do not converge to a fixed point.
- Functionality, in this case, was retained by stable dynamics of global order parameters.

Can oscillations emerge via STDP?

The reciprocal inhibition model

$$\tau_m \dot{r}_1 = -r_1 + g(I_1 - a_1 - J_{12} r_2)$$
$$\tau_a \dot{a}_1 = -a_1 + A r_1$$
$$\tau_m \dot{r}_2 = -r_2 + g(I_2 - a_2 - J_{21} r_1)$$
$$\tau_a \dot{a}_2 = -a_2 + A r_2$$



Outline:

- Understand the dynamics of this system
- Introduce plasticity and study under what conditions this system will develop the capacity to oscillate

Shamir & Sompolinsky, *unpublished*

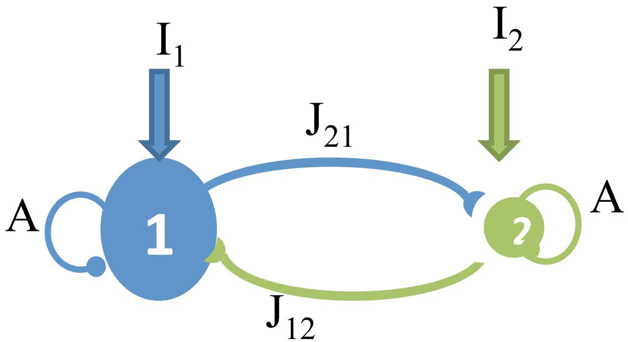
The fixed points

Rival-1 State

$$r_1 = \frac{I_1}{A+1}$$

$$r_2 = 0$$

Existence condition: $1 < \frac{J_{21}}{A+1}$

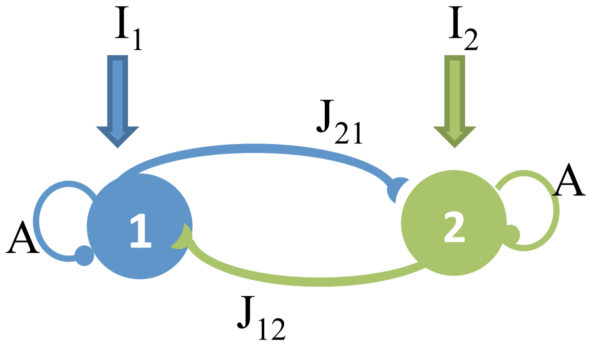


Fusion State

$$r_1 > 0$$

$$r_2 > 0$$

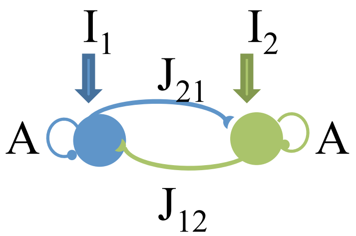
Existence condition: $\frac{J_{xy}}{A+1} < 1$



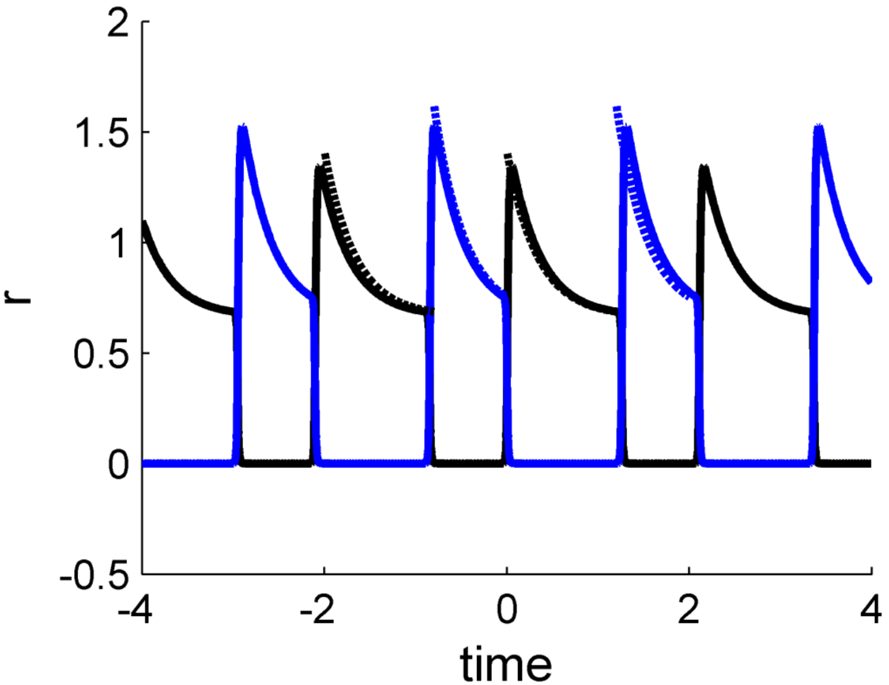
Stability condition: $\sqrt{J_{12}J_{21}} < 1 + \varepsilon$

Shamir & Sompolinsky, *unpublished*

The Limit Cycle solution



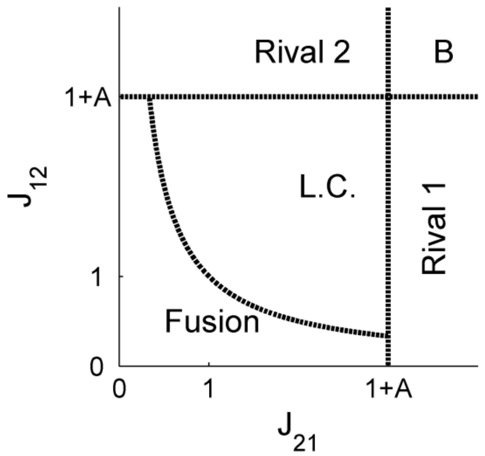
In regions where there are no stable fixed points the system converges to a periodic solution of
Anti-phase Oscillations

