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Equalization Effect in Interpopulation Spike-Timing-Dependent Plasticity in Two Inhibitory and Excitatory Populations



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Abstract We consider two inhibitory (I) and excitatory (E) populations with I to E and E to I interpopulation spike-timing-dependent plasticity (STDP). By changing the noise intensity D, we study the effect of interpopulation STDPs on fast sparsely synchronized rhythms that appear in the two I- and E-populations. Long-term potentiation (LTP) and long-term depression (LTD) for population-averaged values of saturated interpopulation synaptic strengths are thus found to take place. Then, the degree of fast sparse synchronization changes due to the effects of LTP and LTD. In a broad region of intermediate D, the degree of good synchronization (with larger synchronization degree) gets decreased. On the other hand, in a region of large D, the degree of bad synchronization (with smaller synchronization degree) becomes increased. As a result, an "equalization effect" in interpopulation synaptic plasticity occurs in each I- or E-population, where the synchronization degree gets nearly the same in a wide range of D.

1 Introduction

We are interested in fast sparsely synchronized rhythms, related to various cognitive functions (Wang, 2010). This kind of fast sparse synchronization has been much studied in diverse aspects (Wang, 2010; Fisahn et al., 1998; Brunel & Wang, 2003; Geisler et al., 2005; Brunel & Hakim, 2008). In such previous works, synaptic coupling strengths were static. However, in real brains, synaptic strengths may be potentiated (LTP) or depressed (LTD) to adapt to the environment. This kind of adjustment of synaptic strength is called the synaptic plasticity which gives the basis for learning, memory, and development (Abbott & Nelson, 2000).

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Here, we take into consideration, spike-timing-dependent plasticity (STDP) (Song et al., 2000). For the STDP, the synaptic strengths change depending on the relative time difference between the post- and the pre-synaptic spike times. In our recent works (Kim & Lim, 2018), the effects of inhibitory STDP (at I to I synapses) on fast sparse synchronization have been studied in networks of inhibitory fast spiking interneurons.

In contrast to the previous work on the I to I intrapopulation STDP, we consider interpopulation (I to E and E to I) STDPs between the I- and the E-populations. By changing the noise intensity D, we study the effects of interpopulation STDPs on fast sparse synchronization. In Sect. 2, the two I- and E-populations with interpopulation STDPs are described. Then, in Sect. 3, we investigate the effects of interpopulation STDPs on fast sparse synchronization. Finally, summary and discussion are given in Sect. 4.

2 Two I- and E-Populations with Interpopulation Synaptic Plasticity

As in the Ref. (Kim & Lim, 2020), we consider clustered small-world networks (SWNs) consisting of the I- and E-populations. Each I(E)-population is modeled as a directed Watts–Strogatz SWN (Watts & Strogatz, 1998), composed of N_I (N_E) ($N_E : N_I = 4 : 1$) interneurons (pyramidal cells). Connections between the I and the E SWNs are done in random and uniform way. The Izhikevich inhibitory fast spiking interneuron (excitatory regular spiking pyramidal cell) model (which is not only biologically plausible, but also computationally efficient (Izhikevich, 2007)) is chosen as elements in the I SWN (E SWN). Particularly, external noise (i.e., background noise) in our model denotes stochastic fluctuations of random external inputs from other brain regions (not included in the network). It is modeled in terms of a Gaussian white noise in the governing equations for our system, and its intensity is controlled by the parameter *D*. For the whole parameters used in our computations, refer to Table 1 in Kim and Lim (2020).

The coupling strength of the synapse from the pre-synaptic neuron *j* in the source *Y*-population to the post-synaptic neuron *i* in the target *X*-population is $J_{ij}^{(XY)}$. Initial synaptic strengths are normally distributed with the mean $J_0^{(XY)}$ and the standard deviation σ_0 (= 5); $J_0^{(II)} = 1300$, $J_0^{(EE)} = 300$, $J_0^{(EI)} = 800$, and $J_0^{(IE)} = 487.5$. The I to I synaptic strength ($J_0^{(II)} = 1300$) is so strong that fast sparse synchronization may appear in the I-population via balance between strong inhibition and strong external noise (Wang, 2010; Brunel & Wang, 2003; Geisler et al., 2005; Brunel & Hakim, 2008). This I-population is a dominant one, since $J_0^{(II)}$ is much stronger than the E to E synaptic strength ($J_0^{(EE)} = 300$). Moreover, the I to E synaptic strength ($J_0^{(EE)} = 800$) is so strong, and hence fast sparse synchronization may also occur in the E-population when the noise intensity *D* passes a threshold. In contrast, the E to I synaptic strength ($J_0^{(IE)} = 487.5$) is small in comparison with $J_0^{(EI)}$, and hence the

effects of the E-population to the I-population are small. In this way, we consider an inhibition-dominated case.

