Spike-Train Responses of a Pair of Hodgkin-Huxley Neurons with Time-Delayed Couplings

Hideo Hasegawa

Department of Physics, Tokyo Gakugei University
Koganei, Tokyo 184-8501, Japan

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Abstract

Model calculations have been performed on the spike-train response of a pair of Hodgkin-Huxley (HH) neurons coupled by recurrent excitatory-excitatory couplings with time delay. 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 distribution of the output ISI $T_o$ shows a rich of variety depending on the coupling strength and the time delay. The comparison is made between the dependence of the output ISI for the transient inputs and that for the sequential inputs.

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Corresponding Author
Hideo Hasegawa
Department of Physics, Tokyo Gakugei University
4-1-1 Nukui-kita machi, Koganei, Tokyo 184-8501, Japan
Phone: 042-329-7482, Fax: 042-329-7491
e-mail: hasegawa@u-gakugei.ac.jp
1 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 [4].

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 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) has investigated 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][30]. 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 anti-phase state becomes more stable than the synchronized state [22]. Rather, inhibitory couplings with substantial time delay lead to the in-phase synchronized states in the coupled HH oscillators [22]. The similar conclusion is obtained also in the coupled integrate-and-fire (IF) oscillators [22,29,31-34]. 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 [23-26]. Recurrent loops involving two or more neurons with exci-
tatory and/or inhibitory synapses are found in biological systems such as hippocampus [35], neo-cortex [36] and thalamus [37]. It is important to make a detailed study on the coupled HH neurons, which is the simplest but meaningful network unit.

In recent years, much attention has been paid to the delayed-feedback systems described by the delay-differential equation (DDE) [38-43]. 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 [38,39], the bifurcation leading to chaos [39-41], the multistability [39], and the chaotic itinerancy [42,43]. 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 [39] 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 [27] demonstrate this ability in the coupled HH (and IF) neurons with the time-delayed feedback.

The response of DDE is usually discussed by applying the sequential sinusoidal or spike-train inputs to non-linear systems. In real neural systems, however, it is not so often for neurons to receive such sequential, continuous inputs. Rather, it is expected to be more realistic that neurons receive clustered inputs including information to be processed. The purpose of the present paper is to investigate the response of the coupled excitable HH neurons to both the transient and sequential spike-train inputs. We adopt the recurrent excitatory-excitatory (E-E) couplings between a pair of HH neurons, to which we apply the transient spike-train inputs consisting of clustered $M$ impulses for the finite duration ($M$: integer) as well as the sequential inputs with the constant ISI.

Our paper is organized as follows: In the next §2, we describe a simple neural system consisting of neurons, axons, synapses and dendrites, which is adopted for our numerical calculation. We present the calculated results in §3: the response of the coupled HH neurons to the transient, clustered impulses is discussed in §3.1 and that to the sequential spike-train input in §3.2. The dependence of the distribution of the output ISIs on the coupling strength and the time delay are studied. The final §4 is devoted to conclusion and discussion.

2 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 [44][45]. 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, 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

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

(2)

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

$$dm_j/dt = -(a_{mj} + b_{mj}) m_j + a_{mj},$$

(3)

$$dh_j/dt = -(a_{hj} + b_{hj}) h_j + a_{hj},$$

(4)

$$dn_j/dt = -(a_{nj} + b_{nj}) n_j + a_{nj}.$$  

(5)

The coefficients of $a_{mj}$ and $b_{mj}$ etc. are expressed in terms of $V_j$ (their explicit expressions having been given in refs. [20][23]) 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

$$I_j^{\text{ext}} = I_{sj} + A_s \delta_{j1} \sum_n \alpha(t - t_{in}),$$

(6)

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

$$\alpha(t) = (t/\tau_a) e^{-t/\tau_a} \Theta(t).$$

(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

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

(8)
In eqs. (2.6)-(2.8), $\Theta(t) = 1$ 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 $\tau_s = 2$ msec; $t_{in}$ is the $n$-th firing time of the spike-train inputs defined recurrently by

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

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 $t_{in} = n T_i$ for an 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

$$U_{o,j}(t) = V_a \sum_m \delta(t - t_{ojm}), \quad (10)$$
in a similar form to eq. (8), $t_{ojm}$ being the $m$-th firing time of the neuron $j$ when $V_j(t)$ crosses $V_z = 0.0$ mV from below. The output ISI is given by

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

The third term in eq. (1) which expresses the interaction between the two neurons, is assumed to be given by

$$I_{int}^j(\{V_k(t - \tau_{j,k})\}) = \sum_{k(\neq j)} \sum_m C_{jk} \alpha(t - \tau_{j,k} - t_{omk}). \quad (12)$$

We assume the recurrent excitatory-excitatory couplings with positive $C_{ij}$ given by $|C_{21}| = |C_{12}| \equiv c A_s$ and $\tau_{21} = \tau_{12} \equiv \tau_d$.

