

An associative memory of Hodgkin-Huxley neuron networks with Willshaw-type synaptic couplings ^{*}

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(July 13, 2003)

Abstract

An associative memory has been discussed of neural networks consisting of spiking $N (= 100)$ Hodgkin-Huxley (HH) neurons with time-delayed couplings, which memorize P patterns in their synaptic weights. In addition to excitatory synapses whose strengths are modified after the Willshaw-type learning rule with the 0/1 code for quiescent/active states, the network includes uniform inhibitory synapses which are introduced to reduce cross-talk noises. Our simulations of the HH neuron network for the noise-free state have shown to yield a fairly good performance with the storage capacity of $\alpha_c = P_{\max}/N \sim 0.4 - 2.4$ for the low neuron activity of $f \sim 0.04 - 0.10$. This storage capacity of our temporal-code network is comparable to that of the rate-code model with the Willshaw-type synapses. Our HH neuron network is realized not to be vulnerable to the distribution of time delays in couplings. The variability of interspace interval (ISI) of output spike trains in the process of retrieving stored patterns is also discussed.

PACS No. 84.35.+i 87.10.+e 87.18.Sn

Typeset using REVTeX

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I. INTRODUCTION

The Hopfield-type neural networks have been intensively investigated as a model for the learning and memory of brain [1]. In this type of models the information is stored as a content-addressable memory in which synaptic strengths are modified after the Hebbian rule. Its retrieval is made when the network with the symmetric couplings works as the point-attractor with the fixed points. These models have been analyzed by the method of statistical mechanics of spin glasses [2]. Such analysis provides us with most important information of storage capacity, role of noise and recall performance. The Hopfield-type models, however, are an extreme abstraction of real neural networks and they have the following issues from the biological viewpoint.

(i) The dynamical variable in the Hopfield-type model is the firing rate of neurons (*rate coding*). However, the importance of a precise timing of firing (*temporal coding*) is currently realized in many experiments: sonar processing of bats [3], sound localization of owls [4], electrosensation in electric fish [5], visual processing of cats [6] [7], monkeys [8] and human [9].

(ii) The synaptic weight W_{jk} for a given synapse between the pre-synaptic neuron k and the post-synaptic neuron j in the Hopfield-type models is usually assumed to be given by [1]

$$W_{jk} = \sum_{\mu=1}^P (\xi_j^{(\mu)} - a) (\xi_k^{(\mu)} - b), \quad (1)$$

where P stands for the number of patterns to be stored, $\xi_j^{(\mu)} = -1/1$ (or $0/1$) for quiescent/active states and $a = b = f \equiv <\xi_j^{(\mu)}>$, the average activity. Equation (1) shows that a given synapse may be positive (excitatory) or negative (inhibitory) depending on the covariance of the pre- and post-synaptic activities. This is not biologically realized because the synapse is either excitatory or inhibitory with little exception. Furthermore, Eq.(1) shows that the potentiation of the synaptic strength of a given synapse is possible even in the absence of pre- and post-synaptic activities ($\xi_j^{(\mu)} = \xi_k^{(\mu)} = -1$ or 0). The potentiation without the brain activity again contradicts the biological evidence.

In recent years some theoretical studies have been reported of the learning and memory in terms of the temporal coding with the use of spiking neurons [10]- [16] or oscillating neurons [17]- [21]. It has been shown that spiking neurons such as the spike-response and integrate-and-fire neurons with a correlation-based Hebbian learning rule can operate very fast in the order of ten milliseconds [10] [11]. Mueller and Herz [15] showed that the networks consisting of spiking integrate-and-fire (IF) neurons possess the storage capacity similar to those of rate-code neurons. Their model, however, adopts the leaning rule given by Eq.(1) for storing patterns in synapse weights, and then it has the second issue raised above. Based on spiking FitzHugh-Nagumo (FN) neurons with time-delayed couplings, Yoshioka and Shiino [13], and Kanamuru and Okabe [16] discussed the associative memory with the use of the leaning rule given by Eq.(1) but with $a = 0$ and $b = f$ for the $0/1$ code. Their approach has the second issue because their W_{jk} may be positive for negative depending on whether $\xi_k^{(\mu)} = 1$ or 0 for $\xi_j^{(\mu)} = 1$.

Among spiking neuron models having been proposed so far, the Hodgkin-Huxley (HH) model is expected to be the most realistic in the biological sense. Since the HH model was

proposed in 1952 [22], its property has been intensively investigated. Its responses to applied dc [23] and sinusoidal currents [24], and spiking impulses [25] have been studied. The HH model has been generalized with modifications in ion conductances and widely adopted for a study of biological systems such as hippocampus [26] and thalamus [27].

