Effect of Inhibitory Spike-Timing-Dependent Plasticity on Fast Sparsely Synchronized Brain Rhythms

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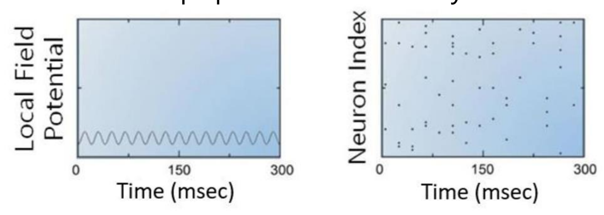
Introduction

- **Fast Spike Synchronization (FSS)**
  Population level: Fast synchronous oscillations [e.g. gamma rhythm (30 ~ 100 Hz) & sharp-wave ripple (100 ~ 200 Hz)]
  Cellular level: Irregular and intermittent discharges like Geiger counters
  Associated with diverse cognitive functions [e.g. sensory perception, feature integration, selective attention, and memory formation and consolidation]

Single-cell firing activity: Distinctly different from population oscillatory behavior



- **Inhibitory Spike-Timing-Dependent Plasticity (iSTDP)**
  Synaptic Plasticity: In real brains synaptic strengths may vary to adapt to environment (potentiated or depressed)
  STDP: Plasticity depending on the relative time difference between the pre-and the post-synaptic spike times
  Study of STDP: Mainly focused on excitatory synapses (eSTDP)
  iSTDP: Less attention because of experimental obstacles and diversity of inhibitory interneurons. (With the advent of fluorescent labeling and optical manipulation iSTDP has begun to be focused.)
- **Purpose of Our Study**
  In previous works on FSS, synaptic coupling strengths were static (i.e., no STDP) [1].
  Investigation of the effect of iSTDP on FSS in an inhibitory population of interneurons

Inhibitory Small-World Network (SWN) of Fast Spiking (FS) Izhikevich Interneurons

- **Governing Equations**

$$C\frac{dv_i}{dt}=k(v_i-v_r)(v_i-v_t)-u_i+I_i+D\xi_i-I_{syn,i},\quad U(v)=\begin{cases}0 & \text{for } v<v_b\\ b(v-v_b)^3 & \text{for } v\ge v_b\end{cases},$$

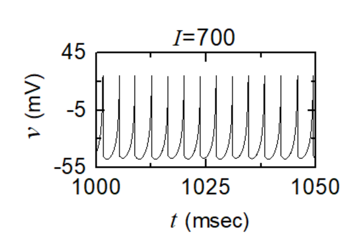
$$\frac{du_i}{dt}=a\{U(v_i)-u_i\},\quad i=1,\dots,N,\qquad I_{syn,i}=\frac{1}{d_i^{in}}\sum_{j=1(j\ne i)}^{N}J_{ij}w_{ij}s_j(t)(v_i-V_{syn}),$$

if $v_i \ge v_p$, then $v_i \leftarrow c$ and $u_i \leftarrow u_i + d$.

$$s_j(t)=\sum_{f=1}^{F_j}E(t-t_f^{(j)}-\tau_l);\qquad E(t)=\frac{1}{\tau_d-\tau_r}(e^{-t/\tau_d}-e^{-t/\tau_r})\Theta(t).$$

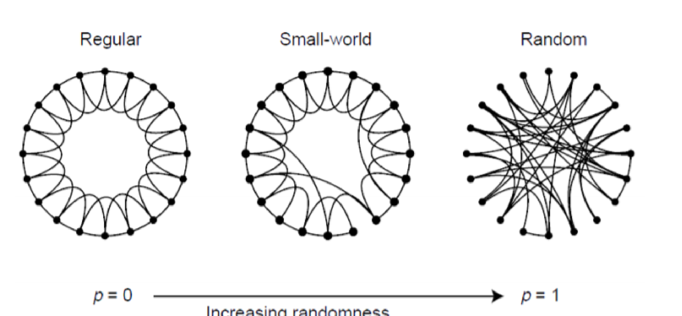
$C=20, v_r=-55, v_t=-40, v_p=25, v_b=-55$
$k=1, a=0.2, b=0.025, c=-45, d=0$
$\tau_l=1, \tau_r=0.5, \tau_d=5, V_{syn}=-80$

Spikings of A Single Suprathreshold Neuron



M_{syn} (Average No. of inward synapses per neuron)=50
Suprathreshold Neurons: $I_i \in$ [680, 720]