As for the functional form of the coupling term of $I_{int}^j(\{V_k(t - \tau_{j,k})\})$, Foss, Longtin, Mensour and Milton [27] adopt a simpler form given by

$$I_{int}^j(\{V_k(t - \tau_{j,k})\}) = \sum_{k(\neq j)} \mu_{jk} V_k(t - \tau_{j,k}), \quad (13)$$
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 $I_{ext}^j$ [eq. (6)].

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

$$V_j(t) = -65 \text{ mV}, m_j(t) = 0.0526, h_j(t) = 0.600,$$
$$n_j(t) = 0.313, \text{ for } j = 1, 2 \text{ at } t = 0, \quad (14)$$
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 1000 msec (100,000 steps).

### 3 Calculated Results

In the present study, we consider only the excitable HH neurons by setting \(I_{sj} = 0\) and \(A_s = g_s(V_a - V_s) = 40 \mu\text{A/cm}^2\) for \(g_s = 0.5\text{mS/cm}^2\), \(V_a = 30\) and \(V_s = -50\text{ mV}\) \([20]\). Our model has additional three parameters, \(T_i\), \(\tau_d\) and \(c\). We treat them as free parameters to be changed because the values of ISI and the time delay observed in biological systems distribute in a fairly wide range \([46]\).

#### 3.1 Transient Spike-Train Inputs

Let us first investigate the response to the transient, clustered spike-train inputs consisting of \(M\) impulses. We have studied in I, the transient response of a single HH neuron to spike-train inputs consisting of \(M = 2 - 5\) impulses with \(T_i = 5, 10\) and \(20\) msec (see Fig. 20 of I). In the case of \(T_i = 20\) msec, we get \(T_o = 20\) msec and the number of output pulses is the same as that of input pulses. On the contrary, in the cases of \(T_i = 5\) and \(10\) msec, the ISI of output is generally larger than that of input because of its character of the low-pass filter, and the number of output pulse is not necessary the same as that of input pulse.

Figure 1 shows the example of the time courses of input \((U_i)\), output pulses \((U_{oj})\), the total postsynaptic current \((I_j = I_j^{\text{ext}} + I_j^{\text{int}})\) 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 \(\tau_{i1} \sim 2\) 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 \(\tau_{i2} \sim 2\) msec, the neuron 2 makes the firing which yields the input current to the neuron 1 after a delay of \(\tau_{l2} = 10\) msec. The input pulses trigger the continuous oscillation in the coupled HH neurons with the output ISI of \(T_o = 24.10\) msec. The time dependence of the output ISI of the neuron 1 and 2 are plotted by solid and dashed lines in Fig. 2(a), 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 value of 24.10 msec.
Figures 2(b) and 2(c) show similar plots for different values of $\tau_d = 13.75$ and 20 msec, respectively. In the case of $\tau_d = 13.75$ msec, output ISIs start the oscillation with $T_o = 20.00$ and 12.36 msec and asymptotically approach the value of 15.93 msec. On the contrary, in the case of $\tau_d = 20$ msec, the oscillation of $T_o$ starting at $t = 0$ continues with the asymptotic values of $T_o = 18.51$ and 25.59 msec. In the following subsections, we will discuss the dependence of output ISIs on the time delay and the coupling strength. Since its behavior of the spike-train outputs of the neurons 1 and 2 is similar, we hereafter take into account only that of the neuron 1 otherwise noticed.

