Studies of phase return map and symbolic dynamics in a periodically driven Hodgkin–Huxley neuron*

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How neuronal spike trains encode external information is a hot topic in neurodynamics studies. In this paper, we investigate the dynamical states of the Hodgkin–Huxley neuron under periodic forcing. Depending on the parameters of the stimulus, the neuron exhibits periodic, quasiperiodic and chaotic spike trains. In order to analyze these spike trains quantitatively, we use the phase return map to describe the dynamical behavior on a one-dimensional (1D) map. According to the monotonicity or discontinuous point of the 1D map, the spike trains are transformed into symbolic sequences by implementing a coarse-grained algorithm — symbolic dynamics. Based on the ordering rules of symbolic dynamics, the parameters of the external stimulus can be measured in high resolution with finite length symbolic sequences. A reasonable explanation for why the nervous system can discriminate or cognize the small change of the external signals in a short time is also presented.

Keywords: Hodgkin–Huxley neuron, return map, symbolic dynamics, chaos

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1. Introduction

Dissipative dynamical systems with two competing frequencies are common in nature.[1] These systems usually exhibit rich dynamical states that include phase-locking, quasiperiod and chaos.[2] A neuron under periodic external stimulus also acts as a dissipative dynamical system with two competing frequencies: the membrane potential firing rate of the neuron and the external current frequency.[3] The neuronal firing pattern reflects the external stimulus information. Studying neuronal action potential firing sequences is the foundation of neuroinformation processing research. In the past several decades, some conventional nonlinear methods, such as Lyapunov exponents, fractal dimension and Kolmogorov complexity, have been used to investigate the dynamical behavior of the neuron.[4,5] However, these methods have high computational complexity and cannot reflect the details of different firing patterns. Here, the phase return map and symbolic dynamics are introduced to explore the external stimulate information from the neuronal spike trains quantitatively.

With the help of well-developed electric techniques, neuroscience has made great development in the past half century. Especially, in 1952, Hodgkin and Huxley[6] modeled a quantitative neuron model based on ionic conductance dynamical characteristics. Nowadays, the Hodgkin–Huxley (HH) model is regarded as the most widely used model for single neuron dynamics studies. As a physical model, the HH model is still considered to be complicated. It is composed of several nonlinear differential equations. Our quantitative knowledge about high-dimensional nonlinear differential equation model is very meager.[1,7] In order to analyze these models, the complexity of the models must be reduced. The map method captures the dynamics of interest from the system while affording substantial simplification from the original differential equations, which makes it one of the most important methods to reduce the dimensions of these models.[8,9]

Return map is a commonly used tool to analyze a nonlinear dynamic system. Through a set of discrete time steps, the dynamical process of a continuous differential equation model is recorded by a string of time series signals. Reconstructing the signals with the iterating operation, we can obtain a one-dimensional (1D) return map of the complicated model. Several classic nonlinear dynamic systems have been investigated by the return map in the past three decades. Examples include Lorenz equations, the Rössler system and Van der Pol system. These results all show that using a return map is much easier to identify periodic, quasiperiodic and chaotic solutions than a cumbersome numerical integration of the differential equations.[10–12]

Symbolic dynamics is a kind of coarse-grained description of a dynamic process. The coarse-grained description does not mean rough or inaccurate; on the contrary, using a finite number of symbols, the states or the parameters of the

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dynamical system can be estimated sensitively and precisely. Zheng[13] and Hao[14] introduced the symbolic dynamics as a powerful tool to study the bifurcations and chaos of the 1D map. With the monotonicity of the 1D map, the "state space" is divided into several regions. Each region is labeled by a letter or symbol. This operation ignores the actual number in the map set, but retains the essential feature of the time evolution of the map. The numerical calculation results of some 1D maps show that the order of the parameter values is equal to the order of the kneading sequences.[15–17]

In this paper, we investigate the neuronal coding of an HH neuron under periodic current stimulus. Firstly, the 1D return map of the HH model is obtained through the stroboscopic sampling of the membrane potential. Secondly, using the symbolic dynamics, the dynamic process of the return map is described by several kinds of symbols. In this step, the firing pattern of the neuron is transformed into the symbolic sequence. Finally, the neuronal coding and neural information process mechanisms are studied by ordering the symbol sequences. The rest of this paper is organized as follows. In Section 2, the HH neuron model, the basic concepts of a return map and the symbolic dynamics of neuronal coding analysis are briefly introduced. In Section 3, the results of the numerical calculation and how the symbolic sequences identify the amplitude or the frequency of the input current are presented. Finally, a discussion of the results is given in Section 4.