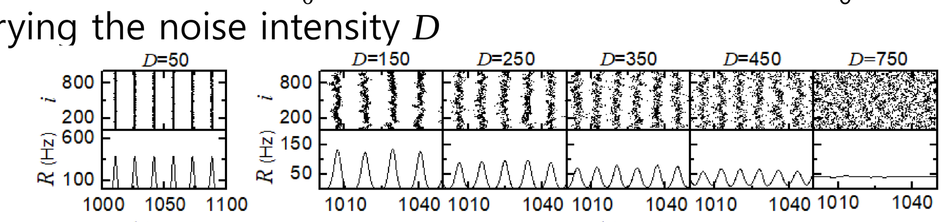
- **Watts-Strogatz SWN**
  Interpolating between the regular lattice (p=0) and the random graph (p=1) via rewiring



FSS in the Absence of iSTDP for p=0.25

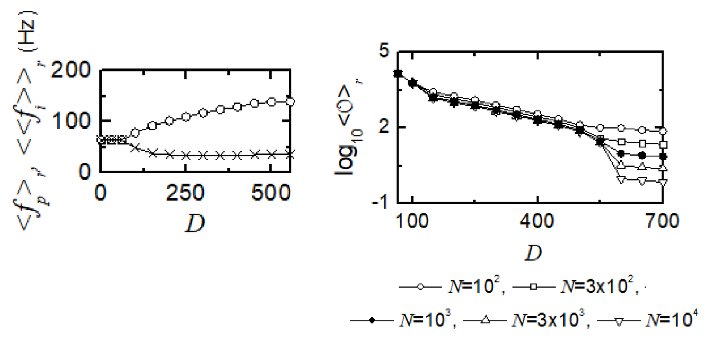
Initial coupling strengths $\{J_{ij}\}$: Gaussian distribution with mean J_0=700 and standard deviation σ_0=5
Aim: Investigation of emergence of FSS by varying the noise intensity D

- **Raster Plots of Spikes**
  Appearance of stripes (composed of spike times and representing the synchronization)
  Desynchronization for D=750:
  Completely scattered without forming any stripes



- **Instantaneous Population Spike Rate (IPSR)**

$$R(t)=\frac{1}{N}\sum_{i=1}^{N}\sum_{s=1}^{n_i}K_h(t-t_s^{(i)});\quad K_h(t)=\frac{1}{\sqrt{2\pi}h}e^{-t^2/2h^2},\ -\infty<t<\infty$$



- **Thermodynamic Order Parameter:** $\mathcal{O}\equiv\overline{(R(t)-\overline{R(t)})^2}$
  Synchronized (desynchronized) state:
  $\mathcal{O}$ approach non-zero (zero) limit values for $N\to\infty$
  Occurrence of FSS in the range of D (D_{th}[~65], D^*[~558])
  Appearance of FSS when passing D_{th} via break-up of full synchronization.
  Disappearance of FSS when passing D^* due to a destructive role of noise to spoil FSS.
- **Statistical-Mechanical Spiking Measure M_s**
  Spiking measure of ith stripe M_i: Product of occupation degree and pacing degree

$$M_i=O_i\cdot P_i$$

Occupation degree O_i: representing the average density of stripes in the raster plot

$$O_i=\frac{N_i^{(s)}}{N}$$

$N_i^{(s)}$: No. of spiking neurons in the ith stripe

Pacing degree P_i: representing the average smearing of stripes in the raster plot (average contribution of all microscopic spike times to the IPSR)

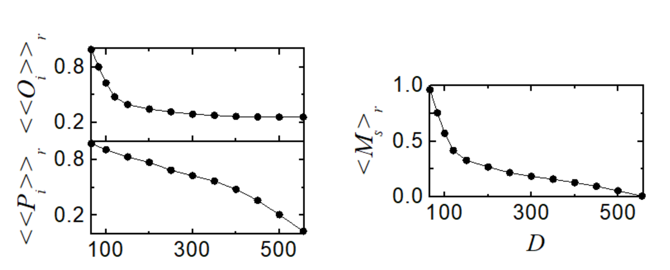
$$P_i=\frac{1}{S_i}\sum_{k=1}^{S_i}\cos\Phi_k$$

S_i: Total No. of microscopic spikes in the ith stripe
Φ_k: global phase at the kth spiking time