3.1.1 The time-delay dependence

Now we study how the output ISIs are determined. When the coupling strength is sufficiently strong for inputs to trigger output impulses and when the feedback time $T_{fb}$ is larger than the duration of clustered impulses (i.e. $T_{fb} = 2\tau_d + \tau_{i_1} + \tau_{i_2} > (M - 1) T_i$), we get two values of $T_o$ given by

$$T_o^{(1)} = T_i,$$
$$T_o^{(2)} = T_{fb} - (M - 1) T_i$$
$$= 2\tau_d + \tau_{i_1} + \tau_{i_2} - (M - 1) T_i. \quad (16)$$

On the other hand, when the feedback time is shorter than input-pulse duration ($2\tau_d + \tau_{i_1} + \tau_{i_2} < (M - 1) T_i$), we get

$$T_o^{(1)} = T_i \Theta(M - 3),$$
$$T_o^{(2)} = | \ell T_{fb} - m T_i |$$
$$= | \ell (2\tau_d + \tau_{i_1} + \tau_{i_2}) - m T_i |. \quad (17)$$

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

Figures 3(a) and 3(b) show the calculated time-delay dependence of $T_o$ for $c = 1.0$ and 1.6, respectively. Filled and open circles denote $T_o$s of the transient ($t \leq 1000$ msec) and asymptotic solutions ($t > 1000$ msec), respectively. As was shown in Figs. 2(a)-2(c), the output ISIs of the asymptotic solutions are $T_o = 24.10$ for $\tau_d = 10$ msec, $T_o = 15.93$ for $\tau_d = 13.75$ msec, and $T_o = 18.51$ and 25.59 msec for $\tau_d = 20$ msec. We note that the behavior of $T_o$ strongly depends on the value of $\tau_d$. In order to see their detailed structures, we show in Figs. 4(a)-4(c), enlarged plots of the narrow regions in Fig. 3(b). Figures 3(a) and 3(b) show three main branches expressed by $T_o \sim 2\tau_d + 5$, $T_o \sim 2\tau_d - 15$ and $T_o \sim 2\tau_d - 35$, which are obtainable for a pair of integers of $(\ell, m) = (1,0), (1,1)$ and (1,2), respectively,
by eq. (17) with $\tau_1 = \tau_2 = 2.5$ and $T_i = 20$ msec. Figure 4(a), in which the narrow region of $10 \leq \tau_d \leq 20$ msec in Fig. 3(b) is enlarged, shows an additional branch of a single ISI given by $T_o \sim \tau_d + 2$ at $11.9 < \tau_d < 12.3$ and $13.7 < \tau_d \approx 19$ msec. Furthermore we note in Fig. 4(b) which shows an enlarged plot at $20 \leq \tau_d \leq 30$ msec in Fig. 3(b), a branch of multiple ISIs given by $T_o \sim 0.5\tau_d + 5$ at $21.9 < \tau_d < 28.5$ msec. These $\tau_d$ dependences of $T_o$ cannot be explained by eq. (17), and may be harmonics of the fundamental ISI with the period of $2\tau_d$. The $\tau_d$ dependence of $T_o$ for $c = 1.0$ shown in Fig. 3(b) is similar to that for $c = 1.0$ shown in Fig. 3(a), except an additional branch given by $T_o \sim 0.5\tau_d + 4$ at $12.3 < \tau_d < 13.7$ msec. The narrow region of $16 \leq \tau_d \leq 20$ msec in Fig. 4(a) is enlarged in Fig. 4(c), where the ISI of the asymptotic solution shows the stair-like structure.

3.1.2 The coupling-strength dependence

Figures 5(a) and 5(b) show the $c$ dependence of the output ISI of the transient (filled circles) and asymptotic solutions (open circles). As was shown in Figs. 2(a) and 2(b), the ISI of the asymptotic solutions with $c = 1.0$ is $T_o = 24$ msec for $\tau_d = 10$ msec and $T_o = 15.93$ msec for $\tau_d = 13.75$ msec. Figure 5(a) shows that as the coupling strength becomes weak, $T_o$ is increased because of the integrator character of the HH neuron. A similar effect is obtained also in a single HH neuron, in which the output ISI becomes larger for smaller spike-train inputs \[20\]. Figure 5(b) shows that ISIs for the transient solutions fluctuate around that for the asymptotic solution as expected. The enlarged plot for $1.5 \leq c \leq 1.7$ of Fig. 5(b) is given in Fig. 6, where a discontinuous change in $T_o$ is clearly realized at $c = 1.61$ msec. For $c < 0.2$ neurons emit only three impulses, returning to rest without oscillations.

3.2 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.

