

Impact of Deviation from Precise Balance between LTP and LTD of STDP on Retrieval Properties of Spatio-Temporal Patterns

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Abstract

Recent biological experimental findings have shown that a synaptic plasticity depends on a relative timing of pre- and post-synaptic spikes and this is called spike timing dependent plasticity (STDP). Many authors have claimed that a precise balance between long-term potentiation (LTP) and long-term depression (LTD) of STDP is crucial in storing spatio-temporal patterns. Some authors *numerically* investigated an impact of the imbalance between LTP and LTD on the network properties. However, this mathematical mechanism remains unknown. We *analytically* show that an associative memory network has the robust retrieval properties

of spatio-temporal patterns against the deviation from the precise balance between LTP and LTD when it contains a *finite* number of neurons.

1 Introduction

Recent biological experimental findings have indicated that a synaptic plasticity depends on a relative timing of pre- and post-synaptic spikes. This relative timing determines whether long-term potentiation (LTP) or long-term depression (LTD) is induced (Bi and Poo, 1998; Markram et al., 1997; Zhang et al., 1998). LTP occurs when a presynaptic firing precedes a postsynaptic firing by no more than about 20 ms. In contrast, LTD occurs when the presynaptic firing follows the postsynaptic firing. A rapid transition between LTP and LTD takes place within a few ms. A learning rule of this type is called spike-timing-dependent plasticity (STDP) (Song et al., 2000) or temporally asymmetric Hebbian learning (TAH) (Abbott and Song, 1999; Rubin et al., 2001). The functional role of STDP has been investigated by many authors (Gerstner et al., 1996; Kempter et al., 1999; Abbott and Song, 1999; Munro and Hernandez, 2000; Rao and Sejnowski, 2000; Song et al., 2000; Rubin et al., 2001; Levy et al., 2001; van Rossum et al., 2001; Song and Abbott, 2001; Yoshioka, 2002; Fu et al., 2002; Karmarkar and Buonomano, 2002; Matsumoto and Okada, 2002b). Particularly, some of them have claimed that the balance between LTP and LTD of STDP is crucial (Song et al., 2000; Munro and Hernandez, 2000; Yoshioka, 2002; Matsumoto and Okada, 2002b). In our previous work, we analytically showed that STDP has the same qualitative effect as the covariance rule when the balance is maintained precisely (Matsumoto and Okada,

2002b). In the brain, it is inconceivable to maintain the balance precisely. Some authors *numerically* investigated the impact of the imbalance between LTP and LTD on the network properties (Song et al., 2000; Munro and Hernandez, 2000; Yoshioka, 2002). Munro and Hernandez showed that spatio-temporal patterns can not be retrieved in a noisy environment in a case without LTD (Munro and Hernandez, 2000). However, this *mathematical* mechanism remains unknown.

In this paper, we *analytically* investigate retrieval properties of spatio-temporal patterns in an associative memory network involving the imbalance between LTP and LTD of STDP using a method of the statistical neurodynamics (Amari and Maginu, 1988; Okada, 1996; Matsumoto and Okada, 2002b). Using this theory, we discuss a macroscopic behavior of the network in a thermodynamic limit: the number of neurons is infinite, $N \rightarrow \infty$. When the balance is maintained precisely, sequential patterns can be stored in the network (Matsumoto and Okada, 2002b). When a mean of deviation from the precise balance is 0 and a fluctuation is finite, the patterns can be stored in the limit of $N \rightarrow \infty$ (Matsumoto and Okada, 2002a). In other words, when the balance is maintained on average, the patterns are retrievable. We also showed that when the mean is not 0, the patterns can not be stored since a cross-talk noise diverge in the limit of $N \rightarrow \infty$. However, previous work using computer simulations has shown that the stored limit cycle is stably retrieved when the number of neurons, N , is *finite* (Munro and Hernandez, 2000; Yoshioka, 2002). In the brain, the number of neurons is considered to be *finite*. Therefore, it is very important to discuss this situation, although there are no analytical works. The purpose of this paper is to *analytically* investigate the retrieval properties when the number of neurons is finite. We found that

the network containing the finite number of neurons becomes robust against this deviation from the precise balance between LTP and LTD of STDP. Since the number of neurons in the brain is considered to be finite, our results might be acceptable in the brain.

We introduce our model for the storage of spatio-temporal patterns in section 2. In section 3, we discuss analytically our model both when the balance between LTP and LTD of STDP is maintained precisely and when it is not maintained precisely. In section 4, we investigate the properties of our model. In section 5, we summarize this paper and discuss our model. The Appendix presents a detailed derivation of dynamical equations of the model when the balance is maintained precisely.

2 Model

The model contains N binary neurons with reciprocal connections. Each neuron takes a binary value: $\{0, 1\}$. We define discrete time steps and the following rule for synchronous updating:

$$u_i(t) = \sum_{j=1}^N J_{ij} x_j(t), \quad (1)$$

$$x_i(t+1) = F(u_i(t) - \theta), \quad (2)$$

$$F(u) = \begin{cases} 1. & u \geq 0 \\ 0. & u < 0, \end{cases} \quad (3)$$

where $x_i(t)$ is the state of the i -th neuron at time t , $u_i(t)$ is the internal potential of that neuron, and θ is a uniform threshold. If the i -th neuron fires at t , its state is $x_i(t) = 1$; otherwise, $x_i(t) = 0$. J_{ij} is the synaptic weight from the j -th neuron to

the i -th neuron. Each element ξ_i^μ of the μ -th memory pattern $\boldsymbol{\xi}^\mu = (\xi_1^\mu, \xi_2^\mu, \dots, \xi_N^\mu)$ is generated independently by

$$\text{Prob}[\xi_i^\mu = 1] = 1 - \text{Prob}[\xi_i^\mu = 0] = f. \quad (4)$$

The expectation of $\boldsymbol{\xi}^\mu$ is $E[\xi_i^\mu] = f$, and thus f is considered to be the mean firing rate of the memory pattern. The memory pattern is sparse when $f \rightarrow 0$, and this coding scheme is called sparse coding.

