Spike-train responses of a pair of Hodgkin-Huxley neurons coupled by excitatory and inhibitory synapses and axons with time delay

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Abstract

Numerical calculations have been made on the spike-train response of a pair of Hodgkin-Huxley (HH) neurons coupled by synapses and axons with time delay. The recurrent excitatory-excitatory, inhibitory-inhibitory, excitatory-inhibitory, and inhibitory-excitatory couplings are adopted. The coupled, excitable HH neurons are assumed to receive the two kinds of spike-train inputs: the transient input consisting of $M$ impulses for the finite duration ($M$: integer) and the sequential input with the constant interspike interval (ISI). The HH neurons in all the kinds of couplings are found to play a role of memory storage with on-off switching. When the coupling strength and the time delay are changed, the distribution of the output ISI $T_o$ shows bifurcation (multifurcation), metastability and chaotic behavior. The calculation of the time correlation shows that the synchronization between the two HH neurons is well preserved even when the distribution of their $T_o$ is chaotic. The correlation dimension of the cycles of $T_o$ is shown to depend not only on the model parameters but also on the type of input ISIs.

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I. INTRODUCTION

Neurons communicate by producing sequence of action potentials or spikes. It has been widely believed that information is encoded in the average rate of firings, the number of action potentials over some suitable intervals. This firing rate hypothesis was first proposed by Andrian [1] from a study of frog, in which the firing rate monotonically increases with an increase of the stimulus strength. By applying the firing rate hypothesis, the properties of many types of neurons in brain have been investigated and the theoretical models have been developed [2].

When all action potentials are taken to be identical and only the times of firing of a given neuron are considered, we obtain a discrete series of times, \( \{ t_n \} \), which is expected to contain the information. In the rate coding, only the average of the rate of the interspike interval (ISI) is taken into account, and then some or most of this information is neglected.

In recent years, the alternative temporal coding, in which detailed spike timing is taken to play an important role, is supported by experiments in a variety of biological systems: 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]. It is now primarily important to understand what kind of code is employed in biological systems: rate code, temporal code or others [10] [11].

Neural functions are performed in the activity of neurons. Since the Hodgkin-Huxley (HH) model was proposed to account for the squid giant axon [12], its property has been intensively investigated. Its responses to an applied dc [13] [17] and sinusoidal currents [18] [19] have been studied. The HH-type models have been widely employed for a study on activities of transducer neurons such as motor and relay neurons, which transform amplitude-modulated inputs to spike-train outputs. Regarding the single HH neuron as a data-processing neuron, the present author [20] (referred to as I hereafter) recently investigates its response to the spike-train inputs whose ISIs are modulated by deterministic, semi-deterministic (chaotic) and stochastic signals.

Several investigations have been reported on the property of a pair of the HH neurons [21]- [27]. In the network of two HH oscillators coupled by excitatory couplings without time delay, the unit fires periodically in the synchronized state. It is, however, not the case when the excitatory couplings have some time delay, for which the antiphase state becomes more stable than the synchronized state [21]. Rather, inhibitory couplings with substantial time delay lead to the in-phase synchronized states in the coupled HH oscillators [21]. The similar conclusion is obtained also in the coupled integrate-and-fire (IF) oscillators [21] [26] [28]- [31]. The phase diagrams for the synchronized state and various cluster states in the coupled HH oscillators are obtained as functions of the synapse strength and the time delay [22]- [24].

In recent years, much attention has been paid to the delayed-feedback systems described by the delay-differential equation (DDE) [32]- [37]. Their property has been investigated with the use of various functional forms for the delay-feedback term in DDE. The exposed properties include the odd-harmonic solutions [32] [33], the bifurcation (multifurcation) leading to chaos [33]- [35], the multistability [33], and the chaotic itinerancy [36]- [37]. Among them the multistability is intrigue because it may be one of conceivable mechanisms for memory storage in biological neural networks. It has been shown by Ikeda and Matsumoto [33] that when the delay time is larger than the response time in the delayed feedback system,
information may be stored in temporal patterns. Actually, Foss, Longtin, Mensour and Milton [25] demonstrate this ability in the coupled HH (and IF) neurons with the time-delayed feedback.

Recurrent loops involving two or more neurons with excitatory and/or inhibitory synapses are found in biological systems such as hippocampus [38], neo-cortex [39] and thalamus [40]. It is important to make a detailed study on the coupled HH neurons, which is the simplest but meaningful network unit. The purpose of the present paper is to investigate the spike-train responses of the coupled, excitable HH neurons, which is treated as data-processing neurons as in our previous study [20]. We consider the four kinds of recurrent couplings between a pair of HH neurons: the excitatory-excitatory (E-E), inhibitory-inhibitory (I-I), excitatory-inhibitory (E-I), and inhibitory-excitatory (I-E) couplings. We apply, to the coupled HH neurons, the two kinds of spike-train inputs: one is the transient inputs consisting of clustered impulses for the finite duration ($M$: integer) and the other is the sequential spike train with the constant ISI. The transient and asymptotic property of their response will be investigated.

Our paper is organized as follows: In the next Sec. II, we describe a simple neural system consisting of neurons, axons, synapses and dendrites, which are adopted for our numerical calculation. We present the calculated results in Sec. III: the response of the coupled HH neurons to the transient, clustered impulses is discussed in Sec. IIIA and that to the sequential spike-train input in Sec. IIIB. The dependences of the distribution of the output ISIs on the coupling strength and the time delay are studied. The final Sec. IV is devoted to conclusion and discussion.

