Effect of Spike-Timing-Dependent Plasticity on Stochastic Spike Synchronization in An Excitatory Neuronal Population

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Introduction

- **Stochastic Spike Synchronization (SSS)**
  Subthreshold neurons: Fire only with the help of noise and exhibit irregular discharges like Geiger counter
  SSS: Population synchronization between complex noise-induced spikings of subthreshold neurons & correlated with brain function of encoding sensory stimuli in the noisy environment
  Previous works on SSS: Synaptic strengths were static.
- **Spike-Timing-Dependent Plasticity (STDP)**
  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
- **Purpose of Our Study**
  Investigation of Effect of the STDP on the SSS in the Small-World Network (SWN)

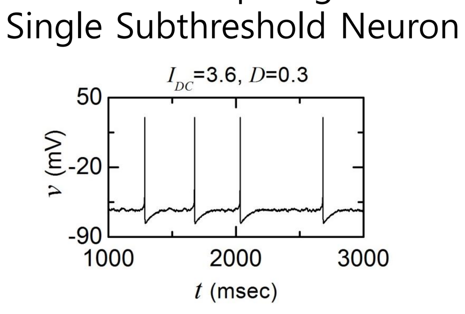
Excitatory SWN of Subthreshold Izhikevich Regular Spiking Neurons

- **Governing Equations**

$$\frac{dv_i}{dt} = f(v_i) - u_i + I_{DC,i} + D\xi_i - I_{syn,i},$$
$$\frac{du_i}{dt} = a(bv_i - u_i), \quad i = 1, \ldots, N,$$
if $v_i \geq v_p$, then $v_i \leftarrow c$ and $u_i \leftarrow u_i + d$.
$a = 0.02, b = 0.2, c = -65, d = 8, v_p = 30$
$\tau_l = 1, \tau_r = 0.5, \tau_d = 2, V_{syn} = 0$

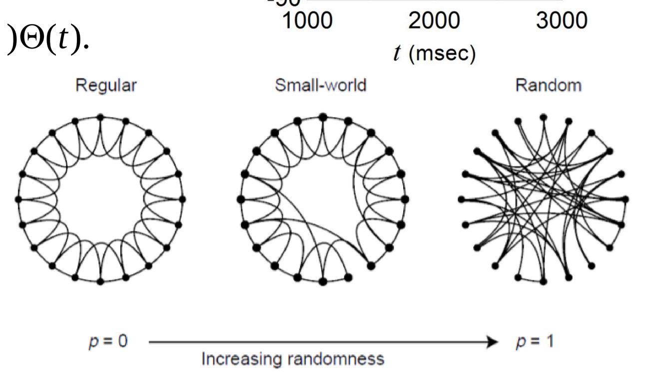
$$f(v) = 0.04v^2 + 5v + 140,$$
$$I_{syn,i} = \frac{1}{d_i^{in}} \sum_{j=1 (j \neq i)}^{N} J_{ij} w_{ij} s_j(t)(v_i - V_{syn}),$$
$$s_j(t) = \sum_{f=1}^{F_j} E(t - t_f^{(j)} - \tau_l);$$
$$E(t) = \frac{1}{\tau_d - \tau_r}(e^{-t/\tau_d} - e^{-t/\tau_r})\Theta(t).$$

Noise-Induced Spikings of A Single Subthreshold Neuron



M_{syn} (Average No. of inward synapses per neuron)=20
Subthreshold Neurons: $I_{DC,i} \in$ [3.55, 3.65]

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



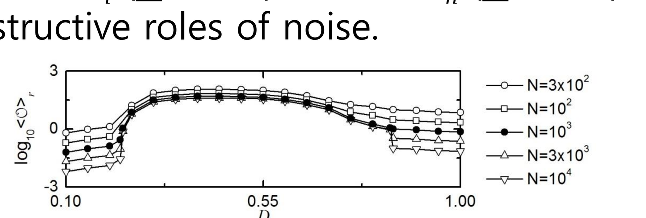
SSS in the Absence of the STDP for p=0.15

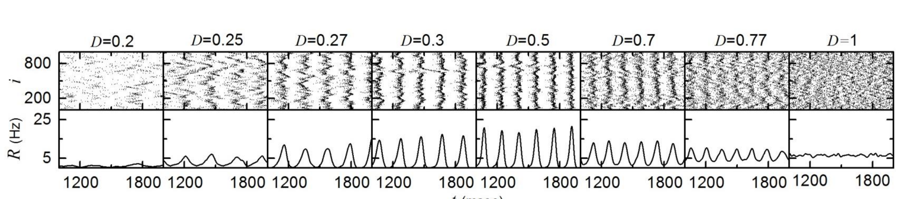
Coupling strengths $\{J_{ij}\}$: Gaussian distribution with mean=0.2 and standard deviation 0.02.