Here, we consider only the I to E and E to I interpopulation synaptic plasticity; in this case, intrapopulation synaptic strengths are static. For the interpopulation synaptic strengths $\{J_{ij}^{(XY)}\}$, we take into consideration a multiplicative STDP (dependent on states) (Kim & Lim, 2018). As the time *t* is increased, synaptic strength for each interpopulation synapse is updated with a nearest spike pair-based STDP rule:

$$J_{ij}^{(XY)} \to J_{ij}^{(XY)} + \delta(J^* - J_{ij}^{(XY)}) |\Delta J_{ij}^{(XY)}(\Delta t_{ij}^{(XY)})|, \tag{1}$$

where $J^* = J_h(J_l)$ for the LTP (LTD) and $\Delta J_{ij}^{(XY)}(\Delta t_{ij}^{(XY)})$ is the synaptic modification depending on the relative time difference $\Delta t_{ij}^{(XY)} (= t_i^{(\text{post},X)} - t_j^{(\text{pre},Y)})$ between the nearest spike times of the post-synaptic neuron *i* in the target *X*-population and the pre-synaptic neuron *j* in the source *Y*-population. For the values of the lower and the upper bounds (J_l and J_h) and the update rate δ , refer to Table 1 in Kim and Lim (2020).

For the I to E STDP, we use a time-delayed Hebbian time window for the synaptic modification $\Delta J_{ij}^{(EI)}(\Delta t_{ij}^{(EI)})$ (Haas et al., 2006); refer to Eqs. (13) and (14) for $\Delta J_{ij}^{(EI)}(\Delta t_{ij}^{(EI)})$ in Kim and Lim (2020). As in the E to E Hebbian time window, LTP occurs for $\Delta t_{ij}^{(EI)} > 0$, while LTD takes place for $\Delta t_{ij}^{(EI)} < 0$. However, the time-delayed Hebbian time window has delayed maximum and minimum for $\Delta J_{ij}^{(EI)}$ [see Fig. 6a in Kim and Lim (2020)], in contrast to the E to E Hebbian time window.

For the E to I STDP, we employ an anti-Hebbian time window for the synaptic modification $\Delta J_{ij}^{(IE)}(\Delta t_{ij}^{(IE)})$ (Bell et al., 1997); refer to Eq. (15) for $\Delta J_{ij}^{(EI)}(\Delta t_{ij}^{(EI)})$ in Kim and Lim (2020). For $\Delta t_{ij}^{(IE)} > 0$, LTD occurs, while LTP takes place for $\Delta t_{ij}^{(IE)} < 0$ [see Fig.6c in Kim and Lim (2020], in contrast to the Hebbian time window for the E to E STDP (Song et al., 2000).

3 Effects of Interpopulation STDPs on Fast Sparse Synchronization

We first consider the case without STDP. In this case, fast sparse synchronization has been found to occur in an wide range (D_1^*, D_2^*) of noise intensity *D* through balance between strong external noise and strong inhibition (Wang, 2010; Brunel & Wang, 2003; Geisler et al., 2005;Brunel & Hakim, 2008). In our model, when passing the first threshold $D_1^* (\simeq 91)$, fast sparse synchronization is found to appear in both the Iand the E-populations. Such population synchronization may be well visualized in the raster plot of neural spikes which is a collection of spike trains of individual neurons. As a collective quantity showing population behaviors, we use an instantaneous population spike rate which may be obtained from the raster plots of spikes (Wang, 2010; Brunel & Wang, 2003; Geisler et al., 2005; Brunel & Hakim, 2008). In the case of fast sparse synchronization, raster plots of spikes in the I- and the E-populations and the corresponding instantaneous population spike rates $R_I(t)$ and $R_E(t)$ are shown for various values of D as shown in Fig. 3b3–b7, c3–c7, and d3–d7 in Ref. (Kim & Lim, 2020). In the I-population, each raster plot is composed of spikes (upper black dots) of N_I (= 600) fast spiking interneurons, while in the E-population, each raster plot consists of spikes (lower gray dots) of N_E (= 2400) regular spiking pyramidal cells. Sparse spiking stripes (consisting of spikes and representing population sparse synchronization) appear successively in the raster plots of spikes in both the I- and the E-populations, and the corresponding instantaneous population spike rates $R_I(t)$ and $R_E(t)$ also show fast in-phase oscillations.