2. Model and method

2.1. The HH model under periodic current stimulus

The HH model consists of the following ordinary differential equations:

$$\begin{aligned} C\dot{V} &= I_{\rm EXT} - \bar{g}_{\rm K} n^4 (V - E_{\rm K}) \\ &\quad - \bar{g}_{\rm Na} m^3 h (V - E_{\rm Na}) - g_{\rm L}(V - E_{\rm L}), \\ \dot{n} &= \alpha_n(V)(1-n) - \beta_n(V) n, \\ \dot{m} &= \alpha_m(V)(1-m) - \beta_m(V) m, \\ \dot{h} &= \alpha_h(V)(1-h) - \beta_h(V) h, \end{aligned} \tag{1}$$

where n is the activation variable for a potassium ion; m is the activation variable for a sodium ion, h is the inactivation variable for a sodium ion; V represents the membrane potential of the neuron in mV; C is the membrane capacitance of the neuron; $I_{\rm EXT}$ is the applied current; the parameters $E_{\rm K}$, $E_{\rm Na}$ and $E_{\rm L}$ represent the Nernst equilibrium potentials of potassium, sodium and a leak current respectively; $\bar{g}_{\rm K}$, $\bar{g}_{\rm Na}$ and $g_{\rm L}$ are the maximal conductances of the corresponding ion channel; and functions $\alpha(V)$ and $\beta(V)$ describe the transition rates between open and close states of the channels. $\alpha(V)$ and $\beta(V)$ are the nonlinear functions of V. The expressions are described as follows:

$$\begin{aligned} \alpha_n(V) &= 0.01(10-V)/(\exp((10-V)/V)-1), \\ \beta_n(V) &= 0.125\exp(-V/80), \\ \alpha_m(V) &= 0.1(25-V)/(\exp((25-V)/10)-1), \\ \beta_m(V) &= 4\exp(-V/18), \\ \alpha_h(V) &= 0.07\exp(-V/20), \\ \beta_h(V) &= 1/(\exp((30-V)/10)+1). \end{aligned} \tag{2}$$

In the numerical calculation, the external current $I_{\rm EXT}$ is a periodic rectangular wave signal. Its expression is defined as follows:

$$I_{\rm EXT} = \begin{cases} 0, & \mod(t,T) > W \cdot T, \\ A, & \mod(t,T) \le W \cdot T. \end{cases} \tag{3}$$

In this expression, A is the amplitude of the current, T is the period of the current and W is the duty cycle.

2.2. Phase return map of the HH model

Given the appropriate parameters of the input current, the neuron generates a series of action potentials or spikes (see Fig. 1(a)). The shapes of action potentials are similar to each other. It is difficult to analyze the neural information from the shape of the action potential. Many neurophysiologists and brain scientists consider that the neural information is encoded by the interval of adjacent neuronal spikes[18–20] (inter-spike interval (ISI)). In this section, the return map is introduced to study the ISI of the neuronal spike trains. The variable θ_n represents the phase of the external current stimulation sampled stroboscopically at the spike of each action potential (see Fig. 1(b)). The continuous membrane potential signal is recorded by a discrete-time phase sequence with the stroboscopic operation. We use θ to denote the phase sequence $(\theta_1, \theta_2, \ldots, \theta_n)$. The phase shift function is defined as $\theta_{n+1} = FS(\theta_n)$. This shift function builds a 1D iteration map of the neuron. We define it as the phase return map of the HH neuron.

The phase return map describes the dynamic process of the HH neuron simply. With the help of the return map, the dynamical states include phase-locking, a quasiperiod and chaos, which can be easily observed from the phase shift map, as shown in Fig. 1(c). According to the KAM theorem, if the return map is invertible, there is no chaos (see Figs. 2(a) and 2(b)).[21] If the dynamical state is chaotic, the return map is irreversible (see Fig. 2(c)). When there are finite points on the return map, the dynamical state of the HH neuron is phase-locking (see Fig. 2(a)). In Fig. 2(b), there are infinite points on the map and the map is invertible, the dynamical state is quasiperiodic.