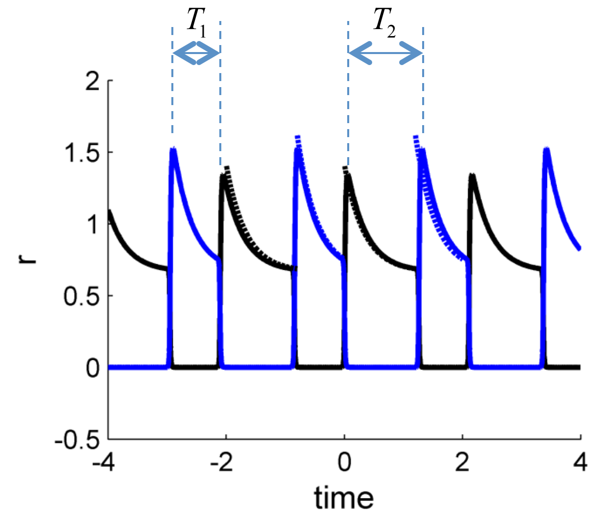


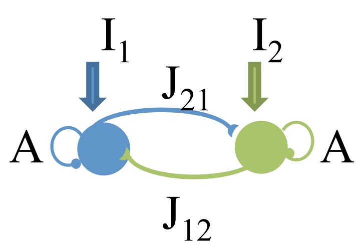
The Phase diagram

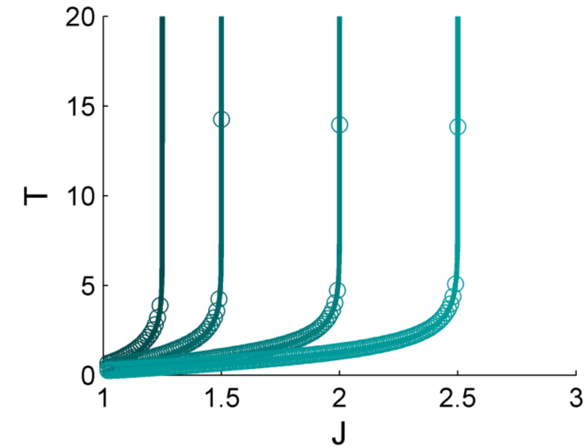
Limit Cycle Solution:
Denote T_i the dominance time of population *i*.

- $T_1 = T_2$ on the diagonal
- T_1 diverges on the border of *Rival-1*
- $T_{1/2}$ goes to zero on the border of *Fusion*



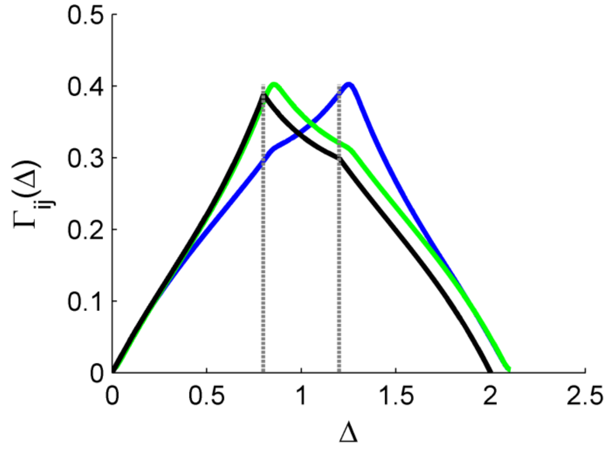






The correlations

The correlations: $\Gamma_{ij}(\Delta) = \int_0^T \frac{dt}{T} r_i(t) r_j(t+\Delta)$

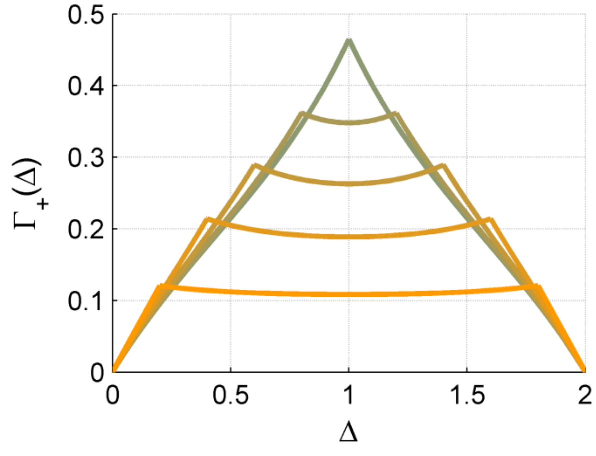


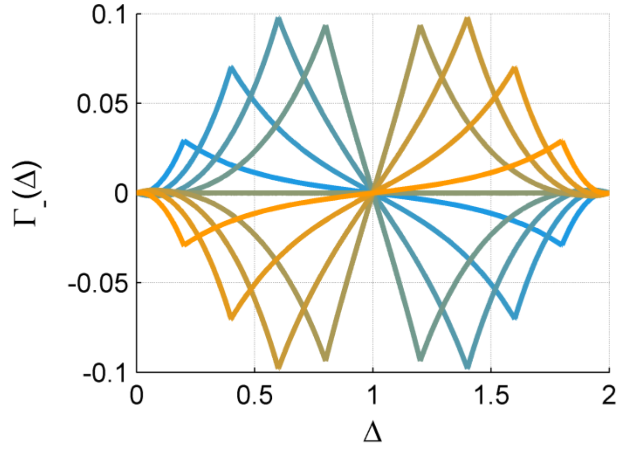
$$\Gamma_+(\Delta) = \frac{\Gamma_{12}(\Delta) + \Gamma_{21}(\Delta)}{2}$$

➢ Always positive and symmetric w.r.t. time.

