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Dynamics analysis on neural firing patterns by symbolic approach*

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Neural firing patterns are investigated by using symbolic dynamics. Bifurcation behaviour of the Hindmarsh–Rose (HR) neuronal model is simulated with the external stimuli gradually decreasing, and various firing activities with different topological structures are orderly numbered. Through constructing first-return maps of interspike intervals, all firing patterns are described and identified by symbolic expressions. On the basis of ordering rules of symbolic sequences, the corresponding relation between parameters and firing patterns is established, which will be helpful for encoding neural information. Moreover, using the operation rule of $*$ product, generation mechanisms and intrinsic configurations of periodic patterns can be distinguished in detail. Results show that the symbolic approach is a powerful tool to study neural firing activities. In particular, such a coarse-grained way can be generalized in neural electrophysiological experiments to extract much valuable information from complicated experimental data.

Keywords: neural firing patterns, interspike interval, first-return map, symbolic sequence
PACC: 8720, 0547

1. Introduction

It is well-known that neural information is mainly transmitted and encoded by rich firing patterns, which have been frequently observed in electrophysiological experiments and simulated by a variety of neuronal models.[1,2] These firing patterns underlie all activities of the brain, including not only basic functions but also complex cognitive behaviour. Therefore, it is of significance to make clear how various firing activities are generated and how these patterns change with external stimuli varying.

For neural systems, complex nonlinear dynamic behaviour and rich bifurcation phenomena have been investigated by using many nonlinear dynamics methods.[3−5] In the conventional study of neural firing activities, time courses, Poincaré maps, Lyapunov exponents and other statistical quantities are used;[6,7] however, how to distinguish details of different firing patterns is still a complicated problem to tackle. Here the symbolic dynamics is introduced in neuronal models to explore various firing rhythms and dynamical behaviour. The motivation is that the first-return maps, $I_{n+1} = f(I_n)$ which are reconstructed from the interspike interval series (abbreviated to ISIs below) of neural firing patterns, generally take unimodal configuration.

A variety of mathematical neuronal models, such as those of Hodgkin–Huxley, FitzHugh–Nagumo, Morris–Lecar, Hindmarsh–Rose (HR) and Chay *et al*, have been constructed based on physiological experiments and theoretical analysis. In this article, the HR neuronal model as a representative example is investigated by means of symbolic dynamics. This model was presented from voltage clamp data to provide a simple description of the patterned activity observed in molluscan neurons. The contents are organized as follows. Some basic concepts of symbolic dynamics for the use of neural firing analysis are briefly introduced in Section 2. Section 3 shows how periodic and chaotic neural firing patterns are described and identified by symbolic sequences. In Section 4, dynamics analysis of firing activities is carried out by the theory of symbolic dynamics. Finally, some conclusions are given in Section 5.

2. Preliminaries on applied symbolic dynamics

The symbolic dynamics[8−10] built on the base of unimodal maps has been developed in the past

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decades, and becomes a useful tool for exploring rich and complex nonlinear phenomena of practical physical systems. For neural systems, it is known that the information is mainly encoded by ISIs of electrical pulses of action potentials. In general, it is found that the first-return map constructed by ISIs shows a unimodal shape. Hence the symbolic dynamics can be effectively applied to exploring the essence of various firing patterns in neural systems. In addition, according to the ordering rules[11] and the composition rule of $*$ product[12] of symbolic sequences, the neural dynamic behaviour can be analysed by the language of symbolic dynamics.

For some ISIs $(I_1, I_2, \ldots, I_n, I_{n+1}, \ldots)$, the maximal value I_m is marked by the symbol R. The ISI just in front of the maximum is defined as the critical value and marked by the symbol C. If I_i $(i = 1, 2, \ldots, n, \ldots)$ is less than the critical value, it is marked by the symbol L; similarly, it is denoted by R (or C) if I_i is larger than (or equal to) I_m. Initiating from the maximal ISI, the symbolic description can be written as $R\ldots$. If the sequence is $(R\ldots C)^\infty$, it indicates that the firing pattern is periodic. Chaotic patterns are described by semi-infinite symbolic sequences.