The synaptic weight J_{ij} follows the form of synaptic plasticity, which depends on the difference in spike times between the i -th (post-) and j -th (pre-) neurons. The difference determines whether LTP or LTD is induced. This type of learning rule is called spike-timing-dependent plasticity (STDP). The biological experimental findings show that LTP or LTD is induced when the difference in the pre- and post-synaptic spike times falls within about 20 ms (Zhang et al., 1998) (Figure 1(a)). We define a single time step in equations (1–3) as 20 ms, and the durations within 20 ms are ignored. The learning rule based on STDP conforms to this equation:

$$J_{ij} = \frac{1}{Nf(1-f)} \sum_{\mu=1}^p (\xi_i^{\mu+1} \xi_j^\mu - (1+\epsilon) \xi_i^{\mu-1} \xi_j^\mu). \quad (5)$$

The number of memory patterns is $p = \alpha N$, where α is defined as the loading rate. LTP is induced when the j -th neuron fires one time step before the i -th neuron, $\xi_i^{\mu+1} = \xi_j^\mu = 1$, while LTD is induced when the j -th neuron fires one time step after the i -th neuron, $\xi_i^{\mu-1} = \xi_j^\mu = 1$. Since the relative magnitude of LTP and LTD is more critical than the absolute magnitudes, the magnitude of LTD changes while that of LTP and the time duration are fixed. ϵ denotes the deviation from the precise balance. When $\epsilon = 0$, the balance is precisely maintained and this

model is equivalent to the previous one (Matsumoto and Okada, 2002b). Figure 1(b) shows the form of STDP in the present model. A sequence of p memory patterns is stored by STDP: $\boldsymbol{\xi}^1 \rightarrow \boldsymbol{\xi}^2 \rightarrow \dots \rightarrow \boldsymbol{\xi}^p \rightarrow \boldsymbol{\xi}^1 \rightarrow \dots$. In other words, $\boldsymbol{\xi}^1$ is retrieved at $t = 1$, $\boldsymbol{\xi}^2$ is retrieved at $t = 2$, and $\boldsymbol{\xi}^1$ is retrieved at $t = p + 1$. There is a critical value α_C of the loading rate, so that a loading rate larger than α_C makes retrieval of the pattern sequence unstable. α_C is called the storage capacity.

3 Theory

3.1 The Case where Balance is Maintained Precisely

We briefly discuss the case where the balance is maintained precisely, which was previously discussed (Matsumoto and Okada, 2002b). This helps a comprehension of the case where the balance is not maintained precisely and keeps a coherence of this paper.

At first, we discuss the simple situation where there are very few memory patterns relative to the number of neurons, i.e., $p \sim O(1)$. Let the state at time t be the equivalent to the t -th memory pattern: $\boldsymbol{x}(t) = \boldsymbol{\xi}^t$. The internal potential $u_i(t)$ of equation (1) is then given by

$$u_i(t) = \xi_i^{t+1} - \xi_i^{t-1}. \quad (6)$$

$u_i(t)$ depends on two independent random variables, ξ_i^{t+1} and ξ_i^{t-1} . The first term ξ_i^{t+1} is the signal term for the recall of the pattern $\boldsymbol{\xi}^{t+1}$, which is intended to be retrieved at time $t + 1$, and the second term ξ_i^{t-1} may interfere with the retrieval

of ξ^{t+1} . According to equation (6), $u_i(t)$ takes a value of 0, -1 or $+1$. The probability distribution of $u_i(t)$ is given by Figure 2(a), i.e.,

$$\text{Prob}(u_i(t)) = (f - f^2)\delta(u_i(t) - 1) + (1 - 2f + 2f^2)\delta(u_i(t)) + (f - f^2)\delta(u_i(t) + 1). \quad (7)$$

If the threshold θ is set between 0 and $+1$, the probability of $u_i(t) = 0$ is $1 - 2f + 2f^2$, that of $u_i(t) = +1$ is $f - f^2$, and that of $u_i(t) = -1$ is $f - f^2$. The overlap between the state $\mathbf{x}(t + 1)$ and the memory pattern ξ^{t+1} is given by

$$m^{t+1}(t + 1) = \frac{1}{Nf(1 - f)} \sum_{i=1}^N (\xi_i^{t+1} - f)x_i(t + 1) = 1 - f. \quad (8)$$

In a sparse limit, the overlap $m^{t+1}(t + 1)$ approaches 1. In other words, the memory pattern ξ^{t+1} is retrievable.

Next, we consider the case where there is a large number of memory patterns, i.e., $p \sim O(N)$. The i -th neuronal internal potential $u_i(t)$ at time t is given using the periodic boundary condition of $\xi_i^{p+1} = \xi_i^1$ and $\xi_i^0 = \xi_i^p$ by

$$u_i(t) = \frac{1}{Nf(1 - f)} \sum_{j=1}^N \sum_{\mu=1}^p (\xi_i^{\mu+1} \xi_j^\mu - \xi_i^{\mu-1} \xi_j^\mu) x_j(t) \quad (9)$$

$$= (\xi_i^{t+1} - \xi_i^{t-1}) m^t(t) + z_i(t), \quad (10)$$

$$z_i(t) = \sum_{\mu \neq t}^p (\xi_i^{\mu+1} - \xi_i^{\mu-1}) m^\mu(t). \quad (11)$$