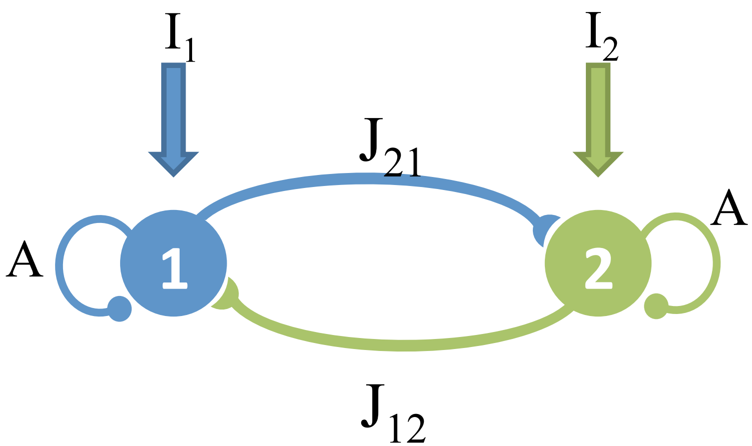
$$\Gamma_-(\Delta) = \Gamma_{21}(\Delta) - \Gamma_{12}(\Delta)$$

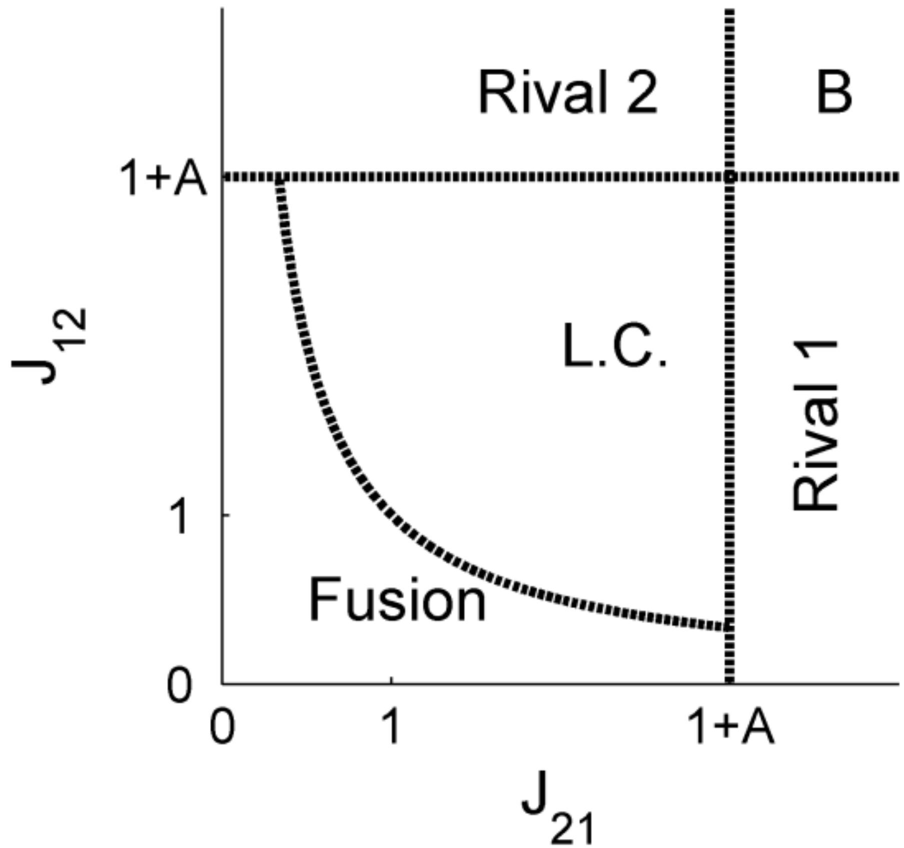
➢ Odd function of time. Zero on the diagonal and anti-symmetric w.r.t. reflection around the diagonal.





Can oscillations emerge via neuronal plasticity?





Hebbian/Anti-Hebbian STDP

The STDP rule:

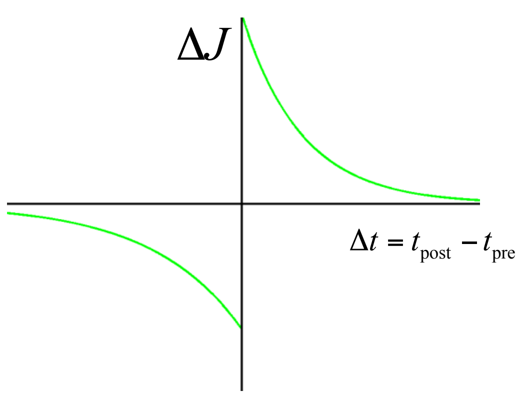
$$\Delta J = \lambda\left(K_{+}(\Delta t) - \alpha K_{-}(\Delta t)\right)$$

$$\Delta t = t_{\text{post}} - t_{\text{pre}} \qquad K_{\pm}(\Delta t) = \frac{1}{\tau_{\pm}} \exp\left\{\mp Ht / \tau_{\pm}\right\} \Theta(\pm Ht)$$

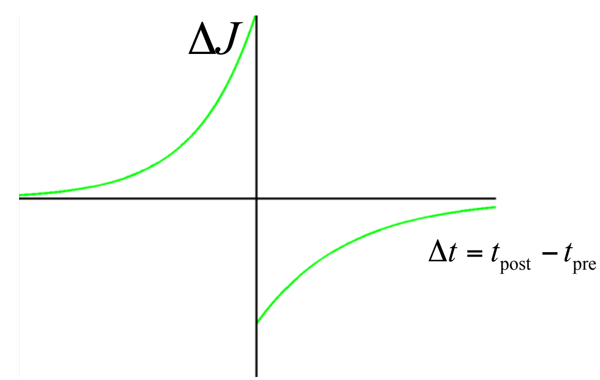
λ is the learning rate, α is the relative strength of depression,

$H = 1 / -1$ for Hebb / Anti-Hebb STDP

Hebbian



Anti-Hebbian



Soloduchin and Shamir (2018)

