Robustness of retrieval properties against imbalance between long-term potentiation and depression of spike-timing-dependent plasticity

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Spike-timing-dependent plasticity (STDP) has recently been shown in some physiological studies. STDP depends on the precise temporal relationship of presynaptic and postsynaptic spikes. Many authors have indicated that a precise balance between long-term potentiation (LTP) and long-term depression (LTD) of STDP is significant for a stable learning. However, a situation in which the balance is maintained precisely is inconceivable in the brain. Using a method of the statistical neurodynamics, we show robust retrieval properties of spatiotemporal patterns in an associative memory model against the imbalance between LTP and LTD. When the fluctuation of LTD is assumed to obey a Gaussian distribution with mean 0 and variance δ^2, the storage capacity takes a finite value even at large δ. This means that the balance between LTP and LTD of STDP need not be maintained precisely, but must be maintained on average. Furthermore, we found that the basin of attraction becomes smaller as δ increases while an initial critical overlap remains unchanged.

I. INTRODUCTION

A recent experimental finding indicates that synaptic modification in cortical neurons depends on the precise temporal relationship between presynaptic and postsynaptic spikes [1–3]. In particular, presynaptic spikes that precede postsynaptic firing induce a long-term potentiation (LTP) by no more than 20 ms, while those that follow postsynaptic firing induce a long-term depression (LTD), with a rapid transition (a few ms). The magnitude of synaptic modification decays exponentially with the time interval between presynaptic and postsynaptic spikes. This form of synaptic modification has been called spike-timing-dependent plasticity (STDP) [4] or temporally asymmetric Hebbian (TAH) learning [5,6].

The functional role of STDP has been investigated by many authors. They showed that STDP is a mechanism for synaptic competition [4–9] or a learning mechanism of sequential patterns [10–16]. An symmetric learning window depending on spike timing similar to STDP has been studied and shown to be an appropriate learning rule for sequential patterns [17–19]. However, this asymmetric learning rule does not involve LTD. Some authors showed that the balance between the LTP and LTD of STDP is significant for stable learning [4,14–16]. In our previous work, we analytically showed that STDP has the same qualitative effect as the covariance rule when the spatiotemporal patterns are stored since the differences between spike times that induce LTP or LTD are capable of canceling out the effect of the firing rate information [16]. In the brain, a situation in which the balance is maintained precisely is inconceivable. The data points obtained by experiments are fluctuated in different trials [1,3]. Therefore, it is meaningful to discuss more biological plausible situation to investigate the neuronal mechanism for sequential learning in the brain. Some authors *numerically* investigated the impact of the imbalance between LTP and LTD on the network properties [4,14].

The aim of this paper is to *analytically* discuss the retrieval properties of spatiotemporal patterns in an associative memory model that incorporates the imbalance between the LTP and LTD of STDP using a method of the statistical neurodynamics [16,20,21]. According to our previous work, when the balance is not precisely maintained, it is impossible to cancel out the information of firing rate. Consequently, cross-talk noise diverges. However, if the magnitudes of the LTP and LTD are equivalent on average in a learning process, it may be possible to stably retrieve spatiotemporal patterns. Since the ratio of the LTP and LTD is crucial, the magnitude of the LTD changes while that of the LTP is fixed. We found that the storage capacity takes a finite value even at large δ when the fluctuation of the LTD is assumed to obey a Gaussian distribution with mean 0 and variance δ^2. This implies that the balance between the LTP and LTD of STDP need not to be maintained precisely, but must be maintained on average. This mechanism might work in the brain. Furthermore, we found that a basin of attraction becomes smaller as δ increases while an initial critical overlap remains unchanged.

II. MODEL

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

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

$$x_i(t+1) = F[u_i(t) - \theta], \tag{2}$$

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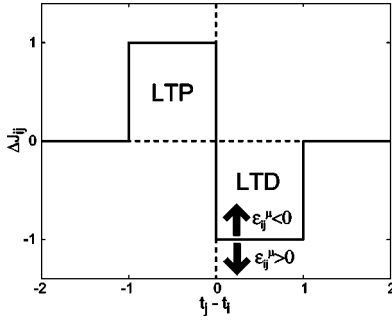†Email address: okada@brain.riken.go.jp

FIG. 1. The time function of STDP in our model. The LTP is induced when the jth neuron fires one time step before the ith one. LTD is induced when the jth neuron fires one time step after the ith one. ϵ_{ij}^{μ} follows a Gaussian distribution with mean ϵ and variance δ^2.

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

where $x_i(t)$ is the state of the ith neuron at time t, $u_i(t)$ is the internal potential of that neuron, and θ is a uniform threshold. If the ith neuron fires at t, its state is $x_i(t) = 1$; otherwise, $x_i(t) = 0$. J_{ij} is the synaptic weight from the jth neuron to the ith neuron. Each element ξ_i^{μ} of the μth memory pattern $\boldsymbol{\xi}^{\mu} = (\xi_1^{\mu}, \xi_2^{\mu}, \ldots, \xi_N^{\mu})$ is generated independently by

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

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 ith (post) and jth (pre) neurons. The time 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 the LTP or LTD is induced when the difference in the presynaptic and postsynaptic spike times falls within about 20 ms [3]. We define a single time step in equations (1)–(3) as 20 ms, and durations within 20 ms are ignored. The learning rule based on STDP conforms to this equation:

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

The number of memory patterns is $p = \alpha N$, where α is defined as a loading rate. The LTP is induced when the jth neuron fires one time step before the ith neuron $\xi_i^{\mu+1} = \xi_j^{\mu} = 1$, while the LTD is induced when the jth neuron fires one time step after the ith neuron $\xi_i^{\mu-1} = \xi_j^{\mu} = 1$. Since the ratio of the LTP and LTD is crucial, the magnitude of the LTD changes while the magnitude of the LTP and the time duration are fixed. ϵ_{ij}^{μ} is generated independently and obeys a Gaussian distribution with mean ϵ and variance δ^2: $\epsilon_{ij}^{\mu} \sim \mathcal{N}(\epsilon, \delta^2)$. Figure 1 shows the time function of STDP in our

model. When $\epsilon_{ij}^{\mu} = 0$, the balance between the LTP and LTD is precisely maintained and then the model is equivalent to the previous model [16]. A sequence of p memory patterns is stored by STDP: $\boldsymbol{\xi}^1 \rightarrow \boldsymbol{\xi}^2 \rightarrow \cdots \rightarrow \boldsymbol{\xi}^p \rightarrow \boldsymbol{\xi}^1 \rightarrow \cdots$. 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 the loading rate larger than α_C makes retrieval of the pattern sequence unstable. α_C is called the storage capacity.