II. ADOPTED MODEL

We adopt a simple neural system consisting of a pair of neurons which is numbered 1 and 2. The neurons which are described by the HH model with identical parameters, are coupled with the time delay of $\tau_{jk}$ ($j, k = 1, 2$) for an impulse propagating from the neuron $k$ to the neuron $j$. This delay time is the sum of conduction times through the axon and dendrite. It has been reported that real biological synapses exhibit temporal dynamics of depression or potentiation during neuronal computation [41][42]. We, however, treat the synapse as a static unit for a simplification of our calculation. The synapse with the coupling strength $C_{jk}$ is excitatory or inhibitory, and it is assumed to be described by the alpha function [Eq.(7)].

Dynamics of the membrane potential $V_j$ of the coupled HH neuron $j (=1, 2)$ is described by the non-linear DDEs given by

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

(1)

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

$$I_j^{\text{ion}}(V_j, m_j, h_j, n_j) = g_{Na}m_j^3h_j(V_j - V_{Na}) + g_Kn_j^4(V_j - V_K) + g_L(V_j - V_L).$$  

(2)

Here the maximum values of conductivities of Na and K channels and leakage are $g_{Na} = 120 \text{ mS/cm}^2$, $g_K = 36 \text{ mS/cm}^2$ and $g_L = 0.3 \text{ mS/cm}^2$, respectively; the respective reversal
potentials are $V_{Na} = 50 \text{ mV}$, $V_K = -77 \text{ mV}$ and $V_L = -54.5 \text{ mV}$. The gating variables of Na and K channels, $m_j, h_j$ and $n_j$, are described by

$$dm_j/dt = -(a_{m_j} + b_{m_j}) m_j + a_{m_j},$$  \hspace{1cm} (3)$$

$$dh_j/dt = -(a_{h_j} + b_{h_j}) h_j + a_{h_j},$$  \hspace{1cm} (4)$$

$$dn_j/dt = -(a_{n_j} + b_{n_j}) n_j + a_{n_j}. \hspace{1cm} (5)$$

The coefficients of $a_{m_j}$ and $b_{m_j}$ etc. are expressed in terms of $V_j$ (their explicit expressions having been given in Refs. [20] [22]) and then the variables $V_j, m_j, h_j$ and $n_j$ are coupled.

The second term in Eq.(1) denotes the external input currents given by

$$I_j^{\text{ext}} = I_{sj} + A_s \delta_j \sum_n \alpha(t - t_{in}), \hspace{1cm} (6)$$

with the alpha function $\alpha(t)$ given by

$$\alpha(t) = (t/\tau_s) e^{-t/\tau_s} \Theta(t), \hspace{1cm} (7)$$

The first term ($I_{sj}$) in Eq.(6) is the dc current which determines whether the neuron is excitable or periodically oscillating. Its second term expresses the postsynaptic current which is induced by the presynaptic spike-train input applied to the neuron 1, given by

$$U_i(t) = V_a \sum_n \delta(t - t_{in}). \hspace{1cm} (8)$$

In Eqs.(6)-(8), $\Theta(t) = 1$ for $x \geq 0$ and 0 for $x < 0$; $A_s = g_s(V_a - V_s)$, $g_s$ and $V_s$ stand for the conductance and reversal potential, respectively, of the synapse; $\tau_s$ is the time constant relevant to the synapse conduction, which is assumed to be $\tau_s = 2 \text{ msec}$; $t_{in}$ is the $n$-th firing time of the spike-train inputs defined recurrently by

$$t_{in+1} = t_{in} + T_{in}(t_{in}), \hspace{1cm} (9)$$

where the input ISI $T_{in}$ is generally a function of $t_{in}$. For the constant input ISI of $T_{in} = T_i$, $t_{in}$ is given by $t_{in} = nT_i$ for an arbitrary integer $n$.

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

$$U_{oj}(t) = V_a \sum_m \delta(t - t_{ojm}), \hspace{1cm} (10)$$

in a similar form to Eq.(8), $t_{ojm}$ being the $m$-th firing time when $V_j(t)$ crosses $V_s = 0.0 \text{ mV}$ from below. The output ISI is given by

$$T_{ojm} = t_{ojm+1} - t_{ojm}. \hspace{1cm} (11)$$

The third term in Eq.(1) which expresses the interaction between the two neurons, is assumed to be given by
\[ I_j^{\text{int}}(\{V_k(t-\tau_{jk})\}) = \sum_{k \neq j} \sum_m C_{jk} \alpha(t-\tau_{jk} - t_{okm}). \] (12)

The positive and negative \( C_{jk} \) denote the excitatory and inhibitory couplings, respectively. Depending on the signs of \( C_{jk} \), we consider the following four types of couplings (Fig.1):

(a) \( C_{21} > 0 \) and \( C_{12} > 0 \) (E-E coupling),
(b) \( C_{21} < 0 \) and \( C_{12} < 0 \) (I-I coupling),
(c) \( C_{21} > 0 \) and \( C_{12} < 0 \) (E-I coupling),
(d) \( C_{21} < 0 \) and \( C_{12} > 0 \) (I-E coupling).

In order to reduce the number of parameters, we assume that \( |C_{21}| = |C_{12}| = c A_s \) and \( \tau_{21} = \tau_{12} = \tau_d \).