Quite recently, Lytton [12] has proposed the feedforward hetero-associative memory network of spiking 40 HH neurons, by employing the notion of the Anderson-Kohonen network. The weight of the excitatory synapses is assumed to be given by the conventional Hebbian rule:

$$W_{jk} = \sum_{\mu=1}^P \xi_j^{(\mu)} \xi_k^{(\mu)}, \quad (2)$$

with $\xi_j^\mu = 0/1$ for quiescent/active states. In addition to the excitatory synapses, Lytton has included inhibitory synapses whose weights are determined by a feedforward rule depending on input patterns, in order to suppress the cross-talk noises arising from the non-orthogonal inputs. Equation (2) shows that the synapse is strengthen only when both pre- and post-synapses are active, in agreement with biological experiments. It is shown, however, that the retrieval of the HH network is only possible in the narrow parameter ranges of conductances of excitatory and inhibitory synapses [12].

Since a naive transplant of the Hebbian rule given by Eq.(2) to HH neuron networks yields the poor performance in retrieving memorized patterns, as was shown by Lytton [12], we adopt, in this paper, the Willshaw rule given by [28]

$$W_{jk} = \Theta\left(\sum_{\mu=1}^P \xi_j^{(\mu)} \xi_k^{(\mu)}\right), \quad (3)$$

where $\Theta(x) = 1$ for $x > 0$ and 0 otherwise, and $\xi_j^{(\mu)} = 0/1$ for quiescent/active states. The synaptic weight given by Eq.(3) is either one or zero, in contrast with that given by Eqs. (1) and (2). Such a dramatic reduction is not biologically justifiable except under some conditions when the postsynaptic membrane of a dendritic spine is active [30]. It has been, however, reported that the Willshaw rule given by Eq.(3) improves the storage efficiency of Hopfield-type neural networks [28]- [33]. Equation (3) shows that the synaptic weight is potentiated only for the simultaneous firings of the pre- and post-synaptic neurons, which is in accord with biological results.

Theoretical studies on memory have extensively pursued the analytical approach, requiring simplified tractable models, which do not necessarily reflect the aspect of the biological reality. As an alternative approach, we may take a simulation method for a better understanding of functioning of real, biological systems to which an analytical method cannot applied.

It is the purpose of the present paper to construct biologically plausible model for an associative memory. We propose HH neuron networks with excitatory and inhibitory synapses, weights of the former are modified by the Willshaw-type learning rule. Simulations of the memory function of the network are performed for sparse coding with the low firing activity ($f \ll 1$) because neurophysical evidences indicate that only a small fraction of neurons are active at a given time [34]. Our simulations demonstrate that our HH neuron networks works fairly well in memory function within the temporal coding.

Our paper is organized as follows: In the next Sec. II, we describe a neural system consisting of N HH neurons which are fully connected with time-delayed couplings. The results of simulations are presented in Sec. III. The retrieval of the stored patterns by perfect and imperfect input patterns are studied in Sec. 3.1 and Sec. 3.2, respectively, and the effect of the distribution of the time delay in couplings is discussed in Sec. 3.3. The final Sec. IV is devoted to discussions concerning the relevant rate-code model and the variability of interspike intervals (ISI) of output spike trains.

II. ADOPTED NETWORK MODEL

We adopt a network of N HH neurons which stores and retrieves sparsely coded P patterns. HH neurons described by identical parameters, are fully coupled by synapses with time-delayed couplings. The input information is assumed to be stored in the synaptic plasticity as will be discussed shortly [Eq.(11)].

Dynamics of the membrane potential V_j of the HH neuron j ($= 1, \dots, N$) is described by the non-linear delay-differential equations given by

$$C dV_j(t)/dt = -I_j^{\text{ion}}(V_j, m_j, h_j, n_j) + I_j^{\text{ext}} + I_j^{\text{int}}, \quad (4)$$

where $C = 1 \mu\text{F}/\text{cm}^2$ is the capacity of the membrane. The first term of Eq.(4) expresses the ion current given by

$$I_j^{\text{ion}}(V_j, m_j, h_j, n_j) = g_{\text{Na}} m_j^3 h_j (V_j - V_{\text{Na}}) + g_{\text{K}} n_j^4 (V_j - V_{\text{K}}) + g_{\text{L}} (V_j - V_{\text{L}}). \quad (5)$$

Here the maximum values of conductivities of Na and K channels and leakage are $g_{\text{Na}} = 120 \text{ mS}/\text{cm}^2$, $g_{\text{K}} = 36 \text{ mS}/\text{cm}^2$ and $g_{\text{L}} = 0.3 \text{ mS}/\text{cm}^2$, respectively, and the respective reversal potentials are $V_{\text{Na}} = 50 \text{ mV}$, $V_{\text{K}} = -77 \text{ mV}$ and $V_{\text{L}} = -54.5 \text{ mV}$. The dynamics of gating variables of Na and K channels, m_j , h_j and n_j , are described by linear-differential equations, whose explicit expressions have been given (for example see [25]).

The second term in Eq.(4) denotes the external input current given by

$$I_j^{\text{ext}} = g_{\text{syn}} (V_a - V_c) \sum_n \alpha(t - t_{in}), \quad (6)$$

which is induced by the pre-synaptic spike-train input applied to the neuron i , given by

$$U_i(t) = V_a \sum_n \delta(t - t_{in}). \quad (7)$$

In Eqs.(6) and (7), t_{in} is the n -th firing time of the spike-train inputs, g_{syn} and V_c denote the conductance and the reversal potential, respectively, of the synapse, τ_s is the time constant relevant to the synapse conduction, and $\alpha(t)$ is the alpha function given by

$$\alpha(t) = (t/\tau_s) e^{-t/\tau_s} \Theta(t). \quad (8)$$

where $\Theta(t)$ is the Heaviside function.