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 $N \to \infty$

SSS in D^*_l ($\simeq$ 0.225) < D < D^*_h ($\simeq$ 0.846) via competition between the constructive and the destructive roles of noise.





Characterization of SSS in the Absence of the STDP

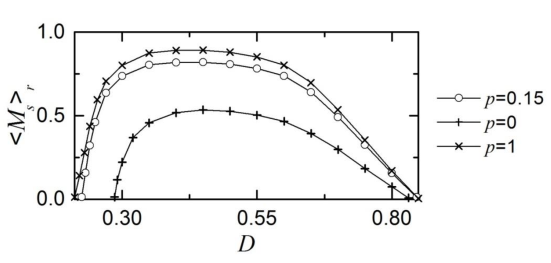
- **Statistical-Mechanical Spiking Measure M_s**
  Pacing degree of the ith stripe: averaging the contributions to $R(t)$ of all microscopic spikes in the ith stripe

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

S_i: Number of spikes in the ith stripe
Φ_k: global phase of spike time

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

N_s: No. of stripe



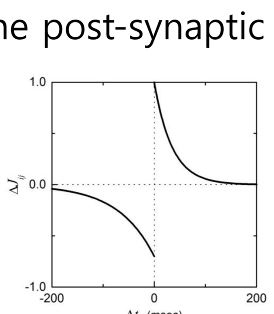
M_s: Bell-shaped curve

Hebbian STDP

- **Additive STDP Rule:** $J_{ij} \to J_{ij} + \delta\,\Delta J_{ij}(\Delta t_{ij});\quad \delta = 0.005,\ J_{ij} \in [0.0001, 1.0]$
  $\Delta t_{ij} (= t_i^{(post)} - t_j^{(pre)})$: Time difference between the nearest spike onset times of the post-synaptic neuron i and the pre-synaptic neuron j.
- **Time Window for the Hebbian STDP**

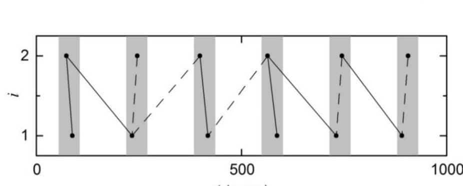
$$\Delta J_{ij} = \begin{cases} A_+ e^{-\Delta t_{ij}/\tau_+} & \text{for } \Delta t_{ij} > 0 \\ -A_- e^{\Delta t_{ij}/\tau_-} & \text{for } \Delta t_{ij} < 0 \end{cases}$$

$A_+ = 1.0,\ A_- = 0.7, \tau_+ = 35$ msec,
$\tau_- = 70$msec, $\Delta J_{ij}(\Delta t_{ij} = 0) = 0$.



When a post synaptic spike follows a pre-synaptic spike (Δt_{ij} > 0), LTP appears; otherwise (Δt_{ij} < 0), LTD occurs

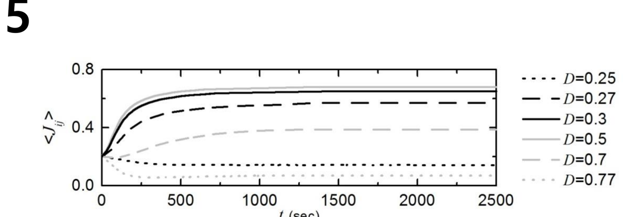
- **Nearest-Spike Pair-Based STDP Rule**
  LTP/LTD may occur between the pre- and the post-synaptic spikes in the same or the nearest-neighboring stripes.