For quantitative analysis, we characterize the degree of fast sparse synchronization in each X-population (X = E or I) in terms of synchronization degree $S_d^{(X)}$, defined by the time-averaged amplitudes of the instantaneous population spike rate $R_X(t)$. As D is increased, the amplitude of $R_I(t)$ decreases monotonically, which results in monotonic decrease in $S_d^{(I)}$ of the I-population. On the other hand, with increasing D, the amplitude of $R_E(t)$ first increases to its peak at $D \sim 250$, and then it becomes decreased. Thus, $S_d^{(E)}$ for a bell-shaped curve. Due to a destructive role of noise to spoil fast sparse synchronization, a transition to desynchronization takes place in both I- and E-populations when passing the second threshold D_2^* ($\simeq 537$). In a desynchronized case, spikes are completely scattered without forming any stripes [see Fig. 3b8 in Kim and Lim (2020)], and the corresponding instantaneous population spike rates $R_I(t)$ and $R_E(t)$ become nearly stationary, as shown in Fig. 3c8, d8 in Kim and Lim (2020). As a result, asynchronous irregular states emerge in the desynchronized region.

From now on, we take into interpopulation (both I to E and E to I) STDPs and investigate their effects on fast sparse synchronization by varying the noise intensity D. Time evolutions of population-averaged I to E synaptic strengths $\langle J_{ij}^{(EI)} \rangle$ and E to I synaptic strengths $\langle J_{ij}^{(IE)} \rangle$ for various values of D are shown in Fig. 7a1, a2, respectively. First, we take into consideration the case of I to E STDP. In each case of intermediate values of D = 110, 250, and 400 (shown in black color), $\langle J_{ij}^{(EI)} \rangle$ increases monotonically above its initial value $J_0^{(EI)}$ (=800), and eventually it converges to a saturated limit value $\langle J_{ij}^{(EI)^*} \rangle$ nearly at t = 1500 s. As a result, inhibitory LTP takes place for these values of D. In contrast, for small and large values of D = 95, 500, and 600 (shown in gray color), $\langle J_{ij}^{(EI)^*} \rangle$. Consequently, inhibitory LTD occurs in the cases of D = 95, 500, and 600.

We next consider the case of E to I STDP. Due to the effect of anti-Hebbian time window, time evolutions of $\langle J_{ij}^{(IE)} \rangle$ are in contrast to those of $\langle J_{ij}^{(EI)} \rangle$ in the case of time-delayed Hebbian time window. For intermediate values of D = 110, 250, and 400 (shown in black color), $\langle J_{ij}^{(IE)} \rangle$ decreases monotonically below its initial value $J_0^{(IE)}$ (=487.5), and eventually, it approaches a saturated limit value $\langle J_{ij}^{(IE)} \rangle$ nearly at t = 1500 s. Consequently, excitatory LTD occurs for these intermediate values of D. On the other hand, for small and large values of D = 95, 500, and 600 (shown in

gray color), $\langle J_{ij}^{(IE)} \rangle$ increases monotonically above $J_0^{(IE)}$ and approaches a saturated limit value $\langle J_{ij}^{(IE)*} \rangle$. Accordingly, excitatory LTP occurs for D = 95, 500, and 600.

Such saturated limit values in the cases of I to E and E to I STDPs are shown in Figs. 7b1 and b2 in Kim and Lim (2020), respectively. In the case of I to E STDP, plot of saturated limit values $\langle J_{ij}^{(E1)*} \rangle \rangle_r$ for a bell-shaped curve. Here, the horizontal dotted line represents the initial average value $J_0^{(E1)}$ (= 800) of I to E synaptic strengths. On the other hand, in the case of E to I STDP, the plot of saturated limit values $\langle J_{ij}^{(IE)*} \rangle \rangle_r$ (open circles) forms a well-shaped graph, where the horizontal dotted line denotes the initial average value of E to I synaptic strengths $J_0^{(IE)}$ (= 487.5). The lower and the higher thresholds, \tilde{D}_l (\simeq 99) and \tilde{D}_h (\simeq 408), for LTP/LTD (where $\langle J_{ij}^{(E1)*} \rangle \rangle_r$ and $\langle J_{ij}^{(IE)*} \rangle \rangle_r$ lie on their horizontal lines) are denoted by solid circles.