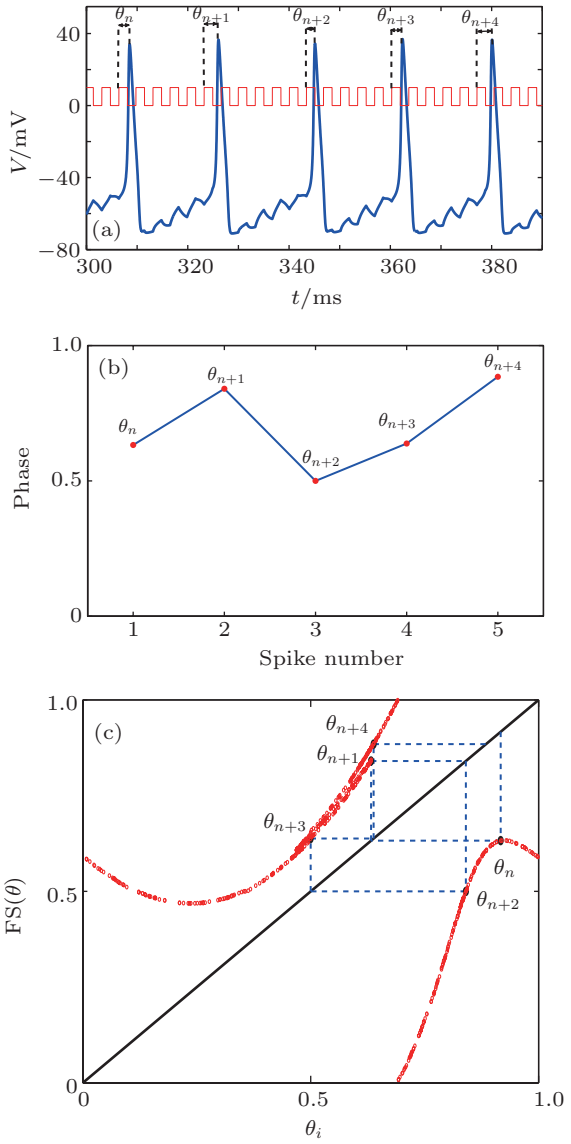


Fig. 1. (color online) Phase return map of the HH neuron. (a) The input periodic current stimulus and the membrane potential of the neuron, θ_i is the phase of the i-th neuron spike in the periodic drive current. (b) The phase sequence of the neuron spike. The phase has been normalized by the current period T. (c) The phase return map of the phase sequence in Fig. 1(b).

2.3. Symbolic dynamics of the HH neuron

With the phase return map operation, the HH neuron is described by a 1D discrete-time map. Symbolic dynamics is a powerful tool to analyze a 1D dynamical system.[22–24] The basic idea of symbolic dynamics is to compute the itineraries of orbits according to the regions of the topological partition in the phase place. X is used to represent the phase topological space, which is composed of a finite collection $P = \{P_1, P_2, \ldots, P_m\}$ of mutually disjoint sets $X = \bigcup_{i=1}^{m} P_i$. Dividing the phase space (X) into a finite collection (P_i) based on the discontinuous point and the monotonicity of the phase return map. We take Fig. 1(c) for example. The map of Fig. 1(c) is a piecewise-continuous map. According to the monotonicity and critical point, the phase space is divided into four regions (P_1, P_2, P_3, P_4), as shown in Fig. 2(c). Each region is labeled by a letter. From left to right, they are M, L, R, N. M and N represent the monotonically decreasing branch. They are assigned to odd parity. Whereas L and R have even parity. The parity of a symbolic sequence is determined by the number of letters M and N it contains. The natural order of single symbols is