When the membrane potential of the j -th neuron $V_j(t)$ oscillates, it yields the spike-train output, which may be expressed by

$$U_{oj}(t) = V_a \sum_m \delta(t - t_{ojm}), \quad (9)$$

in a similar form to Eq.(7), t_{ojm} being the m -th firing time when $V_j(t)$ crosses $V_z = 0.0$ mV from below.

The third term in Eq.(4) expresses the interaction between neurons:

$$I_j^{\text{int}} = G \left(\sum_{k(\neq j)} \sum_m (g_{jk}^{\text{exc}} - g_{jk}^{\text{inh}}) (V_a - V_c) \alpha(t - \tau_{jk} - t_{okm}) \right). \quad (10)$$

with

$$g_{jk}^{\text{exc}} = g_{\text{exc}} \Theta \left(\sum_{\mu=1}^P \xi_j^{(\mu)} \xi_k^{(\mu)} \right), \quad (11)$$

$$G(x) = x \Theta(x), \quad (12)$$

In Eqs.(10)-(12) the self-interaction ($j = k$) is forbidden, g_{jk}^{exc} denotes the conductance of the excitatory synapse, g_{jk}^{inh} that of the inhibitory synapse, and the time delay τ_{jk} ($= \tau_{kj} = \tau_d$) is the sum of conduction times for currents from the neurons k to j through the axon and dendrite. The excitatory synaptic strength g_{jk}^{exc} in Eq.(11) takes either the value of 0 or g_{exc} after Willshaw *et al.* [28] [29]. The synaptic plasticity occurs only when both the pre- and post-synaptic neurons fire simultaneously, in accord with biological findings. The uniform inhibition $g_{jk}^{\text{inh}} = g_{\text{inh}}$ is included to reduce the cross-talk noise.

The function $G(x)$ in Eq.(12) represents the dendrite processing of postsynaptic currents, and its uni-directional form is adopted such that neurons do not fire for resultant inhibitory inputs [35]. It is well known that an HH (and FN) neuron can fire even for an inhibitory input with the inhibitory rebound process [36], whereas an IF neuron cannot. Figure 1(a) and 1(b) show responses of a single HH neuron to excitatory and inhibitory inputs, respectively, which are calculated by setting $I_j^{\text{int}} = 0$ in Eq.(4). With an application of an excitatory input, a HH neuron is depolarized to fire at 2.8 msec after the trigger, and it recovers to the rest state with the refractory period of about 10 msec. When an inhibitory input is applied, on the other hand, a HH neuron is once hyper-polarized and then depolarized to fire after 14.6 msec of the input injection. Because the firing of neurons for inhibitory inputs is not appropriate for the memory retrieval, we introduce the uni-directional function $G(x)$ given by Eq.(12), which suppresses the negative (inhibitory) input, related discussions being given in Sec.IV.

Patterns to be stored are expressed by a vector of $\xi^{(\mu)} = \{\xi_j^{(\mu)} \mid j = 1 - N\}$ where $\mu = 1 - P$ and $\xi_j^{(\mu)} = 0(1)$ for the quiescent (firing) state of the neuron j . We randomly create the patterns to be stored such as to satisfy the condition for a given number of unit-codes, M ($= fN$):

$$M = M^{(\mu)} = \sum_j \xi_j^{(\mu)}. \quad (13)$$

Without a loss of the generality, we take for the $\mu = 1$ pattern that $\xi_j^{(1)} = 1$ for $j \leq M$ and $\xi_j^{(1)} = 0$ for $j > M$. Simulations have been repeated for ten samples, each of which includes

P patterns. The standard deviations in the calculated results are shown by error bars in figures of the following sections.

The retrieval of the first pattern of $\xi^{(1)}$ is made by injecting a proper input pattern of ζ to our network at $t = 0$. The input pattern may be $\zeta = \xi^{(1)}$ (perfect input) or $\zeta \neq \xi^{(1)}$ (imperfect input). Differential equations given by Eqs.(4)-(12) are solved by the forth-order Runge-Kutta method by the integration time step of 0.01 msec with double precision. We assume that all HH neurons are in the same initial conditions given by

$$V_j(t) = -65 \text{ mV}, m_j(t) = 0.0526, h_j(t) = 0.600, n_j(t) = 0.313, \text{ for } j = 1, 2 \text{ at } t = 0, \quad (14)$$

which are the rest-state solution of a single HH neuron ($I_j^{int} = 0$). The initial function for $V_j(t)$ of all HH neurons is given by

$$V_j(t) = -65 \text{ mV} \text{ for } j = 1, 2 \text{ at } t \in [-\tau_d, 0). \quad (15)$$