For a symbolic sequence, if the number of the symbol R is odd, the bunch is defined as an odd bunch, otherwise it is an even bunch. For two different symbolic sequences $x = x_1x_2\ldots$ and $y = y_1y_2\ldots$, if there are $x_1 = y_1, \ldots, x_n = y_n$, but $x_{n+1} \neq y_{n+1}(n \geq 1)$, the bunch $\Sigma = x_1x_2\ldots x_n = y_1y_2\ldots y_n$ is called a common bunch of x and y. Assuming the natural relation $L < C < R$, if the common bunch is an even one the ordering rules are defined as

$$x < y(x > y) \Longleftrightarrow x_{n+1} < y_{n+1}(x_{n+1} > y_{n+1}); \quad (1a)$$

while it is an odd one, the ordering relations are

$$x < y(x > y) \Longleftrightarrow x_{n+1} > y_{n+1}(x_{n+1} < y_{n+1}). \quad (1b)$$

The composition rule of $*$ product is helpful for discussing the self-similarity of periodic patterns and judging their detailed hierarchies and generation mechanisms. For finite symbolic bunches $P = p_1p_2\ldots p_m(p_i = R, L)$ and $Q = q_1q_2\ldots q_n(q_j = R, L, C)$, the $*$ product is defined as

$$P * Q = (P * q_1)(P * q_2)\ldots(P * q_n), \quad (2)$$

where

$$P * q_i = \begin{cases} (PC)_+, & (q_i = R), \\ PC, & (q_i = C), \\ (PC)_-, & (q_i = L). \end{cases} \quad (3)$$

In the above expressions, we take the following notations: if P is an even bunch there are $(PC)_+ = PR$ and $(PC)_- = PL$, whereas $(PC)_+ = PL$ and $(PC)_+ = PR$ when P is an odd one.

Applying the above approaches, the details of various firing activities can be described by corresponding symbolic sequences. The relations between different firing patterns arising from the variation of parameters can be discussed by means of ordering rules. Based on the operation rule of $*$ product, the periodic neural patterns with different topological structures and intrinsic configurations can be distinguished.

3. Symbolic expressions of periodic and chaotic neural firing patterns

As a typical example of symbolic dynamics analysis of neural firing activities, the well-known HR neuron model[13,14] is investigated, here governed by the following differential equations:

$$\begin{aligned} \dot{x} &= y - ax^3 + bx^2 - z + I, \\ \dot{y} &= c - dx^2 - y, \\ \dot{z} &= r(s(x - \chi) - z), \end{aligned} \quad (4)$$

where three variables x, y and z represent the membrane action potential, the recovery variable and the slow adaptation current, respectively. a, b, c, d, r, s, χ and I are parameters. When the external current I is treated as a control parameter to produce various firing patterns, and other parameter values are taken as $a = 1.0$, $b = 3.0$, $c = 1.0$, $d = 5.0$, $r = 0.006$, $s = 4.0$ and $\chi = -1.6$, the bifurcation diagram is constructed as ISIs vs the control parameter I (in Fig.1). This figure includes rich bifurcation phenomena which reflect the transitions of different firing patterns as follows.

(1) The period-adding bifurcation scenario is displayed on the left side of Fig.1. The system lies in a quiescent state for $I \leq 1.31$, from which P1 (period-1) bursting firing pattern is generated via a Hopf bifurcation when the parameter I increases. Subsequently, P2, P3 and P4 bursting rhythms arise one after the other with the bifurcation parameter I increasing. Finally, the P4 pattern terminates via a period-doubling

bifurcation and further leads to chaos.

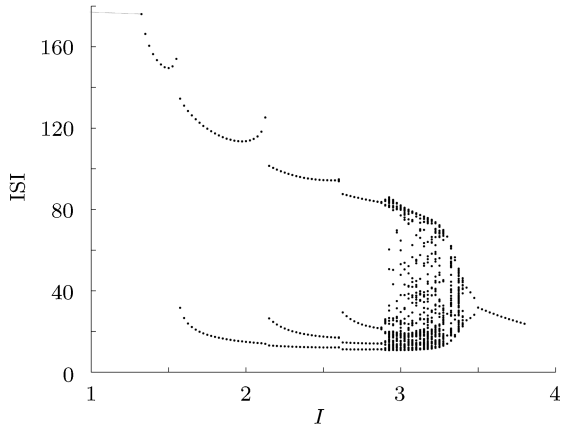


Fig.1. Bifurcation diagram constructed as ISIs vs the external current I.

