

Rate coding in a chain of pulse-coupled oscillators

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The input-output relation of a chain of pulse-coupled oscillators is examined. The oscillators capture the essential aspect of the dynamics of pacemaker neurons. Inputs consist of pacemaker, and noisy trains impinging upon the first unit in the chain. The response of the chain is defined as the spike train emitted by the last unit. We observe two important phenomena in the response of the chain for a given input train, whether pacemaker or noisy. First, the mean output rate of the chain is equal to the mean input rate in the range of input rate in which one input pulse corresponds to one output spike without phase locking (1:1 alternation). Second, for the same input range, the output interspike intervals tend to the average of the input interpulse intervals in a long chain of oscillators. This behavior contrasts with the fact that the response of a single unit depends on both input rate and pattern. We show that the response of the chain is reproduced by the phase transition curve which represents the phase shift due to a single isolated pulse stimulus. This analysis reveals that the averaging of the output interspike intervals is due to the geometrical aspect of the phase transition curve. This geometrical aspect causes the dependence of the response of a single unit on input pattern. [S1063-651X(99)11009-2]

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I. INTRODUCTION

Trains of action potentials emitted by neurons constitute one of the main carriers of information in nervous systems [1,2]. Comprehensive experimental [3,4] and theoretical [5–9] works have clearly established that synapses perform signal transduction based upon the pattern, and hence the timing of the incoming input trains. In this sense, the substrate for temporal coding is present at the level of single synapses. In a seminal work, Segundo *et al.* [10] investigated whether physiologically significant differences in output occur in neurons subjected to a synaptic input that has a given mean frequency but whose higher order statistics are systematically varied. They showed that inputs with the same frequency but with different patterns evoked different output rates. Their results showed that not only the mean frequency of spikes but also the higher order statistics can be information carriers in nervous systems.

In another work, Perkel *et al.* investigated the response of a single oscillator to two kinds of input pulse trains [1], namely, a pacemaker pulse train and a Poisson pulse train (i.e., whose sequence of timings forms a Poisson process). They showed that small changes in the rate of synaptic input or in the input variance can markedly alter the output pattern of a single neuron [1]. They suggested the possibility of highly selective filtering of synaptic inputs in networks of neurons. Kohn *et al.* examined the dependence of the response of a neuron on the input pattern by changing the degree of variability of input pulse trains [11]. They used input pulse trains following a stochastic process leading to variable input intervals. They reported that the output pattern strongly depended on the input variability.

This work examines how the sensitivity of single units to input patterns is reflected on the response of a chain of oscillators. We study whether the sensitivity to the input pattern present at the level of a single unit is also apparent when such units operate sequentially, the input of each unit being the output of the previous one. More precisely, we study

how, in a chain of n oscillators, the range of output spike parameters in the $n - 1$ th order neuron affects the activity of n th order neuron.

To investigate the response of the chain of oscillators, we follow the analysis of a single neuron by Perkel *et al.* [1] and Kohn *et al.* [11] by examining the response of chains of oscillators to both pacemaker and stochastic pulse trains.

This paper is organized as follows. Section II presents the model for the units and the chain. We consider a chain composed of a variant of the radial isochron clock (RIC), which has been shown to be an accurate model for biological oscillators and in particular for Segundo's preparation [6,7,9]. The response of the chains to various types of periodic and noisy input trains are presented in Sec. III. It is shown that the response of the chain depends on both the input rate and coefficient of variation. Moreover, we show that the sensitivity to the input pattern decreases along the chain for input rates within a specific range. Thus, in this regime, the response of a long chain is essentially determined by the input rate. An analysis of this result in terms of the response to a single pulse is also presented. Finally, the results are discussed in Sec. IV.

II. CHAIN MODEL

In this section, we introduce a pacemaker neuron model which captures the essential aspects of the dynamics of a pacemaker neuron. Next we describe the phase transition curve. This curve enables us to analyze the dynamics of the pacemaker neuron by using the knowledge of the response to a single pulse. Finally, we present the chain of the oscillators.