The first term in equation (10) is the signal term for the recall of the pattern ξ^{t+1} . The second term is the cross-talk noise term that represents contributions of non-target patterns other than ξ^{t-1} , and prevents the retrieval of the target pattern, ξ^{t+1} . The cross-talk noise is assumed to obey a Gaussian distribution with mean 0 and time-dependent variance $\sigma^2(t)$. We used the method of the statistical neurodynamics (Amari and Maginu, 1988; Okada, 1995; Matsumoto

and Okada, 2002b) to obtain recursive equations for the overlap $m^t(t)$ between the network state $\mathbf{x}(t)$ and the target pattern $\boldsymbol{\xi}^t$ and the variance $\sigma^2(t)$ of cross-talk noise. The details of the derivation are given in the Appendix. Here, we show the recursive equations for $m^t(t)$ and $\sigma^2(t)$:

$$m^t(t) = \frac{1-2f}{2}\text{erf}(\phi_0) - \frac{1-f}{2}\text{erf}(\phi_1) + \frac{f}{2}\text{erf}(\phi_2), \quad (12)$$

$$\sigma^2(t) = \sum_{a=0}^t {}_2C_{(a+1)} \alpha q(t-a) \prod_{b=1}^a U^2(t-b+1), \quad (13)$$

$$U(t) = \frac{1}{\sqrt{2\pi}\sigma(t-1)} \{ (1-2f+2f^2)e^{-\phi_0^2} + f(1-f)(e^{-\phi_1^2} + e^{-\phi_2^2}) \}, \quad (14)$$

$$q(t) = \frac{1}{2} \left(1 - (1-2f+2f^2)\text{erf}(\phi_0) - f(1-f)(\text{erf}(\phi_1) + \text{erf}(\phi_2)) \right), \quad (15)$$

$$\text{erf}(y) = \frac{2}{\sqrt{\pi}} \int_0^y \exp(-u^2) du, \quad {}_bC_a = \frac{b!}{a!(b-a)!}, \quad a! = a \times (a-1) \times \cdots \times 1,$$

$$\phi_0 = \frac{\theta}{\sqrt{2}\sigma(t-1)}, \phi_1 = \frac{-m^{t-1}(t-1) + \theta}{\sqrt{2}\sigma(t-1)}, \phi_2 = \frac{m^{t-1}(t-1) + \theta}{\sqrt{2}\sigma(t-1)}.$$

3.2 The Case Where Balance is not Maintained Precisely

Here, we discuss the case where the balance is not maintained precisely. It is difficult to treat this case since the mean of cross-talk noise is not 0. However, previous work using computer simulations has shown that the stored limit cycle is stably retrieved when the number of neurons is finite (Munro and Hernandez, 2000; Yoshioka, 2002). This mathematical mechanism remains unknown. To investigate this unknown mechanism, we use the theory derived in section 3.1.

First, let the state at time t be equivalent to the t -th memory pattern: $\mathbf{x}(t) = \boldsymbol{\xi}^t$. Then, the i -th neuronal internal potential $u_i(t)$ at time t is given using the periodic boundary condition of $\xi_i^{p+1} = \xi_i^1$ and $\xi_i^0 = \xi_i^p$ by

$$u_i(t) = \frac{1}{Nf(1-f)} \sum_{j=1}^N \sum_{\mu=1}^p (\xi_i^{\mu+1} \xi_j^\mu - (1+\epsilon) \xi_i^{\mu-1} \xi_j^\mu) x_j(t) \quad (16)$$

$$\begin{aligned}
&= \frac{1}{Nf(1-f)} \sum_{j=1}^N \sum_{\mu=1}^p (\bar{\xi}_i^{\mu+1} - \bar{\xi}_i^{\mu-1}) \bar{\xi}_j^{\mu} x_j(t) \\
&\quad - \frac{\epsilon}{Nf(1-f)} \sum_{j=1}^N \sum_{\mu=1}^p \xi_i^{\mu-1} \xi_j^{\mu} x_j(t),
\end{aligned} \tag{17}$$

where $\bar{\xi}_j^{\mu} = \xi_j^{\mu} - f$. Here, we evaluate the second term, that is, compensation term in equation (17). The average of this term is $\frac{\alpha f}{1-f} \epsilon N q(t)$ where $q(t) = \frac{1}{N} \sum_{j=1}^N x_j(t) = f$ when $\mathbf{x}(t) = \boldsymbol{\xi}^t$. The typical value of this term is 0.19 for $N = 5000$, $\alpha = 0.067$, $\epsilon = 0.05$ and $f = 0.1$, which are typical values used in the following analysis. This value is small enough for the overlap $m^t(t) \simeq 1$ originating the signal term. The fluctuation in the compensation term is able to be eliminated since the order of variance of this term is smaller than that of average. Therefore, the average term of the compensation term adds to the signal term in equation (10).

We will discuss a mechanism that enables memory patterns to be retrieved in the small ϵ and finite N case. The internal potential is given with $\mathbf{x}(t) = \boldsymbol{\xi}^t(t)$ by

$$u_i(t) = \xi_i^{t+1} - \xi_i^{t-1} - \frac{\alpha f^2}{1-f} \epsilon N. \tag{18}$$

When $\epsilon \neq 0$, each distribution of $u_i(t)$ shifts by $\frac{\alpha f^2}{1-f} \epsilon N$ like Figure 2(b). When the typical case at $N = 5000$, $\alpha = 0.067$, $\epsilon = 0.05$, $f = 0.1$ and $\theta = 0.52$ is considered, each distribution of $u_i(t)$ shifts left by 0.19. Since the value of a threshold is 0.52, the probability of $u_i(t+1) = +1$ is little changed. In other words, the small ϵ and finite N case, the retrieval of the next pattern $\boldsymbol{\xi}^{t+1}$ succeeds. Otherwise, the retrieval fails.

Since the average term of the compensation term adds to the signal term in

equation (10), the i -th neuronal internal potential $u_i(t)$ at time t is given by

$$u_i(t) = (\bar{\xi}_i^{t+1} - \bar{\xi}_i^{t-1})m^t(t) + \sum_{\mu \neq t}^p (\bar{\xi}_i^{\mu+1} - \bar{\xi}_i^{\mu-1})m^\mu(t) - \frac{\alpha \epsilon f N}{1-f} q(t). \quad (19)$$

The first term is the signal term and the second is the cross-talk noise term. The third term is the compensation term. The statistical neurodynamics enables us to derive dynamical equations. The equations are almost the same as in section 3.1 other than ϕ_0 , ϕ_1 and ϕ_2 . In ϕ_0 , ϕ_1 and ϕ_2 , θ is replaced by $\theta + \frac{\alpha \epsilon f N}{1-f} q(t-1)$.