The adopted model parameters are summarized as follows: $N = 100$, $V_a = 30 \text{ mV}$, $V_c = -50 \text{ mV}$, $\tau_d = 10 \text{ msec}$, $\tau_s = 2 \text{ msec}$ [25], $g_{syn} = g_{exc} = 0.3 \text{ mS/cm}^2$ and $g_{inh} = 0.24 \text{ mS/cm}^2$. The time delays are taken to be a single constant value of $\tau_{jk} = \tau_{kj} = \tau_d$ in Sec. 3.1 and 3.2, while in Sec. 3.3 they are allowed to uniformly distribute in the limited range. We choose $\tau_d = 10 \text{ msec}$ such that it not only satisfies the condition of $\tau_d > 7 \text{ msec}$, which arises from the absolute refractory period of a HH neuron [Fig. 1], but also it is within the biologically conceivable values [13]. A choice of g_{exc} and g_{inh} will be discussed shortly. Although the size of N (and P and M) is not sufficient large because of a limitation of our computer facility, the calculated results are expected to be useful and meaningful.

III. RESULTS OF SIMULATIONS

3.1 Retrieval by perfect inputs

Firstly we consider, in this subsection, the case in which $\zeta = \xi^{(1)}$ is injected for retrieval of $\xi^{(1)}$ (the perfect input): the retrieval by imperfect-input injection ($\zeta \neq \xi^{(1)}$) will be discussed in the following subsection 3.2.

We define the initial overlap, m_i , between the input pattern ζ and the pattern to be retrieved $\xi^{(1)}$:

$$m_i = (1/N) \sum_j [2\xi_j^{(1)} - 1] [2\zeta_j - 1]. \quad (16)$$

It is easy to see that $m_i = 1.0$ for $\zeta_j = \xi_j^{(1)}$. Similarly the time-dependent overlap, $m(t)$, between the state of the system and the pattern $\xi^{(1)}$, is defined by

$$m(t) = (1/N) \sum_j [2\xi_j^{(1)} - 1] [2\eta_j(t) - 1], \quad (17)$$

where $\eta_j(t)$ is given by

$$\begin{aligned} \eta_j(t) &= 1, & \text{if } U_{oj} = 1 \text{ at } t \in [t_{ojm} - \delta t, t_{ojm} + \delta t], \\ &= 0, & \text{otherwise,} \end{aligned} \quad (18)$$

t_{0jm} ($m = 1, 2, \dots$) being the firing time of the neuron j and δt ($= 2.45 \tau_{syn} \sim 5$ msec) denoting the margin with a magnitude of a half-width of the alpha function given by Eq.(8). We hereafter regard firings with the overlap of $m(t) = 1.0$ at $t \gtrsim 50 \tau_d$ as a *successful retrieval*.

An example of an retrieval of of $\xi^{(1)}$ for a given set of patterns, is shown in Fig. 2. We show the time course of a trigger input U_{ij} , the output U_{oj} , the pre-synaptic current I_j ($= I_j^{ext} + I_j^{int}$) and the membrane potential V_j of the neuron of $j = 1$, for an injection of the input pattern ζ at $t = 0$ with $\alpha = 0.30$, $f = 0.1$, $g_{sys} = g_{exc} = 0.30$ and $g_{inh} = 0.24$ mS/cm². The pre-synaptic current I_1^{ext} starting from $t = 0$ is yielded by the trigger input U_{ij} , while other pre-synaptic currents, for example, starting from $t = 12.6$ msec, arise from the interaction term I_j^{int} through the couplings. The firing of the neuron $j = 1$ is given by $U_{o1}(t) = 1$, and it is compactly depicted in Fig. 3(a), where dots express firings of neurons numbered by the index $j = 1 - 100$ in the vertical scale as a function of time [$U_{oj}(t) = 1$ in Eq.(9)]. Figure 3(a) shows a successful retrieval for $\alpha = P/N = 0.30$ with $f = M/N = 0.10$, $g_{exc} = 0.30$ mS/cm² and $\lambda = 0.8$. The time-dependent overlap $m(t)$ given by Eq.(17) is always unity: $m_i = m(t) = 1.0$ at $t \geq 0$, which is calculated at $t = t_{01m}$ ($m = 1, 2, \dots$), firing times of the neuron 1, and which is plotted at the upper part of Fig. 3(a). The period of firings T_o is determined by $T_o = \tau_d + \tau_r \sim 12.5$ msec where τ_d denotes the delay time of couplings and $\tau_r \sim 2.5$ msec is the response time of a HH neuron. Figure 3(b), on the contrary, shows a failed case for a larger α value of $\alpha = 0.50$, yielding extra firings of neurons of $j > 10$ and non-firings of $j \leq 10$. We note that $m_i = m(t) = 1.0$ at $t = 0$ but $m(t)$ quickly deviates from its initial value at $t > 0$. Figures 3(a) and 3(b) show that a single trigger impulse is sufficient to recall the stored pattern.