As for the functional form of the coupling term of \( I_j^{\text{int}}(\{V_k(t-\tau_{jk})\}) \), Foss, Longtin, Mensour and Milton [25] adopt a simpler form given by

\[ I_j^{\text{int}}(\{V_k(t-\tau_{jk})\}) = \sum_{k \neq j} \mu_{jk} V_k(t-\tau_{jk}). \] (13)

taking no account of the synapse, where \( \mu_{jk} \) is the coefficient of the synaptic coupling. They discuss the memory storage of the pattern in output spike trains, injecting the input information by the initial function, \( V(t) \) for \( t \in [-\tau_d, 0) \), whereas in our calculation input information is given by \( I_{\text{ext}}(t) \) [Eq.(6)].

Differential equations given by Eqs.(1)-(5) including the external current and the coupling given by Eqs.(6)-(12) are solved by the fourth-order Runge-Kutta method. The calculation for each set of parameters is performed for 2 sec (200,000 steps) otherwise noticed by the integration time step of 0.01 msec with double precision. The initial conditions for the variables are given by

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

which are the rest-state solution of a single HH neuron (\( c_{jk} = 0 \)). The initial function for \( V_j(t) \), whose setting is indispensable for the delay-differential equation, is given by

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

For an analysis of asymptotic solutions, we discard results of initial 200 msec (20,000 steps).

### III. Calculated Results

In the present study, we consider only the excitable HH neurons by setting \( I_{ej} = 0 \) and \( A_s = 40 \mu A/cm^2 \). Our model has additional three parameters, \( T_i, \tau_d \) and \( c \). We treat them as free parameters to be changed for the four kinds of E-E, I-I, E-I, and I-E couplings because the values of ISI and the time delay observed in biological systems distribute in a fairly wide range [43].

#### A Transient Spike-Train Inputs
Let us first investigate the response to the transient, clustered spike-train inputs consisting of $M$ impulses. Figure 2(a) shows the example of the time courses of input ($U_i$), output pulses ($U_{oj}$), the total postsynaptic current ($I_j = I_j^{ext} + I_j^{int}$) and the membrane potential ($V_j$) with $M = 3$, $T_i = 20$, $\tau_d = 10$ msec and $c = 1.0$ for the E-E coupling ($c > 0$). The first external pulse applied at $t = 0$ yields the firing of the neuron 1 after the intrinsic delay of $\tau_{11} \sim 2$ msec. The emitted impulse propagates the axon and reaches the synapse of the neuron 2 after $\tau_{21} = 10$ msec. After a more delay of an intrinsic $\tau_{12} \sim 2$ msec, the neuron 2 makes the firing which yields the input current to the neuron 1 after a delay of $\tau_{12} = 10$ msec. The input pulses trigger the continuous oscillation in the coupled HH neurons with the output ISI of $T_o = 24.1$ msec.

Figure 2(b) shows the time dependence of the output ISI of the neuron 1 and 2, respectively. We note that $T_{o1}$ and $T_{o2}$ start from the values of 20.00 and 19.96 msec, respectively, and soon become the fixed value of 24.10 msec.

Figure 3(a) shows the result for the I-I coupling with the parameters same as in Fig. 2(a). After $\tau_{21} = 10$ msec of the firing of the neuron 1, the inhibitory input arrives at the neuron 2, which fires by the inhibitory rebound process with an additional delay of $\tau_{11} \sim 15$ msec beside a delay of $\tau_{12} = 20$ msec of the axon. Subsequently the neuron 1 induced by the recurrent impulse coming from the neuron 2, fires after an total time delay of $\tau_{21} + \tau_{12} \sim 25$ msec due to delays of the axon and the inhibitory rebound. Figure 3(b) shows that the output ISIs of the neuron 1 and 2 start from the values of 20.00 and 21.04 msec, respectively, and asymptotically approach the oscillating two values of 24.33 and 24.45 msec.

In the cases shown in Figs. 2 and 3, the delay of $\tau_d = 10$ msec is shorter than the duration of input pulses (40 msec). On the contrary, when the delay time becomes larger than the duration time of clustered inputs, the situation is changed. Figures 4 shows the time courses of the membrane potentials of the neuron 1 with the four couplings for $M = 3$, $T_i = 20$, $\tau_d = 50$ msec and $c = 1.0$ (hereafter we consider only the output of the neuron 1). We note that the triggered oscillation continues, keeping the original three-impulse form in all the couplings. Then the coupled HH neurons play a role of memory storage [25] [33].

The period of the induced oscillation $T_p$ shown in Fig. 4 is essentially determined by the total delay time of the feedback loop $T_{fb}$ given by

$$T_p \sim T_{fb} = 2\tau_d + \tau_{11} + \tau_{12}$$

where $\tau_{ij}$ denotes the intrinsic time delay of the neuron $j$. It is noted that $\tau_{ij}$ depends on whether an input is excitatory or inhibitory: $\tau_{ij}$ is about 2-3 msec for the excitatory input while it is about 14-15 msec for the inhibitory input. Our simulation shown in Fig. 4 yields $T_p^{EE} = 105$, $T_p^{II} = 129$, $T_p^{EI} = T_p^{IE} = 117$ msec for the E-E, I-I, E-I and I-E couplings, respectively, which follows Eq.(16) with $\tau_1 = 2.5$ and 14.5 msec for the excitatory and inhibitory synapses, respectively ($\tau_d = 50$ msec).

1. The coupling-strength dependence

Figure 5 shows the coupling-strength dependence of the period and the output ISIs of the asymptotic solution in the cases of the four couplings for $M = 3$, $T_i = 20$ and $\tau_d = 50$ msec [44]. The period of the oscillation triggered by input pulses has little dependence on
c, as far as c is larger than the critical value, \(c_{cr}\), above which the oscillation continues. In the case of \(M = 3\), \(T_1 = 20\) and \(\tau_d = 50\) msec, for example, we get \(c_{cr} = 0.20\) for the E-E coupling and 0.42 for the I-I, E-I and I-E couplings: note that at \(0.44 \leq c \leq 0.76\) in the latter cases, we get the two-impulse output against the three-impulse input. This is because the firing by the inhibitory rebound requires a considerable synaptic magnitude [20].