In the case of a bell-shaped graph for $\langle \langle J_{ij}^{(EI)*} \rangle \rangle_r$, inhibitory LTP occurs in a broad region of intermediate D ($\tilde{D}_l < D < \tilde{D}_h$), while inhibitory LTD takes place in the other two (separate) regions of small and large D [$D_1^* < D < \tilde{D}_l$ and $\tilde{D}_h < D < D_{2,\text{inter}}$ ($\simeq 672$)]. We note that inhibitory LTP (inhibitory LTD) disfavors (favors) fast sparse synchronization [i.e., inhibitory LTP (inhibitory LTD) tends to decrease (increase) the degree of fast sparse synchronization] because of increase (decrease) in the mean value of I to E synaptic inhibition.

In contrast, in the case of a well-shaped graph for $\langle \langle J_{ij}^{(IE)*} \rangle \rangle_r$, excitatory LTD takes place in a broad region of intermediate D ($\tilde{D}_l < D < \tilde{D}_h$), while excitatory LTP occurs in the other two (separate) regions of small and large D ($D_1^* < D < \tilde{D}_l$ and $\tilde{D}_h < D < D_{2,\text{inter}}^*$). We also note that the roles of LTP and LTD are reversed in the case of E to I STDP. Excitatory LTP (excitatory LTD) favors (disfavors) fast sparse synchronization [i.e., excitatory LTP (excitatory LTD) tends to increase (decrease) the degree of fast sparse synchronization] due to increase (decrease) in the mean value of E to I synaptic excitation.

The effects of LTP and LTD at inhibitory and excitatory synapses on population states after the saturation time ($t^* = 1500$ s) may be well seen in the raster plot of spikes in the I- and the E-populations and the corresponding instantaneous population spike rates $R_I(t)$ and $R_E(t)$. Raster plots of spikes in the I- and the E-populations and the corresponding instantaneous population spike rates $R_I(t)$ and $R_E(t)$ are shown for various values of D in Figs. 8b1–b6, c1–c6, and d1–d6, respectively. In comparison with the case without STDP, the degrees of fast sparse synchronization for intermediate values of D (D = 110, 250, and 400) are decreased (i.e., the amplitudes of $R_I(t)$ and $R_E(t)$ are decreased) due to increased I to E synaptic inhibition (i.e., increase in inhibitory LTP) and decreased E to I synaptic excitation (decrease in excitatory LTD). On the other hand, for small and large values of D (D = 95 and 500), the degrees of fast sparse synchronization are increased (i.e., the amplitudes of $R_I(t)$ and $R_E(t)$ are increased) due to decreased I to E synaptic inhibition (i.e., decrease in inhibitory LTD) and increased E to I synaptic excitation (decrease in excitatory LTD). On the other hand, for small and large values of D (D = 95 and 500), the degrees of fast sparse synchronization are increased (i.e., the amplitudes of $R_I(t)$ and $R_E(t)$ are increased) due to decreased I to E synaptic inhibition (i.e., decrease in inhibitory LTD) and increased E to I synaptic excitation (increase in excitatory LTP). We note that a desynchronized state for D = 600 in the absence of STDP is transformed into fast sparse synchronization through inhibitory LTD and excitatory LTP. In fact, desynchronized states for D_2^* ($\simeq 537$) $< D < D_{2,inter}^*$ ($\simeq 672$) in the absence of STDP become fast sparsely synchronized ones in the presence of interpopulation STDPs, and thus the region of fast sparse synchronization becomes so much extended. Moreover, we also note that the degree of fast sparse synchronization in the I-(E-)population (i.e., the amplitude of $R_I(t)$ [$R_E(t)$]) tends to be nearly the same in an "extended" wide range of $\tilde{D}_l < D < D_{2,inter}^*$, except for the narrow small-D region ($D_1^* < D < \tilde{D}_l$). Hence, an equalization effect in the interpopulation synaptic plasticity occurs in such an extended wide range of D.

Finally, we make quantitative characterization of the degree of fast sparse synchronization in each X-population (X = E or I) in terms of synchronization degree $S_d^{(X)}$ (defined by the time-averaged amplitudes of the instantaneous population spike rate $R_X(t)$). In each realization, $S_d^{(X)}$ is obtained through time average over 3000 global cycles of $R_X(t)$.