In order to show the importance of the uniform, inhibitory synapse introduced by g_{inh} in Eq.(10), we plot, in Fig. 4, the λ ($= g_{inh}/g_{exc}$) dependence of the critical storage capacity $\alpha_c = P_{max}/N$, above which the retrieval of the input pattern cannot made. We note that α_c decreases as the value of λ decreases. Although the λ dependence of α_c with $g_{exc} = 0.3$ mS/cm² is slightly different from that with $g_{exc} = 0.5$ mS/cm² for $f = 0.06$, the result with $g_{exc} = 0.3$ mS/cm² is identical with that of $g_{exc} = 0.5$ mS/cm² for $f = 0.10$. We have decided to adopt $g_{exc} = 0.3$ mS/cm² and $\lambda = 0.8$ ($g_{inh} = 0.24$ mS/cm²) for our simulations.

The calculated storage capacity α_c as a function of the mean activity f is plotted in Fig. 5, where bars express the standard deviations due to the sample dependence. It clearly shows that α_c increases as f decreases. Theoretical analysis based on the Hopfield model has shown that the storage capacity diverges as $\alpha_c \propto (-1/f \log f)$ in the limit of vanishing f [37]- [41]. Recent calculations of oscillating associative memory made by Aoyagi and Nomura [19] also support the $(-1/f \log f)$ dependence. Although the f values of our simulations for spiking HH neuron networks are not sufficiently small, our result seems to support it: the dotted curve expresses $10/(M \log M)$, which is proportional to $(-1/f \log f)$ in the limit of $f \rightarrow 0$.

3.2 Retrieval by imperfect inputs

Next we discuss the retrieval of $\xi^{(1)}$ when an imperfect input, $\zeta \neq \xi^{(1)}$, is injected. We assume that an input pattern ζ is similar to $\xi^{(1)}$ but some of its codes are modified, keeping unit-code number unchanged: $M = \sum_j \zeta_j$. We adopt ζ whose codes are same as those of $\xi^{(1)}$ except 1-codes in $j \in [M - \Delta M/2, M]$ are changed to 0-codes, and 0-codes in

$j \in [M+1, M+\Delta M/2]$ to 1-codes, where even $\Delta M (\geq 2)$ is the number of changed codes. The initial overlap of ζ thus created is $m_i = 1.0 - 2\Delta M/N$.

Figure 6(a) shows an example of the successful retrieval when an input with the initial overlap of $m_i = 0.84$ is injected for $\alpha = 0.10$ and $f = 0.20$. The time dependence of $m(t)$ plotted in Fig. 7, shows that $m(t) = m_i = 0.84$ just after an input injection and $m(t)$ gradually approaches unity. The time dependence of $m(t)$ for the case of $m_i = 0.92$ also successfully approaches unity. On the contrary, when an input pattern has a smaller initial overlap of $m_i = 0.68$, the retrieval is failed; firings of neurons spread all over the system as shown in Fig. 6(b) and the overlap $m(t)$ decreases from the initial value of $m_i = 0.68$ as shown in Fig. 7. The failed case is plotted also for $m_i = 0.52$, whose transient value of $m(t)$ is not necessarily smaller than that for $m_i = 0.68$.

The dashed curves in Fig. 8 show the storage capacity α_c against the initial overlap m_i for $f = 0.20$. It shows the critical, initial overlap is about $m_i = 0.73$ for $\alpha = 0.1$ and $f = 0.20$ (Fig. 7). We note in Fig. 8 that for $f = 0.20$, the retrieval is effectively possible for $m_i \gtrsim 0.6$. On the contrary, for $f = 0.10$, the retrieval is possible only in the restricted region of $0.92 < m_i \leq 1.0$. Figures 7 and 8 reminds us the similar calculation made by Amari and Maginu for the Hopfield model [42].

3.3 Effect of distributed time delays

So far we have assumed that the time delays are the same for all couplings connecting neurons: $\tau_{jk} = \tau_{kj} = \tau_d$. It is expected to be not the case in real biological systems. In order to study the effect of their distributions, we assume that time delays uniformly (randomly) distribute as

$$\tau_{jk} = \tau_{kj} \in [\tau_d - \Delta\tau/2, \tau_d + \Delta\tau/2], \quad (19)$$

where $\Delta\tau$ is a width of the time-delay distribution.

When the width of the time-delays distribution becomes large, it is difficult for post-synaptic currents to sustain firings of neurons. The solid curve in Fig. 9, expressing the critical storage α_c for $f = 0.06$ as a function of $\Delta\tau$ for the perfect-input retrieval, shows that the critical storage decreases when the width of the distribution becomes wide, and that α_c vanishes for $\Delta\tau \geq 6$ msec. In the case of $f = 0.10$, whose result is plotted by dashed curve, α_c vanishes for $\Delta\tau \geq 9$ msec. Although the time-dependent overlap of $f = 0.10$ deviates from 1.0 for $\Delta\tau > 9$ msec, the oscillating firings may continue with spread firing times. Fig. 10 shows such a case of $\Delta\tau = 10$ msec, in which neurons from $j = 1$ to 10 fire as the pattern $\xi^{(1)}$ but not in a coherent way. The time dependent overlap defined by Eq.(17) oscillates with $0.88 \leq m(t) \leq 1.0$, as is shown in the upper part of Fig. 10.