III. THEORY

In this section, we derive dynamical equations that describe the retrieval properties of the network. In this paper, we consider the thermodynamic limit $N \rightarrow \infty$. The ith neuronal internal potential $u_i(t)$ at time t can be expressed as

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

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

$$- (1 + \epsilon_{ij}^{\mu-1}) \xi_i^{\mu-1} \xi_j^{\mu} \} x_j(t) \tag{6}$$

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

$$- \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu=1}^{p} \epsilon_{ij}^{\mu-1} \xi_i^{\mu-1} \xi_j^{\mu} x_j(t). \tag{7}$$

Using the periodic boundary condition of $\xi_i^{p+1} = \xi_i^1$ and $\xi_i^0 = \xi_i^p$, $\sum_{\mu=1}^{p} (\xi_i^{\mu+1} \xi_j^{\mu} - \xi_i^{\mu-1} \xi_j^{\mu}) = \sum_{\mu=1}^{p} (\bar{\xi}_i^{\mu+1} \bar{\xi}_j^{\mu} - \bar{\xi}_i^{\mu-1} \bar{\xi}_j^{\mu})$ with $\bar{\xi}_i^{\mu} = \xi_i^{\mu} - f$. Using this relationship, $u_i(t)$ is given by

$$u_i(t) = \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu=1}^{p} (\bar{\xi}_i^{\mu+1} - \bar{\xi}_i^{\mu-1}) \bar{\xi}_j^{\mu} x_j(t)$$

$$- \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu=1}^{p} \epsilon_{ij}^{\mu-1} \xi_i^{\mu-1} \xi_j^{\mu} x_j(t) \tag{8}$$

$$= \sum_{\mu=1}^{p} (\bar{\xi}_i^{\mu+1} - \bar{\xi}_i^{\mu-1}) m^{\mu}(t)$$

$$- \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu=1}^{p} \epsilon_{ij}^{\mu-1} \xi_i^{\mu-1} \xi_j^{\mu} x_j(t) \tag{9}$$

$$= (\bar{\xi}_i^{t+1} - \bar{\xi}_i^{t-1}) m^t(t) + \sum_{\mu \neq t}^{p} (\bar{\xi}_i^{\mu+1} - \bar{\xi}_i^{\mu-1}) m^{\mu}(t)$$

$$- \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu=1}^{p} \epsilon_{ij}^{\mu-1} \xi_i^{\mu-1} \xi_j^{\mu} x_j(t), \tag{10}$$

where $m^{\mu}(t)$ is an overlap between $\boldsymbol{\xi}^{\mu}(t)$ and $\boldsymbol{x}(t)$ and is given by

$$m^\mu(t) = \frac{1}{Nf(1-f)} \sum_{i=1}^{N} \overline{\xi}_i^\mu x_i(t). \tag{11}$$

The first term in Eq. (10) is a signal term for the retrieval of the target pattern ξ^{t+1}. The second and third terms are cross-talk noise terms that represent contributions from non-target patterns other than ξ^{t-1} and that prevent ξ^{t+1} from being retrieved. The third term is also a compensation term originated by a deviation from the balance between the LTP and LTD of STDP. Since this term is of order N with respect to N, $O(N)$, when $\epsilon \neq 0$, it diverges in the thermodynamic N limit $N \rightarrow \infty$. This means that the stored limit cycle using the present learning rule [Eq. (5)] is unstable in the limit of $N \rightarrow \infty$ when $\epsilon \neq 0$. Therefore, we will discuss the $\epsilon = 0$ case $\epsilon_{ij}^\mu \sim \mathcal{N}(0, \delta^2)$.

We derive the dynamical equations using the method of statistical neurodynamics [16,20,21]. When it is possible to store a pattern sequence, a cross-talk noise term, that is, the second and third terms in Eq. (10) is assumed to obey a Gaussian distribution with the average 0 and time-dependent variance $\sigma^2(t)$ [16,20]. We derive the recursive equations for $m^t(t)$ and $\sigma^2(t)$ to investigate whether the memory pattern ξ^t is retrieved or not. Since $m^t(t)$ depends on $\sigma^2(t)$, we derive $\sigma^2(t)$. The dynamical equations are derived as

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

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

$$+ \frac{\alpha \delta^2}{(1-f)^2} q(t), \tag{13}$$

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

$$\times (e^{-\phi_1^2} + e^{-\phi_2^2})\}, \tag{14}$$

$$q(t) = \frac{1}{2} \{1 - (1-2f+2f^2)\mathrm{erf}(\phi_0) - f(1-f)[\mathrm{erf}(\phi_1)$$

$$+ \mathrm{erf}(\phi_2)]\}, \tag{15}$$

where $\mathrm{erf}(y) = (2/\sqrt{\pi}) \int_0^y \exp(-u^2) du$ and $\phi_0 = \theta/\sqrt{2}\sigma(t-1)$, $\phi_1 = [-m^{t-1}(t-1) + \theta]/\sqrt{2}\sigma(t-1)$, $\phi_2 = [m^{t-1}(t-1) + \theta]/\sqrt{2}\sigma(t-1)$, ${}_bC_a = b!/a!(b-a)!$, and $a!$ is the factorial with positive integer a. The detail derivation of the dynamical equations is shown in the Appendix.

IV. RESULTS

Figure 2 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. (a) The case at
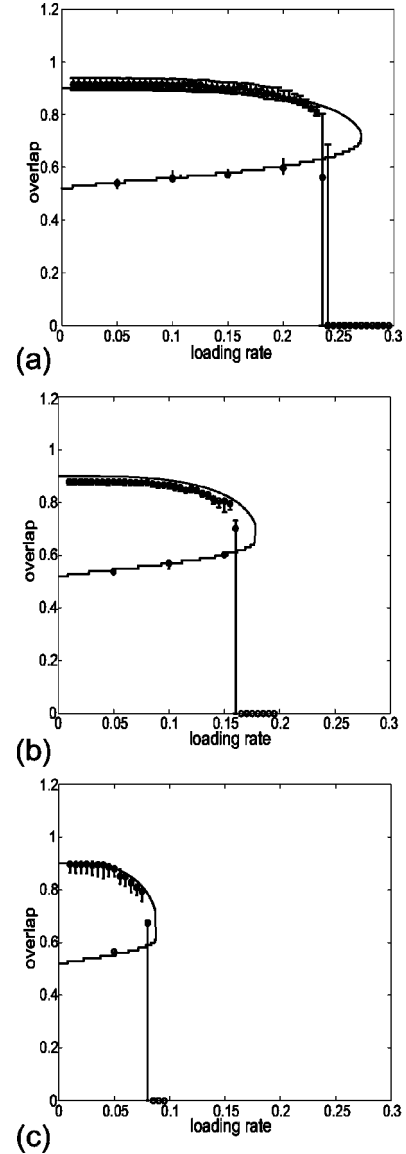

FIG. 2. The dependence of α_C and the basin of attraction on the loading rate at $f = 0.1$ and $\theta = 0.52$. The lower line represents the initial critical overlap and the upper line does the overlap at the steady state. The data points and the error bars show the results of computer simulation of 11 trials at $N = 5000$. (a) $\delta = 0.0$, (b) $\delta = 1.0$, (c) $\delta = 2.0$. $\alpha_C = 0.27$ (a), 0.178 (b), 0.087 (c). The basin of attraction decreases as δ increases.