A. Pacemaker neuron model

The dynamics of the pacemaker neuron model is determined by the following equations in polar coordinates:

$$\dot{r} = Kr(1 - r^2), \quad \dot{\theta} = l_S \text{ if } \theta \in S, \quad \dot{\theta} = l_F \text{ if } \theta \in F, \quad (1)$$

where, $\mathcal{S}=[0.5,0.64)$, $\mathcal{F}=[0,1)-\mathcal{S}$, $l_{\mathcal{S}}=3/20$, $l_{\mathcal{F}}=129/10$, $r \in \mathbb{R}^+$, $\theta \in S^1$ (the unit circle), and K is a positive constant [Fig. 1(a)]. The state point moves slowly and rapidly with angular velocities $l_{\mathcal{S}}$ and $l_{\mathcal{F}}$ when θ is in \mathcal{S} and \mathcal{F} , respectively. We call this model asymmetric modified radial isochron clock (AMRIC).

The unit circle (i.e., $r=1$) is a stable limit cycle of Eqs. (1), with period 1, denoted by γ [Fig. 1(a), left]. Trajectories starting from any initial point in the phase plane, except the origin, wind counterclockwise around the origin, and, as $t \rightarrow \infty$, they approach γ .

The variable $X=r \cos \theta$ (the abscissa of the state point in Cartesian coordinates) represents the ‘‘membrane potential’’ of the AMRIC [Fig. 1(a), middle]. An output discharge is defined as the state point crossing over the positive part of X axis. The time-phase of a point x on γ , denoted by $\tau(x)$, is the time necessary for the state point to move from x_0 to x , where $x_0=(1,0)$.

B. The phase transition curve

A state point on γ , perturbed by a single pulse stimulus of intensity A and duration zero, is displaced by the amount A in the direction of X . Such a stimulation displaces a point x on γ to a point x' with lower ‘‘membrane potential,’’ because X and X' , the abscissas of x and x' in Cartesian coordinates, satisfy $X'=X+A$. Here, for simplicity, we assume that $K \gg 0$, so that a state point perturbed from γ rapidly converges back to it. Thus, following the perturbation, the state point moves instantaneously from x' to a point y on the limit cycle [Fig. 1(a), left]. The following equation gives the relation between the time-phases of x and $y(x, y \in \gamma)$:

$$\tau(y) = \Phi[\tau(x)] \equiv g^{-1}(\Psi\{g[\tau(x)]\}) \pmod{1},$$

where

$$\Psi(\theta) = \frac{1}{2\pi} \tan^{-1} \frac{\sin 2\pi\theta}{A + \cos 2\pi\theta} \quad (2)$$

and

$$\theta = g(\tau) \equiv \int_0^{\tau(x)} \frac{d}{ds} \theta[x(s)] ds.$$

The graph of Φ is the phase transition curve (PTC) [Fig. 1(a), right] of AMRIC. It represents the phase shift due to a single isolated pulse stimulus [7,12].

An important characteristic of the PTC of the AMRIC is that for τ within $[0.039,0.97)$, it can be approximated by a straight line with a positive slope a smaller than 1, for example, $a \approx 0.677$ for $A = -0.5$. The ‘‘linear’’ part of the PTC is approximated as follows:

$$\Phi(\tau) = a\tau + \frac{(1-a)}{2} \quad \text{for } \tau \in [0.039,0.97). \quad (3)$$

The PTC can be used to describe the response of the pacemaker neuron models to an arbitrary sequence of identical pulses. Indeed, from τ_n , the time-phase of the state

point ($x \in \gamma$) before the n th pulse stimulus, we can obtain τ_{n+1} , the time-phase just before the $n+1$ th pulse stimulus, according to

$$\tau_{n+1} = [\Phi(\tau_n) + I_n] \pmod{1} \equiv f(\tau_n, I_n), \quad (4)$$

where I_n is the time interval between the n th and $n+1$ th pulses [7]. We refer to the map $f(\cdot, I): S^1 \rightarrow S^1$ as PTC- I to indicate its dependence on the input interval. For any arbitrary sequence of pulses, and for any initial time-phase τ_1 , we can inductively compute the successive time-phases $\{\tau_n\}$ using Eq. (4). For instance, $\tau_2 = \Phi(\tau_1) + I_1$, $\tau_3 = \Phi[\Phi(\tau_1)I_1] + I_2$, When $k < \Phi(\tau_n) + I_n \leq k+1$, exactly k output spikes occur between the n th and $n+1$ th input pulses [13]. Thus, for any initial time-phase, and sequence of input intervals $\{I_n\}$, the PTC can be used to compute the response of the AMRIC without solving the system of differential equations [Eq. (1)]. We use this method to reproduce and to analyze the response of the chain of oscillators in Sec. III.

