

# Trajectory Segmentation and Symbolic Representation of Dynamics of Delayed Recurrent Inhibitory Neural Loops\*

Jianfu Ma<sup>1</sup> and Jianhong Wu<sup>1,†</sup>

**Abstract** We develop a general symbolic dynamics framework to examine the dynamics of an analogue of the integrate-and-fire neuron model of recurrent inhibitory loops with delayed feedback, which incorporates the firing procedure and absolute refractoriness. We first show that the interaction of the delay, the inhibitory feedback and the absolute refractoriness can generate three basic types of oscillations, and these oscillations can be pinned together to form interesting coexisting periodic patterns in the case of short feedback duration. We then develop a natural symbolic dynamics formulation for the segmentation of a typical trajectory in terms of the basic oscillatory patterns, and use this to derive general principles that determine whether a periodic pattern can and should occur.

**Keywords** Multistability, periodic pattern, neural network, time delay, pattern formation, recurrent inhibitory loops.

**MSC(2010)** 34K13, 34K18, 92B20.

## 1. Introduction

We propose to develop a theoretical framework that allows us to reformulate the delayed feedback as an induced action on a segment of symbols, so we can develop a systematic approach to look at the co-existence of multiple stable periodic oscillations in network of neurons with delayed feedback. For this purpose, we start with a recurrent inhibitory loop that consists of an excitatory neuron  $E$  and an inhibitory neuron  $I$ , where neuron  $E$  gives off collateral branches and excites the inhibitory neuron  $I$ , which in turn inhibits the firing of neuron  $E$ , in a delay time. The incorporation of time delays is necessary, as these are intrinsic properties of both biological and artificial loops due to axonal conduction times, distances of interneurons, the finite switching speeds of amplifiers and the passive propagation of potentials down the dendrites of neurons [6, 7, 21, 22, 24, 28, 29].

The simple recurrent inhibitory loop and its represented coupled network of neuron populations have been used to study how the interaction of the excitatory

---

<sup>†</sup>the corresponding author.

Email address: [jianfu@gmail.com](mailto:jianfu@gmail.com)(J. Ma), [wujh@yorku.ca](mailto:wujh@yorku.ca)(J. Wu)

<sup>1</sup>Laboratory for Industrial and Applied Mathematics, Department of Mathematics and Statistics, Fields-CQUM Laboratory of Mathematics for Public Health, York University, Toronto, Ontario, M3J 1P3, Canada

\*This research was partially supported by the Canada Research Chairs Program (CRC), and by National Sciences and Engineering Research Council of Canada (NSERC).

and the inhibitory neurons, the connection strength and the time delay affects the network's computational performance [1, 2, 15, 26, 27]. In particular, the studies [9, 10, 18] focus on the dynamical behaviors of the excitatory neuron in the loops and hence their model equation takes the form of a scalar delay differential equation that can also arise in modeling a single neuron with delayed self-feedback. The model in [9, 10, 18] takes a quite general form involving membrane potential of the excitatory neuron, ionic currents, an applied current, the effects of the inhibitory feedback on the membrane potential of the excitatory neuron, and the probability that a certain channel is open. In these models, the delay can be large in comparison with the intrinsic spiking period when we consider the recurrent inhibitory loop as a simplification of a large polysynaptic loop or neuron population network. In such a network, many factors can contribute to the delay and consequently the propagation time through the network may be considerably longer than would be estimated from the conduction velocities.

Foss and Milton [9] used the well-known Hodgkin-Huxley model to study recurrent inhibitory loops and found multiple coexisting attracting periodic solutions by computer simulations. Unfortunately, the intrinsic complexity of the conductance-based neuron models such as the Hodgkin-Huxley model makes it difficult for a detailed qualitative and theoretical analysis and hence reduced neuron models such as integrate-and-fire models become desirable from a theoretical point of view. On the other hand, Chow *et. al.* [3] showed that under some assumptions, the full conductance-based dynamics can be approximated by the integrate-and-fire neuron model  $Cv'(\tilde{t}) = -g_L(v - v_L) + \tilde{I}_0 - F(\tilde{t}, \tilde{\tau})$ , with the reset condition:  $v(\tilde{t}+) = v_r$  when  $v(\tilde{t}-) = \tilde{\vartheta}$ . Such a system can be further normalized and simplified as  $V'(t) = -V + I_0 - F(t, \tau)$  by re-scaling  $t = \tilde{t}/\tau_m$ ,  $\tau = \tilde{\tau}/\tau_m$  and letting  $V = (v - v_r)/(\tilde{\vartheta} - v_r)$  with  $\tau_m = C/g_L$ . Under this normalization procedure, the  $V(t)$  is reset to  $V_r = 0$  whenever it reaches the threshold potential  $\vartheta = 1$ .