$\delta = 0.0$, (b) at $\delta = 1.0$, and (c) at $\delta = 2.0$. The lines show analytical results obtained by the dynamical equations (12)–(15). The upper line denotes the steady-state values of the overlap $m^t(t)$ in retrieval of the pattern sequence. $m^t(t)$ is obtained by setting the initial state of the network at the first memory pattern: $x(1) = \xi^1$. Setting the initial values at $m^1(1) = 1$, $\sigma^2(1) = 2\alpha f + \alpha \delta^2 f/(1-f)^2$, $U(1) = 0$, and $q(1) = f$ and using the dynamical equations (12)–(15), $m^t(t)$ is obtained. 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 storage capacity α_C is 0.27 (a), 0.178 (b), and 0.087 (c). The lower line indicates the dependence of an initial critical overlap m_C on α. The stored pattern sequence
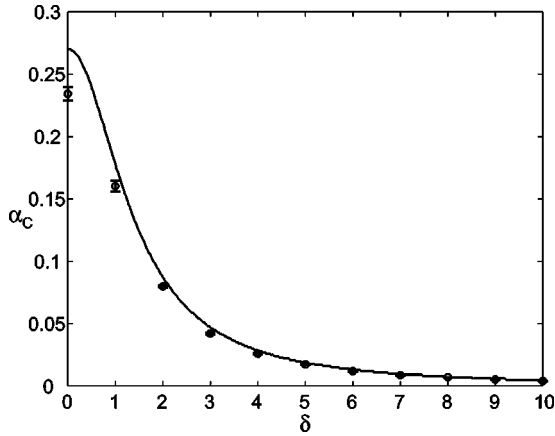
FIG. 3. The dependence of the storage capacity α_C on δ. The solid line shows the analytical results. The data points and error bars show the results of computer simulation of 10 trials at $N = 5000$. Both results are obtained at $f = 0.1$ and $\theta = 0.52$. As the variance δ^2 of the fluctuation increases, α_C decreases.

is retrievable when the initial overlap $m^1(1)$ is greater than the critical value m_C. The region in which $m^1(1)$ is larger than m_C represents the basin of attraction for the retrieval of the pattern sequence. m_C is obtained by setting the initial state of the network at ξ^1 with additional noise. We employ the following method to add noise. $100s\%$ of the minority components $[x_i(1) = 1]$ are flipped, while the same number of majority components $[x_i(1) = 0]$ are also flipped. The initial overlap $m^1(1)$ is given as $1 - 2s/(1-f)$. Then the mean firing rate of the network is kept equal to that of the memory pattern f. The other initial values are equivalent to the upper line case. When the overlap at the steady state is smaller than 0.5, the initial overlap $m^1(1)$ is regarded as the initial critical overlap m_C. The data points and error bars indicate the results of computer simulations of 11 trials with 5000 neurons: $N = 5000$. The results are obtained from Eqs. (1)–(5). The data points indicate median values and both ends of the error bars indicate 1/4 and 3/4 deviations. A discrepancy between the values of m_C obtained by the computer simulations and the analytical results is originated from the finite size effect of the computer simulations [16].

Figure 3 shows the dependence of the storage capacity α_C on the standard derivation δ of the fluctuation of the LTD at $f = 0.1$ and $\theta = 0.52$. The solid line shows the analytical results obtained by the same procedure to obtain α_C in Fig. 2. The data points and error bars show the results of a computer simulation of 10 trials at $N = 5000$. The means and standard deviations of α_C of 10 trials are plotted as the data points and the error bars, respectively. As the variance δ^2 increases, α_C decreases. In other words, the model is robust against the imbalance between the LTP and LTD of STDP. Thus, the balance does not need to be maintained precisely, but must simply be maintained on average.

Figure 4 shows the asymptotic property of α_C in a large limit of δ^2. The solid line shows the analytical results obtained by the same procedure to obtain α_C in Fig. 2 at $f = 0.1$ and $\theta = 0.52$ while the dashed line shows $\log_{10}\alpha_C = \log_{10}(2/\pi\delta^2) - 1.13$. This figure indicates that α_C con-
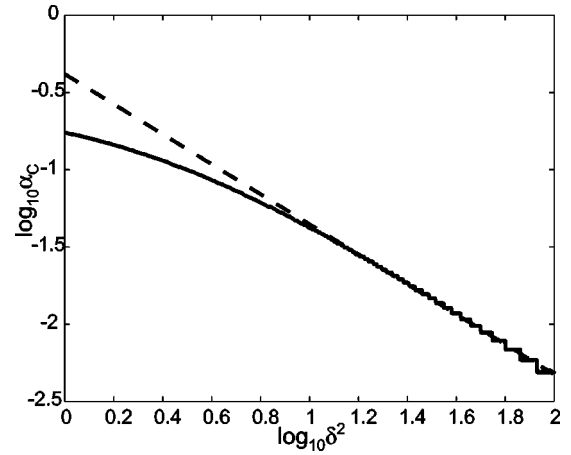

FIG. 4. An asymptotic property of α_C in a large limit of δ^2 at $f = 0.1$ and $\theta = 0.52$. The solid line shows the analytical results while the dashed line shows $\log_{10}\alpha_C = \log_{10}(2/\pi\delta^2) - 1.13$. α_C converges to 0 as order of $1/\delta^2$ with respect to δ, $O(1/\delta^2)$, in the large δ^2 limit.

verges to 0 as an order of $1/\delta^2$ with respect to δ, $O(1/\delta^2)$, in the large δ^2 limit [22].

Next, we discuss the dependency of the basin of attraction on δ. Each region between the upper and lower lines in Figs. 2(a), 2(b), 2(c) shows the basin of attraction at $\delta = 0.0, 1.0, 2.0$, respectively. The basin becomes smaller as a value of δ increases. However, the initial critical overlap m_C is unchanged. To introduce a threshold, the control scheme is known to enlarge the basin of the attraction [16,20,23].

V. DISCUSSION

In this paper, we investigated the impact of the imbalance between the LTP and LTD of STDP on the retrieval properties of spatiotemporal patterns, employing an associative memory network. We analytically investigated the retrieval properties using statistical neurodynamics. When the fluctuation of the LTD is assumed to obey the Gaussian distribution with mean 0 and variance δ^2, the storage capacity takes a finite value even at large δ. This implies that the balance does not need to be maintained precisely, but must be maintained on average. This mechanism might work in the brain. Furthermore, the storage capacity converges to 0 as order $O(1/\delta^2)$ in the large δ^2 limit. Finally, we found that the basin of attraction becomes smaller as the fluctuation of the LTD increases while the initial critical overlap remains unchanged.