For periodic pulse trains ($I_1 = I_2 = \dots = I_n = I = \text{constant}$), the sequence of time-phases $\{\tau_n\}$ becomes $\tau_n = f(\tau_{n-1}, I) = f^2(\tau_{n-2}, I) = f^{n-1}(\tau_1, I)$, where τ_1 is the initial time-phase. If the sequence $\{\tau_n\}$ satisfies $\tau_{p+1} = \tau_1$ and $\tau_n \neq \tau_1, 2 \leq n \leq p$, $\{\tau_n\}$ is called a periodic orbit with period p . If the periodic orbit satisfies $|\partial f^p / \partial \tau(\tau_0)| = \prod_{j=1}^p |\partial f_j / \partial \tau(\tau_j)| < 1$, it is stable. $\rho = \lim_{M \rightarrow \infty} \sum_{n=1}^M \Delta_n / M$, where $\Delta_n = \Phi(\tau_n) + I - \tau_n$, is called rotation number.

If the period of $\{\tau_n\}$ is p , the rotation number ρ becomes q/p with adequate q (p and q are not always incommensurate). We call this response $p:q$ phase locking. In this way, fixed points (periodic orbits with period one) and periodic orbits of the PTC- I correspond to different periodic discharges, and vice-versa. This relation between the geometrical properties of the PTC and the discharge pattern of the pacemaker neuron models plays an important role in our analysis.

C. The chain model

The chain model consists of unidirectionally coupled units [Fig. 1(b)]. The units are AMRICs and the couplings

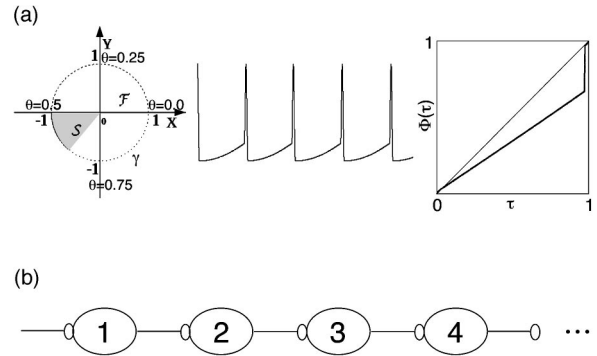


FIG. 1. (a) Left column: the trajectory of the AMRIC in the phase plane; abscissa and ordinate: state variables X and Y , respectively. Middle column: corresponding membrane potential wave form; abscissa: time in arbitrary unit, ordinate: X , the membrane potential of AMRIC in arbitrary unit. Right column: phase transition curve (PTC). (b) Schematic diagram of a chain of pulse-coupled oscillators.

are pulsatile. The input to the chain is the pulse train received by the first unit, while the input pulse train of the $k + 1$ th unit is the output spike train of the k th unit.

In the absence of any external input, the first unit generates a pacemaker train with natural period $N=1$. Thus, the second unit is stimulated by a periodic pulse train with period 1. When the input interpulse interval is 1, the AMRIC exhibits 1:1 phase locking. Thus, in the steady state regime, the second unit also discharges regularly with a period of 1 [Fig. 2(a)]. In this way, all units produce output spike trains with period 1 in the steady state. In the 1:1 phase locking regime, the PTC of the AMRIC has a stable fixed point $\tau^* = 0.0386$ [Fig. 1(a), right]; that is, it receives input pulses at a fixed time-phase $\tau^* = 0.0386$. We choose this state as the initial condition of the chain model.

To calculate the response of the chain model, we have used two methods. One is a numerical simulation scheme that takes advantage of the analytical expression of the solution to Eq. (1) (Appendix V), the other one is by iterating the PTC according to Eq. (4). We have obtained quantitative agreement between the two methods. The figures illustrate the results obtained with the second method. The corresponding figures computed with the first method are not presented because they are visually indistinguishable from those obtained with the second method.

III. RESPONSE TO INPUT TRAINS

In this section, we examine successively the response of the chain model to pacemaker and noisy pulse trains, and clarify the dependence of the output of the chain on the variability of the input intervals. Finally, we discuss the relation between the behavior of the chain model and the geometrical aspect of the PTC.