$$M < L < R < N. \tag{4}$$

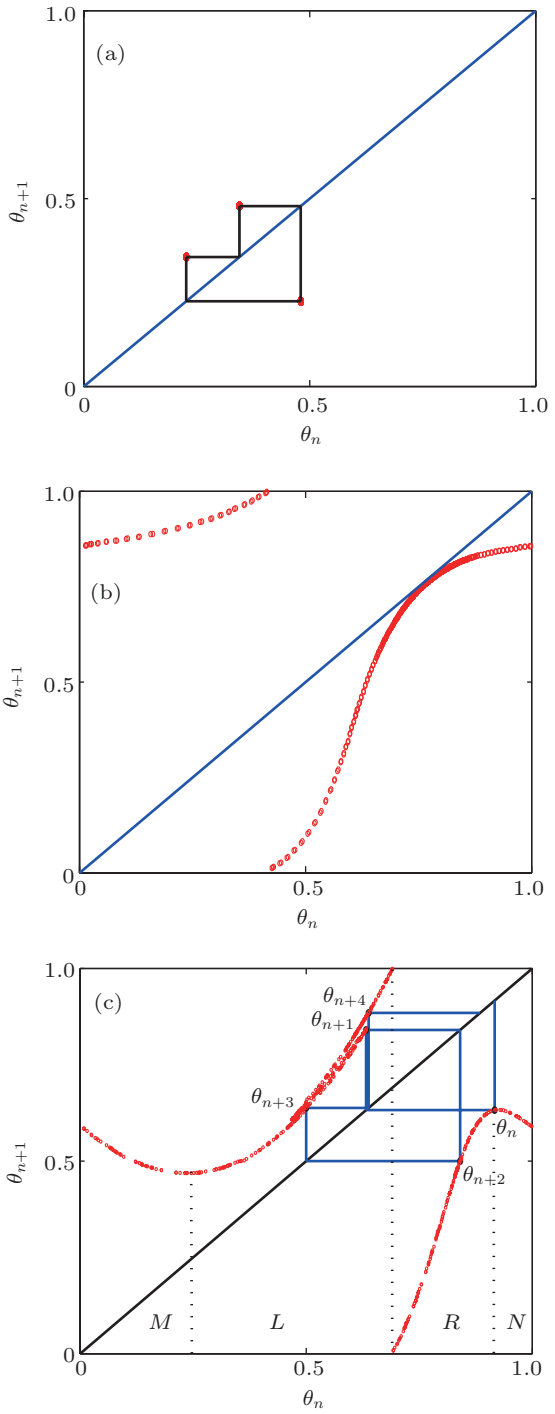


Fig. 2. (color online) Phase return maps under different dynamical states: (a) phase-locking, (b) quasiperiod, (c) chaos. According to the monotonicity of the return map, the phase space is divided into four regions. Each region is labeled by one symbol.

Consider two symbol sequences $S_1 = C^*\alpha\ldots$ and $S_2 = C^*\beta\ldots$, where C^* denotes their common leading symbol and $\alpha \neq \beta$. If the parity of C^* is even, the order of these two symbol sequences is equal to the natural order of α and β. If the parity of C^* is odd, the order is the anti-order of α and β.

$$S_1 > (<) S_2, \quad \text{if } \alpha > (<)\beta \text{ when } C^* \text{ is even}, \tag{5}$$

$$S_1 > (<) S_2, \quad \text{if } \alpha < (>)\beta \text{ when } C^* \text{ is odd}. \tag{6}$$

The neuronal spike trains can be considered as the dynamical itinerary on the return map. With the transformation of symbol sequences, the spike trains are ordered by the parameters of the external stimulus. Figures 2(a) and 2(b) are the degenerated forms of Fig. 2(c). The ordering rule described in expressions (4), (5), and (6) also holds true in Figs. 2(a) and 2(b). The only difference is that symbols M and N are missing in Figs. 2(a) and 2(b).[24–26]

In the above section, we introduced the ordering rule based on the monotonicity of the return map. In fact, it needs enough neural spikes to reach the monotonous zones and critical points of the return map. In order to avoid this defect, a new symbolic method is proposed according to the rotation of the return map.

Definition (winding number) The winding number is the mean number of rotations per iteration. In other words, it is the number of stimulus cycles between the adjacent spikes, which is expressed as

$$W_n = \mathrm{fix}(t_{n+1}/T) - \mathrm{fix}(t_n/T), \tag{7}$$

where t_n is the time of n-th neural spike and T is the period of the input current stimulus. The function $\mathrm{fix}(a)$ returns the integer parts of a. The phase return map contains one discontinuous point. All points on the left side of the discontinuous point have the same winding number (W_L). All points on the right side of the discontinuous point have the other winding number (W_R). The relationship between the phase and the winding number is shown in Fig. 3. The natural order of the winding number symbols is that

$$W_\mathrm{L} < W_R. \tag{8}$$

Given two winding number symbol sequences, $WS_1 = C^*\alpha$ and $WS_2 = C^*\beta$, where C^* denotes their common leading symbol and $\alpha \neq \beta$, the order of these two symbol sequences is

$$WS_1 > (<) WS_2, \quad \text{if } \alpha > (<)\beta. \tag{9}$$

The ordering rule based on the winding number is suitable not only for periodic and quasiperiodic solutions, but also for chaos.