Figure 7 shows the time courses of input ($U_i$), output ($U_o$), the total postsynaptic current ($I_j = I^\text{ext}_j + I^\text{int}_j$) and the membrane potential ($V_j$) for $T_i = 20$ msec, $\tau_d = 10$ msec and $c = 1.0$, which are the same parameters adopted for the clustered inputs shown in Fig. 1. The output ISI in Fig. 1 is 24.1 msec while that in Fig. 7 is 20 msec which is the entrained value with input ISI. The response behavior of the coupled neurons strongly depends on the parameters of $c$, $\tau_d$ and $T_i$. 
3.2.1 The time-delay dependence

Figures 8(a) and 8(b) show the $\tau_d$ dependence of the distribution of $T_o$ for $c = 1.0$ and 1.6, respectively, in the asymptotic solution of the sequential inputs [47]. The calculations in Figs. 8(a) and 8(b) are performed with the same parameters of $T_i$ and $c$ in Figs. 3(a) and 3(b), respectively. The $\tau_d$ dependence of $T_o$ in Fig. 8(a) [Fig. 8(b)] is quite different from that in Fig. 3(a) [Fig. 3(b)]. Figures 8(a) and 8(b) have the bifurcation structure, as commonly observed in systems with the delayed feedback [39]. In order to see more the detailed structure of the bifurcation, we show, in Fig. 9, the enlarged plot for the range of $21 \leq \tau_d \leq 26$ msec between the dotted, vertical lines in Fig. 8(a). The region sandwiched by vertical dotted lines in Fig. 9(a) ($21 \leq \tau_d \leq 26$ msec) is further enlarged in Fig. 9(b). Figures 9(a) and 9(b) clearly show the bifurcation as changing $\tau_d$. The $\tau_d$ dependence for $c = 1.6$ shown in Fig. 8(b) is similar to that for $c = 1.0$ shown in Fig. 8(a), and its enlarged plot also exhibits the bifurcation (not shown).

3.2.2 The coupling-strength dependence

The calculated $c$ dependence of the distribution of $T_o$ with $\tau_d = 10$ and 13.75 msec for $T_i = 20$ msec are shown in Figs. 10(a) and 10(b), respectively [47]. The adopted values of $T_i$ and $\tau_d$ in Figs. 10(a) and 10(b) are the same as those in Figs. 5(a) and 5(b), respectively. The output ISI for the sequential inputs shown in Fig. 10(a) is 20 msec ($= T_i$) independent of the coupling constant, while that for the clustered inputs shown in Fig. 5(a) decreases monotonically as the $c$ value is decreased. We note in Fig. 10(b) that, as increasing the $c$ value, the distribution of the output ISIs for $\tau = 13.75$ msec exhibits the bifurcation. In order to investigate the phenomenon in more detail, we show, in Fig. 11, the enlarged plot for the range of $0.6 \leq c \leq 1.2$ sandwiched by the dotted, vertical lines in Fig. 10(b).

A cycle whose output ISIs almost continuously distribute, is expected to be chaotic although in the strict sense, the distribution of our $T_o$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. 11, we pay our attention to the result of $c = 0.95$, 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 temporal 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 [18]

\[
\nu = \lim_{\epsilon \to 0} \frac{\log C(\epsilon)}{\log \epsilon}, \quad (18)
\]
with
\[ C(\epsilon) = N^{-2} \sum_{m,n=1}^{N} \Theta(\epsilon - |X_m - X_n|), \tag{19} \]
\[ X_m = (T_{om}, T_{om+1}, \ldots, T_{om+k-1}), \tag{20} \]
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 embedding dimensions \( k \) calculated for the cycle shown in Fig. 12(a) with the data size of \( N \sim 1200 \). 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 = \( e^{-4.6} \) < \( \epsilon < e^0 \)). When the relevant spike-train output given by \( U_{\alpha i}(t) \) [eq. (10)] is Fourier transformed, its spectrum shows a broad distribution. These suggest that the cycle shown in Fig. 12(a) may be chaos, although we cannot draw any definite conclusion until a detailed calculation of its Lyapunov spectrum is performed, related discussion being given in §4.