A. Response to pacemaker input

We investigate the response of the chain model to pacemaker pulse trains. Figure 2(a) shows the steady state mean output rate of the chain model as a function of the mean input rate. This figure includes the response of the first, second, third, 50th, and 100th units to a pacemaker pulse train delivered to the first unit.

The plot of mean output rate of the first unit (i.e., one single unit), though globally decreasing, is interrupted by wide ranges of input rate where an increase in inhibitory input pulse rate accelerates the pacemaker rate (paradoxical acceleration) [Fig. 2(a)]. In this region, p input intervals correspond to q output interspike intervals with fixed time-phases, namely, $p:q$ phase locking occurs. To consider the relation between mean input rate and mean output rate of $p:q$ phase locking, we denote by $\bar{r}_{in} = 1/I$ the input rate and by $\bar{r}_{out} = q/(T_1 + T_2 + \dots + T_q)$ the mean output rate, where $\{T_1, T_2, \dots, T_q\}$ are the successive output intervals in $p:q$ phase locking region. From $T_1 + T_2 + \dots + T_q = pI$, we obtain

$$\bar{r}_{out} = \frac{p}{q} \bar{r}_{in}. \quad (5)$$

Thus, a line with slope p/q appears in the $p:q$ phase locking region accounting for paradoxical acceleration.

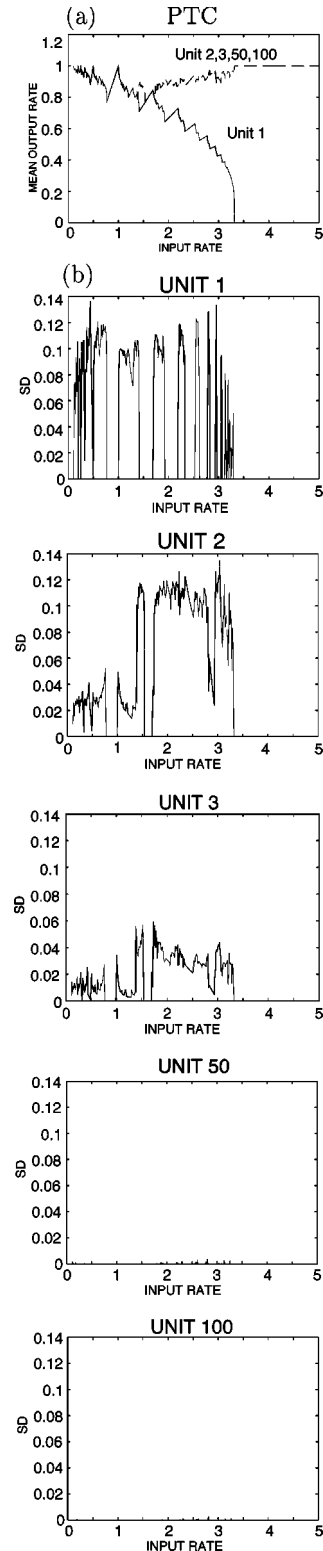


FIG. 2. Response of chain of oscillators to pacemaker input by using PTC. (a) Mean firing rate of the chain of oscillators, as a function of mean input rate. Abscissa and ordinate: mean input rate in spikes per unit time and mean output rate in spikes per unit time, respectively. (b) Standard deviation of the chain of oscillators, as a function of mean input rate. Abscissas: mean input rate in spikes per unit time; ordinates: standard deviation of interspike interval in arbitrary units. Response of simulated chain of oscillators also shows the same response.

Figure 2(a) shows that no matter what values the input rate takes, the mean output rate of the first unit is always bounded: $0.0 \leq \bar{r}_{out} \leq 1.0$. This, in turn, implies that the second unit receives an input train with mean rate within 0 and 1. Therefore, the mean output rate of this unit varies between $0.77 \leq \bar{r}_{out} \leq 1.0$. This range corresponds to 1:1 phase locking region. Similarly, the mean output rate of all units beyond the second one also varies within the 1:1 phase locking range.

Thus, the overall behavior of the chain is determined by the way an AMRIC responds to an input train with a rate within the 1:1 phase locking range. We have previously reported that within this range, the relation $1 < \Phi(\tau_n) + I_n \leq 2$ holds except for special values of time phase and intervals [13]. This implies that to one input pulse corresponds exactly one output pulse, i.e., there is 1:1 alternation. At the level of the chain, this property means that the mean output rate of all units is the same as the input rate. This phenomenon accounts for the fact that units 2, 3, 50, and 100 have all the same output rate in Fig. 2(a), and that this common value matches the discharge rate of the first unit for low input rates. The difference between the firing rate of the first unit and that of the others appears when the input rate increases, leading to discharge rates at the level of the first unit that are below the 1:1 locking (or equivalently 1:1 alternation range). Eventually, when the input rate becomes too large ($r_{in} > 3.32$), the first unit remains quiescent, and the second unit acts like the entry to the chain which stabilizes into its initial pattern with all units firing at the natural period.