2. The time-delay dependence

Next we study how the output ISIs are determined. When the feedback time \(T_{fb}\) is larger than the duration of clustered impulses \(i.e. T_{fb} = 2\tau_d + \tau_{i1} + \tau_{i2} > (M - 1) T_1\), we get two values of \(T_o\) given by

\[
T_o^{(1)} = T_1, \quad T_o^{(2)} = T_{fb} - (M - 1) T_1 = 2\tau_d + \tau_{i1} + \tau_{i2} - (M - 1) T_1.
\]  

(17)

On the other hand, when the feedback time is shorter than input-pulse duration \((2\tau_d + \tau_{i1} + \tau_{i2} < (M - 1) T_1)\), we get

\[
T_o^{(1)} = T_1 \Theta(M - 3), \quad T_o^{(2)} = \lfloor \ell T_{fb} - m T_1 \rfloor = \lfloor \ell (2\tau_d + \tau_{i1} + \tau_{i2}) - m T_1 \rfloor,
\]  

(18)

where integers \(\ell\) and \(m\) satisfy \(1 \leq \ell \leq [(M - 1) T_1/T_{fb}] + 1\) and \(0 \leq m \leq M - 1, \lfloor \cdot \rfloor\) is the Gauss sign and \(T_o^{(1)}\) is vanishing for \(M \leq 2\).

We have obtained the \(\tau_d\) dependence of the output ISI from the asymptotic solution in our simulations. Results for clustered inputs of \(M = 3\) are shown in Fig. 6(a)-6(d), where filled circles denote the values of \(T_o\) for a given \(\tau_d\) [14]. Figure 6(a) shows the result for inputs with \(T_1 = 20\) msec in the E-E couplings. We try to analyze the calculated \(T_o\) with the use of Eqs.(17) and (18). Three dashed lines in Fig. 6(a) are given by \(2\tau_d + 5, 2\tau_d - 15\) and \(2\tau_d - 35\), which are obtained by Eqs.(17) and (18) with \(\tau_{i1} = \tau_{i2} = 2.5\) and \(T_1 = 20\) msec. Dashed lines in Fig. 6(b) are given by \(2\tau_d + 29, 2\tau_d + 9\) and \(2\tau_d - 11\), which are obtained by Eqs.(17) and (18) with \(\tau_{i1} = \tau_{i2} = 14.5\) and \(T_1 = 20\) msec. Similar analysis is made for the E-I and I-E couplings, whose results are expressed by dashed lines in Figs. 6(c) and 6(d). Agreement of the dashed lines with filled circles in Fig. 6(a) and 6(b) are fairly good. On the contrary, the agreement between them is not satisfactory in Fig. 6(c) and 6(d) for \(T_1 = 50\) msec. The deviation of filled circles from the dashed lines is due to the effects of non-linearity of the HH neurons.

The time courses of the membrane potentials for \(M = 1 - 5\) are plotted in Fig. 7 for \(T_1 = 20, \tau_d = 50\) msec and \(c = 1.0\). In all the couplings, the form of input pulse is preserved and the coupled neurons play a role of memory storage.

It is possible to control the switching of the oscillations by input pulses. Figure 8 demonstrates such a switching in the E-I coupled HH neurons. The oscillation is triggered by the external input \(U_1\) at \(t = 0\). When we apply the external excitatory input at \(t = 543\) msec, it cancels out the recurrent inhibitory input to the neuron 1 and suppress the firing of the neuron 1. Then the oscillation is switched off by the control input pulse at \(t = 543\) msec. At \(t = 700\) mec, the oscillation is again triggered by input pulse. In this example, the control pulse is applied to the neuron 1. We can alternatively switch off the oscillation by applying the inhibitory (excitatory) input to the neuron 2 in the E-I (I-E or I-I) coupling. These show the feasibility of the on-off switching of the oscillation in the simplest neuronal unit.
B. Sequential Spike-Train Inputs

Next we discuss the response to the sequential spike-train. Our calculations in I show that when an isolated HH neuron \((c = 0)\) receives the sequential inputs with the constant ISI of \(T_i\), it behaves as a low-pass filter: it emits the spike train with \(T_o > 10\) msec for \(T_i < 12\) msec while for \(T_i > 12\) msec its output ISI is given by \(T_o = T_i\) (see Fig. 7 of Ref. [20]). This response may be modified when the coupling is introduced to a pair of HH neurons. Figures 9(a) and 9(b) show the time courses of input \((U_i)\), output \((U_o)\), the total postsynaptic current \((I_j = I_{j}^{\text{ext}} + I_{j}^{\text{int}})\) and the membrane potential \((V_j)\) for \(T_i = 20\) msec, \(\tau_d = 10\) msec and \(c = 1.0\) for the E-E and I-I couplings, respectively. They should be compared with Figs. 2(a) and 3(a) for the transient spike-train inputs with the same values of \(T_i\) and \(\tau_d\). The output ISI in Fig. 2 is 24.1 msec while that in Fig. 9(b) is 20 msec which is the entrained value with input ISI. Although \(T_o\) in Fig. 3 are two values of 24.3 and 24.5 msec, we get, in Fig. 9(b), ten values of 20.6, 21.2, 37.3, 19.2, 22.1, 20.6, 21.7, 35.7, 19.9 and 21.8 msec.