4 Conclusion and Discussion

We have performed model calculations of the spike-train responses of a pair of coupled HH neurons, applying the two types of inputs of the transient and sequential spike-train impulses. Calculations for the transient inputs shown in Figs. 3(a) and 3(b) [Fig. 5(a) and 5(b)] are performed with the same model parameters as those for the sequential inputs shown in Figs. 8(a) and 8(b) [10(a) and 10(b)]. When we make a comparison of the response to transient inputs with the corresponding result to sequential inputs, we notice the difference and similarity between them. When we regard a neuron as a data-processing element, the relation between input and output ISIs is one of the important factors for its quality. Our previous calculation in I shows that a single HH neuron emits a single ISI of \( T_o = T_i \) for \( T_i < 12 \) msec whereas for shorter ISI of \( T_i < 12 \) msec it emits multiple ISIs of \( T_o > 10 \) msec (see Fig. 7 of I). Figures 13(a) and 13(b) show the \( T_i \) dependence of \( T_o \) of coupled HH neurons for the transient and sequential inputs, respectively, with \( \tau_d = 50 \) msec and \( c = 1.0 \). Dashed lines in Figs. 13(a) and 13(b) are obtained with the use of eq. (17) for a pair of integers \((\ell, m)\) shown in the brackets. It is apparent that the distribution of \( T_o \) in Fig. 13(a) is not the same as that in Fig. 13(b), but they are partly similar.

On the theoretical point of view, the sequential input is taken as the limit of \( M \to \infty \) of the \( M \)-impulse clustered input. In order to understand the transition of the response behavior as increasing \( M \), we plot, in Fig. 14, the time dependence of \( T_o \) for this set of parameters by changing the \( M \) value. For \( M = 3 \), \( T_o \) oscillates with the values of 19.6, 20.0 and 64.54 msec, as mentioned before. The calculated \( T_o \) 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 $M = 10$, $T_o$ remains 20 msec until $t \sim 200$ msec, after which $T_o$ oscillates with the values of 19.9, 20.0 and 24.2 msec. In the limit of $M \to \infty$ corresponding to the sequential inputs, the state with $T_o = 20$ msec continues from $t = 0$ to $\infty$. Thus as increasing $M$, the time region of $T_o = 20$ msec is increased. Figure 15 shows the similar plot of the time dependence of the distribution of $T_o$ 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. 3.2 (see Fig. 12(a)). In the case of $M = 3$, we get the oscillation in $T_o$ which asymptotically approaches the value of 15.97 msec. In the case of $M = 10$ (50), the chaotic behavior is realized at $0 \leq t \lesssim 180$ ($0 \leq t \lesssim 980$) msec during the application of inputs. After inputs are switched off, the output ISI gradually approaches the asymptotic value of 15.97 msec. In the limit of $M \to \infty$, the chaotic oscillation eternally continues.

We have shown in §3.2 that the cycle of the output ISIs shown in Fig. 12(a) may be chaos because of its correlation dimension of $\nu \sim 0.94$ 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]

$$T_i(t) = d_0 + d_1 \sin(2\pi t/T_p),$$  \hspace{1cm} (21)$$

where $d_0$ denotes the average of $T_i(t)$, $d_1$ the magnitude of the sinusoidal modulation, and $T_p$ its period. Figure 16(a) shows the Lorentz plot of the output ISIs of the single HH neuron ($c = 0.0$) receiving sequential inputs modulated by sinusoidal ISIs [eq. (21)] with $d_0 = 2d_1 = 20$ and $T_p = 100$ msec (see Fig. 9(d) of I, where points in the Lorentz plot are connected by lines in the temporal order). We note that $T_o$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 sinusoidal spike-train input to the coupled HH neurons with $\tau_d = 10$ msec and $c = 1.0$, whose Lorentz plot is shown in Fig. 16(b). Its structure is rather different from that shown in Fig. 16(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. 16(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 $\nu_i$, 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 $\nu_i$ 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 and 2, defined by

\[
\Gamma_{12}(\tau) = \int_{t_a}^{t_b} [V_1(t) - <V_1(t)>] [V_2(t + \tau) - <V_2(t)>] \, dt,
\]