While the upper panel in Fig. 2(a) represented the averaged response of the units within the chain, the lower panels show how the variability of the interdischarge intervals changes across the chain. The five panels in Fig. 2(b) show, from top to bottom, the standard deviation of interspike intervals of the first, second, third, 50th, and 100th units. Globally, the standard deviation decreases unit by unit thereby indicating that the firing becomes more pacemakerlike as one moves along the chain. Since the first unit generates a periodic discharge with a constant interval in $p:1$ phase locking regions, its standard deviation is zero in this regime. For this range of input rates, the standard deviation of the other units is also zero. This is because the output spike train from the first unit is a pacemaker spike train and such trains are transmitted unaltered when they are in the 1:1 phase locking region.

The standard deviation is also zero for all units when $\bar{r}_{in} > 3.32$ because the first unit is silent in this case. Outside of the above two conditions, the standard deviation of the intervals is different from 0. Notably, even when the first unit generates a periodic spike train in the $p:q$ phase locking region, with $q \geq 2$, the corresponding standard deviation is not zero because the intervals form a repetitive sequence composed of q distinct values.

B. Response to stochastic input

When all interpulse intervals are independent and identically distributed with probability density function $\rho \exp(-\rho x)$, we refer to the pulse train as a Poisson input because the timing of the events follows a Poisson process [14]. Moreover, if we pick up one pulse every k input pulses

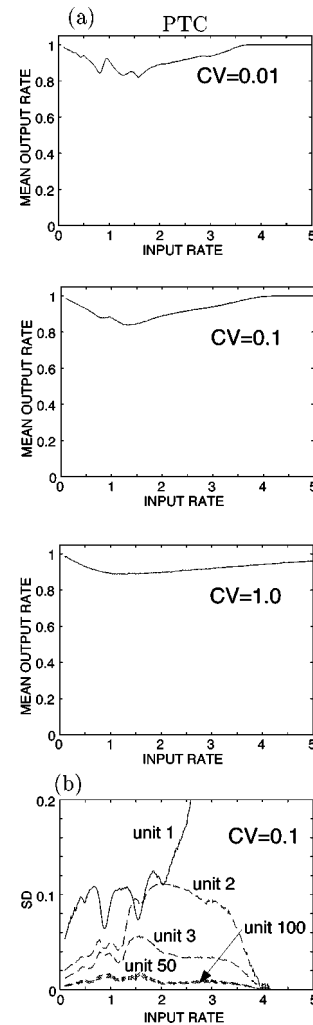


FIG. 3. Response of chain of oscillators to γ input by using PTC. (a) Mean firing rate of the chain of oscillators, as a function of mean input rate. Abscissas: mean input rate in spikes per unit time; ordinates: mean output rate in spikes per unit time. From top to bottom, the CV of γ input are 0.01, 0.1, 1. (b) Standard deviation of chain of oscillators. Abscissa: mean input rate in spikes per unit time; ordinate: standard deviation of output inter-spike interval in arbitrary unit. The CV of γ input is 0.1. Response of simulated chain of oscillators produces the same response.

from a Poisson input, the resulting train follows the k th order γ process [14]. We call this input γ input. As k increases, the mean and standard deviation of input intervals increase as k and \sqrt{k} , respectively. Hence, the coefficient of variation (CV), namely, the ratio of the standard deviation to the mean, decreases as $1/\sqrt{k}$. In other words, the first order γ process is a Poisson process and increasing the order of the process leads to more regular input trains. Thus, stimulation with γ processes with different orders provides a standard method to analyze the influence of input variability on the behavior of the chain.