4 Results

We used the statistical neurodynamics and computer simulation to investigate the properties of our model and examine its behavior.

Figure 3 shows the dependence of the overlap $m^t(t)$ on the loading rate α when the mean firing rate of the memory pattern is $f = 0.1$, and the threshold is $\theta = 0.52$, which is optimized to maximize the storage capacity. The solid line denotes the steady-state values of the overlap $m^t(t)$ in retrieval of the pattern sequence at $\epsilon = 0.0$ in (a) and $\epsilon = 0.05$ in (b). $m^t(t)$ is obtained by setting the initial state of the network at the first memory pattern: $\mathbf{x}(1) = \boldsymbol{\xi}^1$. The storage capacity is $\alpha_C = 0.27$ in (a) and $\alpha_C = 0.067$ in (b). The data points and error bars indicate the results of computer simulation of 11 trials with 5000 neurons: $N = 5000$, with the former indicating median values and the latter indicating 1/4 and 3/4 deviations. A discrepancy between the values of m_C obtained by the computer simulations and the analytical result is originated from the finite size effect of the computer simulations (Matsumoto and Okada, 2002b).

Figure 4 shows the storage capacity α_C as a function of ϵ . When the overlap at the steady state is smaller than 0.5, the critical loading rate α is regarded as the storage capacity α_C . The data points and error bars show the results of computer simulation of 10 trials at $f = 0.1$, $\theta = 0.52$ and $N = 3000$ (\square) or $N = 5000$ (\circ), with the former indicating mean values and the latter indicating standard deviations. The solid line shows the theoretical results at $N = 3000$, while the dashed line and the gray solid line show the results at $N = 5000$ and $N = 100000$, respectively. As $|\epsilon|$ increases, α_C decreases. When $\epsilon = 0.5$, the storage capacities of $N = 3000$ and $N = 5000$ are 0.017 and 0.011, respectively. However, the storage capacity of $N = 100000$ is 0. In other words, when the number of neurons is finite, α_C takes a finite value. The results of computer simulation coincide with the theoretical results at small ϵ .

Figure 5 shows α_C as a function of ϵ . The solid line shows the theoretical results at $f = 0.1$ and $\theta = 0.52$ while the dashed line shows $\log_{10} \alpha_C = \log_{10} \frac{4}{\pi N \epsilon} + 1.33$ at $N = 5000$, $f = 0.1$ and $\theta = 0.52$. This figure indicates that α_C converges to 0 as $O(\frac{1}{N\epsilon})$ in a large $N\epsilon$ limit.

5 Summary and Discussion

In this paper, we investigated the impact of the balance between LTP and LTD of STDP on the retrieval properties of spatio-temporal patterns, employing an associative memory network. Some authors *numerically* investigated that the impact of the imbalance between LTP and LTD on the network properties. We *analytically* investigated the retrieval properties using the statistical neurodynamics. In

this paper, we discussed the case where the value of LTD deviates from the precise balance. The stored limit cycle using STDP is unstable in the thermodynamic limit: $N \rightarrow \infty$. However, the stored limit cycle is stable when the number of the neurons is *finite*. Moreover, the results of computer simulations *coincide* with the theoretical results at small ϵ . Thus, a network containing a *finite* number of neurons becomes robust against deviation from the precise balance. Since the number of neurons in the brain is considered to be finite, our results might be acceptable in the brain. Furthermore, the storage capacity converges to 0 as $O(\frac{1}{N\epsilon})$ in a large $N\epsilon$ limit.

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Appendix. Derivation of the Dynamical Equations when Balance is Maintained Precisely

In this appendix, we derive recursive equations for the overlap $m^t(t)$ and the variance $\sigma^2(t)$ when the balance between LTP and LTD of STDP is maintained precisely. The internal potential $u_i(t)$ at time t is derived from equation (5) and the periodic boundary condition of $\xi_i^{p+1} = \xi_i^1$ and $\xi_i^0 = \xi_i^p$ in the following way:

$$u_i(t) = \frac{1}{Nf(1-f)} \sum_{j=1}^N \sum_{\mu=1}^p (\xi_i^{\mu+1} \xi_j^\mu - \xi_i^{\mu-1} \xi_j^\mu) x_j(t) \quad (20)$$

$$= (\xi_i^{t+1} - \xi_i^{t-1}) m^t(t) + z_i(t). \quad (21)$$

The cross-talk noise is assumed to obey a Gaussian distribution with a mean of 0 and time-dependent variance $\sigma^2(t)$: $E[z_i(t)] = 0$, $E[(z_i(t))^2] = \sigma^2(t)$. The overlap is $m^t(t) = \frac{1}{Nf(1-f)} \sum_{i=1}^N (\xi_i^t - f) x_i(t)$. We use a Taylor expansion to derive the following expression for the i -th neuronal state at time $t + 1$.

$$x_i(t+1) = F\left(\sum_{\nu=1}^p (\xi_i^{\nu+1} - \xi_i^{\nu-1}) m^\nu(t) - \theta\right) \quad (22)$$

$$\begin{aligned}
&= F\left(\sum_{\nu \neq \mu}^p (\bar{\xi}_i^{\nu+1} - \bar{\xi}_i^{\nu-1})m^\nu(t) - \theta\right) \\
&\quad + \bar{\xi}_i^\mu(m^{\mu-1}(t) - m^{\mu+1}(t))F'\left(\sum_{\nu \neq \mu}^p (\bar{\xi}_i^{\nu+1} - \bar{\xi}_i^{\nu-1})m^\nu(t) - \theta\right) \quad (23)
\end{aligned}$$

$$= x_i^{(\mu)}(t+1) + \bar{\xi}_i^\mu(m^{\mu-1}(t) - m^{\mu+1}(t))x_i'^{(\mu)}(t+1), \quad (24)$$

where $x_i^{(\mu)}$ is independent of ξ_i^μ and $\bar{\xi}_i^\mu = \xi_i^\mu - f$. Using this relationship, the cross-talk noise at time t , $z_i(t)$, is derived below.