We found that the storage capacity takes a finite value even at large δ. When δ is larger than 1.0, the LTD sometimes disappears in the learning process. The spatiotemporal patterns do not seem to be retrievable. Surprisingly, even in this situation, the patterns are retrievable. This implies that the present model achieves strong robustness against the imbalance between the LTP and LTD.

APPENDIX: DERIVATION OF DYNAMICAL EQUATIONS BY THE STATISTICAL NEURODYNAMICS

The detail derivation of the dynamical equations (12)–(15) is given in this appendix. At first, we give a sketch of

the derivation. The main point in this derivation is to divide an internal potential $u_i(t)$ into two parts, a signal term for the retrieval of a target pattern and a cross-talk noise term that represents contributions from nontarget patterns and prevents the target pattern from being retrieved. We evaluate the cross-talk noise term. Specifically, the internal potential $u_i(t)$ of the ith neuron at time t is expressed as [see Eq. (9)]

$$u_i(t) = \sum_{\mu=1}^{p} (\bar{\xi}_i^{\mu+1} - \bar{\xi}_i^{\mu-1}) m^\mu(t) - \frac{1}{Nf(1-f)}$$

$$\times \sum_{j=1}^{N} \sum_{\mu=1}^{p} \epsilon_{ij}^{\mu-1} \xi_i^{\mu-1} \xi_j^\mu x_j(t) \tag{A1}$$

$$= (\bar{\xi}_i^{t+1} - \bar{\xi}_i^{t-1}) m^t(t) + \sum_{\mu \neq t} (\bar{\xi}_i^{\mu+1} - \bar{\xi}_i^{\mu-1}) m^\mu(t)$$

$$- \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu=1}^{p} \epsilon_{ij}^{\mu-1} \xi_i^{\mu-1} \xi_j^\mu x_j(t) \tag{A2}$$

$$= (\bar{\xi}_i^{t+1} - \bar{\xi}_i^{t-1}) m^t(t) + z_i(t), \tag{A3}$$

where $\bar{\xi}_i^\mu = \xi_i^\mu - f$, $m^\mu(t)$ is the overlap between $\boldsymbol{\xi}^\mu(t)$, and $\boldsymbol{x}(t)$ and is given by

$$m^\mu(t) = \frac{1}{Nf(1-f)} \sum_{i=1}^{N} \bar{\xi}_i^\mu x_i(t) \tag{A4}$$

and

$$z_i(t) = \sum_{\mu \neq t}^{p} (\bar{\xi}_i^{\mu+1} - \bar{\xi}_i^{\mu-1}) m^\mu(t)$$

$$- \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu=1}^{p} \epsilon_{ij}^{\mu-1} \xi_i^{\mu-1} \xi_j^\mu x_j(t). \tag{A5}$$

The first term in Eq. (A3) is the signal term and the second term is the cross-talk noise term. Since $x_i(t)$ in Eq. (A4) depends on ξ_i^μ, the distribution of the cross-talk noise term $z_i(t)$ is unknown. The dependence on ξ_i^μ is extracted from $x_i(t)$ using the Taylor expansion [see Eq. (A10)]. In the thermodynamic limit $N \to \infty$, $m^\mu(t)$ tends to be deterministic. Therefore, $x_i^{\{\mu\}}(t)$, which denotes that it does not include ξ_i^μ, is independent of ξ_i^μ. This enables us to assume that the cross-talk noise term $z_i(t)$ obeys a Gaussian distribution with mean 0 and variance σ^2 [16,20]. Since the distribution of the cross-talk noise term is known, the recursive equation of the overlap is obtained [see Eq. (A35)].

To extract the dependence on ξ_i^μ from $x_i(t)$, the state of the ith neuron at time $t+1$ is transformed:

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

$$= F \left(\sum_{\nu=1}^{p} (\bar{\xi}_i^{\nu+1} - \bar{\xi}_i^{\nu-1}) m^\nu(t) \right.$$

$$\left. - \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\nu=1}^{p} \epsilon_{ij}^{\nu-1} \xi_i^{\nu-1} \xi_j^\nu x_j(t) - \theta \right). \tag{A6}$$

The first term in the function $F(\cdots)$ of Eq. (A6) is transformed using the periodic boundary condition of $\xi_i^{p+1} = \xi_i^1$ and $\xi_i^0 = \xi_i^p$:

$$\sum_{\nu=1}^{p} (\bar{\xi}_i^{\nu+1} - \bar{\xi}_i^{\nu-1}) m^\nu(t)$$

$$= \sum_{\nu=1}^{p} \bar{\xi}_i^{\nu+1} m^\nu(t) - \sum_{\nu=1}^{p} \bar{\xi}_i^{\nu-1} m^\nu(t),$$

$$= \sum_{\nu'=1}^{p} \bar{\xi}_i^{\nu'} m^{\nu'-1}(t) - \sum_{\nu'=1}^{p} \bar{\xi}_i^{\nu'} m^{\nu'+1}(t),$$

$$= \sum_{\nu=1}^{p} \bar{\xi}_i^\nu \{ m^{\nu-1}(t) - m^{\nu+1}(t) \}. \tag{A7}$$

The second term in the function $F(\cdots)$ of Eq. (A6) is transformed using the periodic boundary condition

$$\frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\nu=1}^{p} \epsilon_{ij}^{\nu-1} \xi_i^{\nu-1} \xi_j^\nu x_j(t)$$

$$= \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\nu'=1}^{p} \epsilon_{ij}^{\nu'} \xi_i^{\nu'} \xi_j^{\nu'+1} x_j(t). \tag{A8}$$

To extract the dependency on ξ_i^μ from $x_i(t+1)$, using Eqs. (A7) and (A8), $x(t+1)$ is divided into two parts, the terms which include ξ_i^μ and the terms which do not include ξ_i^μ:

$$x_i(t+1) = F \left(\sum_{\nu=1}^{p} \bar{\xi}_i^\nu \{ m^{\nu-1}(t) - m^{\nu+1}(t) \} \right.$$

$$\left. - \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\nu=1}^{p} \epsilon_{ij}^\nu \xi_i^\nu \xi_j^{\nu+1} x_j(t) - \theta \right)$$

$$= F \left(\bar{\xi}_i^\mu \{ m^{\mu-1}(t) - m^{\mu+1}(t) \} \right.$$

$$- \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \epsilon_{ij}^\mu \xi_i^\mu \xi_j^{\mu+1} x_j(t)$$

$$+ \sum_{\nu \neq \mu}^{p} \bar{\xi}_i^\nu \{ m^{\nu-1}(t) - m^{\nu+1}(t) \}$$

$$\left. - \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\nu \neq \mu}^{p} \epsilon_{ij}^\nu \xi_i^\nu \xi_j^{\nu+1} x_j(t) - \theta \right). \tag{A9}$$