The three panels in Fig. 3(a) show the mean input rate versus the mean output rate of the 100th unit in a chain stimulated by γ processes with CVs of 0.01, 0.1, and 1 (from top to bottom). The range of the output rate of the chain model is in the 1:1 phase locking region of a single unit since the mean output rate is restricted to this range for

all units after the first one. Similar to the case of pacemaker inputs, high input rates effectively prevent the first unit from firing, thereby leading to a period 1 firing in all subsequent units. In the case of stochastic inputs this phenomenon occurs at higher mean rates than for pacemaker forcing. This shifting is due to the variability of the input intervals.

The preceding section established how for pacemaker inputs, the response of a long chain varies with the input period. When the input has some variability, the locking regions, characterized by the positive slopes in the figures representing the relation between input and output rates, progressively disappear as the CV is increased. The smaller the size of the locking region, the smaller the variability required to smooth out the corresponding positive slope [Fig. 3(a)]. This phenomenon implies that the mean output rate of the chain depends not only on the mean input rate but also on the input variability. This dependence is consistent with previous studies that examined the response of single units [10,11].

The main difference between the response of the chain and that of a single unit appears at the level of the variability of the interspike intervals. This is shown in Fig. 3(b) where the standard deviations of the interdischarge intervals of units one, two, three, fifty, and one hundred are represented. For the first unit, the standard deviation presents valleys in regions of $p:1$ (noisy) phase lockings and humps in $p:q$ phase locking with $q \geq 2$. Similarly, the standard deviations of the other units are smoothed versions of the ones obtained with pacemaker forcing [lower panels in Fig. 2(b)]. Furthermore, for the 50th and 100th units, they take on larger values when the input is stochastic. Nevertheless, in the same way as for pacemaker inputs, the standard deviation decreases along the chain, thereby indicating that the discharge trains of the units become more regular and pacemaker like along the chain.

This phenomenon is further illustrated in Fig. 4, which shows the time evolution of input interpulse intervals and output inter-spike intervals of the first, second, third, 50th, and 100th units. Figures 4(a) and 4(b) show, respectively, the responses to a pacemaker within the 1:2 phase locking region and to a γ input with mean rate equal to 1 and CV of 0.1. The abscissas are the order of interval and the ordinates are the interpulse or interspike intervals. Due to the input-output relation of a single AMRIC, the output intervals of the first unit are bounded within $0 \leq T_n \leq 1.30$. Those of the subsequent units are further restricted to $1.0 \leq T_n \leq 1.30$, which corresponds to the 1:1 locking region. For both pacemaker and stochastic inputs, the higher order units have a marked lower variability than the first one. For the periodic input, units two and three display already close to pacemaker discharges, while for the stochastic input, the decrease in the variability is slower as some low level fluctuations still appear in the output train of unit 100. Figure 5 shows the progressive monotonic decrease of the standard deviation as the unit number increases. Thus, in a long chain the output resembles pacemaker firing, with intervals displaying little variability around their mean value. Therefore, the two characteristics of the input, namely, its mean rate and CV, are both encoded in the mean output rate.

When the input rate varies within the 1:1 locking region, our numerical results show that the mean output rate tends to the mean input rate, whether the input is pacemaker or sto-