The reset condition has so far been considered as an impulse: the potential is reset immediately after it reaches the threshold. In real biological neurons, however, the reset process involves a firing procedure followed by the absolute refractory period. It turns out that the firing procedure and the absolute refractoriness have very important impact on the timing of the inhibitory feedback, and this impact is particularly significant if the feedback is delayed. Indeed, numerical results [18] showed that an integrate-and-fire model incorporating the firing procedure and absolute refractoriness is capable of generating a large number of asymptotically stable periodic solutions with predictable patterns of oscillations, in agreement with some earlier studies in [9, 13, 23, 25].

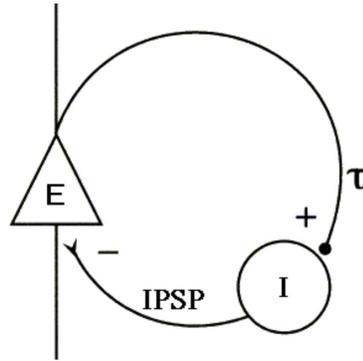
In this series of papers, we hope to develop a systematical approach to rigorously analyze the mechanism for the observed multistability in recurrent inhibitory loops. In particular, we shall show how the interaction of the time lag, the inhibition, the firing procedure and the absolute refractory period can generate some basic and analytically trackable types of oscillations, and how these basic oscillations can then be pinned together to form a large class of periodic patterns. We shall also illustrate by numerical simulations that these periodic patterns can be easily observed. In subsequent work, we will link the periodic patterns exhibited in our simple integrate-and-fire model to a variety of rhythms displayed in the nervous system.

The rest of this paper is organized as follows: we first formulate the integrate-and-fire model of recurrent inhibitory loops by incorporating the firing procedure

and the absolute refractoriness in Section 2. We identify three possible scenarios by comparing the feedback duration with the firing and the absolute refractory period when the feedback duration is relatively short. We show that the inhibition delivered by delayed feedback eventually stabilizes a trajectory composed of the aforementioned basic oscillations to a stable periodic pattern and different possible combinations of these basic oscillations within a time interval of length  $\tau$  then lead to the coexistence of multiple stable periodic patterns. We outline the symbolic dynamics approach in Section 3, present some general results in Section 4, and illustrate these with a case study in Section 5.

## 2. Spiking neuron model

We consider the following normalized integrate-and-fire model for the membrane potential of the excitatory neuron in the recurrent inhibitory loop depicted in Figure 1:



**Figure 1.** A schematic illustration of a recurrent integrate-and-fire neuron loop that consists of an excitatory neuron  $E$  and an inhibitory neuron  $I$ , where neuron  $E$  excites the neuron  $I$  instanttly, which in turns delivers an inhibitory postsynaptic potential (IPSP) to the neuron  $E$  with a delay  $\tau$ .

$$V'(t) = -V(t) - F(t) + I_0, \quad (2.1)$$

where  $I_0$  is the external input (assumed to be a constant) and  $F(t)$  describes the delay feedback, which will be described in detail later.

The dynamical behaviors of the model solutions are subject to a *resetting mechanism*: when the membrane potential  $V(t)$  reaches the *threshold*  $\vartheta$  at a firing time  $t_f$ , the membrane potential increases from  $\vartheta$  to a constant  $c > \vartheta$  (at  $t_f + s_1$ ) and then decays to the so-called *reset potential*  $V_r$  (at  $t_f + T_F$ ). We normalize the system so that the rest potential  $V_r = 0$ .

For simplicity, we shall use the following piecewise linear function  $V_f$  to describe this firing procedure, though much of the analysis and simulation in this paper remains true if this function is replaced by any one with the aforementioned features. So,

$$V_f(t) = \begin{cases} \vartheta + \frac{c-\vartheta}{s_1}(t - t_f) & \text{if } t \in [t_f, t_f + s_1); \\ V_r + \frac{c-V_r}{T_F-s_1}(t_f + T_F - t) & \text{if } t \in [t_f + s_1, t_f + T_F], \end{cases} \quad (2.2)$$

where  $T_F$  is the width of spike and the firing time  $t_f$  is defined by the threshold condition:

$$V(t_f) = \vartheta \quad \text{and} \quad V(t_f - \varepsilon) < \vartheta$$

for sufficiently small  $\varepsilon > 0$ .