(2) The right side shows the period-doubling bifurcation cascades. With the parameter I gradually decreasing, initiating from P1, the firing patterns in the form of P2, P4, P8, etc., orderly vary via a series of period-doubling bifurcations, and finally turns into chaos.

(3) There are many periodic windows coexisting in the chaos region, which occur via fold bifurcations and end through period-doubling ways. These periodic windows can be located according to the tangential positions of dark-lines (shown in Fig.2) obtained by the regression algorithm[15], and the corresponding super-stable periodic patterns are orderly arranged as P6, P5, P3, P6, P5, P6 and P4 with the bifurcation parameter I decreasing.

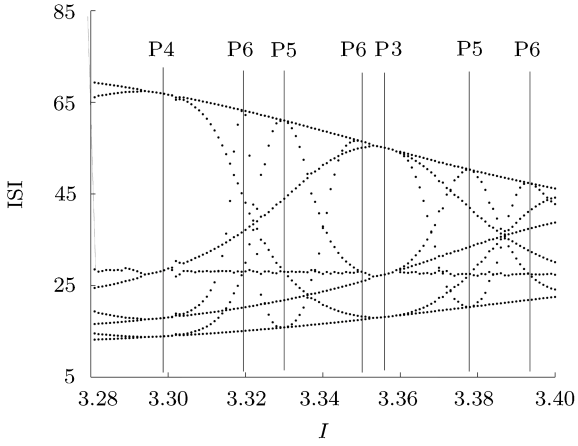


Fig.2. Dark-lines spectrum diagram in which the periodic patterns embedded in the chaos region are marked.

The periodic firing rhythms within P6 are revealed in the whole parameter range. A challenging task of how the details of these patterns with different topological structures can be symbolically identified is discussed in the following subsection.

3.1. Identifying periodic firing rhythms by symbolic sequences

For exploring the intrinsically evolving mechanisms and topological structures of neural firing patterns, these firing patterns are numbered with the parameter I decreasing. The symbolic sequences describing these patterns are shown in Table 1.

Table 1. Ordering periodic firing rhythms within P6.

No.	Firing pattern	parameter I	ISI series	Symbolic sequence
1	P1	3.800	23.8094	C
2	P2	3.450	26.5908, 39.2934	*RC*
3	P4	3.420	26.0421, 42.6914, 24.6649, 41.2470	*RLRC*
4	P6	3.393	27.6134, 47.4109, 21.8230, 37.3544, 32.6836, 41.0902	*RLRRRC*
5	P5	3.378	27.5058, 50.3204, 20.3018, 33.4521, 41.9265	*RLRRC*
6	P3	3.355	27.2437, 55.2504, 18.0560	*RLC*
7	P6	3.352	27.3515, 55.9672, 17.7554, 26.4483, 55.3631, 18.0663	*RLLRLC*
8	P5	3.330	27.9995, 61.0252, 15.8305, 21.8007, 43.9659	*RLLRC*
9	P6	3.31929	28.0050, 63.2602, 15.0677, 20.1691, 36.7368, 44.5223	*RLLRRC*
10	P4	3.298	28.0722, 67.0119, 13.8749, 17.8336	*RLLC*
11	P6	3.241	29.1059, 72.8447, 12.1713, 14.9073, 20.4543, 48.0516	*RLLLRC*
12	P6	2.97778	32.7030, 80.2195, 10.8305, 13.1396, 17.8493, 65.3067	*RLLLRC*
13	P4	2.800	22.4064, 84.5314, 11.1844, 14.1249	*RLLC*
14	P3	2.300	20.1586, 96.9293, 12.5375	*RLC*
15	P2	1.800	17.3574, 117.3687	*RC*
16	P1	1.400	156.3795	*C*