The critical width of the time-delay distribution, $\Delta\tau_c$, above which the retrieval of the stored patterns is failed, depends on the average time delay of τ_d . Figure 11 shows $\Delta\tau_c$ for three cases of $(f, \alpha) = (0.06, 0.30)$, $(0.06, 0.10)$ and $(0.10, 0.10)$. We should note that the time delay has the lower bound of 7 msec below which the retrieval is not possible because of the absolute refractory period of a HH neuron [Fig.1], while it has no upper bounds. For both $\alpha=0.30$ and 0.10 , the critical width for $f = 0.06$ has a maximum value of $\Delta\tau_c = 13$ msec at $\tau_d = 15$ msec, and $\Delta\tau_c \sim 8$ msec at $\tau_d \geq 25$ msec. The critical width for $f = 0.10$ is $\Delta\tau_c = 13$ msec at $\tau_d \gtrsim 15$ msec, which is larger than that for $f = 0.06$. Our HH neuron network is fairly robust against the distribution of the time delays in couplings.

IV. DISCUSSION AND CONCLUSION

Our simulations have demonstrated that neural networks consisting of spiking HH neurons may show a fairly good performance as an associative memory with the memory capacity of $\alpha_c \sim 0.4 - 2.4$ for $f \sim 0.04 - 0.10$ [Fig. 5]. It is worth to compare the storage capacity of our HH neuron networks with that of the *rate-code* model in which the dynamics of the firing rate $x_j(t)$ is given by

$$x_j(t+1) = \Theta\left(\sum_{k(\neq j)} (W_{jk} - \nu) x_k(t) - \theta\right). \quad (20)$$

In Eq.(20) W_{jk} is determined by the Willshaw-type rule given by Eq.(2), and ν ($0 < \nu < 1$) and θ are the inhibitory coupling and the threshold, respectively, which are introduced to suppress cross-talk noises [29]- [33]. The storage capacity α_c depends on f , ν and θ . The calculated α_c of this *rate-code* model is shown as a function of f by the solid curve in Fig. 12, where parameters of $N = 100$, $\nu = 0.8$ and $\theta = 0.5$ are adopted [43]. We get the memory capacity of $\alpha_c \sim 0.4 - 3.7$ for $f \sim 0.04 - 0.10$, which is comparable to that of our HH neuron network.

For a comparison, we have repeated calculations of the storage capacity of the *rate-code* model mentioned above, employing the conventional Hebb-type rule given by Eq.(2) instead of the Willshaw-type one given by Eq.(3). The calculated f dependence of the memory capacity is plotted by the dashed curve in Fig. 12. The storage capacity becomes $\alpha_c \sim 0.2 - 1.5$ for $f \sim 0.04 - 0.10$, which is about a half of the values in the *rate-code* model with the Willshaw-type synapses. The critical storage capacities in the Hopfield model with Willshaw-type [Eq.(2)] and Hebb-type synapses [Eq.(3)] increase as the activity f decreases, which is in agreement with the theoretical analysis [38]- [40].

We now examine the following two assumptions adopted in Eq.(10) for the interaction term in our HH neuron network:

- (i) the Willshaw-type rule for weights of excitatory synapses and the uniform inhibitory synapses [Eq.(11)], and
- (ii) the uni-directional function, $G(x)$ [Eq.(12)] for dendrite processing.

We have employed the assumption (i) to enhance the storage capacity. In order to show this explicitly, we calculate the f dependence of the storage capacity α_c when the Willshaw-type learning rule given by Eq.(11) in our HH neuron network is replaced by the conventional Hebb-type one:

$$g_{jk} = g_{exc} \sum_{\mu=1}^P \xi_j^{(\mu)} \xi_k^{(\mu)}. \quad (21)$$

The calculated storage capacity α_c is plotted by the solid curve in Fig. 13 as a function of the average activity f . The memory capacity is $\alpha_c \sim 0.03 - 0.14$ for $f \sim 0.04 - 0.10$, which is much smaller than the corresponding value of $\alpha_c \sim 0.4 - 2.4$ obtained with Willshaw-type rule [Fig. 5]. This clearly shows that the storage capacity with the Willshaw-type rule [Eq.(11)] is enhanced by a factor of ten. The reason why the solid curve in Fig. 13 has a discontinuous change at $f \sim 10$, is not clear at the moment. The solid curve loosely follows the dotted curve expressing $1/(M \log M)$, which is proportional to $(-1/f \log f)$ at $f \rightarrow 0$.

The assumption (ii) on $G(x)$ has been introduced to prevent firings for inhibitory (negative) inputs. This function $G(x)$ may be regarded to mimic the *inward rectification* of dendrites [44], which make the response of a neuron to hyperpolarizing outward currents much worse than that to depolarizing inward currents. If the uni-directional function: $G(x) = x \Theta(x)$ given by Eq.(12) is replaced by the linear one: $G(x) = x$, HH neurons fire for both excitatory and inhibitory inputs, and then the neural networks cannot retrieve the stored patterns. In this case, the weight of inhibitory synapses, g_{jk}^{inh} , in Eq.(10) is properly determined by a learning rule depending on the stored patterns, as Lytton [12] has proposed for the feedforward HH network. Such a procedure, however, yields a poor performance as an associative memory working only in a narrow parameter range [12]. It would be necessary that the assumptions (i) and (ii) adopted in our HH neuron network are examined and sought physiologically.