The firing is followed by an absolute refractory period, where the membrane potential follows a particular pattern independent of the external input and feedback. We assume, based on the work [12], that this particular pattern is given by

$$V(t) = E[1 - e^{-(t-t_f-T_F)}] \quad \text{for } t \in (t_f + T_F, t_f + T_{FR}), \quad (2.3)$$

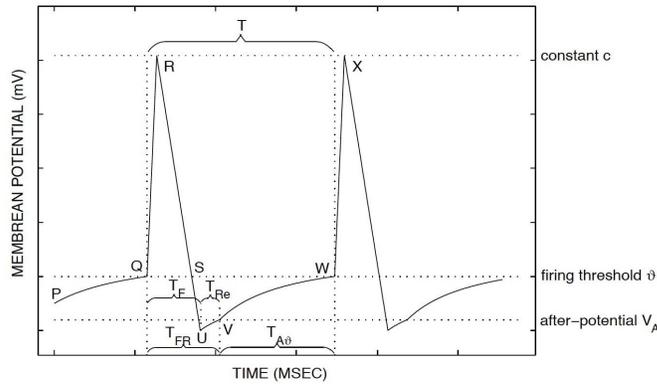
with  $E$  being a constant. We define by  $T_{Re} := T_{FR} - T_F$  the duration of the absolute refractoriness and  $T_{FR}$  as the sum of the width of spike and the duration of the absolute refractory period. The membrane potential at time  $t_f + T_{FR}$  is called the *after-potential* and is denoted by  $V_A$ . It is obvious that

$$V_A = E(1 - e^{-T_{Re}}).$$

The inhibitory feedback is given by

$$F(t) = \begin{cases} a & \text{if } t \in [t_f^\tau + \tau, t_f^\tau + \tau + T_{FD}]; \\ 0 & \text{otherwise,} \end{cases} \quad (2.4)$$

where  $T_{FD}$  is the duration of the inhibitory feedback and  $t_f^\tau$  is the firing time of the neuron prior to the time  $t - \tau$ . More precisely,  $t_f^\tau = \sup\{s; s \leq t - \tau, V(s) = \vartheta \text{ and } V(s - \varepsilon) < \vartheta \text{ for sufficiently small } \varepsilon > 0\}$ . Therefore, if  $T_{FD}$  coincides the amount of time that the membrane potential is above the threshold  $\vartheta$  during a spike (from  $Q$  to  $S$  in Figure 2), then  $F(t) = G(V(t - \tau))$  where  $G(x)$  is the step function with  $G(x) = a$  if  $x \geq \vartheta$  and  $G(x) = 0$  otherwise. In this case, equation (2.1) can be written in the standard form of a scalar delay differential equation  $V'(t) = -V(t) - G((V(t - \tau))) + I_0$ .



**Figure 2.** In the absence of recurrent inhibition ( $F \equiv 0$ ), an intrinsic spiking period  $T$  is the period from  $Q$  to  $W$ ;  $T_F$  from  $Q$  to  $U$ ;  $T_{Re}$  from  $U$  to  $V$ ;  $T_{FR}$  from  $Q$  to  $V$ ;  $T_{A\vartheta}$  from  $V$  to  $W$ .

In what follows, we always assume that the stimulus  $I_0$  is sufficiently large so that

$$I_0 > \vartheta.$$

Under this assumption, in the absence of recurrent inhibition ( $F \equiv 0$ ), the action potential described by (2.1) subject to the firing procedure and absolute refractoriness is a periodic function. We call the period of such a periodic function the *intrinsic spiking period* of the excitatory neuron. This period, denoted by  $T$ , is the duration between two consecutive firing times of the spike train, and is divided into two parts:  $T_{FR}$  and  $T_{A\vartheta}$  (from  $Q$  to  $V$  and from  $V$  to  $W$  in Figure 2, respectively),  $T_{A\vartheta}$  is the time that it takes the membrane potential to increase from the after-potential  $V_A$  to the threshold  $\vartheta$  (from time  $t_f + T_{FR}$  to the next firing time), given by

$$T_{A\vartheta} = \log \left[ \frac{I_0 - V_A}{I_0 - \vartheta} \right]. \quad (2.5)$$

To consider the impact of the recurrent inhibition on the dynamical behaviors of the excitatory neuron, we note that each time the excitatory neuron fires a spike, an inhibitory feedback is delivered but with a time lag  $\tau$ . In what follows, we always assume that

$$a > I_0$$

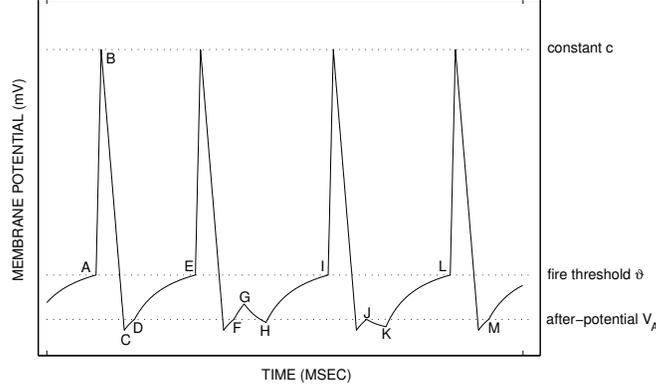
so that an inhibitory feedback can cause the membrane potential of the excitatory neuron to decline. Note that, however, if the feedback is delivered during the firing period or the absolute refractoriness of the excitatory neuron, the feedback has no effect on the membrane potential.