From Table 1 we can see that some firing patterns have the same periodicity, but they are denoted by different symbolic sequences which represent their distinct topological structures, such as the P4 patterns of No.3 and No.10, the P5 patterns of No.5 and No.8, and also the P6 patterns of No.7, No.9 and No.11; However, some patterns are provided by the same symbolic expressions, for instance, P1 rhythms of No.1 and No.16, the P2 ones of No.2 and No.15, the P3 ones of No.6 and No.14, the P4 ones of No.10 and No.13, and the P6 ones of No.11 and No.12. Therefore, it is interesting to study their detailed intrinsic relationships and dynamical mechanisms later in Section 4.

3.2. Symbolic description of chaotic firing rhythms

Similarly, some chaotic firing rhythms can be described by semi-infinite symbolic sequences. From the chaos region, the parameter values are taken as $I = 3.395, 3.385, 3.365, 3.340, 3.325, 3.305$. The first-return maps of ISIs are constructed and shown in Fig.3, with the corresponding symbolic expressions given in Table 2.

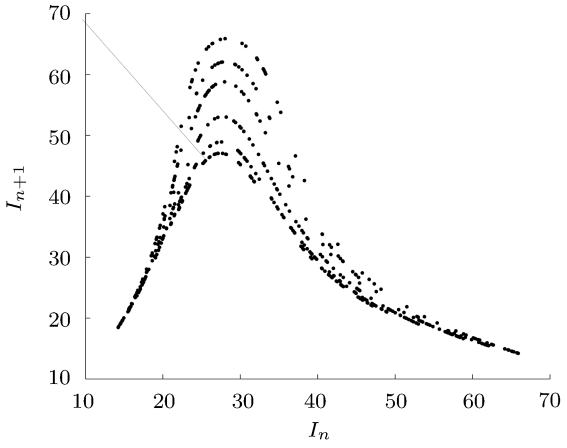


Fig.3. The first-return maps constructed by ISIs of neural chaotic firing rhythms, with a perfect unimodal shape. From the bottom to the top, six curves correspond to the parameter values $I = 3.395, 3.385, 3.365, 3.340, 3.325, 3.305$, respectively.

Table 2. Symbolic expressions of chaotic firing rhythms.

No.	Parameter	Symbolic sequences
1	3.395	$RLRRRLRLRRRLRLRL\ldots$
2	3.385	$RLRRRRRRLRRRRLRRR\ldots$
3	3.365	$RLRRLRRLRLRLRLRL\ldots$
4	3.340	$RLLRLRRRRRLLRLLR\ldots$
5	3.325	$RLLRRRLRRRRLLRRR\ldots$
6	3.305	$RLLRRLLRRLLRLLRL\ldots$

For these chaotic patterns, graphical description of time courses and phase space configurations is less valuable to accurately distinguish their topological structures. In what follows, it is indicated that chaotic firing rhythms can be effectively identified by corresponding symbolic sequences. The inherent dynamic features of the chaotic patterns will be also analysed by the symbolic approach in Section 4.

4. Dynamics analysis of neural firing patterns

4.1. Relationship between parameters and symbolic sequences

According to the ordering rules of symbolic sequences introduced in Section 2, the relations between parameters, which denote the external stimuli, and symbolic sequences of ISIs encoding neural firing activities are explored. The executing approach comparing symbolic sequences is illustrated through several examples. (1) Comparing the P4 pattern (No.3 in Table 1, with $RLRC$ and $I = 3.420$) and the P5 pattern (No.5 in Table 1, with $RLRRC$ and $I = 3.378$), the common bunch RLR is even, so the relation $C < R \Longrightarrow RLRC < RLRRC$ is satisfied. (2) For the chaotic patterns of No.2 (with $RLRRRRRR\ldots$ and $I = 3.385$) and No.3 (with $RLRR\ LRRL\ldots$ and $I = 3.365$) in Table 2, the common bunch $RLRR$ is odd, so the relation is $R > L \Longrightarrow RLRR\ RRRR\ldots < RLRRLRRL\ldots$. (3) The ordering rules are likely to be used to compare periodic pattern in Table 1 and chaotic pattern in Table 2. For example, the periodic pattern $RLRRC$ at $I = 3.378$ is larger than the chaotic one at $I = 3.385$, and less than the sequence at $I = 3.365$.