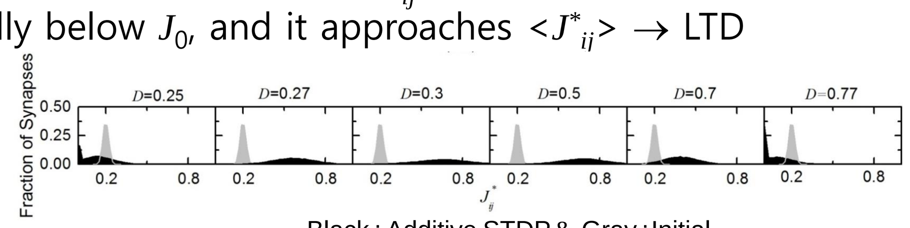
Solid line : LTP
Dashed line : LTD

Effect of the Additive STDP on SSS for p=0.15

- **Time-Evolutions of Population-Averaged Synaptic Strength $\langle J_{ij} \rangle$**
  D=0.27, 0.3, 0.5 and 0.7: $\langle J_{ij} \rangle$ increases monotonically above its initial value J_0 (=0.2), and it approaches a saturated limit value $\langle J^*_{ij} \rangle \to$ LTP
  D=0.25 and 0.77: $\langle J_{ij} \rangle$ decreases monotonically below J_0, and it approaches $\langle J^*_{ij} \rangle \to$ LTD

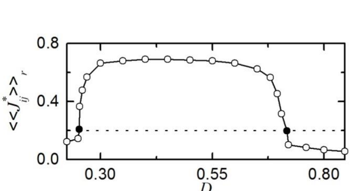


- **Histograms for Fraction of Synapses J^*_{ij}**
  $\langle J^*_{ij} \rangle$ become larger (smaller) than the initial value for LTP (LTD).
  The standard deviations are very larger than the initial one (=0.02).

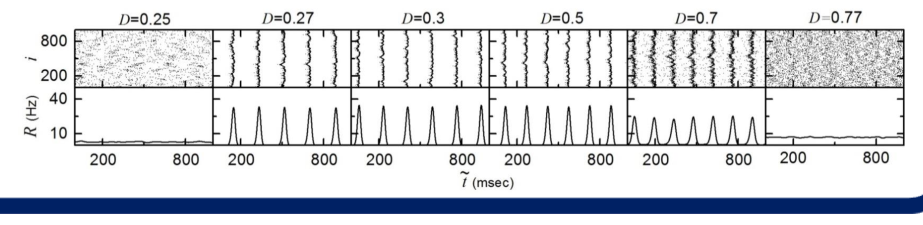


Black : Additive STDP & Gray : Initial

- **Population-Averaged Limit Values of Synaptic Strengths $\langle\langle J^*_{ij} \rangle\rangle_r$ versus D**
  LTP occurs in ($\widetilde{D}_l$, $\widetilde{D}_h$); ($\widetilde{D}_l \simeq 0.253, \widetilde{D}_h \simeq 0.717$).
  In most range of the SSS LTP occurs, while LTD takes place only near both ends.



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

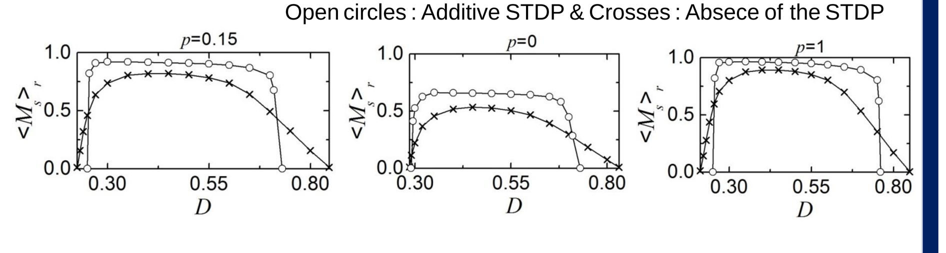


Effect of the Additive STDP on M_s

- **"Matthew" Effect in Synaptic Plasticity**
  LTP $\to$ Good synchronization gets better.
  LTD $\to$ Bad synchronization gets worse.

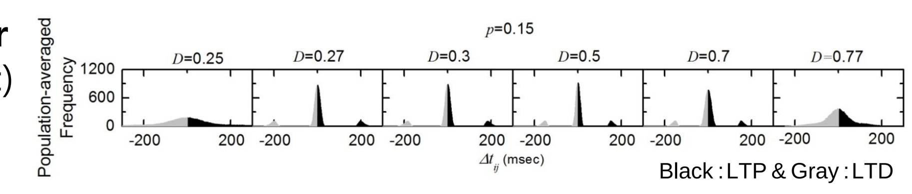
Increase in p: Step-like transitions become more rapid due to the increased Mathew effect.