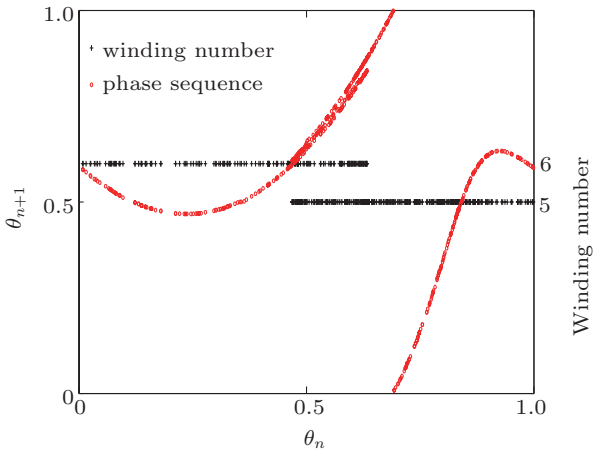


Fig. 3. (color online) Relationship between the phase and the winding number on the phase return map. The discontinuous point of the phase trajectory is identical to the discontinuous point of the winding number.

3. Results

To explore the dynamical state of the HH neuron under periodic current, we study the model through the numerical simulation. The simulation is implemented using the fourth order Runge–Kutta method. The parameters of the HH neuron are shown in Table 1. The initial conditions of the model for all simulations are the same. The initial values are the resting values of the system variables when the HH neuron is silent. The different dynamical states of the HH neuron are investigated via the ISI bifurcation diagram and phase return map. The parameters of the current stimuli are estimated or measured via symbolic dynamics.

Table 1. Parameters for the HH neuron model.

Parameters	Values
C/μF·cm^{-2}	1
$\bar{g}_\mathrm{K}$/ms·cm^{-2}	36
$\bar{g}_\mathrm{Na}$/ms·cm^{-2}	120
g_L/ms·cm^{-2}	0.3
E_K/mV	–71.967
E_Na/mV	54.98
E_L/mV	–49

3.1. Inter-spike interval (ISI) bifurcation diagram

In Eq. (3), the waveform of the external current is determined by three parameters (A, T, W). The amplitude of the current (A) is chosen to be 10 μA. The width of the current waveform is set to be 50%. The period changes from 3 ms to 20 ms. Figure 4(a) shows the ISIs under different periodic current stimuli.

For extremely long periods of the input current, the neuron exhibits periodic bursting. For a long period of the inputs (13 ms–20 ms), the neuron exhibits periodic firing. Also, this periodic firing exists in the period ranges from 6.3 ms to 9.6 ms, from 4.6 ms to 5.5 ms, etc. In the period range from

10 ms to 13 ms, the neuron exhibits multiperiodic oscillator. The firing patterns are aperiodic and irregular when the input period changes from 3.3 ms to 4.5 ms. In some narrow period ranges, the period-double bifurcation is found. In order to study the relationship between the external force frequency (current period) and the model intrinsic frequency (firing rate), the phase sequences under different period stimuli are plotted in Fig. 5. In Fig. 5, the phase-locking range corresponds to the period or multiperiodic oscillation range in Fig. 4.

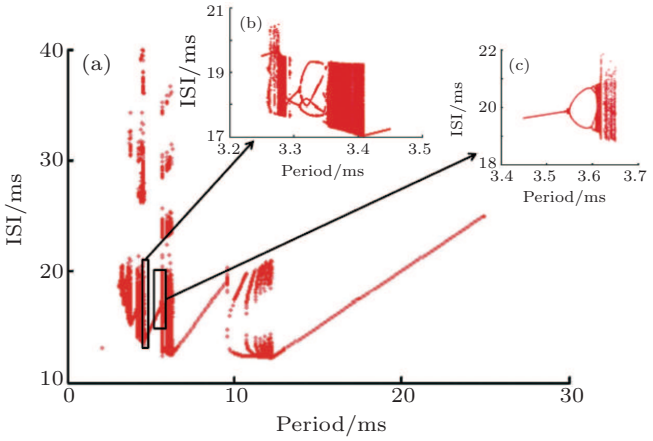


Fig. 4. (color online) ISI bifurcation diagrams under different periods.