$$\begin{aligned}
z_i(t) &= \sum_{\mu \neq t}^p (\xi_i^{\mu+1} - \xi_i^{\mu-1})m^\mu(t) \quad (25) \\
&= \frac{1}{Nf(1-f)} \sum_{\mu \neq t}^p \sum_{j=1}^N (\bar{\xi}_i^{\mu+1} - \bar{\xi}_i^{\mu-1})\bar{\xi}_j^\mu x_j^{(\mu)}(t) \\
&\quad + \sum_{\nu \neq t}^p U(t)(\bar{\xi}_i^{\nu+1}m^{\nu-1}(t-1) - 2\bar{\xi}_i^{\nu-1}m^{\nu-1}(t-1) + \bar{\xi}_i^{\nu-1}m^{\nu+1}(t-1)) \quad (26)
\end{aligned}$$

where $U(t) = E[x_i'^{(\mu)}(t)]$. $x_i'^{(\mu)}(t)$ is the differential of $x_i^{(\mu)}(t)$. Therefore, the square of $z_i(t)$ is given by

$$\begin{aligned}
(z_i(t))^2 &= \left(\frac{1}{Nf(1-f)}\right)^2 \sum_{\mu \neq t}^p \sum_{j=1}^N (\bar{\xi}_i^{\mu+1} - \bar{\xi}_i^{\mu-1})^2 (\bar{\xi}_j^\mu)^2 (x_j^{(\mu)}(t))^2 \\
&\quad + \sum_{\nu \neq t}^p U(t)^2 (\bar{\xi}_i^{\nu+1}m^{\nu-1}(t-1) - 2\bar{\xi}_i^{\nu-1}m^{\nu-1}(t-1) \\
&\quad + \bar{\xi}_i^{\nu-1}m^{\nu+1}(t-1))^2 \quad (27)
\end{aligned}$$

$$\begin{aligned}
&= (1^2 + (-1)^2)\alpha q(t) + (1^2 + (-2)^2 + 1^2)\alpha q(t-1)U^2(t) \\
&\quad + (1^2 + (-3)^2 + 3^2 + (-1)^2)\alpha q(t-2)U^2(t)U^2(t-1) + \dots \quad (28)
\end{aligned}$$

$$= \sum_{a=0}^t {}_{2(a+1)}C_{(a+1)}\alpha q(t-a) \prod_{b=1}^a U^2(t-b+1), \quad (29)$$

where $p = \alpha N$, $q(t) = \frac{1}{N} \sum_{i=1}^N (x_i^{(\mu)}(t))^2$, ${}_bC_a = \frac{b!}{a!(b-a)!}$ and $a!$ is the factorial with positive integer a . We applied the relationship $\sum_{a=0}^b ({}_bC_a)^2 = {}_{2b}C_b$ in this

derivation. The expectation of $z_i(t)$ is assumed to be 0, so the variance $\sigma^2(t)$ is equal to $E[(z_i(t))^2]$. We then get a recursive equation for $\sigma^2(t)$:

$$\sigma^2(t) = \sum_{a=0}^t 2_{(a+1)} C_{(a+1)} \alpha q(t-a) \prod_{b=1}^a U^2(t-b+1). \quad (30)$$

Replacing the average over the sites with the average over the Gaussian noise term, a recursive equation for the overlap $m^t(t)$ between the network state $\mathbf{x}(t)$ and the retrieval pattern $\boldsymbol{\xi}^t$ is obtained as follows:

$$m^t(t) = \frac{1}{Nf(1-f)} \sum_{i=1}^N (\xi_i^t - f)x_i(t) \quad (31)$$

$$= \frac{1}{f(1-f)} \langle \langle \int Dz (\xi^t - f)x(t) \rangle \rangle \quad (32)$$

$$= \frac{1}{\sqrt{2\pi}f(1-f)} \int_{-\infty}^{\infty} dz e^{-\frac{z^2}{2}} \langle \langle (\xi^t - f)F((\xi^t - \xi^{t-2})m^{t-1}(t-1) + \sigma(t-1)z - \theta) \rangle \rangle \quad (33)$$

$$= \frac{1-2f}{2} \text{erf}(\phi_0) - \frac{1-f}{2} \text{erf}(\phi_1) + \frac{f}{2} \text{erf}(\phi_2), \quad (34)$$

where $\text{erf}(y) = \frac{2}{\sqrt{\pi}} \int_0^y \exp(-u^2) du$, and $\phi_0 = \frac{\theta}{\sqrt{2\sigma(t-1)}}$, $\phi_1 = \frac{-m^{t-1}(t-1)+\theta}{\sqrt{2\sigma(t-1)}}$, $\phi_2 = \frac{m^{t-1}(t-1)+\theta}{\sqrt{2\sigma(t-1)}}$. $U(t)$ is derived in the following way:

$$U(t) = \frac{1}{N} \sum_{i=1}^N x_i^{(\mu)}(t) = \frac{1}{N} \sum_{i=1}^N x_i'(t) \quad (35)$$

$$= \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} dz e^{-\frac{z^2}{2}} \langle \langle F'((\xi^t - \xi^{t-2})m^{t-1}(t-1) + \sigma(t-1)z - \theta) \rangle \rangle \quad (36)$$

$$= \frac{1}{\sqrt{2\pi}\sigma(t-1)} \{(1-2f+2f^2)e^{-\phi_0^2} + f(1-f)(e^{-\phi_1^2} + e^{-\phi_2^2})\}. \quad (37)$$

Finally, we derive $q(t)$.

$$q(t) = \frac{1}{N} \sum_{i=1}^N (x_i^{(\mu)}(t))^2 = \frac{1}{N} \sum_{i=1}^N (x_i(t))^2 \quad (38)$$

$$= \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} dz e^{-\frac{z^2}{2}} \langle \langle F^2((\xi^t - \xi^{t-2})m^{t-1}(t-1) + \sigma(t-1)z - \theta) \rangle \rangle \quad (39)$$

$$= \frac{1}{2} (1 - (1-2f+2f^2)\text{erf}(\phi_0) - f(1-f)(\text{erf}(\phi_1) + \text{erf}(\phi_2))) . \quad (40)$$

Figure captions

Figure 1: Spike-timing-dependent plasticity. (a): The results of the biological experiment (Zhang et al., 1998). (b): STDP in our model. LTP occurs when the j -th neuron fires one time step before the i -th one. LTD occurs when the j -th neuron fires one time step after the i -th one.