Open circles : Additive STDP & Crosses : Absece of the STDP



Distribution of Microscopic Time Delays between the Pre- and Post-Synaptic Spike Times and Synaptic Modifications

- **Population-Averaged Histograms $H(\Delta t_{ij})$ for $\{\Delta t_{ij}\}$** during t=0~saturation time t^* (=2000sec)
  LTP (D=0.27, 0.3, 0.5, & 0.7): 3 peaks.
  One main central peaks (same spiking stripe) and two minor left and right peaks (different nearest-neighboring spiking stripes)
  LTD (D=0.25 & 0.77): Single broad peak via a merging of the above main and minor peaks

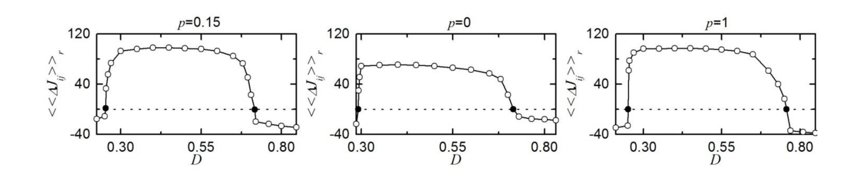


Black : LTP & Gray : LTD

- **Population-Averaged Synaptic Modification $\langle\langle \Delta J_{ij} \rangle\rangle_r$ Obtained from $H(\Delta t_{ij})$**

$$\langle\langle \Delta J_{ij} \rangle\rangle_r \simeq \sum_{bins} H(\Delta t_{ij}) \cdot \Delta J_{ij}(\Delta t_{ij})$$

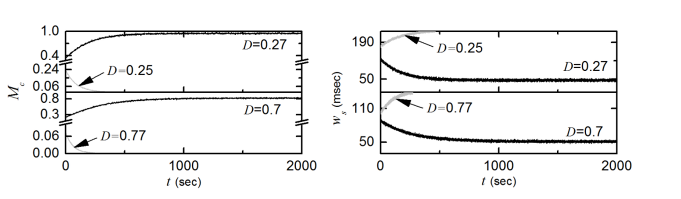
Population-averaged limit values of synaptic strengths $\langle\langle J^*_{ij} \rangle\rangle_r$ (=J_0 + $\delta\langle\langle \Delta J_{ij} \rangle\rangle_r$) agree well with direct-obtained values.



Microscopic Cross-Correlations between Synaptic Pairs

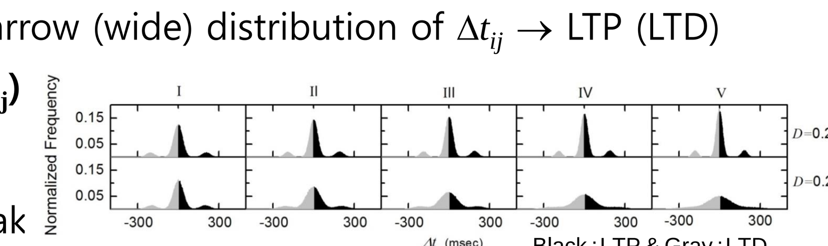
- **Microscopic Correlation Measure M_c**
  M_c: Average "in-phase" degree between the pre- and the post-synaptic pairs

$$M_c = \frac{1}{N_{syn}}\sum_{(i,j)} C_{i,j}(0), \quad C_{i,j}(\tau) = \frac{\overline{\Delta r_i(t+\tau)\Delta r_j(t)}}{\sqrt{\overline{\Delta r_i^2(t)}}\sqrt{\overline{\Delta r_j^2(t)}}}$$



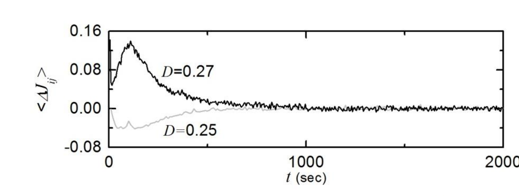
LTP (D=0.25 & 0.77): M_c increases and approaches a limit value.
LTD (D=0.27 & 0.7): M_c decreases and approaches zero.

- **Widths w_s of Spiking Stripes**
  Strong (weak) $M_c \to w_s$ decreases (increases) $\to$ Narrow (wide) distribution of $\Delta t_{ij} \to$ LTP (LTD)
- **Time-Evolutions of Normalized Histogram $H(\Delta t_{ij})$**
  LTP: 3 peaks $\to$ Peaks become narrowed.
  $\to$ Main peak becomes symmetric.
  LTD: 3 peaks $\to$ Merged into the single broad peak
  $\to$ Peak becomes symmetric.