At time t, the pattern ξ^t is designed to be retrieved. Therefore, we can assume that $m^t(t)$ is of order 1 with respect to N, $m^t(t) \sim O(1)$, and $m^\mu(t)(\mu \neq t)$ is of order $1/\sqrt{N}$ with respect to N, $m^\mu(t) \sim O(1/\sqrt{N})$. Since $m^\mu(t) \sim O(1/\sqrt{N})$, $m^{\mu-1}(t)$ and $m^{\mu+1}(t)$ are of order $1/\sqrt{N}$ with respect to N. Since $m^{\mu+1}(t) \sim O(1/\sqrt{N})$ and $\epsilon_{ij}^\mu \sim O(1)$, the second term in Eq. (A9) can be considered to be of order $1/\sqrt{N}$ with respect to N. In the thermodynamic limit, $N \to \infty$, the first and second terms in Eq. (A9) are small. Using the Taylor expansion up to first order of $x_i(t+1)$, $x_i(t+1)$ is transformed:

$$x_i(t+1) = x_i^{(\mu)}(t+1) + u_i^{\{\mu\}}(t) x_i'^{(\mu)}(t+1), \quad (A10)$$

where $x_i^{(\mu)}(t+1)$ is independent of ξ_i^μ, $x_i'^{(\mu)}(t+1)$ is differential of $x_i^{(\mu)}(t+1)$, and

$$u_i^{\{\mu\}}(t) = \bar{\xi}_i^\mu \{ m^{\mu-1}(t) - m^{\mu+1}(t) \}$$
$$- \frac{1}{Nf(1-f)} \sum_{j=1}^N \epsilon_{ij}^\mu \xi_i^\mu \xi_j^{\mu+1} x_j(t), \quad (A11)$$

$$x_i^{(\mu)}(t+1) = F(u_i(t) - u_i^{\{\mu\}}(t) - \theta), \quad (A12)$$

$$x_i'^{(\mu)}(t+1) = F'(u_i(t) - u_i^{\{\mu\}}(t) - \theta). \quad (A13)$$

We assume that the function $F(\cdots)$ is differentiable. This assumption is valid since the average of $F(\cdots)$ over a Gaussian noise term will be taken in a later step [see Eq. (A34)]. For $\mu \neq t$, the overlap $m^\mu(t)$ is expressed as

$$m^\mu(t) = \frac{1}{Nf(1-f)} \sum_{i=1}^N (\xi_i^\mu - f) x_i(t)$$
$$= \frac{1}{Nf(1-f)} \sum_{i=1}^N \bar{\xi}_i^\mu \{ x_i^{(\mu)}(t) + u_i^{\{\mu\}}(t-1) x_i'^{(\mu)}(t) \}$$
$$(A14)$$

$$= \frac{1}{Nf(1-f)} \sum_{i=1}^N \bar{\xi}_i^\mu x_i^{(\mu)}(t) + \frac{1}{Nf(1-f)}$$
$$\times \sum_{i=1}^N (\bar{\xi}_i^\mu)^2 \{ m^{\mu-1}(t-1) - m^{\mu+1}(t-1) \} x_i'^{(\mu)}(t)$$
$$- \left(\frac{1}{Nf(1-f)} \right)^2 \sum_{i=1}^N \bar{\xi}_i^\mu \sum_{j=1}^N \epsilon_{ij}^\mu \xi_i^\mu \xi_j^{\mu+1}$$
$$\times x_j(t-1) x_i'^{(\mu)}(t). \quad (A15)$$

If the averages over $\xi_j^\mu(\mu \neq t)$ and $\epsilon_{ji}^\mu(\mu \neq t)$ are taken on the right-hand side of Eq. (A15), the third term vanishes since $E[\epsilon_{ji}^\mu] = 0$. Since the third term including $x_j(t-1)$ depends on both ξ_j^μ and ϵ_{ji}^μ, ξ_j^μ and ϵ_{ji}^μ are extracted from $x_j(t)$ before the averages are taken

$$x_j(t+1) = F \Bigg(\bar{\xi}_j^\mu \{ m^{\mu-1}(t) - m^{\mu+1}(t) \}$$
$$- \frac{1}{Nf(1-f)} \sum_{k \neq i}^N \epsilon_{jk}^\mu \xi_j^\mu \xi_k^{\mu+1} x_k(t)$$
$$- \frac{1}{Nf(1-f)} \sum_{\nu \neq \mu}^p \epsilon_{ji}^\nu \xi_j^\nu \xi_i^{\nu+1} x_i(t)$$
$$- \frac{1}{Nf(1-f)} \epsilon_{ji}^\mu \xi_j^\mu \xi_i^{\mu+1} x_i(t)$$
$$+ \sum_{\nu \neq \mu}^p \bar{\xi}_j^\nu \{ m^{\nu-1}(t) - m^{\nu+1}(t) \}$$
$$+ \frac{1}{Nf(1-f)} \sum_{k \neq i}^N \sum_{\nu \neq \mu}^p \epsilon_{jk}^\nu \xi_j^\nu \xi_k^{\nu+1} x_k(t) - \theta \Bigg)$$
$$(A16)$$

$$= x_j^{(\mu)(\epsilon_{ji}^\mu)}(t+1) + u_j^{\{\mu, \epsilon_{ji}^\mu\}}(t) x_j'^{(\mu)(\epsilon_{ji}^\mu)}(t+1), \quad (A17)$$

where $x_j'^{(\mu)(\epsilon_{ji}^\mu)}(t)$, which is independent of both $\xi_j^\mu(t)$ and ϵ_{ji}^μ is the differential of $x_j^{(\mu)(\epsilon_{ji}^\mu)}(t)$ and

$$u_j^{\{\mu, \epsilon_{ji}^\mu\}}(t) = \bar{\xi}_j^\mu \{ m^{\mu-1}(t) - m^{\mu+1}(t) \}$$
$$- \frac{1}{Nf(1-f)} \sum_{k \neq i}^N \epsilon_{jk}^\mu \xi_j^\mu \xi_k^{\mu+1} x_k(t)$$
$$- \frac{1}{Nf(1-f)} \sum_{\nu \neq \mu}^p \epsilon_{ji}^\nu \xi_j^\nu \xi_i^{\nu+1} x_i(t)$$
$$- \frac{1}{Nf(1-f)} \epsilon_{ji}^\mu \xi_j^\mu \xi_i^{\mu+1} x_i(t), \quad (A18)$$

$$x_j^{(\mu)(\epsilon_{ji}^\mu)}(t+1) = F(u_j(t) - u_j^{\{\mu, \epsilon_{ji}^\mu\}}(t) - \theta), \quad (A19)$$

$$x_j'^{(\mu)(\epsilon_{ji}^\mu)}(t+1) = F'(u_j(t) - u_j^{\{\mu, \epsilon_{ji}^\mu\}}(t) - \theta). \quad (A20)$$