It has been reported that a large variability ($c_v = 0.5 \sim 1.0$) is observed in spike trains of non-bursting cortical neurons in visual V1 and MT of monkey [45], which is in strong contrast with a small c_v ($= 0.05 \sim 0.1$) in motor neurons [46]. There have been much discussions how to understand the observed large variability [47]- [52]: a balance between excitatory and inhibitory inputs [47], the high physiological gain in the plot of input current vs. output frequency [48], correlation fluctuations in recurrent networks [49], the active dendrite conductance [50], input ISIs with the distribution of a slow-decreasing tail [51], and input ISIs with large c_v [25] [52]. Based on our simulations, we discuss the behavior of the interspike interval (ISI) of output spike trains which is defined by

$$T_{ojm} = t_{ojm+1} - t_{ojm}, \quad (22)$$

where t_{ojm} ($m = 1, 2, \dots$) is the firing time of the neuron j [Eq.(9)]. Histograms shown in Figs. 14(a)-14(c) express the distribution of ISIs of *all* HH neurons for $0 \leq t \leq 500$ msec. Figure 14(a) denotes the distribution of output ISIs of a successful retrieval with the initial overlap of $m_i = 0.84$, which have been discussed in Sec. 3.2: the time course of its firings of neurons is plotted in Fig. 6(a) with parameters of $f = 0.20$, $\alpha = 0.10$ and $\tau_d = 10$ msec. The mean and root-mean-square (RMS) values of the output ISI are $\mu_o = 11.98$ and $\sigma_o = 1.42$ msec, which yield the dimensionless *variability* of $c_v \equiv \sigma_o/\mu_o = 0.12$. The histogram of Fig. 14(b), on the other hand, shows the distribution of ISI for a failed retrieval case with a smaller initial overlap of $m_i = 0.68$: the time course of neuron firings are plotted in Fig. 6(b). We note that ISIs distribute up to 30 msec, obtaining $\mu_o = 13.98$, $\sigma_o = 5.69$ msec, and $c_v = 0.41$. The histogram of Fig. 14(c) expresses also a failed case with more smaller $m_i = 0.56$, which leads to $\mu_o = 16.17$, $\sigma_o = 17.76$ msec and $c_v = 1.10$. Note that there is a small distribution of ISI even at $30 < T_o < 60$ msec, where plotted result is magnified by a factor of ten. Repeating these calculations, we obtain, in Fig. 15, the m_i dependence of μ_o , σ_o and c_v (for $f = 0.20$, $\alpha = 0.10$ and $\tau_d = 10$ msec). For $m_i > 0.9$, we get $\mu_o = 11.76$ and $\sigma_o \sim 0$ msec, then $c_v \sim 0$. When m_i is more reduced, μ_o is increased because ISIs with $T_o > 20$ msec appear, which make σ_o and c_v increase. Figure 15 shows that c_v is larger for smaller m_i , and that the variability becomes considerable ($c_v \sim 0.5$) even for successful retrievals with $m_i > 0.7$ [Fig. 6]. The situation is similar when a retrieval is worsen because of spread distributions of time delays in couplings. For example, in the case having been shown in Fig. 10, where we plot the time course of firings for $\Delta\tau = 10$ msec with the parameters of $f = 0.10$, $\alpha = 0.10$, $\tau_d = 10$ msec and $m_i = 1.0$, a considerable value of

$c_v = 0.45$ is obtained which arises from $\mu_o = 18.61$ and $\sigma_o = 8.31$ msec. Our simulations show that the variability of ISIs may be considerable while neurons are trying to retrieve the stored memory. We hope that results of our simulations might have some relevance to the observed large variability.

To summarized, taking account of the two issues on the Hopfield-type neural networks raised in the Introduction, we have proposed the biologically plausible network consisting of spiking HH neurons with the Willshaw-type synapses, whose simulations demonstrate its storage capacity to be comparable to that of the rate-code network. We may extend and modify our model into various directions. For example, it is straightforward to apply our method to the feedforward hetero-associative memory of temporal-code Anderson-Kohonen-type networks. When the excitatory synapse given by Eq.(11) is changed as

$$g_{jk}^{exc} = g_{exc} \Theta \left(\sum_{\mu=1}^{P-1} \xi_j^{(\mu+1)} \xi_k^{(\mu)} \right), \quad (23)$$

the patterns of $\mu = 1 - P$ can be retrieved in a temporal sequence. This shows a possibility of the storing and retrieval of temporal patterns. The synapse given by Eq.(23) corresponds to the asymmetric coupling in the Hopfield model [53]. It has been shown that the Hopfield model with asymmetric couplings shows intrigue dynamics like chaos. In the present paper, we have taken no account of noises. Quite recently, Kanamaru and Okabe [16] have investigated the effect of noises on an associative memory of the FN neuron network, showing that a retrieval of the stored patterns may be improved by noises, just like the stochastic resonance. It would be the case also in our HH neuron network. We cannot, however, draw any definite conclusion until performing simulations because their leaning rule given by Eq.(1) with $a = 0$ and $b = f$ is different from ours given by Eq.(11). It is well known that temporal-code neurons are more efficient in data processing than the rate-code neurons because the former can carry much information than the latter [54]. It is expected to be true also in the memory function. We suppose that there could be alternative, more efficient mechanisms, by which real temporal-code networks might be operating for learning and memory.