Statistical-mechanical spiking measure:

$$M_s=\frac{1}{N_s}\sum_{i=1}^{N_s}M_i$$

N_s: No. of stripes



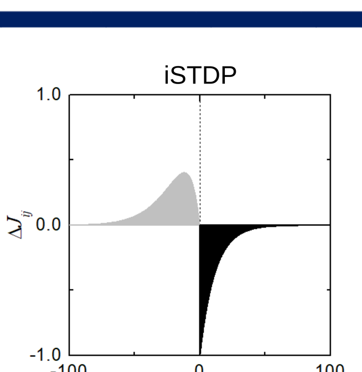
With increasing D from D_{th},
$\langle\langle O_i\rangle\rangle_r$ decreases rapidly due to stochastic spike skipping, and tends to approach a limit value (~ 0.26).
$\langle\langle P_i\rangle\rangle_r$ decreases and converges to zero rapidly due to complete overlap of sparse spiking stripes.
$\langle M_s\rangle_r$ decreases rapidly due to the rapid decrease in $\langle\langle O_i\rangle\rangle_r$, and converges to zero.

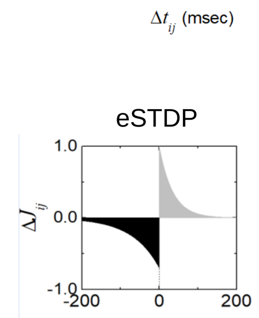
Anti-Hebbian iSTDP

- **Multiplicative STDP Rule:** $J_{ij}\to J_{ij}+\delta(J^*-J_{ij})\,|\Delta J_{ij}(\Delta t_{ij})|$;
  δ(=0.05): Updated rate. $J_{ij}\in[J_l,J_h]$; $J_l=0.0001$ & $J_h=2000$
  $J^*=J_h$ (J_l) for LTP (LTD).
  $\Delta t_{ij}(=t_i^{(post)}-t_j^{(pre)})$: Time difference between the nearest spike onset times of the post-synaptic neuron i and the pre-synaptic neuron j.
- **Time Window for the Anti-Hebbian iSTDP**

$$\Delta J_{ij}=\begin{cases}-A_+e^{-\Delta t_{ij}/\tau_+} & \text{for } \Delta t_{ij}>0\\ -A_-\dfrac{\Delta t_{ij}}{\tau_-}e^{\Delta t_{ij}/\tau_-} & \text{for } \Delta t_{ij}\le 0\end{cases}\qquad A_+=1.0,\ A_-=1.1,\ \tau_+=31.5\text{ msec},\ \tau_-=12\text{msec}.$$

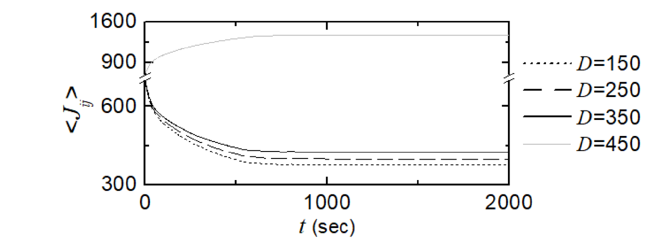
When a post synaptic spike follows a pre-synaptic spike (Δt_{ij} > 0), LTD appears; otherwise (Δt_{ij} < 0), LTP occurs.
(c.f. eSTDP: Hebbian STDP [2]-[3]; Δt_{ij}>0 → LTP, Δt_{ij}<0 → LTD)



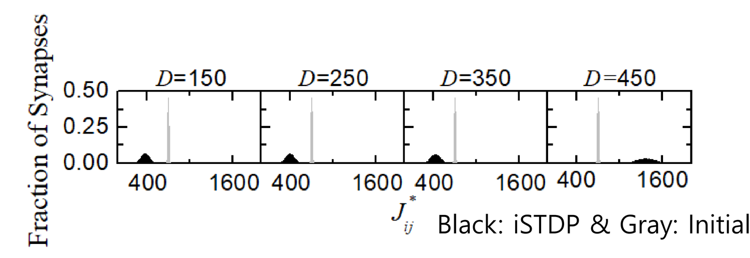


Effect of iSTDP on FSS for p=0.25

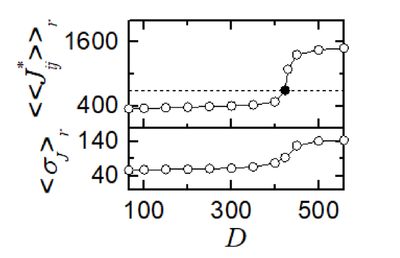
- **Time-Evolutions of Population-Averaged Synaptic Strength $\langle J_{ij}\rangle$**
  D=150, 250, and 350: $\langle J_{ij}\rangle$ decreases monotonically below its initial value J_0 (=700), and it approaches a saturated limit value $\langle J^*_{ij}\rangle$ → LTD
  D=450: $\langle J_{ij}\rangle$ increases monotonically above J_0, and it approaches $\langle J^*_{ij}\rangle$ → LTP