Figure 2: The probability distribution of the i -th neuronal potential $u_i(t)$ at time t . (a): The balance between LTP and LTD of STDP is maintained precisely: $\epsilon = 0$. (b): The balance is not maintained precisely: $\epsilon \neq 0$. Each distribution shifts by $\frac{\alpha f^2}{1-f}\epsilon N$.

Figure 3: The solid line shows the overlap in the steady state when the firing rate of stored patterns is 0.1 at $\epsilon = 0.0$ in (a) and $\epsilon = 0.05$ in (b). The storage capacity is 0.27 in (a) and 0.067 in (b). In both figures, the threshold is 0.52 and the number of neurons is 5000. The data points indicate the median values and both ends of the error bars indicate 1/4 and 3/4 derivations, respectively. They are obtained in 11 computer simulation trials.

Figure 4: The storage capacity α_C as a function of ϵ . The data points and error bars show the results of computer simulation of 10 trials at $N = 3000$ (\square) or $N = 5000$ (\circ), with the former indicating the mean values and latter indicating standard deviations. The solid line, dashed line and gray solid line show the theoretical results at $N = 3000$, $N = 5000$ and $N = 100000$, respectively. All results are obtained at $f = 0.1$ and $\theta = 0.52$. As $|\epsilon|$ increases, α_C decreases.

Figure 5: The storage capacity α_C as a function of ϵ at $N = 5000$, $f = 0.1$ and $\theta = 0.52$. The solid line shows the theoretical results while the dashed line shows $\log_{10} \alpha_C = \log_{10} \frac{4}{\pi N \epsilon} + 1.33$. α_C converges to 0 as $O(\frac{1}{N\epsilon})$ in a large $N\epsilon$ limit.

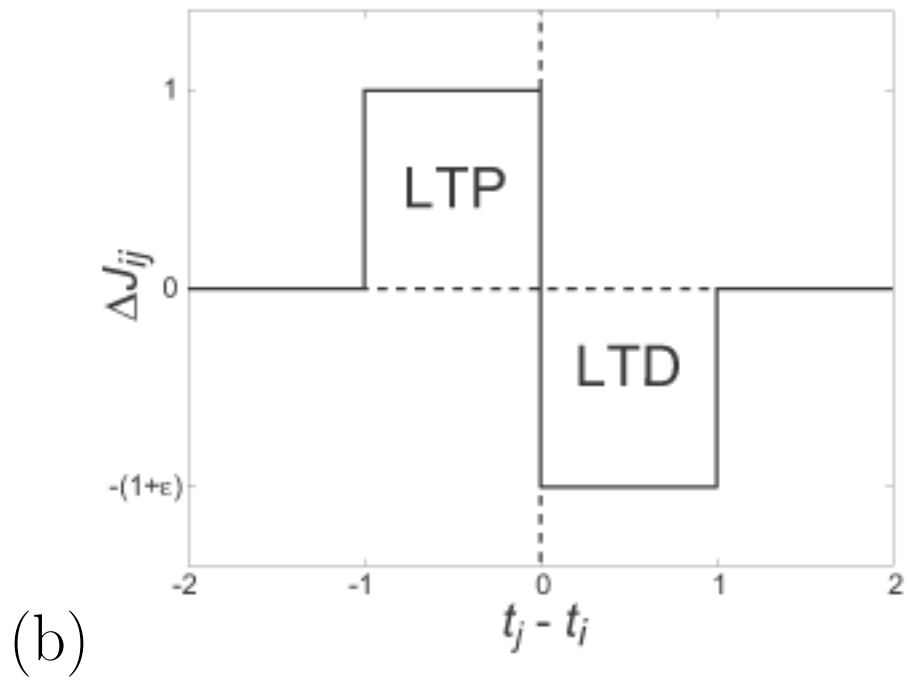
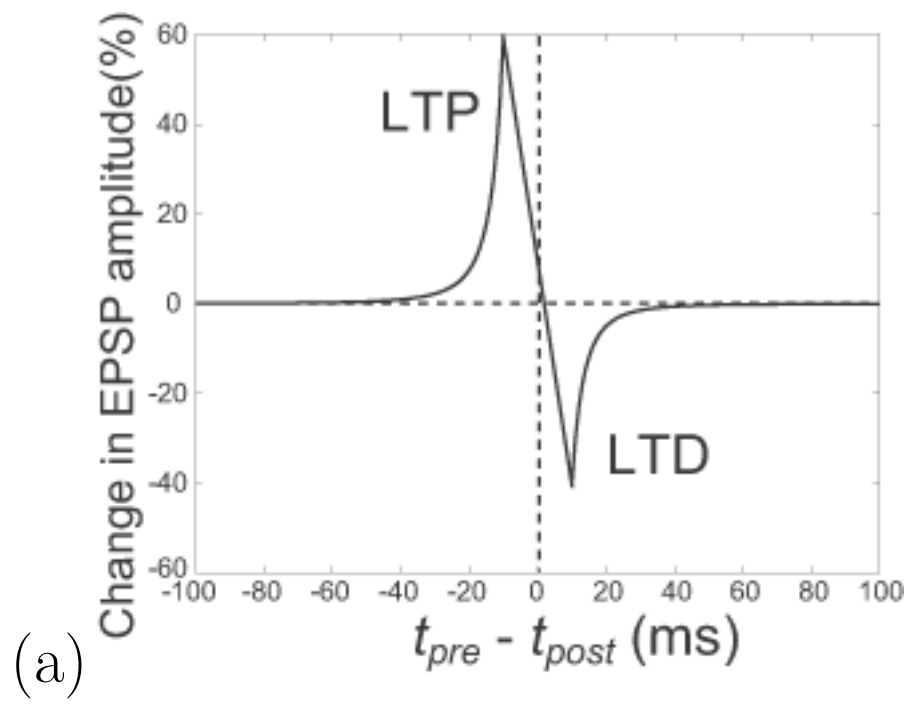