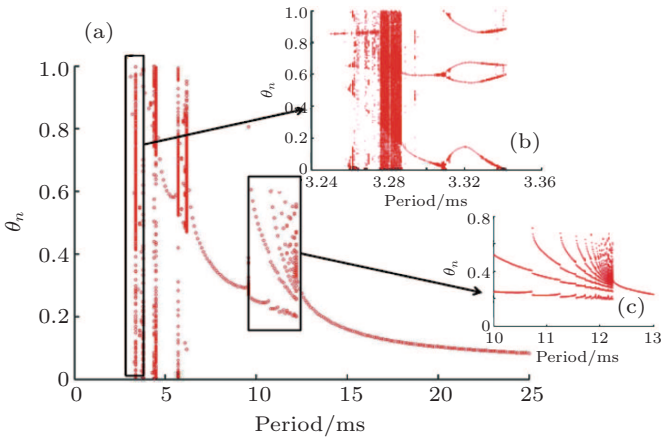


Fig. 5. (color online) Phase sequence diagrams under different periods.

3.2. Phase return maps under different periods

In the ISI sequence figure or the phase sequence figure, it is difficult to find out some orders in the chaos ranges. In the input period range from 3.0 ms to 20 ms, the neuron fires with an irregular pattern. It includes chaos, quasiperiod and phase-locking. These dynamical states can be easily analyzed using the phase return map. The coordinates of the first 25 points are rejected in Fig. 6.