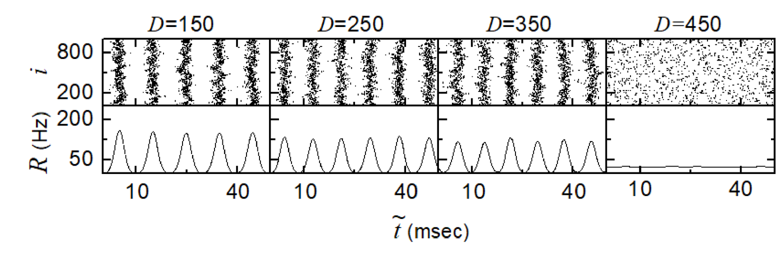
- **Histograms for Fraction of Synapses J^*_{ij}**
  $\langle J^*_{ij}\rangle$ becomes smaller (larger) than the initial value for the case of LTD (LTP).
  The standard deviations are very larger than the initial one (=5).



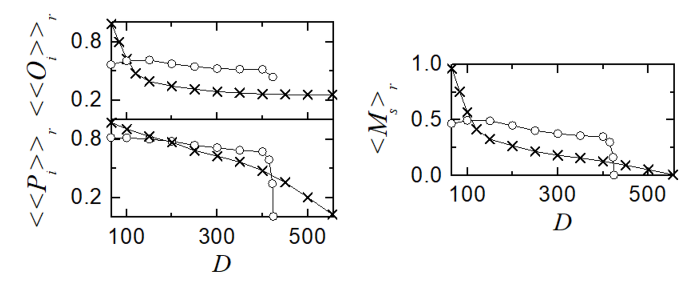
- **Population-Averaged Limit Values of Synaptic Strengths $\langle\langle J^*_{ij}\rangle\rangle_r$ versus D**
  LTD occurs in $D<\tilde{D}(\sim423)$ (solid circles); otherwise, occurrence of LTP.
  $\langle\sigma_J\rangle_r$ are larger than the initial value for both cases of LTD & LTP.



- **Raster Plots of Spikes and IPSR $R(t)$**
  LTD → The degrees of FSS are increased.
  LTP → The population states become desynchronized.



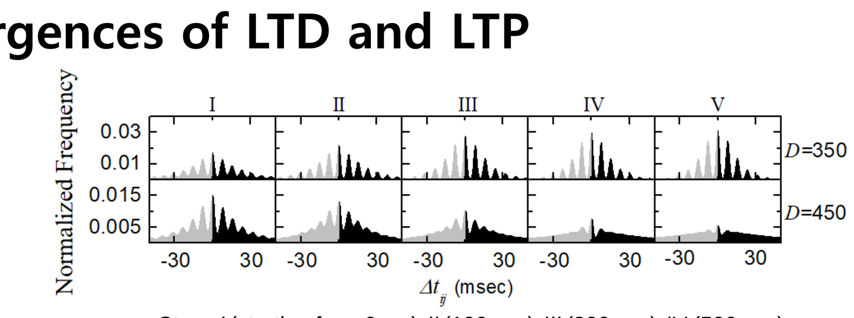
- **"Matthew" Effect in Inhibitory Synaptic Plasticity**
  Occupation degree: Increased in most cases due to LTD (decreased mean synaptic inhibition) (For small D, decreased due to increased standard deviation σ_J)
  Pacing degree: Increase due to dominant effect of LTD (overcoming the effect of increased σ_J)
  Rapid step-like transition to Desynchronization due to LTP
  Occurrence of "Mathew Effect" in Synaptic Plasticity:
  Good FSS gets better via LTD, while bad FSS gets worse via LTP.