### 3. Building blocks and connection to symbolic dynamics

To describe three basic types of oscillations ( $V$ ,  $W_d$ ,  $W_u$ ) that give the building blocks of periodic patterns, we start from a firing time  $t_f$  of the neuron and consider the situation when a feedback is delivered at time  $t_f + s_2$ . After a firing procedure and the absolute refractoriness, at least three scenarios can occur:

- (i) **Ineffective feedback**,  $s_2 \in (t_f, t_f + T_{FR})$  and  $T_{FR} - s_2 > T_{FD}$ : In this case the feedback has arrived too early and ended too soon, and thus has no impact on the membrane potential. The neuron generates a natural spike: the membrane potential arises from  $V_A$  to  $\vartheta$  (via equation (2.1) with  $F(t) = 0$ ). This oscillation from the firing time  $t_f$  to the next firing time is illustrated by the graph from  $A$  to  $E$  in Figure 3. We call this type of oscillation a *V-oscillation*.
- (ii) **Partial feedback**,  $s_2 \in (t_f, t_f + T_{FR})$  and  $T_{FR} - s_2 < T_{FD}$ : In this case the feedback has arrived too early and but will not end before the absolute refractoriness period, the membrane potential goes down first (via equation (2.1) with  $F(t) = a$ ), then goes up (via equation (2.1) with  $F(t) = 0$ ) until reaching the firing threshold  $\vartheta$ . This is shown in the graph from  $I$  to  $L$  in Figure 3, and we call this type of oscillation a *W<sub>d</sub>-oscillation*.
- (iii) **Full feedback**,  $s_2 \in (t_f + T_{FR}, t_f + T_{FR} + T_{A\vartheta})$ , In this case the feedback arrived after the absolute refractoriness period and the feedback has its full effect during the feedback duration, the membrane potential goes up first (via equation (2.1) with  $F(t) = 0$ ), then goes down (via equation (2.1) with

$F(t) = a$ ), finally goes up again (via equation (2.1) with  $F(t) = 0$ ) until reaching the firing threshold  $\vartheta$ . This is illustrated by the graph from  $E$  to  $I$  in Figure 3, and we call this type of oscillation a  $W_u$ -oscillation.



**Figure 3.** Three basic types of oscillations generated by the integrate-and-fire model. From  $A$  to  $E$  is a  $V$ -oscillation; from  $E$  to  $I$  is a  $W_u$ -oscillation; from  $I$  to  $L$  is a  $W_d$ -oscillation.

### 3.1. Pattern formation from three basic oscillations

Observe that the corresponding solution  $V(t)$  for  $t \geq 0$  for a given initial function on  $[-\tau, 0]$  satisfies the following properties:

- If  $I_0 > \vartheta$ , then the sequence of firing times is unbounded. For otherwise, we have  $V(t) \leq \vartheta$  and  $V'(t) = -V(t) + I_0$  for large  $t$ , and this leads to a contradiction since  $I_0 > \vartheta$ .
- The duration between two consecutive firing times is always greater than or equal to the intrinsic spiking period  $T$ .

Therefore, for a given initial function, after a transit time, the excitatory neuron must fire. We will use  $r_1$  to denote the first firing time, we denote the series of firing times of the excitatory neuron by  $\{r_1, r_2, r_3, \dots\}$ , the action potential in the interval  $[r_i, r_{i+1}]$  by  $\tilde{\pi}_i$ , and the duration of  $\tilde{\pi}_i$  by  $\tilde{T}_i$  ( $\tilde{T}_i := r_{i+1} - r_i$ ).