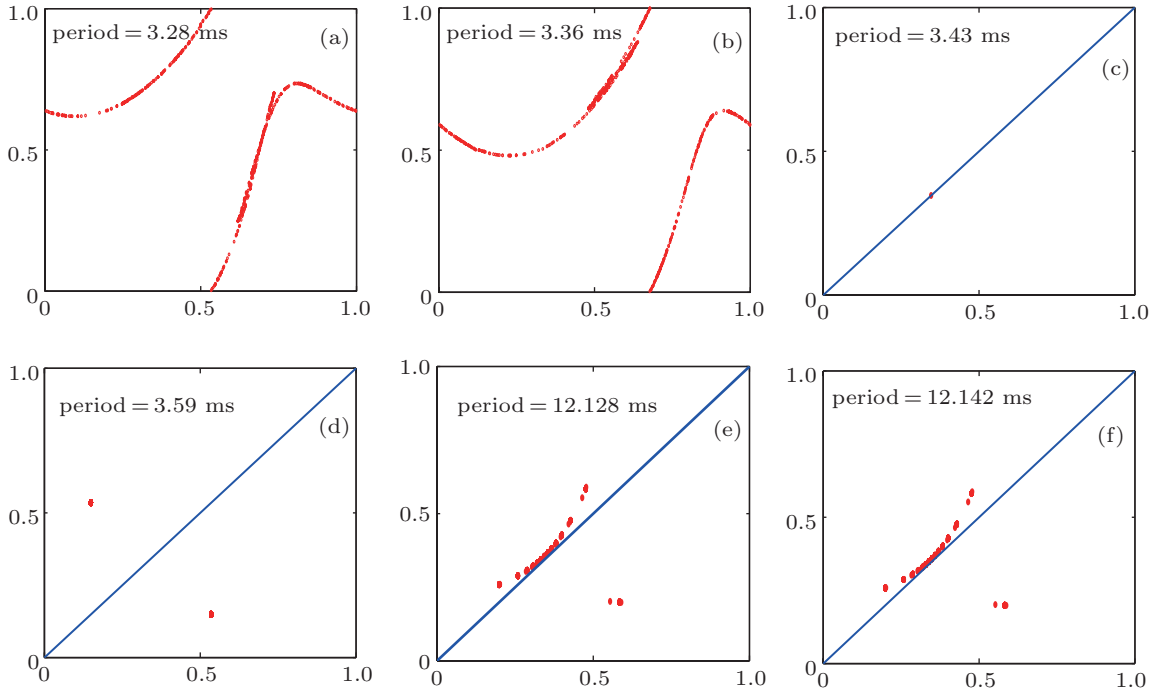


Fig. 6. (color online) Phase return maps under different periods. The parameters of the external current stimuli are $A = 10$ μA, $W = 50\%$. (a) $T = 3.28$ ms, chaos. (b) $T = 3.36$ ms, chaos. (c) $T = 3.43$ ms, phase-locking. (d) $T = 3.59$ ms, phase-locking. (e) $T = 12.128$ ms, quasiperiod. (f) $T = 12.142$ ms, quasiperiod.

The return map captures the interesting dynamical features of the spiking neuron. From the trajectory on the phase return map, the dynamical states can be easily distinguished. The chaotic trajectory of the HH neuron is simply described on the phase return map. More importantly, the phase return map reveals some orders when the neuron works in a chaotic

motion. According to the monotonicity and the discontinuous point on the return map, the external force strength is described qualitatively via the symbolic dynamics.

3.3. Using symbolic dynamics to measure the model parameters

The phase return map records the trajectory of the neuron motion on the 1D map. According to the principle of the 1D symbolic dynamics introduced in Subsection 2.3, we can describe the neuronal spike trains through the symbolic sequences. The motion of the HH neuron is chaotic when the period range of the input current is from 3.28 ms to 3.38 ms. The shape of the phase return map in this range is similar to that of the map shown in Fig. 6(a). The symbol sequences of these periodic stimuli are listed in Table 2.

Table 2. Symbolic sequences under different periods stimuli.

Periods/ms	Symbolic sequences
3.378	*R M L L R L L L R L L*
3.376	*R M L L R L L* ***R*** *M L L*
3.374	*R M L L R L L* ***N*** *L R L*
3.372	*R M L L R L* ***R*** *L L L R*
3.370	*R M L L R L R L L* ***R*** *M*
3.368	*R M L L* ***N*** *L R L L R L*
3.366	*R M L L N L R L L R* ***M***
3.364	*R M L* ***R*** *M L R L L L N*

The symbols which are marked as both bold and underlined letters in the whole table are the first different symbols between the neighboring symbolic sequences. The ordination of these symbolic sequences is obvious according to the ordering rule defined in expression (5). The relationship between the symbolic sequence and the period of the external current is monotonically ascending. When the period of the external current is bigger, the symbolic sequence is bigger. The results show that the symbolic sequences are very sensitive to the change of the stimulus parameter. With this characteristic, the parameter of the external force or model can be effectively estimated through several symbols.

The symbolic sequences can also reflect the small changes of the other parameters of the periodic current. Table 3 shows the symbolic sequences under different amplitudes (A) of the current. Table 4 shows the symbolic sequences under different values of duty cycle (W). The periods of the external current in these simulations are all 3.4 ms. The results in Tables 2–4 are obtained from the symbolic method according to the monotonicity of the phase return map. The symbolic method based on the winding number is also suitable for the estimation of model parameters. Table 5 shows the symbolic sequences generated from the winding number defined in expression (3), which implies that by using the winding number symbolic sequences, the model parameters can also be measured. However, its sensitivity or resolution is lower than when using monotonicity to divide the symbols.

Table 3. Symbolic sequences under different values of A.

A/μA	Symbolic sequences
10.4	*L L L L L L L L L L L L L R*
10.2	*L L L L L L L L L* ***R*** *L L L*
10	*L L L L L* ***R*** *M L L L L L L*
9.98	*L L* ***R*** *M L L R M L L L L*
9.96	*L* ***R*** *L L L L L R M L L L L*
9.94	***R*** *M L L L R M L R M L R*
9.92	*R* ***R*** *M M R M M N M N M*

Table 4. Symbolic sequences under different values of W.

W	Symbolic sequences
50.4	*L L L L L L L L L L L L*
50.2	*L L L L L L L L L L* ***R*** *L*
50.0	*L L L L L* ***R*** *M L L L L L*
49.8	*L L* ***R*** *L L L L L L R M L*
49.6	*L* ***N*** *L R M L L L L R L L*
49.4	*L N L* ***N*** *L R L L L R L N*
49.2	*L N L N L* ***N*** *M L N M L N*

Table 5. Winding symbolic sequences under different periods.