(22)

where the bracket denotes the time average, and \( t_a = 1000 \) and \( t_b = 2000 \) msec are adopted for our calculation. Figure 17(a) shows the result for the case of the sequential input to the coupled HH neurons with \( T_i = 20, \tau_d = 10 \) msec and \( c = 1.0 \) (see Fig. 7 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 § 3.2, and then \( \Gamma_{12}(\tau) \) shown in Fig. 17(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. 17(b) and 17(c). We have discussed in § 3.2 that the cycle of \( T_o \) depicted in Fig. 12 may be chaotic. Figure 17(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 \( \tau = -45.34, -30.69, -16.13, 0.0, 16.07, 30.54, 48.17, \ldots \) msec with the period of about 16 msec, which is the sum of \( \tau_d \) and \( \tau_i \). More evident peaks are found in Fig. 17(c) showing also the chaotic case discussed in the preceding paragraph: the E-E coupled neurons receiving the sinusoidal inputs given by eq. (21) with \( d_0 = 2d_1 = 20, T_p = 100, T_i = 20, \tau_d = 10 \) msec and \( c = 1.0 \) [see Fig. 16(b)]. We note peaks in \( \Gamma_{12}(\tau) \) at \( \tau = -37.63, -25.03, -12.52, 0.0, 12.72, 25.30, 37.88, \ldots \) msec with the period of about 12.6 msec. These results are not modified even when the initial condition of one of the HH neurons is slightly changed from the values in eq. (14). It is interesting that the synchronization is well preserved between the coupled HH neurons in the chaotic state [49].

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 [50]. 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]

\[
P(T) = s^r \, T^{r-1} \, e^{-sT} / \Gamma(r),
\]

(23)

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 18 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 $T_o$ [see Fig. 8(a)]. This fine structure is, however, washed out for $c_{vi} = 0.43$, as expected.

Finally we discuss the relevance of the calculated properties to biological experiments. Many experimental data have shown the complex behavior of electroencephalographic (EEG) waves in brain. The macroscopic characteristics of their activity are aperiodic and unpredictable oscillations with amplitude histograms that are near Gaussian, auto-correlation functions that rapidly approach zero and intermittent burst of oscillations having spectral peaks [51]. It has been reported that the activity of EEG in the olfactory bulb shows the significance of chaos in an animal’s motivated behaviors [52]. The complex behavior of EEG is nothing but the reflection of that of action potentials generated by neurons. It has been shown that neurons in different regions of the brain have different firings property. In hippocampus, for example, gamma oscillation ($20 \sim 70$ Hz) occurs in vivo, following sharp waves [35]. In neo-cortex, gamma oscillation is observed under conditions of sensory signal as well as during sleep [36]. In thalamus burst firings are found during slow-sleep, and single spiking is found during arousal [37]. One of the reasons of this variety of firings is that different class of neurons has different ion conductances. Physiological experiments have shown that these biological systems include recurrent loops connecting two or more neurons with excitatory and/or inhibitory synapses. It is conceivable that the distributed processing of brain function may be due to differences not only in ion conductances of the neuron but also in synaptic strength and in delay times of axons and dendrites connecting neurons. Although many theoretical studies have been made, the origin of the complexity in neuron firings has not been well clarified at the moment. We should note that synaptic strengths may be modified by Hebb’s learning rule, which changes the state of the network including given synapses. Our calculations for a pair of HH neurons, which is a simplest, plausible model simulating recurrently connected network, have demonstrated that depending on the coupling strength and the time delay, the coupled HH neurons show a much variety, yielding not only regular spike trains but also irregular (chaotic) impulses. We hope that our calculations might have some relevance to the complex activities in real, biological systems.

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Figure Captions

Fig.1 The time dependence of the clustered input ($U_i$), output ($U_{oj}$), the total postsynaptic current ($I_j$) and the membrane potential ($V_j$) with $M = 3$, $T_i = 20$, $\tau_d = 10$ msec and $c = 1.0$. The result of $V_2$ is shifted downward by 200 mV and scales for $U_i$, $U_{oj}$ and $I_j$ are arbitrary.

Fig.2 The time dependence of the output ISI ($T_o$) of neuron 1 (filled circles) and 2 (open circles) for (a) $\tau_d = 10$, (b) 13.75 and (c) 20 msec for clustered inputs with $M = 3$, $T_i = 20$ msec and $c = 1.0$.

Fig.3 The $\tau_d$ dependence of the distribution of $T_o$ of (a) $c = 1.0$ and (b) 1.6 for the clustered inputs with $M = 3$ and $T_i = 20$ msec. Filled and open circles denote the results of the transient ($t < 1000$ msec) and asymptotic solutions ($t > 1000$ msec), respectively. The dashed lines are expressed by the equations written beside the lines. The enlarged plots of the regions between dotted, vertical lines in Fig. 3(b) are shown in Figs. 4(a)-4(c) (see text).