We will denote by  $t_{A\vartheta, i}$  the duration from the time when the inhibition of feedback (after  $r_i$ ) wears off to the next firing time. If no confusion arises, we will eliminate the subindex  $i$  and denote this by  $t_{A\vartheta}$ . This duration is depicted by the time from  $D$  to  $E$ , from  $H$  to  $I$ , or from  $K$  to  $L$  in Figure 3. Let  $\Delta t = t_{A\vartheta} - T_{A\vartheta}$ . It is obvious that  $\Delta t = 0$  for a  $V$ -oscillation. Each  $W_d$ -oscillation is characterized by  $(t_{down}, \Delta t)$  and a  $W_u$ -oscillation is characterized by  $(t_{up}, T_{FD}, \Delta t)$ . In Figure 3,  $t_{down}$  is the duration between  $J$  and  $K$  for a  $W_d$ -oscillation, while  $t_{up}$  is the duration between  $F$  and  $G$  for a  $W_u$ -oscillation. It is obvious that  $\Delta t > 0$  for a  $W_d$ -oscillation. For a  $W_u$ -oscillation, if the feedback inhibition brings the membrane potential below  $V_A$ ,  $\Delta t > 0$  and it is the time between the offset of inhibition and the time when  $V_A$  is reached again; otherwise,  $\Delta t < 0$ .

We then define  $\Delta t_{max}$  as the maximum value of all possible values  $\Delta t$ . This maximum occurs when  $t_{down} = T_{FD}$  for a  $W_d$ -oscillation or  $t_{up} = 0$  for a  $W_u$ -oscillation. A specific formulae will be given in (4.5). Note that  $\Delta t_{max} \rightarrow 0$  as

$T_{FD} \rightarrow 0$ . Therefore,  $T_{FD} < T_{FR}$  and  $\Delta t_{max} \leq T_{FR} - T_{FD}$  hold simultaneously if  $T_{FD}$  is small.

When  $T_{FD} < T_{FR}$  and  $\Delta t_{max} \leq T_{FR} - T_{FD}$ , the duration from the time when a feedback arrives to the next firing time is always less than or equal to the intrinsic spiking period  $T$ . Therefore, the action potential  $\tilde{\pi}_i$  with  $r_i \geq T_f + T$  must be one of three oscillations described above. More precisely, we have

**Lemma 3.1.** *If  $T_{FD} < T_{FR}$  and  $\Delta t_{max} \leq T_{FR} - T_{FD}$ , then  $\tilde{\pi}_i \in \{V, W_d, W_u\}$  for any segment of the action potential  $\tilde{\pi}_i$  with  $r_i \geq T_f + T$ .*

**Proof.** We first note that the distance/duration between two feedbacks is greater than or equal to  $T$ . We want to show that between two feedbacks, the neuron must fire. In other words, we want to prove that once the first feedback arrives, the membrane potential will reach the threshold before the next feedback is delivered. We denote by  $T^*$  the duration between the time when the first feedback arrives and the time when the membrane potential reaches the threshold. We claim that  $T^* \leq T$  for all the three oscillations.

This is obvious for an  $V$ -oscillation. For a  $W_d$ -oscillation, the duration of the inhibitory feedback is  $T_{FD}$ , that is the sum of  $t_{down}$  and the time within the absolute refractoriness and the firing procedure. The fact that  $t_{A\vartheta} = T_{A\vartheta} + \Delta t$  with  $\Delta t \leq \Delta t_{max}$  and the condition  $\Delta t_{max} \leq T_{FR} - T_{FD}$  lead to  $T^* = T_{FD} + t_{A\vartheta} \leq T_{A\vartheta} + T_{FR} = T$ . Similarly, for a  $W_u$ -oscillation, we have  $T^* = T_{FD} + t_{A\vartheta} \leq T$ .

In summary,  $T^* \leq T$  for each basic oscillation  $V, W_d$  and  $W_u$ . Therefore, the neuron will fire before the next feedback arrives.  $\square$

### 3.2. Representation by a sequence of symbols

Then the solution can be expressed as  $\{\tilde{\pi}_1, \tilde{\pi}_2, \dots, \tilde{\pi}_n, \dots\}$  with  $\tilde{\pi}_i \in \{W_d, W_u, V\}$  if  $r_i \geq T_f + T$ . Furthermore, when  $r_i \geq T_f + T$ ,  $\tilde{T}_i$  can be calculated as follows:

$$T(\tilde{\pi}_i) := \tilde{T}_i = \begin{cases} T & \text{if } \tilde{\pi}_i = V; \\ T + t_{down} + \Delta t & \text{if } \tilde{\pi}_i = W_d; \\ T + t_{up} + T_{FD} + \Delta t & \text{if } \tilde{\pi}_i = W_u. \end{cases} \quad (3.1)$$

Note that at this stage,  $t_{down}, t_{up}$  and  $\Delta t$  should all have the subindex  $i$  since theoretically they are supposed to be different for different  $\tilde{\pi}_i$ . We drop such a subindex here for simplicity of notation. Later on, we shall show that these numbers are indeed independent of the subindex.