Applying the above ordering approach, it is found that for the symbolic sequences describing periodic patterns from No.1 to No.11 in Table 1 and chaotic patterns in Table 2, the order increases with the external parameter I gradually decreasing. Such corresponding relationship between parameters and symbolic sequences is valid in the parameter range where periodic and chaotic patterns alternately occur. Thus, parameter values, firing patterns and symbolic sequences can be associated together. As ISIs are measured from electrophysiological experiments or simulated by mathematical models, the corresponding symbolic sequence can be easily obtained by means of

symbolic dynamics. No matter whether the sequence is periodic or chaotic, its position in the parameter region can be approximately fixed, and further the relation between external stimuli and neural activities is determined.

4.2. Symbolic structure of chaotic attractor

As is known, the phenomenon that chaos is extremely sensitive to initial values is one of the primary properties in nonlinear systems. A tiny variation of initial condition can induce completely different evolving routes. It is challenging how to depict such different chaos structures. Especially for neural systems, at each moment the cellular activities are affected by changes of external circumstance and ceaseless metabolism, so the firing patterns are more diverse and complex. The structural details of different chaotic firing patterns can be effectively expressed through the symbolic sequences.

For the HR neuronal model, at the bifurcation parameter $I = 3.365$, the chaotic firing rhythm with the symbolic description $RLRRLRRL\ RLRL\ RLRL\ RLRL\ RRLR\ldots$ is simulated by the initial values (0,0,0). With the initial values (0.001,0,0) and the same other conditions taken, a chaotic pattern is obtained, which corresponds to $RLRR\ LRRL\ RLRL\ RLRR\ LRRR\ LRLR\ldots$. With less variation of the initial values, e.g. $(0.00001, 0, 0)$, the chaotic firing pattern is symbolically described as $RLRR\,LRRL\,RLRL\,RLRR\,RRRL\,RLRR\ldots$. The three patterns are compared by the time courses of variables x and z, which are shown in Fig.4.

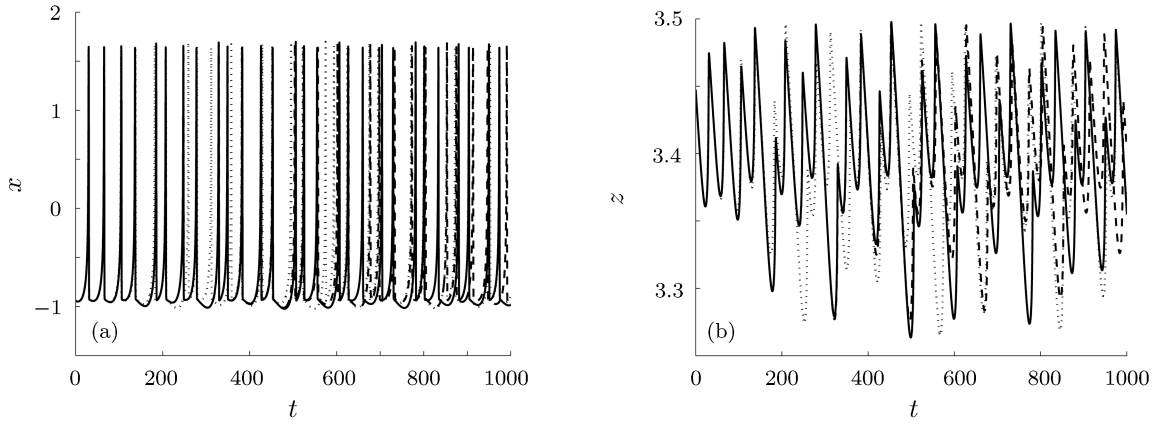


Fig.4. The time courses of variable x (a) and z (b) for three chaotic firing patterns with different initial values. The dotted $(\cdots)$, dashed $(--)$ and solid $(-)$ curves correspond to the initial values $(0, 0, 0)$, $(0.00001, 0, 0)$ and $(0.001, 0, 0)$, respectively.