The first, second, and third terms on the right-hand side of Eq. (A18) are of order $1/\sqrt{N}$ with respect to N and the fourth term is of order $1/N$ with respect to N. In the thermodynamic limit, $N \to \infty$, $u_j^{\{\mu, \epsilon_{ji}^\mu\}}(t)$ is small and Eq. (A16) equals Eq. (A17). Substituting Eq. (A17) into the right-hand side of Eq. (A15) and averaging the resultant expressions over ξ_j^μ and ϵ_{ji}^μ and using $E[\epsilon_{ji}^\mu] = 0$ yield the following equation for $m^\mu(t)(\mu \neq t)$:

$$m^\mu(t) = \frac{1}{Nf(1-f)} \sum_{i=1}^{N} \bar{\xi}_i^\mu x_i^{(\mu)}(t) + \frac{1}{Nf(1-f)} \sum_{i=1}^{N} (\bar{\xi}_i^\mu)^2 \{m^{\mu-1}(t-1) - m^{\mu+1}(t-1)\} x_i'^{(\mu)}(t) \tag{A21}$$

$$= \frac{1}{Nf(1-f)} \sum_{i=1}^{N} \bar{\xi}_i^\mu x_i^{(\mu)}(t) + U(t)\{m^{\mu-1}(t-1) - m^{\mu+1}(t-1)\}, \tag{A22}$$

where $U(t) = (1/N)\sum_{i=1}^{N} x_i'^{(\mu)}(t)$. Substituting Eq. (A22) into Eq. (A2) yields

$$u_i(t) = (\bar{\xi}_i^{t+1} - \bar{\xi}_i^{t-1}) m^t(t) + \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu \neq t}^{p} (\bar{\xi}_i^{\mu+1} - \bar{\xi}_i^{\mu-1}) \bar{\xi}_j^\mu x_j^{(\mu)}(t) + \sum_{\mu \neq t}^{p} U(t)\{\bar{\xi}_i^{\mu+1} m^{\mu-1}(t-1) - 2\bar{\xi}_i^{\mu-1} m^{\mu-1}(t-1)$$

$$+ \bar{\xi}_i^{\mu-1} m^{\mu+1}(t-1)\} - \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu=1}^{p} \epsilon_{ij}^{\mu-1} \bar{\xi}_i^{\mu-1} \bar{\xi}_j^\mu x_j(t). \tag{A23}$$

Substituting Eq. (A17) into the last term of Eq. (A23) yields the following expression for $u_i(t)$:

$$u_i(t) = (\bar{\xi}_i^{t+1} - \bar{\xi}_i^{t-1}) m^t(t) + \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu \neq t}^{p} (\bar{\xi}_i^{\mu+1} - \bar{\xi}_i^{\mu-1}) \bar{\xi}_j^\mu x_j^{(\mu)}(t) + \sum_{\mu \neq t}^{p} U(t)\{\bar{\xi}_i^{\mu+1} m^{\mu-1}(t-1) - 2\bar{\xi}_i^{\mu-1} m^{\mu-1}$$

$$\times (t-1) + \bar{\xi}_i^{\mu-1} m^{\mu+1}(t-1)\} - \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu=1}^{p} \epsilon_{ij}^{\mu-1} \bar{\xi}_i^{\mu-1} \bar{\xi}_j^\mu \{x_j^{(\mu)(\epsilon_{ji}^\mu)}(t) + u_j^{\{\mu, \epsilon_{ji}^\mu\}}(t-1) x_j'^{(\mu)(\epsilon_{ji}^\mu)}(t)\} \tag{A24}$$

$$= (\bar{\xi}_i^{t+1} - \bar{\xi}_i^{t-1}) m^t(t) + \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu \neq t}^{p} (\bar{\xi}_i^{\mu+1} - \bar{\xi}_i^{\mu-1}) \bar{\xi}_j^\mu x_j^{(\mu)}(t) + \sum_{\mu \neq t}^{p} U(t)\{\bar{\xi}_i^{\mu+1} m^{\mu-1}(t-1)$$

$$- 2\bar{\xi}_i^{\mu-1} m^{\mu-1}(t-1) + \bar{\xi}_i^{\mu-1} m^{\mu+1}(t-1)\} - \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu=1}^{p} \epsilon_{ij}^{\mu-1} \bar{\xi}_i^{\mu-1} \bar{\xi}_j^\mu x_j^{(\mu)(\epsilon_{ji}^\mu)}(t)$$

$$- \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu=1}^{p} \epsilon_{ij}^{\mu-1} \bar{\xi}_i^{\mu-1} \bar{\xi}_j^\mu \bar{\xi}_j^\mu \{m^{\mu-1}(t-1) - m^{\mu+1}(t-1)\} x_j'^{(\mu)(\epsilon_{ji}^\mu)}(t)$$

$$+ \left(\frac{1}{Nf(1-f)}\right)^2 \sum_{j=1}^{N} \sum_{\mu=1}^{p} \epsilon_{ij}^{\mu-1} \bar{\xi}_i^{\mu-1} \bar{\xi}_j^\mu \sum_{k \neq i}^{N} \epsilon_{jk}^\mu \xi_j^\mu \xi_k^{\mu+1} x_k(t-1) x_j'^{(\mu)(\epsilon_{ji}^\mu)}(t)$$

$$+ \left(\frac{1}{Nf(1-f)}\right)^2 \sum_{j=1}^{N} \sum_{\mu=1}^{p} \epsilon_{ij}^{\mu-1} \bar{\xi}_i^{\mu-1} \bar{\xi}_j^\mu \sum_{\nu \neq \mu}^{p} \epsilon_{ji}^\nu \xi_j^\nu \xi_i^{\nu+1} x_i(t-1) x_j'^{(\mu)(\epsilon_{ji}^\mu)}(t)$$

$$+ \left(\frac{1}{Nf(1-f)}\right)^2 \sum_{j=1}^{N} \sum_{\mu=1}^{p} \epsilon_{ij}^{\mu-1} \bar{\xi}_i^{\mu-1} \bar{\xi}_j^\mu \epsilon_{ji}^\mu \xi_j^\mu \xi_i^{\mu+1} x_i(t-1) x_j'^{(\mu)(\epsilon_{ji}^\mu)}(t). \tag{A25}$$