Fig.4 The enlarged plot of the $\tau_d$ dependence for (a) $10 \lesssim \tau_d \lesssim 20$ msec, (b) $20 \lesssim \tau_d \lesssim 30$ msec, and (c) $16 \lesssim \tau_d \lesssim 20$ msec for $M = 3$, $T_i = 20$ and $c = 1.6$ @ (see Fig. 3(b)).

Fig.5 The $c$ dependence of the distribution of $T_o$ for (a) $\tau_d = 10$ and (b) 13.75 msec to the clustered inputs with $M = 3$ and $T_i = 20$ msec. Filled and open circles denote the results of the transient ($t < 1000$ msec) and asymptotic solutions ($t > 1000$ msec), respectively. The enlarged plot of the regions between dotted, vertical lines in Fig. 5(b) is shown in Fig. 6.

Fig.6 The enlarged plot of the $c$ dependence of the $T_o$ for $M = 3$, $T_i = 20$ and $\tau_d = 13.75$ msec (see Fig. 5(b)).

Fig.7 The time course of sequential input ($U_i$), output ($U_{oj}$), the total postsynaptic current ($I_j$), and the membrane potential ($V_j$) with $T_i = 20$, $\tau_d = 10$ msec and $c = 1.0$. The result of $V_2$ is shifted downward by 200 mV and scales for $U_i$, $U_{oj}$ and $I_j$ are arbitrary.

Fig.8 The $\tau_d$ dependence of the distribution of $T_o$ of (a) $c = 1.0$ and (b) 1.6 for the sequential input with $T_i = 20$ msec. The enlarged plot of the region between dotted, vertical lines in Fig. 8(a) is shown in Fig. 9.
Fig. 9 The enlarged plot of the $\tau_d$ dependence of $T_o$ at (a) $21 \leq \tau_d \leq 26$ msec and (b) $23 \leq \tau_d \leq 24$ msec [the region sandwiched by vertical dotted lines in 9(a)] for $T_i = 20$ msec and $c = 1.0$ (see Fig. 8(a)).

Fig. 10 The $c$ dependence of the distribution of $T_o$ for (a) $\tau_d=10.0$ and (b) 13.75 msec to the sequential inputs with $T_i=20$ msec. The enlarged plot of the regions between dotted, vertical lines in 10(b) is shown in Fig. 11.

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

Fig. 12 (a) The Lorenz plot of $T_{om}$ for $c = 0.95$ with $T_i = 20$ and $\tau_d=13.75$, 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 $\nu = 0.94$ [eqs.(3.3)-(3.5)].

Fig. 13 The $T_i$ dependence of the distribution of $T_o$ for (a) the clustered input ($M = 3$) and (b) sequential spike-train input with $\tau_d = 50$ msec and $c = 1.0$. Filled and open circles in (a) denote the results of the transient ($t \leq 1000$ msec) and asymptotic solutions ($t > 1000$ msec), respectively, while in (b) filled circles express the results of asymptotic solutions ($t > 1000$ msec). Dashed lines are expressed by a pair of integers of $(\ell, m)$ in eq. (17) (see text).

Fig. 14 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 $c = 1.0$, results of $M=3, 10$ and 50 being shifted upward by 60, 40 and 20 msec, respectively. The arrows denote the time below which the inputs are continuously applied.

Fig. 15 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 $c = 0.95$, results of $M=3, 10$ and 50 being shifted upward by 30, 20 and 10 msec, respectively.

Fig. 16 The Lorenz plots of $T_{om}$ of (a) the single HH neuron ($c = 0.0$) and (b) the 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. (21) with $d_0 = 2d_1 = 20$ and $T_p = 100$ msec (see text).
Fig. 17 The time correlation $\Gamma_{12}(\tau)$ between the membrane potentials of the neurons 1 and 2 [eq. (22)] 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 spike-train input given by eq. (21) 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. 18 The $\tau_d$ dependence of the mean ($\mu_o$) and rms ($\sigma_o$) of output ISIs of the coupled HH neurons ($c = 1$) receiving sequential inputs of $\mu_i =< T_i >= 20$ msec with $c_vi = 0.0$ (dashed curves) and $c_vi = 0.43$ (solid curves) (see text).
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