For these chaotic patterns, their first-return maps constructed by ISIs display the same trace (not shown here). However, in Fig.4 it is noted that their structural details are different. The difference between these chaotic patterns can be effectively described by the corresponding symbolic sequences.

4.3. Generation mechanisms and intrinsic configurations of periodic firing patterns

Not only neural firing pattern can be depicted and identified by symbolic sequences, but also the bifurcation ways via which the periodic patterns are generated can be judged by the operation rule of $*$ product. If a symbolic sequence describing some firing pattern can be written as the format $P*RC$ or $P*LC$ (where the symbolic bunch P is made up of R and L), the pattern is generated via a period-doubling bifurcation of the pattern with PC. If some sequence cannot be decomposed into such an expression of $*$ product, it generally comes from a fold bifurcation.

For the periodic firing rhythms in Table 1, certainly it is impossible that P3 and P5 patterns occur through period-doubling bifurcations. We mainly focus on the generation mechanism of the P4 and P6 patterns. No.3 pattern (P4 with $RLRC$) can be written as $R*RC$, which means that this pattern is period-doubling from P2 pattern with RC. Moreover, No.7 pattern (P6 with $RLLRLC$) satisfies the relation $RL*RC$, which indicates that this P6 pattern is generated via a period-doubling bifurcation of P3 pattern

with RLC. It is found that except this P6 pattern the other P6 ones are generated via fold bifurcations.

Furthermore, the patterns of No.4, No.7, No.9 and No.11, which have the same periodicity P6 but are provided by distinct topological structures and symbolic sequences, are graphically compared by the time courses of the membrane potential x in Fig.5. The intrinsic configuration of these periodic rhythms can be imaged through the elementary words decomposed from the symbolic sequence. (1) No.4 firing rhythm ($RLRRRC = R * RLC$) indicates that it is a period-3 pattern with RLC embedded in the chaos region with two patches. (2) No.7 pattern with $RLLRLC = RL * RC$ is period-doubling from the P3 pattern in the one-patch chaos region. (3) No.9 pattern with $RLLRRC$ and No.11 one with $RLLLRC$, which cannot be decomposed into any format of $*$ product, are embedded in the one-patch chaos region.