The fifth, sixth, seventh, and eighth terms vanish since $E[\epsilon_{ij}^\mu] = 0$, and this yields

$$u_i(t) = (\bar{\xi}_i^{t+1} - \bar{\xi}_i^{t-1}) m^t(t) + \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu \neq t}^{p} (\bar{\xi}_i^{\mu+1} - \bar{\xi}_i^{\mu-1}) \bar{\xi}_j^\mu x_j^{(\mu)}(t) + \sum_{\mu \neq t}^{p} U(t)\{\bar{\xi}_i^{\mu+1} m^{\mu-1}(t-1) - 2\bar{\xi}_i^{\mu-1} m^{\mu-1}(t-1)$$

$$+ \bar{\xi}_i^{\mu-1} m^{\mu+1}(t-1)\} - \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu=1}^{p} \epsilon_{ij}^{\mu-1} \bar{\xi}_i^{\mu-1} \bar{\xi}_j^\mu x_j^{(\mu)(\epsilon_{ji}^\mu)}(t) \tag{A26}$$

$$= (\bar{\xi}_i^{t+1} - \bar{\xi}_i^{t-1}) m^t(t) + z_i(t), \tag{A27}$$

where

$$
z_i(t) = \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu \neq t}^{p} (\bar{\xi}_i^{\mu+1} - \bar{\xi}_i^{\mu-1}) \bar{\xi}_j^\mu x_j^{(\mu)}(t) + \sum_{\mu \neq t}^{p} U(t) \{ \bar{\xi}_i^{\mu+1} m^{\mu-1}(t-1) - 2\bar{\xi}_i^{\mu-1} m^{\mu-1}(t-1) + \bar{\xi}_i^{\mu-1} m^{\mu+1}(t-1) \}
$$

$$
- \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu=1}^{p} \epsilon_{ij}^{\mu-1} \xi_i^{\mu-1} \xi_j^\mu x_j^{(\mu)(\epsilon_{ji}^\mu)}(t). \tag{A28}
$$

$z_i(t)$ is the cross-talk noise term. We assume that the cross-talk noise obeys a Gaussian distribution with mean 0 and time-dependent variance $\sigma^2(t)$: $E[z_i(t)]=0, E[(z_i(t))^2]=\sigma^2(t)$ [16,20]. The first and second terms of $z_i(t)$ are the same cross-talk noise terms as those of our previous work [16]. The square of $z_i(t)$ is given by

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

$$
+ \bar{\xi}_i^{\nu-1} m^{\nu+1}(t-1) \}^2 + \left(\frac{1}{Nf(1-f)} \right)^2 \sum_{j=1}^{N} \sum_{\mu=1}^{p} (\epsilon_{ij}^{\mu-1})^2 (\xi_i^{\mu-1})^2 (\xi_j^\mu)^2 \{x_j^{(\mu)(\epsilon_{ji}^\mu)}(t)\}^2 + \frac{2}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu \neq t}^{p} (\bar{\xi}_i^{\mu+1}
$$

$$
- \bar{\xi}_i^{\mu-1}) \bar{\xi}_j^\mu x_j^{(\mu)}(t) \sum_{\mu' \neq t}^{p} U(t) \{ \bar{\xi}_i^{\mu'+1} m^{\mu'-1}(t-1) - 2\bar{\xi}_i^{\mu'-1} m^{\mu'-1}(t-1) + \bar{\xi}_i^{\mu'-1} m^{\mu'+1}(t-1) \} + 2 \sum_{\mu \neq t}^{p} U(t)
$$

$$
\times \{ \bar{\xi}_i^{\mu+1} m^{\mu-1}(t-1) - 2\bar{\xi}_i^{\mu-1} m^{\mu-1}(t-1) + \bar{\xi}_i^{\mu-1} m^{\mu+1}(t-1) \} \frac{1}{Nf(1-f)} \sum_{j=1}^{N} \sum_{\mu=1}^{p} \epsilon_{ij}^{\mu-1} \xi_i^{\mu-1} \xi_j^\mu x_j^{(\mu)(\epsilon_{ji}^\mu)}(t)
$$

$$
+ 2 \left(\frac{1}{Nf(1-f)} \right)^2 \sum_{j=1}^{N} \sum_{\mu'=1}^{p} \epsilon_{ij}^{\mu'-1} \xi_i^{\mu'-1} \xi_j^{\mu'} x_j^{(\mu')(\epsilon_{ji}^{\mu'})}(t) \sum_{k=1}^{N} \sum_{\mu' \neq t}^{p} (\bar{\xi}_i^{\mu'+1} - \bar{\xi}_i^{\mu'-1}) \bar{\xi}_k^{\mu'} x_k^{(\mu')}(t) \tag{A29}
$$

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

$$
+ \bar{\xi}_i^{\nu-1} m^{\nu+1}(t-1) \}^2 + \left(\frac{1}{Nf(1-f)} \right)^2 \sum_{j=1}^{N} \sum_{\mu=1}^{p} (\epsilon_{ij}^{\mu-1})^2 (\xi_i^{\mu-1})^2 (\xi_j^\mu)^2 \{x_j^{(\mu)(\epsilon_{ji}^\mu)}(t)\}^2 \tag{A30}
$$

$$
= \sum_{a=0}^{t} {}_{2(a+1)}C_{(a+1)} \alpha q(t-a) \prod_{b=1}^{a} U^2(t-b+1) + \frac{\alpha \delta^2}{(1-f)^2} q(t), \tag{A31}
$$

where $p = \alpha N$, $q(t) = (1/N) \Sigma_{i=1}^{N} \{x_i^{(\mu)}(t)\}^2$, $_bC_a = b!/a!(b-a)!$, $a!$ is the factorial with positive integer a, and $E[(\epsilon_{ij}^\mu)^2] = \delta^2$. Since $E[\epsilon_{ij}^\mu] = 0$, the fourth, fifth, and sixth terms in Eq. (A29) vanish. We applied the relationship $\Sigma_{a=0}^{b} (_bC_a)^2 = _{2b}C_b$ in this derivation. Since $E[z_i(t)] = 0$, the variance $\sigma^2(t)$ is equal to $E[\{z_i(t)\}^2]$. We then get the recursive equation for $\sigma^2(t)$