STDP dynamics induce a flow on the phase diagram

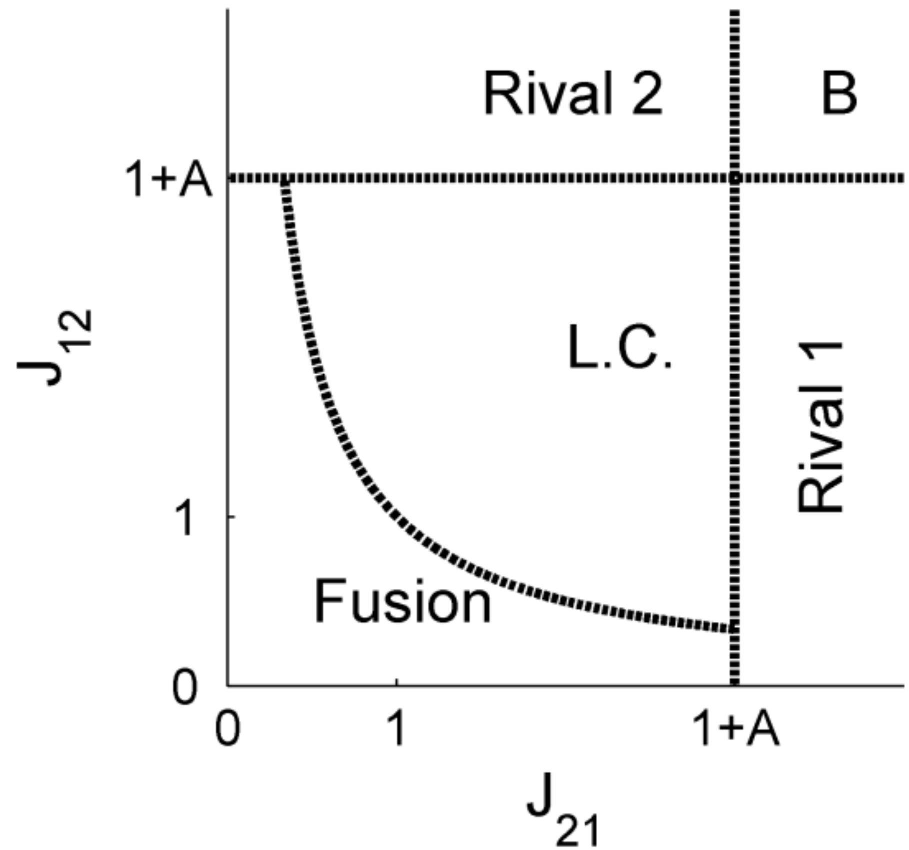
$$\dot{J}_{ij} = \lambda \int \Gamma_{ij}(t)\left[K_{+}(t) - \alpha K_{-}(t)\right]dt$$

Transition from stable Fusion to the Limit Cycle region requires:

$$\alpha < 1$$

$$J_{+} = \frac{J_{21} + J_{12}}{2}$$

$$\dot{J}_{+} = \lambda \int \Gamma_{+}(t)\left[K_{+}(t) - \alpha K_{-}(t)\right]dt$$



Soloduchin and Shamir (2018)

STDP dynamics on the diagonal

$$J_+ = \frac{J_{21} + J_{12}}{2}$$

$$\dot{J}_+ = \lambda \left\{ \dot{J}_{+\mathrm{pot}} - \alpha \dot{J}_{+\mathrm{dep}} \right\}$$