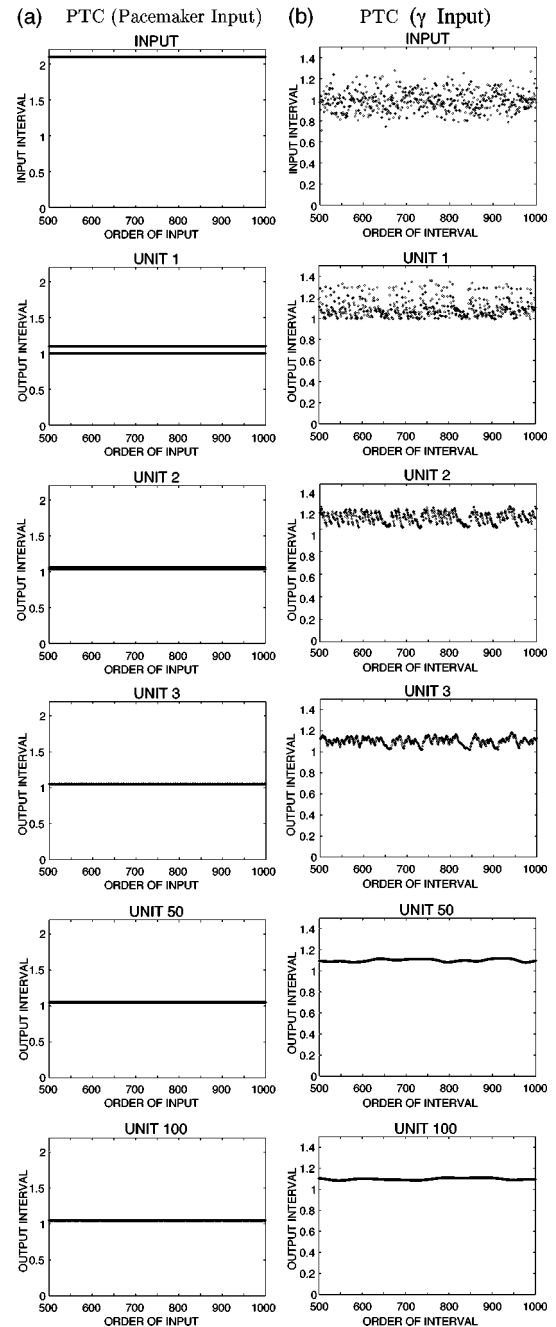


FIG. 4. Basic plot of chain of oscillators. (a) Response of chain of oscillators to pacemaker input by PTC. (b) Response of chain of oscillators to γ input by PTC. Abscissas: order of interpulse or interspike interval in arbitrary units; ordinates: interpulse or interspike interval in arbitrary units. The rate of pacemaker input is 2.1 in (a). The mean rate of γ input is 1.0 and the CV of γ input is 0.1 in (b).

chastic. This remarkable averaging effect can serve as the basis for the computation of the mean output rate of the chain from the response of a single unit. Indeed, as pointed out previously, the interdischarge intervals of the second unit of the chain lie within the 1:1 locking range. This property holds for both pacemaker and stochastic inputs. Consequently, the chain composed of units three and beyond is stimulated by an input train whose rate is within the 1:1 locking region. This, in turn, implies that (i) the output of a long chain is close to pacemaker spike train with interspike

intervals displaying some small variability around their mean value, and, furthermore, that (ii) this mean value is given by the mean interspike interval of the second unit within the chain.

Figure 4(a) illustrates this phenomenon. The output of the first unit is formed by two intervals T_1 and T_2 , both of which lie within the 1:1 locking region. The response of the chain at the level of the 100th unit is a pacemaker firing with period $(T_1 + T_2)/2$. A similar regularization effect takes place along the chain when the input is stochastic, as illustrated in Fig. 4(b). Such averaging effects that take place along the chain constitute the main characteristic of its input-output response. The next paragraph shows how the progressive reduction of the variability of the intervals can be accounted for by the geometrical properties of the PTC.

To understand the mechanisms underlying the averaging effect, we consider the response of a single unit to an input pulse train such that all the input intervals fall within the 1:1 phase locking region. Our previous study indicates that for such inputs, the unit displays in general 1:1 alternation, that is, the AMRIC generates exactly one discharge for every input pulse [13]. Thus, the n th output interspike interval, denoted by T_n , is given by

$$T_n = I_n + \tau_n - \tau_{n+1}, \quad (6)$$

where τ_n and τ_{n+1} are the time phases of the n th and $(n+1)$ th input pulses. Furthermore, in this regime, the discharge phases occur mainly in the ‘‘linear’’ part of the PTC, so that we have

$$\tau_{n+1} = a\tau_n + b + I_n \pmod{1}. \quad (7)$$

Taking ensemble averages over input trains, we obtain

$$\bar{\tau}_{n+1} = a\bar{\tau}_n + b + \bar{I} \pmod{1}, \quad (8)$$

where $\bar{\tau}_k$ and \bar{I} represent averages of the phase and the input intervals. Letting $n \rightarrow \infty$, we have $\bar{\tau} = a\bar{\tau} + b + \bar{I}$, where $\bar{\tau}$ is the steady state average discharge phase. This final expression yields $\bar{\tau} = \bar{I} + b/(1-a)$ and $\bar{T} = \bar{I}$, where \bar{T} is the steady state average output interval. The above relation confirms that the output rate coincides with the input rate.

Using Eqs. (6) and (7), we obtain the following relation:

$$T_n = (1-a)\tau_n - b. \quad (9)$$

From this relation we obtain that

$$V(T_n) = (1-a)^2 V(\tau_n), \quad (10)$$

where $V(T_n)$ and $V(\tau_n)$ represent the variances of the T_n and τ_n . Letting $n \rightarrow \infty$, we find the following relation for the steady state variances: $V(T) = (1-a)^2 V(\tau)$. From Eq. (7), it can be seen that $V(\tau) = V(I)/(1-a^2)$.