Periods/ms	Symbolic sequences
3.378	5 6 5 5 5 6 5 5 5 6 5 5
3.376	5 6 5 5 5 6 5 5 **6** 5 5 5
3.374	5 6 5 5 5 6 5 5 6 5 **6** 5
3.372	5 6 5 5 5 6 5 **6** 5 5 5 6
3.370	5 6 5 5 5 6 5 6 5 5 **6** 5
3.364	5 6 5 5 **6** 5 5 6 5 5 5 6
3.355	5 6 5 5 6 5 5 6 5 5 **6** 5

4. Discussion

In the conventional study of neuronal spike trains, the ISI bifurcation diagram, entropy and other statistical methods are used to investigate the information coding of the nervous system.[27,28] However, these methods can only distinguish the dynamical states in several classes, with a long computing simulation. In this paper, the dynamical states of the Hodgkin–Huxley neuron under periodic forcing are investigated quantitatively with the help of a phase return map and symbolic dynamics. The numerical simulation shows that with a phase return map, we could change a complicated dynamical system into a tractable problem. The phase return map is obtained from a stroboscopic sampling of the neuronal membrane potential. According to the monotonicity of the phase return map, the quasperiodic or chaotic solution of the neuron motion can be easily discriminated. With the theoretical basis of 1D symbolic dynamics, the stimulus parameters are measured by a series of symbolic sequences. Compared with conventional nonlinear analytical methods, the symbolic dynamics can distinguish the tiny difference between neuronal

fire patterns in a short time. This means that the phase return map and symbolic dynamics are proper ways to explain the strange neural coding.

In this study, we introduce two symbolic methods. One is based on the monotonicity of the trajectory on the phase return map. The other is based on the winding number. Both of the two methods have their own advantages. The first one has higher resolution, but it needs a large number spikes to determine the knee point of the phase trajectory. The ordering rule of this method is confined to a narrow parameter space. If the number of monotonic branch changes, this ordering rule is no longer suitable. Compared with the first symbolic method, the winding symbolic method has lower resolution. However, it does not need a long simulation time to find out the discontinuous point. For each neuron spike, we obtain one winding number. The ordering rule of the symbolic dynamics based on the winding number is suitable for a wider parameter space, not only for chaotic solutions, but also for quasiperiodic and periodic solutions.

In nature, animals can perceive and cognize the external signal precisely in a short time. This function and the neuronal coding are inseparable. A phase return map and symbolic dynamics are two efficient methods to reflect the mechanism of neural information processing in the nervous system. Compared with the rate code, phase code or ISI histogram, the symbolic sequences can distinguish smaller differences among external signals in several neural spikes. This characteristic is consistent with the information encoding processing in the nervous system.

The basic ideas of these two methods are to perform dimensionality reduction and conduct a coarse-grained description. They provide an effective way to analyze a high-dimensional dynamical system quantitatively. The neuronal code of other real neurons, such as the pyramidal neuron, ganglion neuron or mitral cell, can also be investigated by the phase return map and symbolic dynamics. These two methods are robust to the waveforms of the input stimulus and the distribution of the ion channels of the neuron. In fact, these two methods are also useful in analyzing complex neural networks under periodic force stimulus. The equations of a neural network driven by a periodic current are shown as follows:

$$C\dot{V}_i = I_{\mathrm{EXT}} + \sum_{j=1}^{N} \mathrm{R_{ij}} - \bar{g}_{\mathrm{K}} n_i^4 (V_i - E_{\mathrm{K}}) - \bar{g}_{\mathrm{Na}} m_i^3 h_i (V_i - E_{\mathrm{Na}}) - g_{\mathrm{L}} (V_i - E_{\mathrm{L}}). \quad (10)$$

In this neural network, there are N neurons. The coupling current between the i-th neuron and j-th neuron is R_{ij}. I_{EXT} is considered as the external force. Selecting any neuronal spike train as the subject to analyze, this model can also be considered as a dissipative dynamical system with two competing frequencies. This is similar to the single neuron model. Through the symbolic dynamics, the parameters of the external periodic current can be measured in high resolution. This is suitable for signal measurement and analysis on neural cell-based biosensors.

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