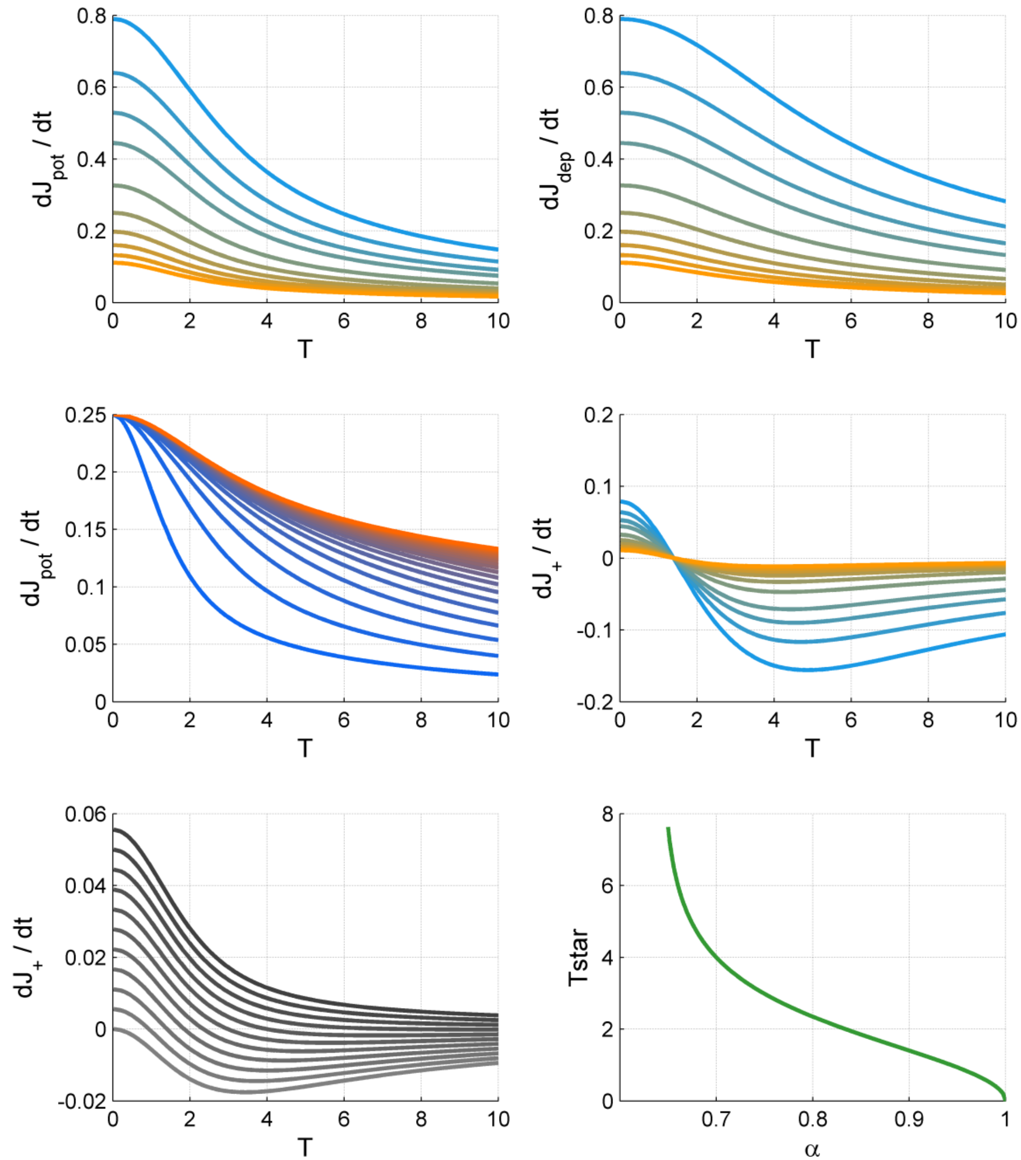
It is convenient to study

$$\dot{J}_{+\mathrm{pot/dep}} = \int \Gamma_+(t) K_{+/-}(t) dt$$

As $T \to 0$ $\quad \dot{J}_+ = (1-\alpha) I^2 / \left(2 + A\right)^2$

For $\tau_+ < \tau_-$ we obtain $\dot{J}_{+\mathrm{pot}} \leq \dot{J}_{+\mathrm{dep}}$

with equality only at *T=0*



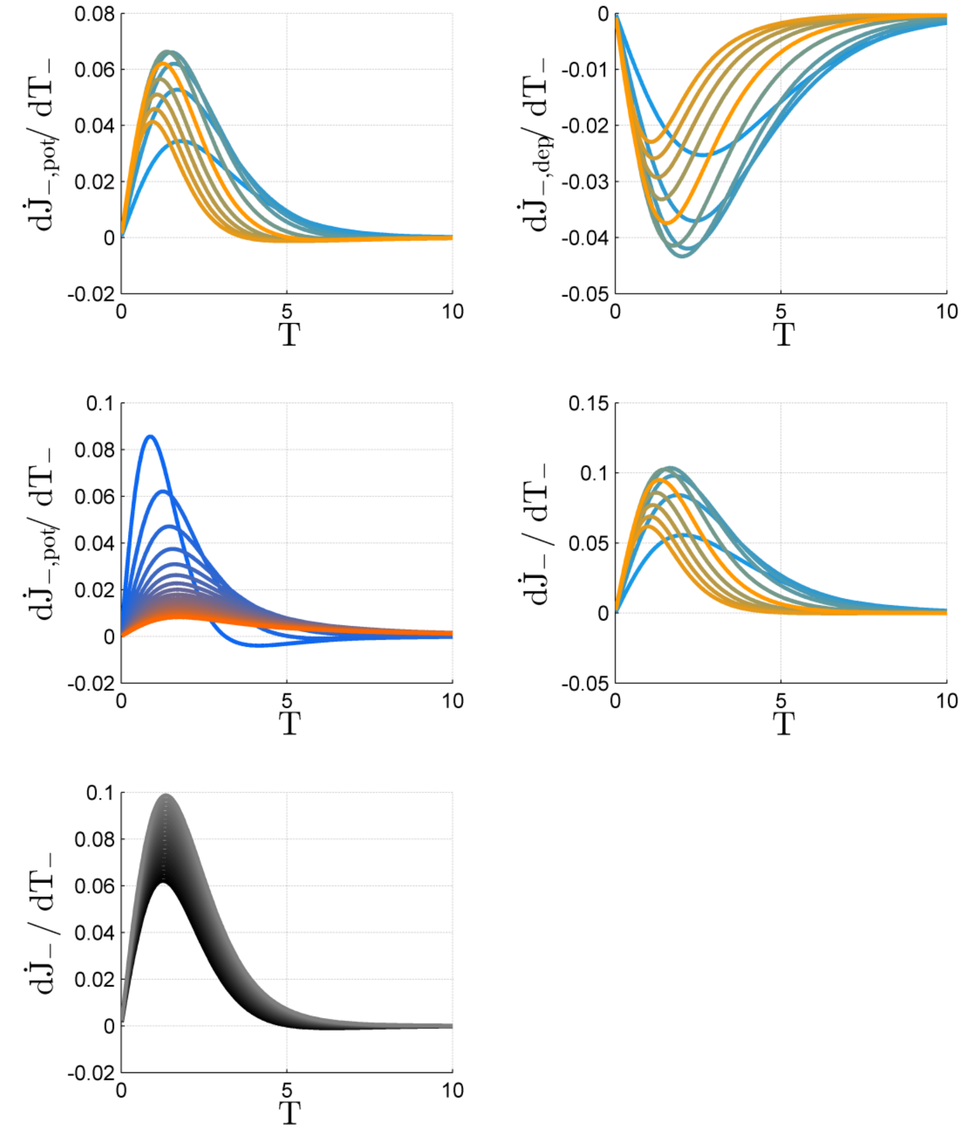
Soloduchin and Shamir (2018)

STDP dynamics in the orthogonal direction

$$J_- = J_{21} - J_{12}$$

$$\dot{J}_- = \lambda\left\{\dot{J}_{-\mathrm{pot}} - \alpha \dot{J}_{-\mathrm{dep}}\right\}$$