ACKNOWLEDGEMENTS

This work is partly supported by a Grant-in-Aid for Scientific Research from the Japanese Ministry of Education, Science and Culture.

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FIGURES

FIG. 1. Responses of the membrane potentials, V (solid curve), of a HH neuron to (a) excitatory and (b) inhibitory external currents, I^{ext} (dashed curve): a HH neuron fires not only by excitatory input but also by inhibitory inputs.

FIG. 2. The time course of (a) input U_{i1} , (b) output U_{o1} , (c) the post-synaptic current $I_1 (= I_1^{ext} + I_1^{int})$ and (d) the membrane potential V_1 of the neuron $j = 1$ when an input pattern is injected at $t = 0$ with $\alpha = 0.3$, $f = 0.10$, $g_{exc} = 0.30 \text{ mS/cm}^2$ and $\lambda = 0.8$; the vertical scale is for V_1 only, and I_1^{int} , U_{o1} and U_{i1} are shown in arbitrary units.

FIG. 3. The time course of firings of neurons for (a) $\alpha = 0.30$ and (b) $\alpha = 0.50$ with $f = 0.10$, $g_{exc} = 0.30 \text{ mS/cm}^2$ and $\lambda = 0.8$; dots express firings of neurons numbered by index shown in the vertical scale: the upper part shows the relevant overlap of $m(t)$.

FIG. 4. The storage capacity α_c as a function of $\lambda (= g_{inh}/g_{exc})$ for $f = 0.06$ and 0.10 with $g_{exc} = 0.3 \text{ mS/cm}^2$ (solid curve) and $g_{exc} = 0.5 \text{ mS/cm}^2$ (dashed curve).

FIG. 5. The storage capacity α_c as a function of the average activity f . The solid curve denotes the calculated results and the dotted curve expresses $10/(M \log M)$, error bars denoting the standard deviations for ten samples.

FIG. 6. The time course of neuron firings for an injection of imperfect input patterns with initial overlaps of (a) $m_i = 0.84$ and (b) $m_i = 0.68$ for $f = 0.20$ and $\alpha = 0.10$.

FIG. 7. The time dependence of the overlap $m(t)$ for various m_i with $f = 0.20$ and $\alpha = 0.1$.

FIG. 8. The storage capacity α_c as a function of the initial overlap m_i for $f = 0.10$ (solid curve) and $f = 0.20$ (dashed curve).

FIG. 9. The storage capacity α_c as a function of a width of the time-delay distribution, $\Delta\tau$, for $\tau_d = 10 \text{ msec}$. The solid and dashed denotes the calculated results for $f = 0.06$ (solid curve) and $f = 0.10$ (dashed curve), respectively.

FIG. 10. The time course of firings of neurons for $f = 0.10$, $\alpha = 0.10$, $\Delta\tau = 10$ and $\tau_d = 10 \text{ msec}$: the upper part shows the relevant overlap of $m(t)$ (see text).

FIG. 11. The critical width, $\Delta\tau_c$, of the time-delay distribution as a function of τ_d for $(f, \alpha) = (0.06, 0.30)$ (solid curve), $(0.060, 0.10)$ (dotted curve) and $(0.10, 0.10)$ (dashed curve). Calculations are made with a step of $\Delta\tau = 1.0 \text{ msec}$ for a given τ_d .

FIG. 12. The storage capacity α_c as a function of the average activity f of the *rate-code* neuron network with the Willshaw-type synapses (solid curve) and the Hebb-type synapses (dashed curve), the dotted curve denoting $10/(M \log M)$ (see text).

FIG. 13. The storage capacity α_c as a function of the average activity f of the HH neuron network with the Hebb-type synapses [Eq.(21)]. The solid curve denotes the calculated result and the dotted curve expresses $1/(M \log M)$.

FIG. 14. Histograms of ISIs of spike-train outputs in a retrieval process with the initial overlap of (a) $m_i = 0.84$, (b) 0.68 and (c) 0.56 for $f = 0.20$, $\alpha = 0.10$ and $\tau_d = 10$ msec, the histogram at $T_o > 30$ msec of (c) being enlarged by a factor of ten. The time course of neurons firings for (a) and (b) are plotted in Fig. 6(a) and 6(b), respectively.

FIG. 15. The average (μ_o , thin solid curve) and RMS values of ISIs (σ_o , dashed curve), and the variability (c_v , bold solid curve) as a function of the initial overlap (m_i) for $f = 0.20$, $\alpha = 0.10$ and $\tau_d = 10$ msec, the left (right) vertical scale being for μ_o and σ_o (c_v). Error bars denote the standard deviation of c_v , and those for μ_o and σ_o are not shown for illegibility of the figure.

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