Figure 1

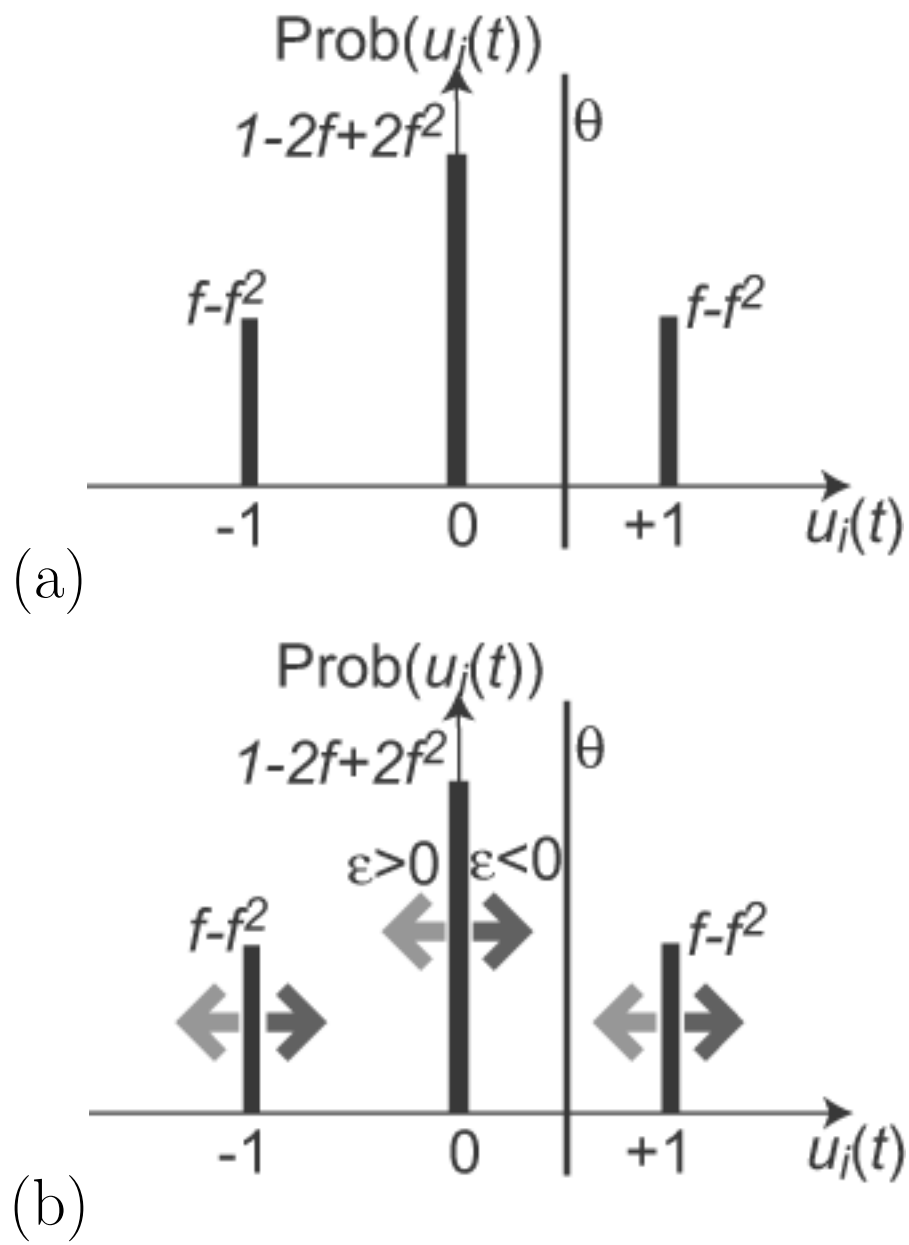


Figure 2

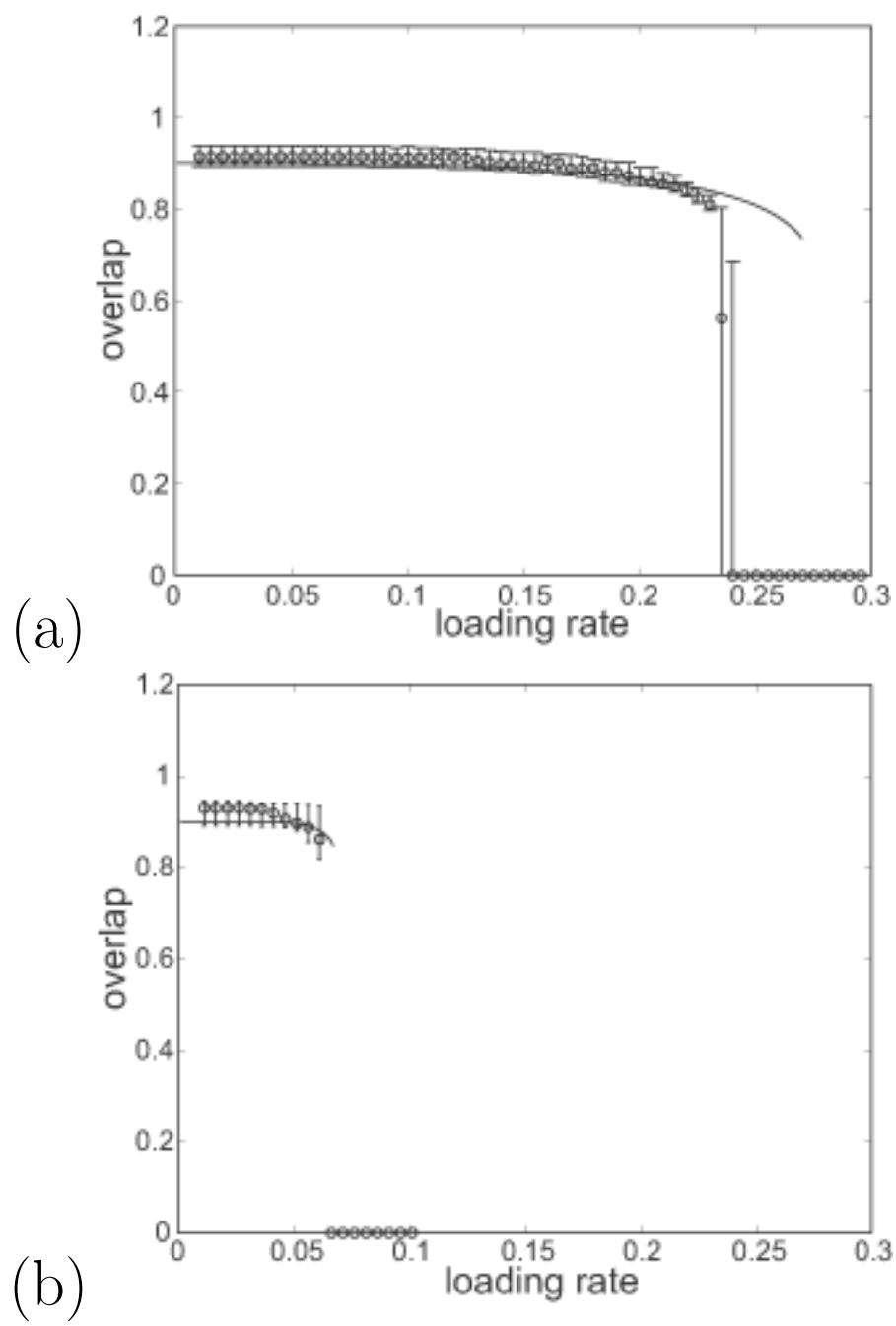


Figure 3

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