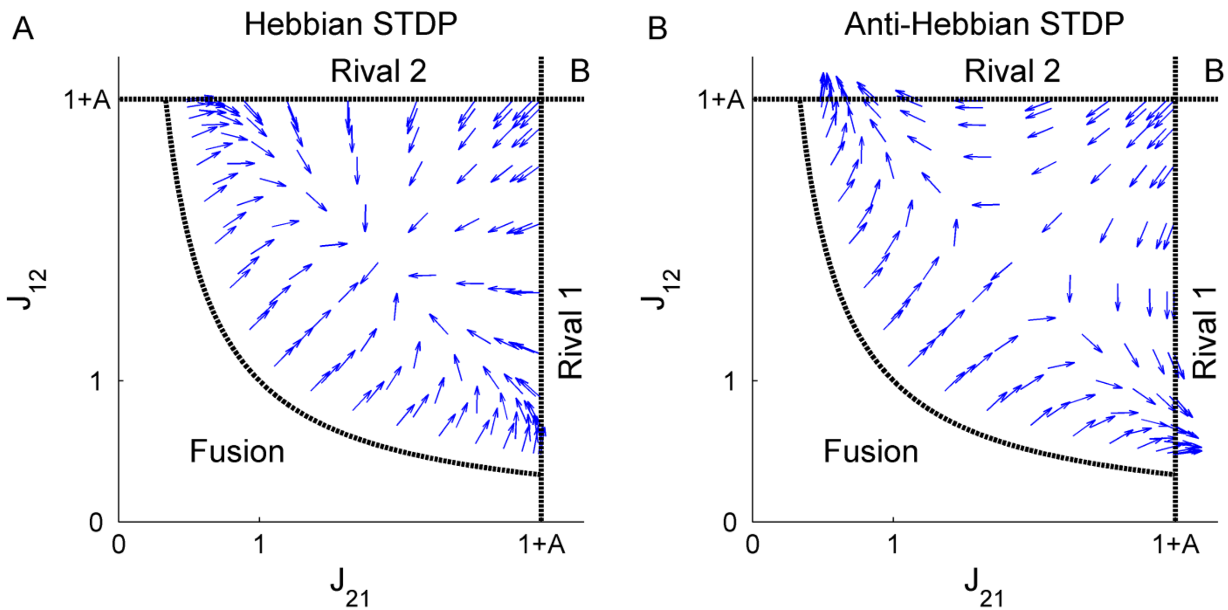
On the diagonal $\dot{J}_-$ is zero.



If STDP dynamics are unstable in the direction J_- for Hebbian plasticity they will be stable for Anti-Hebbian rule and vice versa.

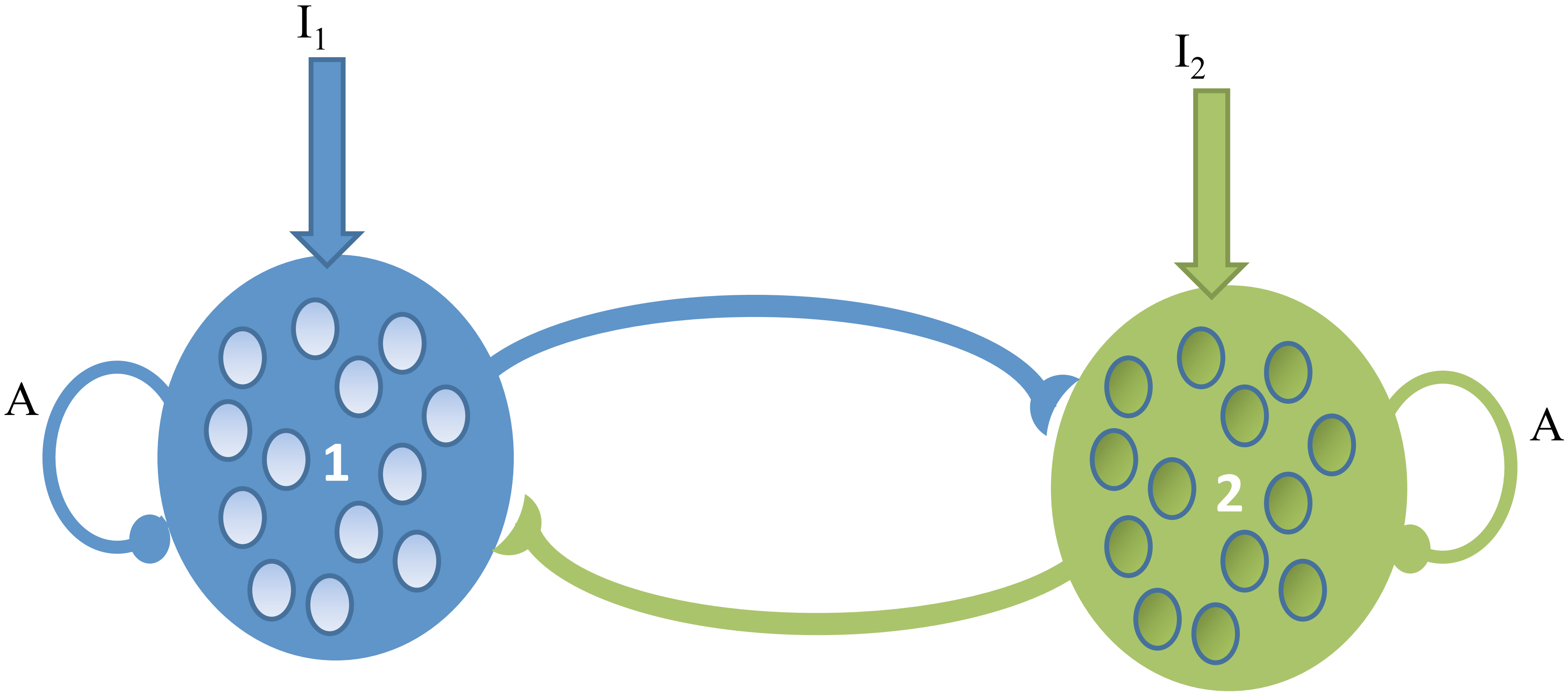
Soloduchin and Shamir (2018)