1. The coupling-strength dependence

The response behavior of the coupled neurons strongly depends on the parameters of \(c\), \(\tau_d\) and \(T_i\). Figure 10(a)-10(d) show the examples of the \(c\) dependence of the distribution of \(T_o\) of the E-E, I-I, E-I and I-E couplings for various parameters [44]. We note that, as increasing the \(c\) value, the distribution of the output ISIs show the bi(multi)furcation, as commonly observed in systems with the delayed feedback [33]. In order to investigate the phenomenon in more detail, we show, in Fig. 11(a), the enlarged plot for the range of \(0.6 \leq c \leq 1.2\) sandwiched by the dotted, vertical lines in Fig. 10(a). Figure 11(b) is the enlarged plot of Fig. 10(d) for the narrow range of \(0.3 \leq c \leq 1.0\). These figures clearly show the bi(multi)furcation with many windows.

A cycle whose output ISIs almost continuously distribute, is expected to be chaotic although in the strict sense, the distribution of \(T_o\)s never becomes continuous because they are quantized by the integration time step of 0.01 msec. Among many candidates of chaos-like behavior in Figs. 10 and 11, we pay our attention to the result of \(c = 0.95\) in Fig. 11(a), for which the Lorentz plot (return map) of its \(T_o\) is shown in Fig. 12(a) (calculations are performed for 20 sec of two million steps). The output ISIs seem to distribute on the folded ring. When these points are connected by lines in the chronological order, the inside of the ring is nearly filled by them. In order to examine the property of this cycle, we calculate the correlation dimension \(\nu\) given by [45]

\[
\nu = \lim_{\epsilon \to 0} \frac{\log C(\epsilon)}{\log \epsilon},
\]

with

\[
C(\epsilon) = N^{-2} \sum_{m,n=1}^{N} \Theta(\epsilon - |X_m - X_n|),
\]

\[
X_m = (T_{om}, T_{om+1}, ...., T_{om+k-1}).
\]
where \( C(\epsilon) \) is the correlation integral, \( X_m \) is the \( k \)-dimensional vector generated by \( T_{om} \), \( N \) the size of data, and \( \Theta(\cdot) \) the Heaviside function. Figure 12(b) shows the log \( C(\epsilon) \)-log \( \epsilon \) plot for various \( k \) calculated for the cycle shown in Fig. 12(a) with \( N \sim 1200 \). We note that \( C(\epsilon) \) behaves as \( C(\epsilon) \propto \epsilon^\nu \) with the correlation dimension of \( \nu = 0.94 \pm 0.02 \) for small \( \epsilon \) (\( 0.01 = e^{-4.6} < \epsilon < e^0 \)). The non-integral \( \nu \) implies that this cycle may be chaos, the related discussion being given in Sec. IV.

2. The time-delay dependence

A simple generalization of the discussion given in the previous Sec. IIIA2 yields that the output ISIs for the sequential spike-train input with the constant \( T_i \) are given by

\[
T_o = |\ell T_{fb} - m T_i| - |\ell (2\tau_d + \tau_{i1} + \tau_{i2}) - m T_i|,
\]

(22)

where \( \ell, m \) are integers. In the above analysis, we do not take into account the absolute refractory period and the merging of recurrent inputs with external inputs at synapse, which eliminate some of the candidates of \( T_o \) obtained from Eq.(22) for many choices of a pair of \( \ell \) and \( m \), as will seen shortly.

Figure 13(a)-13(d) show the \( \tau_d \) dependence of the distribution of \( T_o \) in the asymptotic solution for the sequential inputs [44]. We try to analyze the obtained distribution of \( T_o \) with the use of Eq.(22) by adopting \( \tau_{ij} = 2.5 \) and 14.5 msec for the excitatory and inhibitory couplings, respectively, as was made in Sec. IIIA2. Dashed curves in Fig. 13(c)-13(d) denote the lines generated by Eq.(22) for these values of \( \tau_{ij} \) and \( T_i = 50 \) msec with a choice of a pair of integers \((\ell, m)\) shown beside the lines. Although many lines can be drawn for various choices of the integers, we plot only results with \( \ell = 1 \) in order to avoid a disfigurement by them. Some of filled circles representing the distribution of \( T_o \) in Figs. 13(c)-13(d) may be explained by dashed lines. Most of filled circles, however, cannot be well understood by this analysis due to the effects not included in our simple analysis. Furthermore our analysis with the use of Eq.(22) does not work at all for the results shown in Fig. 13(a) and 13(b), which plot the distribution of \( T_o \) in the E-E and I-I couplings for inputs with \( T_i = 20 \) msec. We note that the result shown in Fig. 13(a) (13(b)) for the sequential inputs is quite different from that shown in Fig. 6(a) (6(b)) for the transient inputs although both the calculations adopt the same parameters of \( T_i \) and \( c \).

In order to see more the detailed structure of the bi(multi)furcation, we show, in Fig. 14(a), the enlarged plot for the range of \( 21 < \tau_d < 26 \) msec between the dotted, vertical lines in Fig. 13(a). Figure 14(b) is the enlarged plot of Fig. 13(c) for the narrow range of \( 33 < \tau_d < 38 \) msec. They clearly show the bi(multi)furation as changing \( \tau_d \).