Open circles : iSTDP, Crosses : Absence of iSTDP

Microscopic Investigation on Emergences of LTD and LTP

- **Normalized Histogram $H(\Delta t_{ij})$ for the Distribution of $\{\Delta t_{ij}\}$**
  LTD (D = 350): Multi-peaks appear.
  Stage I: Effect of right black part (causality) is dominant. → LTD
  As t is increased: Peaks become narrow and sharper. → Increasing the degree of FSS
  Effect of LTD (black part) tends to cancel out the effect of LTP (gray part).
  LTP (D = 350): Stage I: Effect of left gray part (acausality) is dominant. → LTP
  As t is increased: Peaks become wider and merging → Decreasing the degree of FSS → Appearance of one broad single peak



Stage I (starting from 0sec), II (100 sec), III (300 sec), IV (500 sec) & V (800 sec). Duration : 0.2 sec

- **Population-Averaged Multiplicative Synaptic Modification $\langle\langle\Delta J_{ij}\rangle\rangle_r$**
  Recurrence relation for the population-averaged synaptic strength:

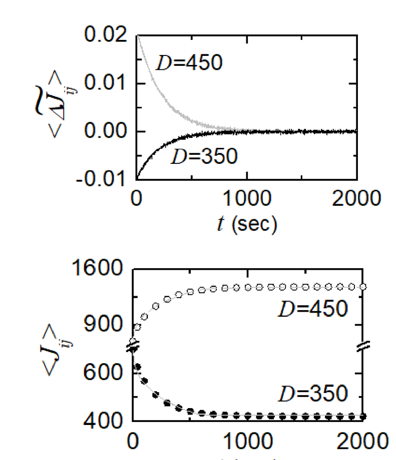
$$\langle J_{ij}\rangle_k=\langle J_{ij}\rangle_{k-1}+\delta\cdot\langle\Delta J_{ij}(\Delta t_{ij})\rangle_k$$

Population-averaged multiplicative synaptic modification:

$$\langle\Delta J_{ij}(\Delta t_{ij})\rangle_k \simeq (J^*-\langle J_{ij}\rangle_{k-1})\langle|\Delta J_{ij}(\Delta t_{ij})|\rangle_k$$

where $\langle|\Delta J_{ij}(\Delta t_{ij})|\rangle_k\simeq\sum_{bins}H_k(\Delta t_{ij})\cdot|\Delta J_{ij}(\Delta t_{ij})|$

Population-averaged limit values of synaptic strengths:
Agree well with the directly-calculated values.



Summary

- **Fast Spike Synchronization (FSS)**
  FSS (associated with diverse cognitive functions) occurs in the inhibitory SWN.
- **Effect of Inhibitory Spike-Timing-Dependent Plasticity (iSTDP) on the FSS**
  "Matthew" effect in inhibitory synaptic plasticity (governed by anti-Hebbian rule)
  → Good FSS gets better via long-term depression (LTD) of synaptic strengths, while bad FSS gets worse via long-term potentiation (LTP).
  [c.f. Matthew effect in excitatory synaptic plasticity: Good (bad) synchronization gets better (worse) via LTP (LTD).]
  In addition to the effect of mean value (LTP or LTD) (for the distribution of synaptic inhibition strengths), the effect of standard deviation on population synchronization may also become significant (e.g., small D) (c.f. eSTDP: The effect of mean of LTP/LTD is always dominant.)
- **Investigation of Emergences of LTP and LTD**
  Microscopic studies based on the distributions of time delays between the pre- and the post-synaptic spike times

References

[1] S.-Y. Kim and W. Lim, "Effect of small-world connectivity on fast sparsely synchronized cortical rhythms," Physica A 421, 109-123 (2015).
[2] S.-Y. Kim and W. Lim, "Stochastic spike synchronization in a small-world neural network with spike-timing-dependent plasticity," Neural Networks 97, 92-106 (2018).
[3] S.-Y. Kim and W. Lim, "Effect of spike-timing-dependent plasticity on stochastic spike synchronization in an excitatory neuronal population," in "Advances in Cognitive Neurodynamics (VI)," edited by J. Delgado-Garcia, X. Pan, R. Sanchez-Campusano, and R. Wang , Ch. 42, pp. 335-341 (Springer, Singapore, 2018).
[4] S.-Y. Kim and W. Lim, "Effect of inhibitory spike-timing-dependent plasticity on fast sparsely synchronized rhythms in a small-world neuronal network," Neural Networks 106, 50-66 (2018)

Acknowledgments

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