Flow on the phase plane



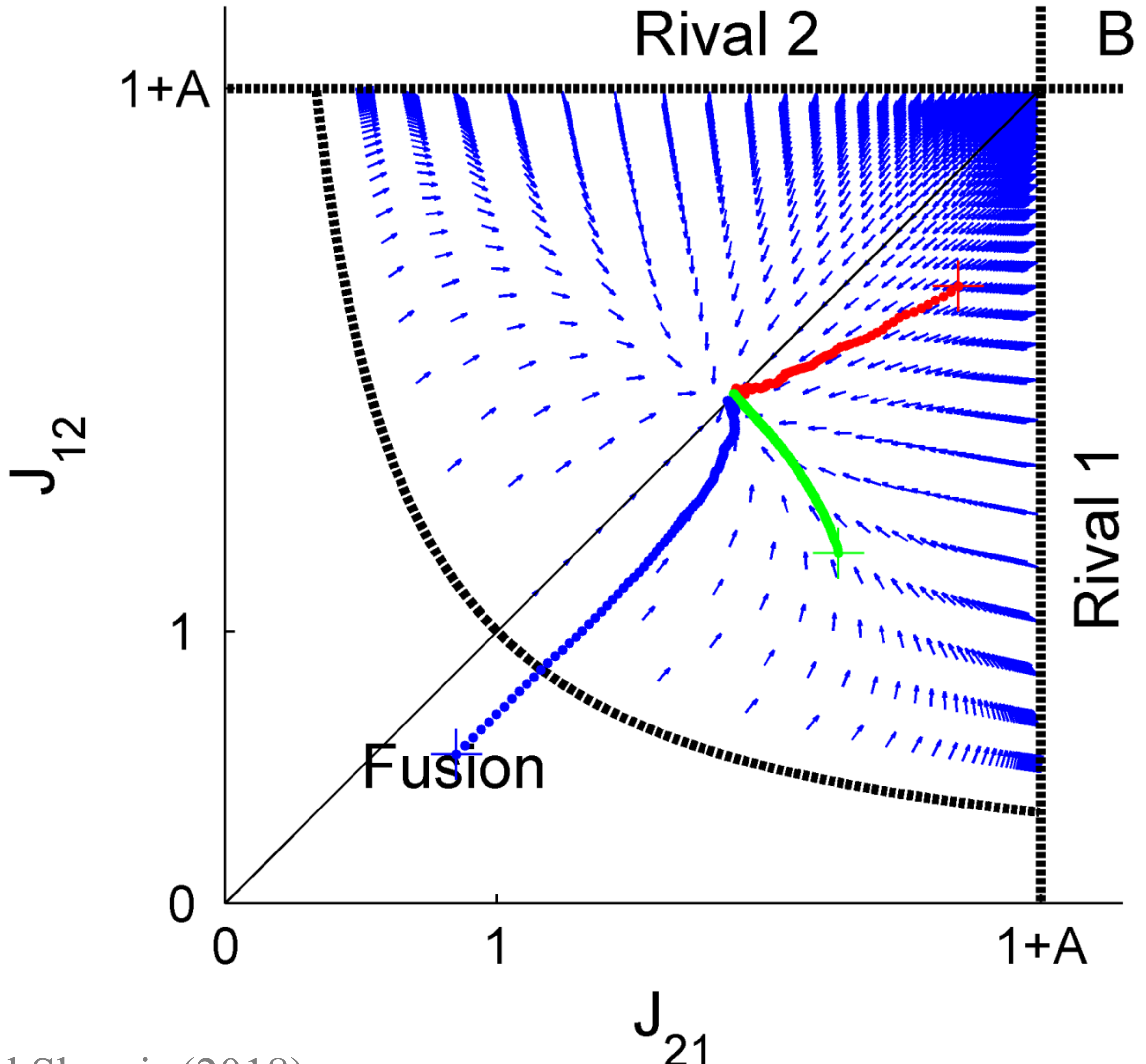
Soloduchin and Shamir (2018)

Learning synaptic population



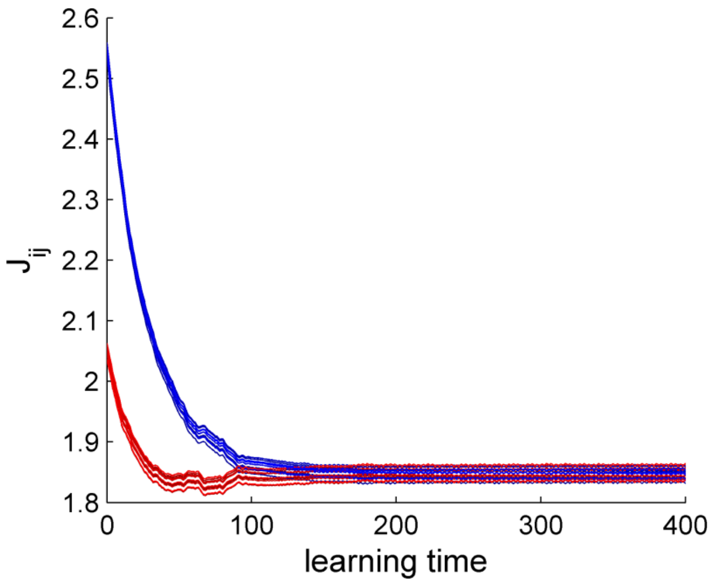
Soloduchin and Shamir (2018)