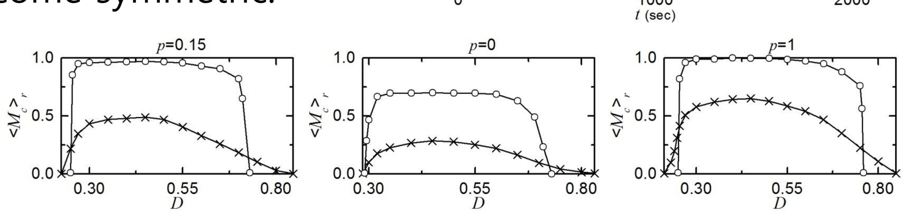
Black : LTP & Gray : LTD

- **Time-Evolutions of $\langle\Delta J_{ij}\rangle$**
  LTP (D=0.27) [LTD (D=0.25)]: $\langle\Delta J_{ij}(t)\rangle$ is positive (negative)
  $\langle\Delta J_{ij}(t)\rangle$ approach 0 because $H(\Delta t_{ij})$ become symmetric.



- **Mathew Effect in M_c**
  M_c: Matthew effect also occurs.

Increase in p: Step-like transitions become more rapid due to the increased Mathew effect.



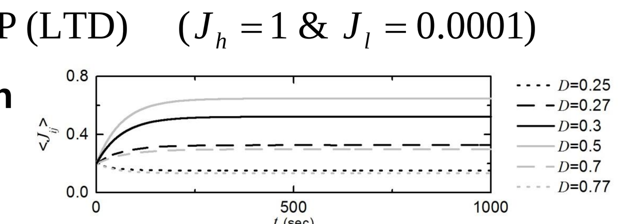
Open circles : Multiplicative STDP, Crosses : Absece of the STDP

Effect of the Multiplicative STDP on the SSS

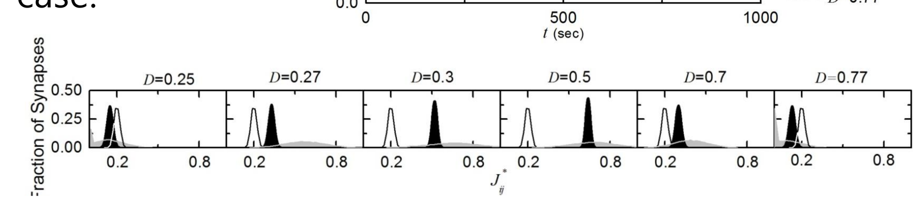
- **Multiplicative STDP Rule**: Soft bound for the synaptic strength

$$J_{ij} \to J_{ij} + (J^* - J_{ij})\,|\,\delta\Delta J_{ij}(\Delta t_{ij})\,| \qquad J^* = J_h(J_l) \text{ for the LTP (LTD)} \quad (J_h = 1\ \&\ J_l = 0.0001)$$

- **Time-Evolutions of Population-Averaged Synaptic Strength**
  Soft bound $\to$ Saturation time is shorter and $\langle J^*_{ij} \rangle$ are smaller than the additive STDP case.



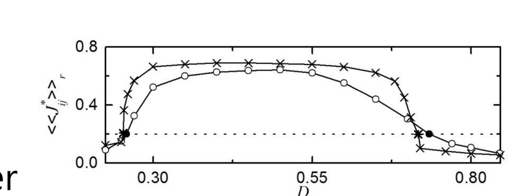
- **Histograms for Fraction of J^*_{ij}**
  LTP (D=0.27, 0.3, 0.5, & 0.7): $\langle J^*_{ij} \rangle$ become larger than the initial value
  LTD (D=0.25 & 0.77): $\langle J^*_{ij} \rangle$ become smaller than the initial value



Black : Multiplicative STDP, Gray : Additive STDP, Black curve : Initial

Both cases, standard deviations of $\{J^*_{ij}\}$ are smaller than the initial value (=0.02).