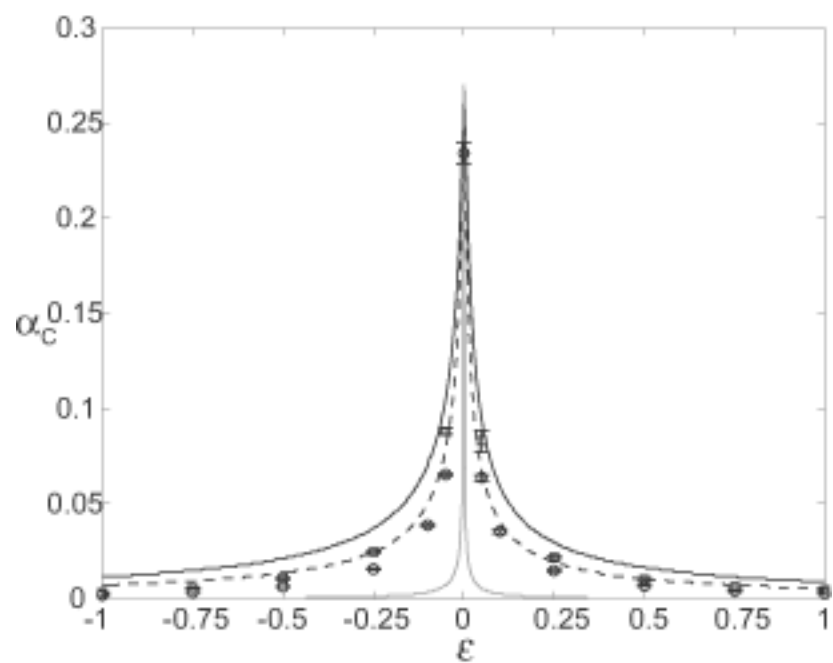


Figure 4

Matsumoto

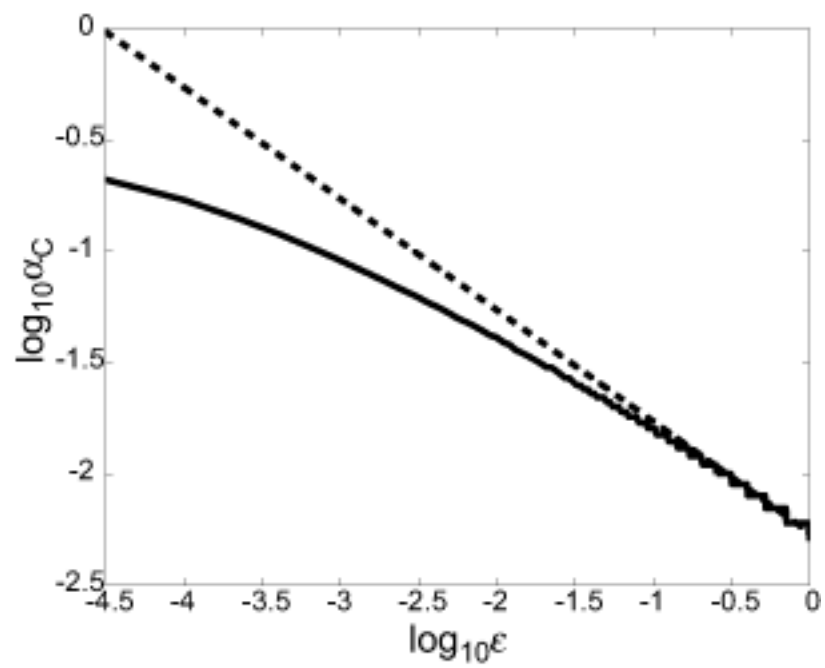


Figure 5

Matsumoto