Thus, finally we obtain the following relation between the variances of the input and output intervals:

$$V(T) = \alpha V(I), \quad (11)$$

where $\alpha = (1-a)^2/(1-a^2)$. Since $a < 1$, we have $\alpha < 1$, which implies that the interval variance of the output is smaller than that of the input.

Equation (11) shows the decrease in the variance across a single unit. In a chain of length k , we have that the mean output interspike interval coincides with the mean input interspike interval, while the variances satisfy $V(T) = \alpha^k V(I)$. Thus the output variance decreases to zero with the length of the chain. This reduction of the variability of the intervals accounts for the averaging effect observed across the chain.

IV. DISCUSSION

This work examined how the sensitivity of single units to input patterns is reflected on the response of the chain of oscillators. We analyzed the response of the chain to pacemaker input and stochastic input. The investigation revealed that the response of the chain depends on the input rate and coefficient of variation. However, the latter does not have a significant effect when the input rate remains within the 1:1 phase locking range. Indeed, in this regime, the output interspike intervals tend to the average of input interspike intervals in a long chain of oscillators. This property implies that the response of the chain is completely determined by the input rate. In this sense, the response of a long chain contrasts with that of the first unit whose output depends both on the input rate and the input pattern. One consequence of this behavior of a long chain, with potential functional implication, is that when the input rate is confined to the 1:1 locking regime, the chain model performs rate coding (i.e., the information carrier is mean rate). More precisely, the mean output rate is equal to the mean input rate. We analyzed the mechanism underlying this averaging effect in terms of the geometrical properties of the PTC. This description of the response of a long chain to an input with rate within the 1:1 locking range opened the way for the analysis of the response to other input signals. This extension hinged upon the observation that for a broad range of input intervals, the interdischarge intervals of a single unit lay within the 1:1 locking range. This, in turn, implies that the output of a long chain consists of a (close to) pacemaker discharge train with a period equal to the mean output rate of the first unit. Thus, for a broad class of inputs, the response of the chain is completely characterized by the mean discharge rate of the first unit. This quantity, in turn, depends on the organization of the locking regions in response to pacemaker inputs. In this way, we established a link between the response characteristics of a single unit and that of a long chain. The similarity

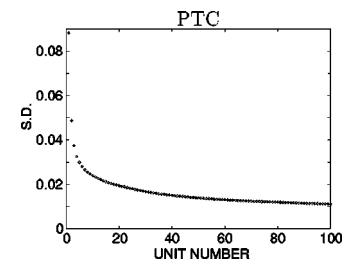


FIG. 5. Standard deviation of output interspike interval in each unit of chain of oscillators by using PTC. Abscissa: unit number; ordinate: standard deviation of output interspike interval in arbitrary unit. The mean input rate and the CV of γ input are 1.0 and 0.1, respectively. Standard deviation calculated by a simulation of chain of oscillators shows the same result.

between the response of the pacemaker model, namely, the AMRIC and experimental recordings of living neurons [1,11] suggests that our results could hold for chains of pacemaker neurons.

V. SIMULATION METHOD

To get the output sequence, we use special simulation method as follows.

Let $r(t_0), \theta(t_0)$ be the initial values of AMRIC at $t=t_0$. If there is no stimulus, the next output spike occurs at $t=t_0+N-\tau(t_0)$, where $N-\tau(t_0)$ is necessary time to the next spike from the initial condition without input. Let us

consider the case that the first stimulus arrives before the next spike. Set the input pulse arrives at t' and $r(t'^-)$ and $\theta(t'^-)$ are the variables just before the stimulus, and $r(t'^+)$ and $\theta(t'^+)$ are the variables just after the stimulus. When the stimulus arrives at t' , the state point moves to the direction of X axis by the amount of amplitude of the stimulus A . Then we get $r(t'^+)$ and $\theta(t'^+)$. From $\tau(t'^+)=g^{-1}[\theta(t'^+)]$, the next spike occurs at $t=N-\tau(t'^+)$. If the AMRIC get other stimulus before the time t , we repeat the above procedure. If there is no other stimulus, we get the occurrence time of next output spike. In this way, we can get the sequence of output spikes.

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