VI. CONCLUSION AND DISCUSSION

We have performed numerical investigation on the spike-train responses of a pair of HH neurons with four kinds of the recurrent E-E, I-I, E-I and I-E couplings. The response of the coupled, excitable HH neurons to the transient, clustered impulses and to the sequential inputs shows a rich of variety. The former input triggers the synchronous oscillation in the coupled HH neurons, which may play a role of memory storage. The response to the latter
sequential input strongly depends on the coupling strength and the time delay, yielding bi(multi)furcation, multistability and chaotic behavior.

We have applied the two types of inputs of the transient and sequential spike-train impulses. On the theoretical point of view, the latter is taken as the limit of $M \rightarrow \infty$ of the former. Figure 15(a) and 15(b) show the $T_i$ dependence of the distribution of $T_0$ for the transient and sequential inputs, respectively, with $\tau_d = 50$ msec and $c = 1.0$ in the E-E coupling. Dashed curves in Fig. 15(a) are given by the equations shown beside the lines which are obtained from Eqs.(17) and (18), as mentioned in Sec. IIIA2. On the other hand, dashed lines in Fig. 15(b) are obtained with the use of Eq.(22) for a pair of integers $(\ell, m)$ shown in the brackets. It is apparent that the distribution of $T_0$ in Fig. 15(a) is not the same as that in Fig. 15(b), but they are partly similar. For example, we obtain for $T_i = 20$ msec, $T_0 = 19.6, 20.0$ and $64.54$ msec in Fig. 15(a) whereas only $20.0$ msec in Fig. 15(b). In order to understand this difference, we plot, in Fig. 16, the time dependence of $T_0$ for this set of parameters by changing the $M$ value. For $M = 3$, $T_0$ oscillates with the values of $19.6, 20.0$ and $64.54$ msec, which is mentioned above. The calculated $T_0$ for $M=4$ are $18.7, 19.8, 20.0$, and $45.6$ msec, and those for $M = 5$ are $19.9, 20.0$ and $24.2$ msec. For $M = 10$, $T_0$ remains $20$ msec until $t \sim 200$ msec, after which $T_0$ oscillates with the values of $19.9, 20.0$ and $24.2$ msec. In the limit of $M \rightarrow \infty$ corresponding to the sequential inputs, the state with $T_0 = 20$ msec continues from $t = 0$ to $\infty$. Thus as increasing $M$, the time region of $T_0 = 20$ msec is increased.

Figure 17 shows the similar plot of the time dependence of the distribution of $T_0$ for various $M$ with $T_i = 20$, $\tau_d = 13.75$ and $c = 0.95$, for which the sequential input leads to the chaotic behavior, as was discussed in Sec. IIIB1 (see Fig.12(a)). In the case of $M = 3$, we get the oscillation in $T_0$ which asymptotically approaches the value of $15.97$ msec. In the case of $M = 10$ (50), the chaotic behavior is realized at $0 \leq t < 180$ (0 $\leq t < 980$) msec during the application of inputs. After inputs are switched off, the output ISI gradually approach the fixed value of $15.97$ msec. In the limit of $M \rightarrow \infty$, the chaotic oscillation eternally continues.

We have shown in Sec. IIIB1 that the cycle of the output ISIs shown in Fig. 12(a) may be chaos because its correlation dimension of $\nu \sim 0.94$ is derived from the log $C(\epsilon)$-log $\epsilon$ plot in Fig. 12(b). This is not surprising because the response of single HH neurons to some kinds of external inputs may be chaotic [18] [19] [20]. In particular, it has been shown in I that the response of a single HH neuron may be chaos when the ISI of the spike-train input is modulated by the sinusoidal signal [20]:

$$T_i(t) = d_0 + d_1 \sin(2\pi t/T_p).$$

(23)

Figure 18(a) shows the Lorentz plot of the output ISIs of the single HH neuron receiving sequential inputs with ISIs sinusoidally modulated by Eq.(23) with $d_0 = 2d_1 = 20$ and $T_p = 100$ msec (see Fig.7(d) of I). We note that $T_0$s distribute on the deformed ring. From the log $C(\epsilon)$-log $\epsilon$ plot (not shown) of this cycle, we get its correlation dimension of $\nu \sim 1.04$. We apply this spike-train input to the E-E coupled HH neurons with $\tau_d = 10$ msec and $c = 1.0$, whose Lorentz plot is shown in Fig. 18(b). Its structure is rather different from that shown in Fig. 18(a). Actually the correlation dimension of this cycle for the coupled HH neurons is $\nu \sim 1.83$, which is different from and larger than $\nu \sim 1.04$ of the cycle shown
in Fig. 18(a) for the single HH neuron. From similar calculations for the coupled HH neurons, we obtain the correlation dimensions of $\nu \sim 0.95$ for $\tau_d = 5$ msec and $c = 1.0$, and $\nu \sim 1.03$ for $\tau_d = 10$ msec and $c = 0.5$. These results clearly show that the correlation dimension of the output ISIs depend not only on the model parameters ($c$ and $\tau_d$) of the coupled HH neurons but also on the correlation dimension of input ISIs ($\nu_i = 0$ for the constant ISI and $\nu_i = 1$ for the sinusoidally modulated ISI). We expect that spike-train inputs with larger correlation dimension lead to spike-train outputs with larger $\nu$. One of the disadvantages of the present calculation of the correlation dimension is a lack of the data size of $N \sim 1200$ with million-step calculations. A more accurate analysis requires a larger size of data and then a computer with the larger memory storage.