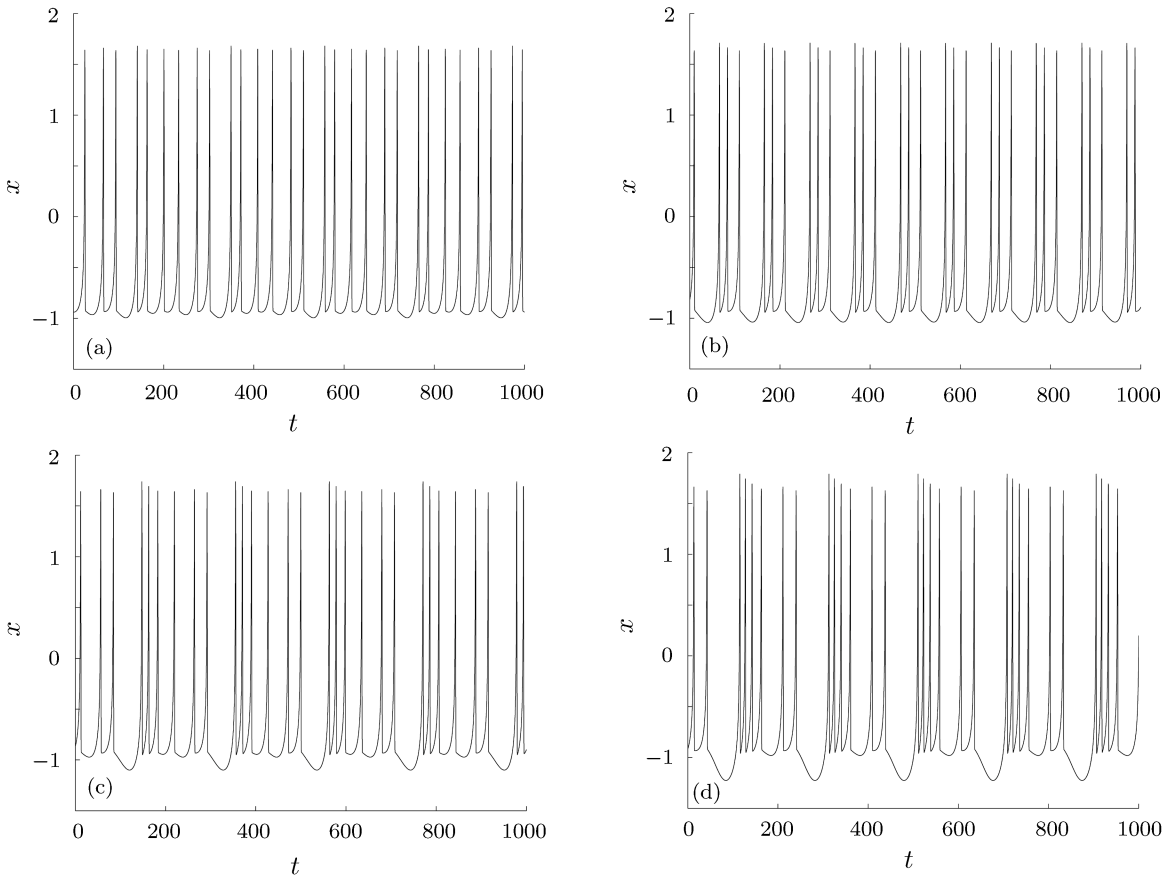


Fig.5. The time courses of different P6 patterns at $I = 3.393$ ($RLRRRC$) (a), $I = 3.352$ ($RLLRLC$) (b), $I = 3.31929$ ($RLLRRC$) (c), and $I = 3.241$ ($RLLLRC$) (d), respectively.

4.4. Genesis of periodic bursting firing patterns

For the periodic firing rhythms described by the same symbolic expressions, their time courses are provided with similar structural features, such as No.12 and No.11, No.13 and No.10, No.14 and No.6, No.15 and No.2, and also No.16 and No.1. However, it should be noted that the patterns from No.12 to No.16 show bursting behaviour, while the No.11, No.10, No.6, No.2 and No.1 display spiking behaviour. So it is suspected that the periodic bursting patterns from No.12 to No.16 on the left of the bifurcation diagram in Fig.1 are closely related to the spiking patterns with the same symbolic sequences as theirs, which either exist in the period-doubling cascades or are embedded in the chaos region. The problem will be further studied to clarify the explanation for the genesis of period-adding bursting firing patterns in Ref.[16].

5. Conclusions

In the present work, various bifurcation phenomena and complex behaviour have been found with

the bifurcation parameter changing, such as period-adding bifurcations, period-doubling cascades, and also periodic windows embedded in the chaos region. These aspects are investigated in detail by means of symbolic dynamics, and some conclusions are drawn as follows.

(1) For various firing patterns, either periodic or chaotic, their ISIs can be effectively described and identified by different symbolic sequences. Hence, the dynamics analysis of these firing patterns can be performed in the context of symbolic dynamics.

(2) According to the ordering rules of symbolic sequences, the corresponding relation between parameters of external stimuli and firing patterns of neural activities is revealed. In the further work, some quantitative definitions, such as topological entropy and complexity index, will be investigated by the formal language, and it means that the symbolic dynamics may be applied to encoding the neural information.

(3) The structural details of chaotic firing patterns can be rigorously expressed by symbolic sequences. It is significant to identify the complex firing activities of chaos for implementing pharmacological experiments and encoding neural information.

(4) Based on the operation rule of $*$ product, the generation mechanisms and intrinsic configurations of periodic firing patterns can be discussed by the symbolic dynamics.

In a word, the symbolic dynamics is a powerful tool for studying neural firing activities, no matter which are measured in electrophysiological experiments or simulated by mathematical models.

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