### 3.3. Feedback-induced action on symbol segments

We define

$$\tilde{\sigma}_n = (\tilde{\pi}_n, \tilde{\pi}_{n+1}, \dots, \tilde{\pi}_{n+N_n-1}, \tilde{\pi}_{n+N_n}) \text{ such that } N_n = \min_k \left( \sum_{i=0}^k \tilde{T}_{n+i} \geq \tau \right) \quad (3.2)$$

for  $n = 1, 2, \dots$ . The duration of  $\tilde{\sigma}_n$  is  $p_n := T(\tilde{\sigma}_n) = \sum_{i=0}^{N_n} \tilde{T}_{n+i}$ . According to the the above definition of  $\tilde{\sigma}_n$ , the spike of  $\tilde{\pi}_n$  may deliver an inhibitory feedback to a segment of  $\tilde{\pi}_{n+N_n}$ . Therefore, the feedback can be considered as an action of the

first item  $\tilde{\pi}_n$  on the last item  $\tilde{\pi}_{n+N_n}$  within  $\tilde{\sigma}_n$ , and our ultimate goal is to describe how such an action will eventually stabilize  $\tilde{\sigma}_n$  to a periodic pattern.

It is therefore natural to consider a general periodic pattern  $\sigma = \{\pi_i; i \geq 1\}$ . Such a pattern is uniquely determined by the *initial segment of symbols* below:

$$(\pi_1, \pi_2, \dots, \pi_N), N := \min_k \sum_{i=1}^k T(\pi_i) \geq \tau.$$

Therefore, in what follows, we write such a pattern as

$$\begin{cases} \sigma = (\pi_1, \pi_2, \dots, \pi_{N-1}, \pi_N) & \text{where } \pi_i \in \{W_d, W_u, V\}, \\ N = \min_k \left( \sum_{i=1}^k T(\pi_i) \geq \tau \right). \end{cases} \quad (3.3)$$

Define a shift operator  $\varphi : \Sigma \rightarrow \Sigma$  with  $\Sigma := \{\sigma; \sigma \text{ is a periodic pattern}\}$  by

$$(\varphi\sigma)_i := \varphi\pi_i = \begin{cases} \pi_{i+1} & \text{if } i \in \{1, 2, \dots, N-1\}; \\ \pi_1 & \text{if } i = N. \end{cases}$$

**Definition 3.1.** Two periodic patterns  $\sigma_1$  and  $\sigma_2$  are said to be equivalent, if there exists an integer  $j \in \{1, \dots, N\}$  such that  $\sigma_2 = \varphi^j \sigma_1$ .

### 3.4. Characterization of feedback-induced actions

For a periodic pattern defined by (3.3), the action of the feedback from  $\pi_1$  on  $\pi_N$  yields

$$\begin{cases} \sum_{i=1}^{N-1} T(\pi_i) + T_{FR} \geq \tau + T_{FD} & \text{if and only if } \pi_N = V; \\ \sum_{i=1}^{N-1} T(\pi_i) + T_{FR} + t_{down} = \tau + T_{FD} & \text{if and only if } \pi_N = W_d; \\ \sum_{i=1}^{N-1} T(\pi_i) + T_{FR} + t_{up} = \tau & \text{if and only if } \pi_N = W_u. \end{cases} \quad (3.4)$$

Analogously,  $\varphi\sigma, \dots, \varphi^{N-1}\sigma$  give other  $N-1$  similar relationships. As will be shown, these relationships determine the types of periodic patterns that can be generated by the recurrent inhibitory loop for a given time delay  $\tau$ .

An important property of a periodic pattern  $\sigma$  defined by (3.3), which will be shown in Lemma 4.1, is that within a given periodic pattern  $\sigma$ , all  $W_d$ -oscillations are the same in terms of  $(t_{down}, \Delta t)$  and all  $W_u$ -oscillations are the same in terms of  $(t_{up}, T_{FD}, \Delta t)$ . In view of the above definition of equivalence, therefore, we can simply describe a periodic pattern in terms of the numbers and orderings of  $W_d$ ,  $W_u$  and  $V$  oscillations as follows:

$$\sigma = (n_1\pi_1, n_2\pi_2, \dots, n_k\pi_k) \text{ or } \sigma = (n_1\pi_1 n_2\pi_2 \dots n_k\pi_k) \text{ where } \pi_i \in \{W_d, W_u, V\}.$$

For example,  $(W_u W_u W_u V V)$  can be simply written as  $(3W_u, 2V)$  or  $(3W_u 2V)$ . Note also that  $(W_u W_u W_u V V)$  and  $(W_u W_u V V W_u)$  are equivalent periodic patterns. In what follows, we shall use  $(3W_u 2V)$  to denote the equivalence class of  $(W_u W_u W_u V V)$  under the equivalence defined in Definition 3.1, so that  $(W_u W_u V V W_u)$  also belongs to  $(3W_u 2V)$ . Note that  $(W_u V W_u W_u V) \notin (3W_u 2V)$ . On the other

hand, if  $\sigma = (1W_u2V1W_u2V)$ , the minimum periodic pattern should be  $\sigma_{min} = (1W_u2V)$ . Hence, we give the definition of the minimum periodic pattern.