We first consider the case of I-population. Figure 1a shows plots of $\langle S_d^{(I)} \rangle_r$ versus D. In the gray region of intermediate $D[\widetilde{D}_l (\simeq 99) < D < \widetilde{D}_h (\simeq 408)]$, the degrees of good synchronization (solid circles) in the absence of STDP get decreased to lower ones (open circles) via (E to I) excitatory LTD, while in the region of large $D[\widetilde{D}_h < D < D_{2,\text{inter}}^* (\simeq 672)]$, the degrees of bad synchronization (solid circles) in the absence of STDP become increased to higher values (open circles) through (E to I) excitatory LTP. Consequently, in a wide region of $\widetilde{D}_l < D < D_{2,\text{inter}}^*$ (including both the intermediate and the large D regions), the values of $S_d^{(I)}$ become nearly the same. This kind of equalization effect may also be well seen in the histograms for



Fig. 1 Characterization of spiking degrees for fast sparse synchronization. Plots of **a** [(**b**)] the synchronization degree $\langle S_d^{(I)} \rangle_r (\langle S_d^{(E)} \rangle_r)$ (open circles) versus *D* in the I(E)-population. For comparison, those in the absence of STDP are also denoted by solid circles. Histograms for distribution of synchronization degrees $\langle S_d^{(I)} \rangle_r (\langle S_d^{(E)} \rangle_r)$ in the I(E)-population in the **c1** [(**d1**)] absence and the **c2** [(**d2**)] presence of interpopulation STDP

the distribution of $\langle S_d^{(I)} \rangle_r$ in the region of $\widetilde{D}_l < D < D_{2,\text{inter}}^*$. The gray histogram in the absence of STDP is shown in Fig. 1c1 and the hatched histogram in the presence of interpopulation STDP is given in Fig. 1c2. The standard deviation (\simeq 12.4) in the hatched histogram is much smaller than that (\simeq 20.4) in the gray histogram, and hence equalization effect emerges. Moreover, a dumbing-down effect also occurs because the mean value (\simeq 23.7) in the hatched histogram is smaller than that (\simeq 27.9) in the gray histogram.

Next, we consider the case of E-population. Figure 1b shows plots of $\langle S_d^{(E)} \rangle_r$ versus D. In the gray region of intermediate D ($\tilde{D}_l < D < \tilde{D}_h$), the degrees of good synchronization (solid circles) in the absence of STDP become decreased to lower ones (open circles) through (I to E) inhibitory LTP, while in the region of large D ($\tilde{D}_h < D < D_{2,inter}^*$), the degrees of bad synchronization (solid circles) in the absence of STDP get increased to higher values (open circles) via (I to E) inhibitory LTD. As a result, in a broad region of $\tilde{D}_l < D < D_{2,inter}^*$ (including both the intermediate and the large D regions), the values of $S_d^{(E)}$ get nearly the same, as in the case of $S_d^{(I)}$. This type of equalization effect may also be well seen in the histograms for the distribution of $\langle S_d^{(E)} \rangle_r$ in the region of $\tilde{D}_l < D < D_{2,inter}^*$. The gray histogram in the absence of STDP and the hatched histogram in the presence of interpopulation STDP are shown in Fig. 1d1, d2, respectively. The standard deviation ($\simeq 0.9$) in the hatched histogram is much smaller than that ($\simeq 3.1$) in the gray histogram, and hence equalization effect appears. Furthermore, a dumbing-down effect also takes place because the mean value ($\simeq 3.0$) in the hatched histogram is smaller than that ($\simeq 6.0$) in the gray histogram.

4 Summary and Discussion

We considered clustered small-world networks consisting of I- and E-populations with interpopulation STDPs. A time-delayed Hebbian time window has been employed for the I to E STDP update rule. On the other hand, an anti-Hebbian time window has been used for the E to I STDP update rule. By changing the noise intensity D, we have studied the effects of interpopulation STDPs on fast sparsely synchronized rhythms. Thus, LTP and LTD have been found to occur, depending on D. These LTP and LTD affect the degree of fast sparse synchronization. In a broad region of intermediate D, the degree of good synchronization (with larger synchronization degree) has been found to get decreased. On the other hand, in the region of large D, the degree of fast sparse synchronization become increased. Accordingly, the degree of fast sparse synchronization becomes nearly the same (i.e., a kind of "equalization effect" occurs) in a wide range of D. We note that this kind of equalization effect is distinctly in contrast to the Matthew effect in intrapopulation (I to I and E to E) synaptic plasticity where good (bad) synchronization becomes better (worse) (Kim & Lim, 2018).

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