Learning synaptic population



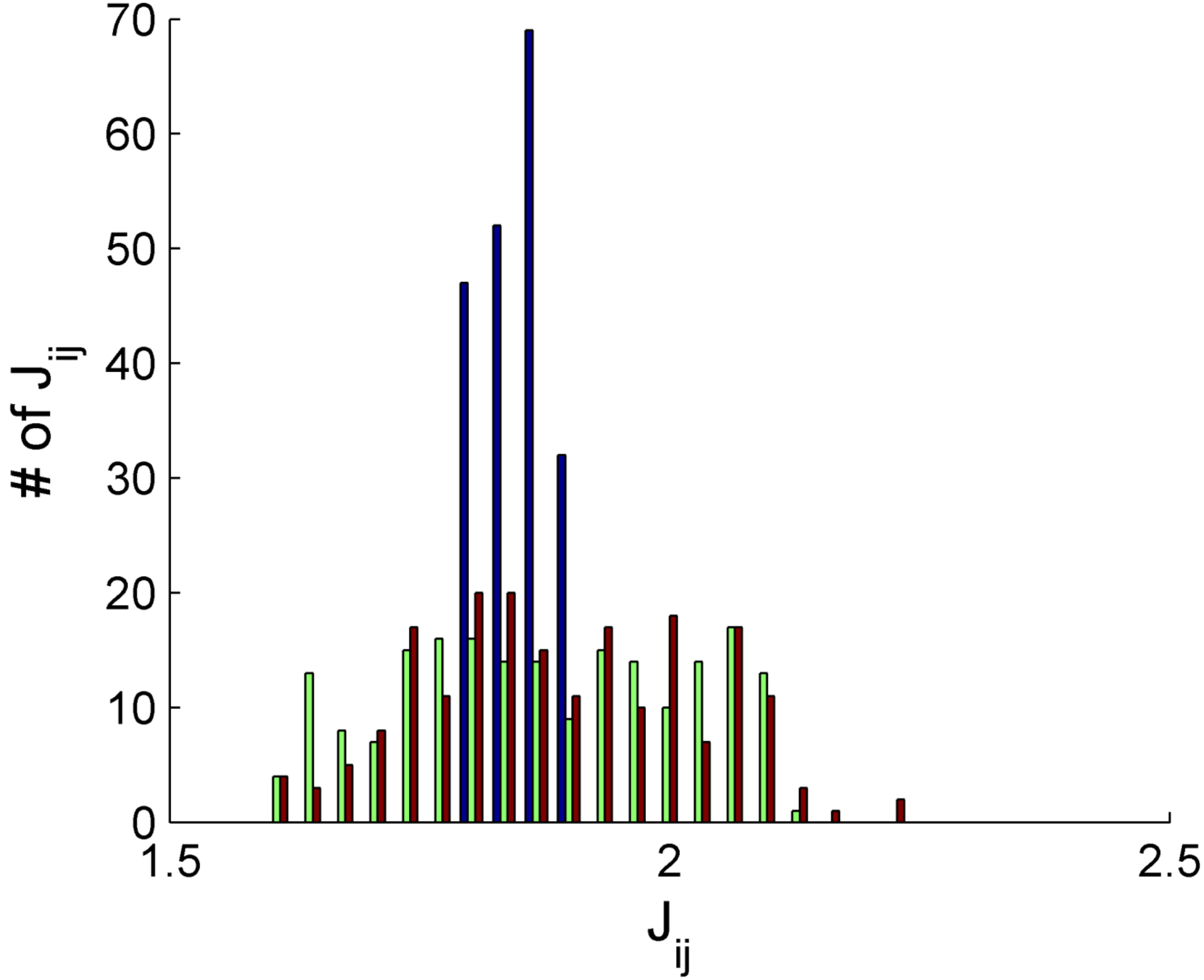
Soloduchin and Shamir (2018)

Learning synaptic population



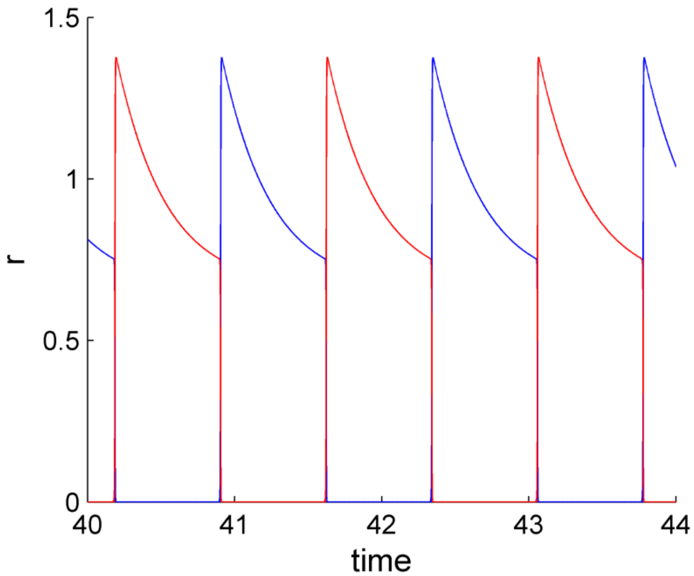
Soloduchin and Shamir (2018)

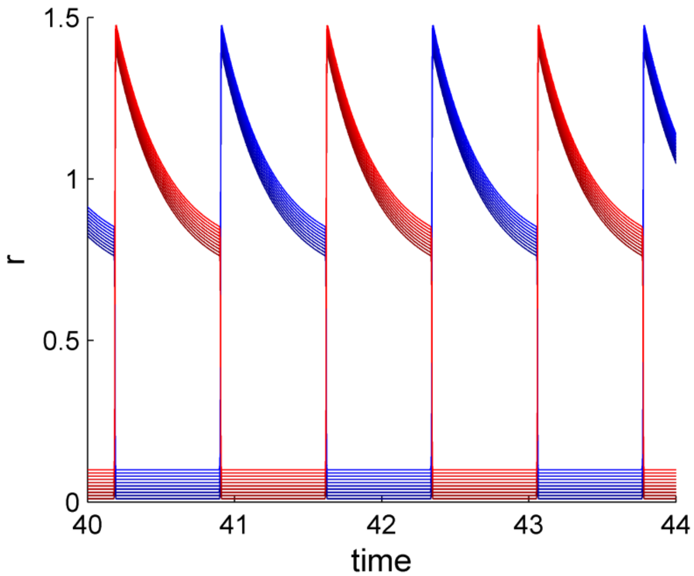
Learning synaptic population



Soloduchin and Shamir (2018)

Learning synaptic population





$T = 1.433$ $T = 1.432$ $T = 1.436$

Soloduchin and Shamir (2018)

Summary

- The phase diagram of the neuronal activities is the phase plane of the STDP dynamics.
- STDP can provide a mechanism that enables the emergence of oscillatory activity in the brain.
- The STDP rule governs and stabilizes the resultant oscillatory activity.
- The specific architecture and the non-linear nature of the neuronal dynamics may have a major effect on the STDP dynamics as well.
- Disruption to the STDP rule may alter the oscillatory behavior.

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