**Definition 3.2.** For a  $p$ -periodic pattern  $\sigma$  described by (3.3), we call  $\sigma_{min} = (\pi_1, \pi_2, \dots, \pi_{\tilde{N}-1}, \pi_{\tilde{N}})$  the minimum  $p_{min}$ -periodic pattern of  $\sigma$ , if there exists the maximum integer  $1 < \tilde{k} < N$  such that  $N = \tilde{k}\tilde{N}$ ,  $p = \tilde{k}p_{min}$  and  $\sigma = \tilde{k}\sigma_{min} := (\sigma_{min}, \dots, \sigma_{min})$  ( $\tilde{k}$  times).

If there is no such an integer  $\tilde{k}$ , then  $\sigma_{min} = \sigma$ . In what follows, we shall use

$$\Omega_{m,h,j} = \left\{ p_{min}; \sigma_{min} = (n_1\pi_1, n_2\pi_2, \dots, n_k\pi_k) : m = \sum_{\pi_i=W_d} n_i, \right. \\ \left. h = \sum_{\pi_i=W_u} n_i, j = \sum_{\pi_i=V} n_i \right\} \quad (3.5)$$

to denote the set of all periodic patterns composed of  $m$   $W_d$ -oscillations,  $h$   $W_u$ -oscillations and  $j$   $V$ -oscillations with the minimum period  $p_{min}$ . Then the set of all periodic patterns for a given time delay  $\tau$  is give by  $\Omega_\tau = \cup \Omega_{m,h,j}$ . For example,

$$\Omega_{0,3,2} = \{5T + 3t_{up} + 3T_{FD} + 3\Delta t; (3W_u2V), (2W_u1V1W_u1V)\}.$$

Note that, up to the equivalence given in Definition 3.1,  $(3W_u2V)$  and  $(2W_u1V1W_u1V)$  are the only possible periodic patterns with 3  $W_u$ -oscillations, 2  $V$ -oscillations and the minimum period  $5T + 3t_{up} + 3T_{FD} + 3\Delta t$ , so the notation  $\Omega_{0,3,2}$  is a pattern set specified by all possible 3  $W_u$ -oscillations and 2  $V$ -oscillations arranged in a ring. Since the system of equations (3.4) is independent of the orders of those oscillations  $\pi_i$ , we conclude that if  $(3W_u2V)$  can be generated, then  $(2W_u1V1W_u1V)$  can also be generated by the model with the same set of parameters.

## 4. Pattern formation and transition

We first recall the notation  $(t_{up}, T_{FD}, \Delta t)$  of a  $W_u$ -oscillation. We note that  $t_{up}$  should satisfy  $0 < t_{up} < T_{A\theta}$  and the sign of  $\Delta t$  depends on the value of  $t_{up}$ . In particular, there exists an important quantity

$$T_c = \log \left[ \frac{I_0 - V_A}{(I_0 - V_A - a)e^{T_{FD}} + a} \right] > 0 \quad (4.1)$$

such that

$$\Delta t \begin{cases} = 0 & \text{if } t_{up} = T_c; \\ > 0 & \text{if } t_{up} < T_c; \\ < 0 & \text{if } t_{up} > T_c. \end{cases} \quad (4.2)$$

We shall show that interesting transitions of dynamical behaviors of the recurrent inhibitory loop occur at certain critical values of the time delay. In order to define these critical values, we need to introduce two functions: one is a positive and increasing continuous function  $f_1$ , given by

$$f_1(\Delta t) = \log \left[ \frac{I_0 - V_A - a}{(I_0 - V_A)e^{\Delta t} - a} \right] \quad (4.3)$$

which describes the relationship of  $t_{down}$  and  $\Delta t$  for a  $W_d$ -oscillation; and another is a decreasing continuous function  $f_2$ , given by

$$f_2(\Delta t) = \log \left[ \frac{I_0 - V_A}{(I_0 - V_A)e^{T_{FD} + \Delta t} - ae^{T_{FD}} + a} \right] \quad (4.4)$$

which describes the relationship of  $t_{up}$  and  $\Delta t$  for a  $W_u$ -oscillation. Obviously,  $T_c = f_2(0)$ . These functions are then used to define four critical values  $T_1, T_2, T_3$  and  $T_4$  in (4.10), (4.16), (4.17) and (4.18).