Next we discuss the time correlation $\Gamma_{12}(\tau)$ between the membrane potentials, $V_1$ and $V_2$, of the neurons 1 an 2, defined by

$$\Gamma_{12}(\tau) = \int_{t_a}^{t_b} V_1(t) V_2(t + \tau) \, dt, \quad (24)$$

where $t_a = 1000$ and $t_b = 2000$ msec are adopted for our calculation. Figure 19(a) shows the result for the case of the sequential input to the E-E coupled HH neurons with $T_i = 20$, $\tau_d = 10$ msec and $c = 1.0$ (see Fig. 9(a) for the time courses of $V_1$ and $V_2$). In this case we obtain the constant $T_o = 20$ msec as was discussed in Sec. IIIIB, and then $\Gamma_{12}(\tau)$ shown in Fig. 19(a) has peaks at $\tau = 12.04 + 20n$ msec ($n$: integer) with the period of 20 msec, as expected. We are interested in the time correlation for the case when the distribution of $T_o$ is chaotic. Results for such cases are shown in Figs. 19(b) and 19(c). We have discussed in Sec. IIIIB1 that the cycle of $T_o$ depicted in Fig. 12 may be chaotic. Figure 19(b) shows the result of this case for the E-E coupling with $T_i = 20$, $\tau_d = 13.75$ msec and $c = 0.95$. We note that $\Gamma_{12}(\tau)$ has peaks at $\tau = 0.0, 16.07, \sim 3.2, 48.17, 62.71, \ldots$ msec with the period of about 16 msec, which is the sum of $\tau_d$ and $\tau_{11}^i$. More evident peaks are found in Fig. 19(c) showing also the chaotic case discussed in the preceding paragraph: the E-E coupled neurons receiving the sinusoidal inputs given by Eq.(23) with $d_0 = 2d_1 = 20$, $T_p = 100$, $T_i = 20$, $\tau_d = 10$ msec and $c = 1.0$ [see Fig. 18(b)]. We note peaks in $\Gamma_{12}(\tau)$ at $\tau = 0.0, 12.72, 25.30, 37.88, 50.43, \ldots$ msec with the period of about 12.6 msec. It is interesting that the synchronization is well preserved between the coupled HH neurons even when the distribution of their output ISIs shows the chaotic behavior.

A fairly large variability ($c_v = 0.5 \sim 1.0$) has been reported for spike trains of non-bursting cortical neurons in V1 and MT of monkey [14]. It is possible that when the appreciable variability in neuronal signals is taken into account in our calculations, much of the fine structures in the $c-$ and $\tau_d$-dependent distributions of $T_o$ will be washed out. In order to study this speculation, we apply the spike-train input with ISI whose distribution is given by the gamma distribution defined by [20]

$$P(T) = s^r \quad T^{r-1} \quad e^{-sT} / \Gamma(r), \quad (25)$$

where $\Gamma (r)$ is the gamma function. The average of input ISI is given by $\mu_i = r/s$, its root-mean-square (RMS) by $\sigma_i = \sqrt{r}/s$ and its variability by $c_{vi} = \sigma_i/\mu_i = 1/\sqrt{r}$. Figure 19 shows the $\tau_d$ dependence of the mean ($\mu_o$) and RMS values ($\sigma_o$) of the output ISIs for $c_{vi} = 0.0$ (dashed curves) and $c_{vi} = 0.43$ (solid curves) with $T_i = 20$ msec and $c = 1.0$. Note that $\sigma_o$ provides us with the measure of the width of the distribution of $T_o$. The distribution
for $c_{vi} = 0$ has a fine structure reflecting the strong $\tau_d$ dependence of $T_\alpha$ [see Fig. 13(a)]. This fine structure is, however, washed out for $c_{vi} = 0.43$, as expected. Detailed calculations of the response of the coupled HH neurons to stochastic spike-train inputs are now under way and will be published elsewhere.

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FIGURES

FIG. 1. Adopted pairs of HH neurons with (a) the E-E, (b) I-I, (c) E-I, and (d) I-E couplings, open and filled circles denoting excitatory and inhibitory synapses, respectively.

FIG. 2. The time dependence of (a) the transient input \( U_i \), output \( U_{oj} \), the total postsynaptic current \( I_j \) and the membrane potential \( V_j \), and (b) the output ISI \( (T_{oj}) \) with \( M = 3 \), \( T_i = 20 \) and \( \tau_d = 10 \) msec in the E-E couplings. The result of \( V_2 \) in (a) is shifted downward by 200 mV and scales for \( U_i \), \( U_{oj} \) and \( I_j \) are arbitrary.

FIG. 3. The time dependence of (a) the transient input \( U_i \), output \( U_{oj} \), the total postsynaptic current \( I_j \) and the membrane potential \( V_j \), and (b) the output ISI \( (T_{oj}) \) with \( M = 3 \) and \( T_i = 20 \) msec in the I-I couplings. Same as in Fig. 2.

FIG. 4. The time course of the input \( (U_i) \) and membrane potentials \( (V) \) for \( M = 3 \), \( T_i = 20 \) and \( \tau_d = 50 \) msec in the four couplings, results of I-I, E-I and I-E couplings being shifted downward by 200, 400 and 600 mV, respectively.

FIG. 5. The coupling-strength dependence of the oscillation period \( T_p \) and the output ISIs \( T_o \) of the E-E (solid curve, open circles), I-I (dashed curve, filled circles), and E-I and I-E couplings (dotted curve, open triangles) for the transient inputs with \( M = 3 \), \( T_i = 20 \) and \( \tau_d = 50 \) msec. The left (right) ordinate is for \( T_o \) (\( T_p \)).