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

$$
+ \frac{\alpha \delta^2}{(1-f)^2} q(t). \tag{A32}
$$

The overlap between the state $x(t)$ and the retrieval pattern ξ^t is given by

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

$$
= \frac{1}{Nf(1-f)} \sum_{i=1}^{N} (\xi_i^t - f) F((\xi_i^t - \xi_i^{t-2}) m^{t-1}(t-1)
$$

$$
+ z_i(t-1) - \theta). \tag{A33}
$$

Since $u_i(t)$ is an independent and identical distribution, by the law of large numbers, the average over i can be replaced

by an average over the memory patterns ξ^μ and the Gaussian noise term $z \sim \mathcal{N}(0, \sigma^2)$. Then, the recursive equation for the overlap $m^t(t)$ is transformed:

$$m^t(t) = \frac{1}{f(1-f)} \frac{1}{\sqrt{2\pi}\sigma} \int_{-\infty}^{\infty} dz\, e^{-z^2/2\sigma^2} \langle\langle (\xi^t - f)$$

$$\times F((\xi^t - \xi^{t-2})m^{t-1}(t-1) + z - \theta) \rangle\rangle$$

$$= \frac{1}{f(1-f)} \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} d\tilde{z}\, e^{-\tilde{z}^2/2} \langle\langle (\xi^t - f) F((\xi^t - \xi^{t-2})$$

$$\times m^{t-1}(t-1) + \sigma(t-1)\tilde{z} - \theta) \rangle\rangle \tag{A34}$$

$$= \frac{1-2f}{2} \operatorname{erf}(\phi_0) - \frac{1-f}{2} \operatorname{erf}(\phi_1) + \frac{f}{2} \operatorname{erf}(\phi_2), \tag{A35}$$

where $\tilde{z} = z/\sigma$, $\operatorname{erf}(y) = (2/\sqrt{\pi}) \int_0^y \exp(-u^2) du$, and $\phi_0 = \theta/\sqrt{2}\sigma(t-1)$, $\phi_1 = [-m^{t-1}(t-1) + \theta]/\sqrt{2}\sigma(t-1)$, $\phi_2 = [m^{t-1}(t-1) + \theta]/\sqrt{2}\sigma(t-1)$, and $\langle\langle \cdots \rangle\rangle$ denotes an average over the memory pattern ξ^μ. Since $x_i'(t) - x_i'^{(\mu)}(t) \sim O(1/\sqrt{N})$ and the thermodynamic limit, $N \to \infty$, is considered, $x_i'^{(\mu)}(t) = x_i'(t)$. Using this relationship, we derive $U(t)$:

$$U(t) = \frac{1}{N} \sum_{i=1}^{N} x_i'^{(\mu)}(t) = \frac{1}{N} \sum_{i=1}^{N} x_i'(t) \tag{A36}$$

$$= \frac{1}{f(1-f)} \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} dz\, e^{-z^2/2} \langle\langle F'((\xi^t - \xi^{t-2})m^{t-1}$$

$$\times (t-1) + \sigma(t-1)z - \theta) \rangle\rangle \tag{A37}$$

$$= \frac{1}{f(1-f)} \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} dz\, e^{-z^2/2} z \langle\langle F((\xi^t - \xi^{t-2})m^{t-1}$$

$$\times (t-1) + \sigma(t-1)z - \theta) \rangle\rangle \tag{A38}$$

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

$$\times (e^{-\phi_1^2} + e^{-\phi_2^2}) \}. \tag{A39}$$

Since $x_i(t) - x_i^{(\mu)}(t) \sim O(1/\sqrt{N})$ and $N \to \infty$, $x_i^{(\mu)}(t) = x_i(t)$. Using this relationship, we derive $q(t)$:

$$q(t) = \frac{1}{N} \sum_{i=1}^{N} \{x_i^{(\mu)}(t)\}^2 = \frac{1}{N} \sum_{i=1}^{N} \{x_i(t)\}^2 \tag{A40}$$

$$= \frac{1}{f(1-f)} \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} dz\, e^{-z^2/2} \langle\langle F^2((\xi^t - \xi^{t-2})$$

$$\times m^{t-1}(t-1) + \sigma(t-1)z - \theta) \rangle\rangle \tag{A41}$$

$$= \frac{1}{2} \{ 1 - (1 - 2f + 2f^2) \operatorname{erf}(\phi_0) - f(1-f)$$

$$\times (\operatorname{erf}(\phi_1) + \operatorname{erf}(\phi_2)) \}. \tag{A42}$$

[1] G.Q. Bi and M.M. Poo, J. Neurosci. **18**, 10464 (1998).
[2] H. Markram, J. Lübke, M. Frotscher, and B. Sakmann, Science **275**, 213 (1997).
[3] L.I. Zhang, H.W. Tao, C.E. Holt, W.A. Harris, and M.M. Poo, Nature (London) **395**, 37 (1998).
[4] S. Song, K.D. Miller, and L.F. Abbott, Nat. Neurosci. **3**, 919 (2000).
[5] L. F. Abbott and S. Song, in *Advances in Neural Information Processing Systems*, edited by M. S. Kearns, S. Solla, and D. Cohn (MIT Press, Cambridge, MA, 1999), Vol. 11, pp. 69–75.
[6] J. Rubin, D.D. Lee, and H. Sompolinsky, Phys. Rev. Lett. **86**, 364 (2001).
[7] N. Levy, D. Horn, I. Meilijson, and E. Ruppin, Neural Networks **14**, 815 (2001).
[8] M.C.W. van Rossum, G.Q. Bi, and G.G. Turrigiano, J. Neurosci. **20**, 8812 (2001).
[9] S. Song and L.F. Abbott, Neuron **32**, 339 (2001).
[10] W. Gerstner, R. Kempter, J.L. van Hemmen, and H. Wagner, Nature (London) **383**, 76 (1996).
[11] R. Kempter, W. Gerstner, and J.L. van Hemmen, Phys. Rev. E **59**, 4498 (1999).
[12] W.M. Kistler and J.L. van Hemmen, Neural Comput. **12**, 385 (2000).
[13] R. P. N. Rao and T. J. Sejnowski, in *Advances in Neural Information Processing Systems*, edited by S. A. Solla, T. K. Leen, and K. R. Müller (MIT Press, Cambridge, MA, 2000), Vol. 12, pp. 164–170.
[14] P. Munro and G. Hernandez, in *Advances in Neural Information Processing Systems*, edited by S. A. Solla, T. K. Leen, and K. R. Müller (MIT Press, Cambridge, MA, 2000), Vol. 12, pp. 150–156.
[15] M. Yoshioka, Phys. Rev. E **65**, 011903 (2002).
[16] N. Matsumoto and M. Okada, Neural Comput. **14**, 2883 (2002); in *Advances in Neural Information Processing Systems*, edited by T. G. Dietterich, S. Becker and Z. Ghahramani (MIT Press, Cambridge, MA, 2002), Vol. 14, 245–252.
[17] A. Herz, B. Sulzer, R. Kuhn, and J.L. van Hemmen, Biol. Cybern. **60**, 457 (1989).
[18] W. Gerstner, R. Ritz, and J.L. van Hemmen, Biol. Cybern. **69**, 503 (1993).
[19] L.F. Abbott and K.I. Blum, Cereb. Cortex **6**, 406 (1996).
[20] M. Okada, Neural Networks **9**, 1429 (1996).
[21] S. Amari and K. Maginu, Neural Networks **1**, 63 (1988).
[22] K. Mimura, T. Kimoto, and M. Okada, Phys. Rev. E. **68**, 031930 (2003).
[23] K. Kitano and T. Aoyagi, J. Phys. A **31**, L613 (1998).