- **Population-Averaged Limit Values of Synaptic Strengths $\langle\langle J^*_{ij} \rangle\rangle_r$ versus D**
  LTP occurs in ($\widetilde{D}_l$, $\widetilde{D}_h$); ($\widetilde{D}_l \simeq 0.258, \widetilde{D}_h \simeq 0.735$).
  Both $\langle J^*_{ij} \rangle$ and its standard deviation are smaller than those for the case of the additive STDP.
  Gradual change near the thresholds in contrast to the case of the additive STDP



Open circles : Multiplicative STDP
Crosses : Additive STDP

- **Raster Plots of Spikes and IPSR $R(t)$**
  LTP $\to$ The degrees of SSS are increased.
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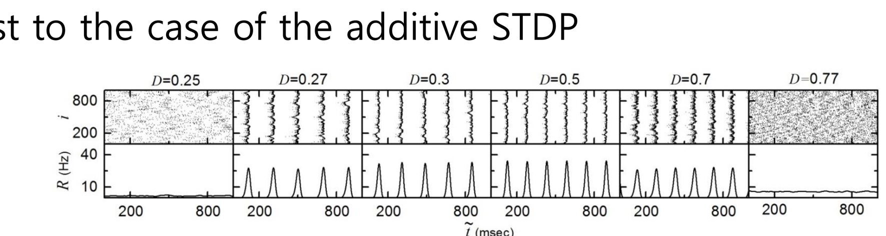
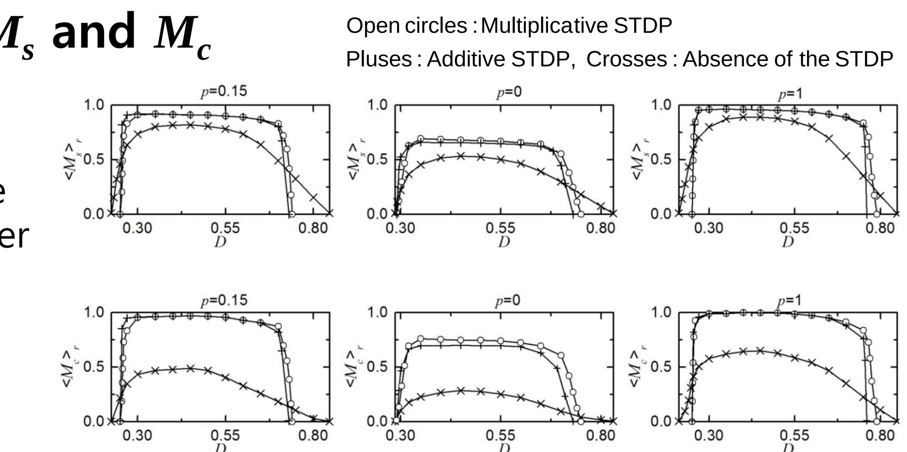


Effect of Multiplicative STDP on M_s and M_c

Open circles : Multiplicative STDP
Pluses : Additive STDP, Crosses : Absence of the STDP

Smaller $\langle J^*_{ij} \rangle$ (standard deviation of J^*_{ij})
$\to$ Decreasing (Increasing) M_s and M_c,
$\Rightarrow M_s$ and M_c: Nearly the same as those in the the additive case, although $\langle J^*_{ij} \rangle$ are smaller

Changes in M_s and M_c near the thresholds:
Relatively less rapid than the additive case due to soft bounds



Matthew Effect occurs in both M_s and M_c.
Increase in p: Step-like transitions become more rapid due to the increased Mathew effect similar to the case of the additive STDP.

Summary

- **Stochastic Spike Synchronization (SSS)**
  - SSS between complex noise-induced spikings of subthreshold neurons: Correlated with brain function of encoding sensory stimuli in the noisy environment.
  - Previous works on SSS: Synaptic strengths were static.
  - Occurrence of SSS in intermediated noise intensities via competition between the constructive and the destructive roles of noise.
- **Investigation of The Effect of Additive STDP on the SSS**
  - Occurrence of "Matthew" effect in synaptic plasticity
    $\to$ Good synchronization gets better via LTP, while bad synchronization gets worse via LTD.
  - Intensive investigation of emergences of LTP and LTD via microscopic studies based on both the distributions of time delays and the pair-correlations between the pre- and the post-synaptic IISRs.
- **Investigation of The Effect of Multiplicative STDP on the SSS**
  - Soft bounds in the synaptic strengths in contrast to the hard bounds for the additive case.
  - Both $\langle J^*_{ij} \rangle$ and the standard deviation σ of $\{J^*_{ij}\}$: Smaller than those for the case of additive STDP
  - Degrees of SSS in most cases: Nearly the same as those in the additive case.
    Near the thresholds, changes in M_s are also relatively less rapid due to soft bounds, when compared with the additive case.