FIG. 6. The \( \tau_d \) dependence of the distribution of \( T_o \) of (a) E-E \( (T_i = 20 \) msec), (b) I-I \( (T_i = 20 \) msec), (c) E-E \( (T_i = 50 \) msec), and (d) I-E couplings \( (T_i = 50 \) msec) for the clustered inputs with \( M = 3 \) and \( c = 1 \). The dashed lines are expressed by the equations written beside the lines (see text).

FIG. 7. The time course of the membrane potentials \( (V_1) \) for \( M = 1 - 5 \) for \( T_i = 20 \) and \( \tau_d = 50 \) msec with the E-E coupling.

FIG. 8. The time course of the external input \( (U_1) \), the postsynaptic current \( (I_1) \), and the membrane potential \( (V_1) \) in the E-I coupling with \( \tau_d = 50 \) msec, demonstrating the switching of the oscillation by \( U_1 \). Scales for \( U_1 \) and \( I_1 \) are arbitrary.

FIG. 9. The time course of input \( (U_i) \), output \( (U_{oj}) \), the total postsynaptic current \( (I_j) \), and the membrane potential \( (V_j) \) for sequential input with \( T_i = 20 \) and \( \tau_d = 10 \) msec in the (a) E-E and (b) I-I couplings.
FIG. 10. The distribution of $T_o$ as a function of the coupling strength $c$ of (a) E-E ($T_i=20$, $\tau_d=13.75$ msec), (b) I-I ($T_i=20$, $\tau_d=20$ msec), (c) E-I ($T_i=20$, $\tau_d=15$ msec), and (d) I-E couplings ($T_i=20$, $\tau_d=20$ msec) for the sequential inputs. The enlarged plots of the regions between dotted, vertical lines in (a) and (c) are shown in Fig. 11(a) and (b), respectively.

FIG. 11. The enlarged plots of the distribution of $T_o$ for (a) the E-E coupling with $T_i=20$ and $\tau_d=13.75$ msec (see Fig. 10(a)), and for (b) the I-E coupling with $T_i=20$ and $\tau_d=20$ msec (see Fig. 10(c)). The arrow in (a) denotes the $c$ value for which the Lorentz plot is shown in Figs. 12(a).

FIG. 12. (a) The Lorenz plot of $T_o$ for $c = 0.95$ with $T_i = 20$ and $\tau_d = 13.75$ in the E-E coupling, the computation being performed for 20 sec (two million steps). (b) The correlation integral $C(\epsilon)$ of the cycle shown in (a) as a function of $\epsilon$ in the log-log plot for various dimensions $k$, the dashed line denoting $C(\epsilon) \propto \epsilon^\nu$ with the correlation dimension of $\nu = 0.94$ (see text).

FIG. 13. The $\tau_d$ dependence of the distribution of $T_o$ of (a) E-E ($T_i = 20$ msec), (b) I-I ($T_i = 20$ msec), (c) E-E ($T_i = 50$ msec), and (d) I-I couplings ($T_i = 50$ msec) for the sequential input with $c = 1.0$. Dashed lines in (c) and (d) are given by Eq.(22) with a pair of integers $(\ell, m)$ shown beside the line. The enlarged plots of the regions between dotted, vertical lines in (a) and (c) are shown in Fig. 14(a) and (b), respectively.

FIG. 14. The enlarged plot of the distribution of $T_o$ for (a) $T_i = 20$ msec (see Fig. 13(a)) and (b) $T_i = 50$ msec (see Fig. 13(c)).

FIG. 15. The $T_i$ dependence of the distribution of $T_o$ for (a) the transient ($M = 3$) and (b) sequential spike-train input with $\tau_d = 50$ msec and $c = 1.0$. Dashed lines are given by Eqs.(17), (18) and (22) (see text).

FIG. 16. The time dependence of $T_o$ for the clustered impulse inputs with $M = 3, 10, 50$ and $\infty$ with $T_i = 20$, $\tau_d = 50$ msec and $c = 1.0$ in the E-E coupling, results of $M=3, 10$ and 50 being shifted upward by 30, 20 and 10 mV, respectively. The arrows denote the time below which the inputs are continuously applied.

FIG. 17. The time dependence of $T_o$ for the clustered impulse inputs with $M = 3, 10, 50$ and $\infty$ with $T_i = 20$, $\tau_d = 13.75$ msec and $c = 0.95$ in the E-E coupling. Same as in Fig.16.

FIG. 18. The Lorenz plots of $T_o$ of (a) the single HH neuron and (b) the E-E coupled HH neurons ($\tau_d = 10$ msec and $c = 1.0$) receiving spike-train inputs whose ISIs are modulated by sinusoidal signal given by Eq.(23) with $d_0 = 2d_1 = 20$ and $T_p = 100$ msec (see text).
FIG. 19. The time correlation $\Gamma_{12}(\tau)$ between the membrane potentials of the neurons 1 and 2 for (a) the constant-ISI input with $T_i = 20$, $\tau_d = 10$ msec and $c = 1.0$, (b) that with $T_i = 20$, $\tau_d = 13.75$ msec and $c = 0.95$, and (c) the sinusoidal input given by Eq. (23) with $d_1 = 2d_2 = 20$, $T_p = 100$, $\tau_d = 10$ msec and $c = 1.0$. The results of (b) and (c) are shifted downward by 1.0 and 2.0, respectively (see text).

FIG. 20. The $\tau_d$ dependence of the mean ($\mu_o$) and rms ($\sigma_o$) of output ISIs of the E-E coupled HH neurons ($c = 1$) receiving sequential inputs of $T_i = 20$ msec with $c_vi = 0.0$ (dashed curves) and $c_vi = 0.43$ (solid curves) (see text).
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