We note that  $t_{down} \in [0, T_{FD}]$  and  $\Delta t \geq 0$  for a  $W_d$ -oscillation. There are two extreme cases:  $t_{down} = T_{FD}$  for a  $W_d$ -oscillation and  $t_{up} = 0$  for a  $W_u$ -oscillation. The action potentials in these two cases are the same and  $\Delta t$  reaches its maximum value, given by

$$\Delta t_{max} = f_1^{-1}(T_{FD}) = \log \left[ \frac{(I_0 - V_A - a)e^{-T_{FD}} + a}{I_0 - V_A} \right] > 0. \quad (4.5)$$

On the other hand, for a  $W_u$ -oscillation, when  $t_{up}$  approaches the value  $T_{A\vartheta}$ ,  $\Delta t$  approaches its minimum value, given by

$$\Delta t_{min} = f_2^{-1}(T_{A\vartheta}) = -T_{FD} + \log \left[ e^{-T_{A\vartheta}} + \frac{a(e^{T_{FD}} - 1)}{I_0 - V_A} \right] < 0. \quad (4.6)$$

We shall use these extreme cases to define the minimum value  $\tau_{min}$  and the maximum value  $\tau_{max}$  of the time delay for the existence of certain periodic patterns.

We now fix an integer  $n \geq 1$  and assume  $\tau/T \in [n, n+1)$ . We start with general conditions to ensure  $\Omega_{m,h,j} \subseteq \Omega_\tau$ .

**Lemma 4.1.** *All  $W_u$ -oscillations in a periodic pattern are the same in terms of  $(t_{up}, T_{FD}, \Delta t)$  and all  $W_d$ -oscillations in a periodic pattern are the same in terms of  $(t_{down}, \Delta t)$ .*

**Proof.** We first illustrate our argument in a simple case where  $\sigma = (\pi_1, \pi_2) = (W_u^{(1)}, W_u^{(2)})$ ,  $W_u^{(1)}$  is characterized by  $(t_{up,1}, T_{FD}, \Delta t_1)$  and  $W_u^{(2)}$  is characterized by  $(t_{up,2}, T_{FD}, \Delta t_2)$ . By condition (3.4),  $\pi_2 = W_u$  can be generated if and only if

$$T + t_{up,1} + T_{FD} + \Delta t_1 + T_{FR} + t_{up,2} = \tau.$$

Similarly, in terms of  $\varphi\sigma = (\pi_2, \pi_1)$ , we have

$$T + t_{up,2} + T_{FD} + \Delta t_2 + T_{FR} + t_{up,1} = \tau.$$

The above two equations give rise to  $\Delta t_1 = \Delta t_2$ . Hence,  $t_{up,1} = t_{up,2}$ .

Similarly, if  $\sigma = (\pi_1, \dots, \pi_N) = (W_u^{(1)}, \dots, W_u^{(N)})$  with each  $W_u^{(i)}$  being characterized by  $(t_{up,i}, T_{FD}, \Delta t_i)$ ,  $\pi_N = W_u$  can be generated if and only if

$$\left[ (N-1)T + \sum_{1 \leq i \leq N, i \neq N} (t_{up,i} + T_{FD} + \Delta t_i) \right] + T_{FR} + t_{up,N} = \tau.$$

Analogously, in terms of  $\varphi\sigma, \varphi^2\sigma, \dots, \varphi^{N-1}\sigma$ , we have

$$\left[ (N-1)T + \sum_{1 \leq i \leq N, i \neq j} (t_{up,i} + T_{FD} + \Delta t_i) \right] + T_{FR} + t_{up,j} = \tau$$

for each  $1 \leq j \leq N-1$ . The above system of equations gives rise to  $\Delta t_1 = \dots = \Delta t_N$ , and hence,  $t_{up,1} = \dots = t_{up,N}$ .

The same argument can be used to show that all  $W_u$ -oscillations in a periodic pattern of  $\Omega_{m,h,j}$  with  $h \geq 1$  and  $m+j \geq 1$  must be the same in terms of  $(t_{up}, T_{FD}, \Delta t)$  and all  $W_d$ -oscillations in a periodic pattern are the same in terms of  $(t_{down}, \Delta t)$ .  $\square$

As will be shown in Lemma 4.8, there exists at most one  $W_d$ -oscillation in a given periodic pattern. Therefore, we only consider the case  $m = 1$  for a periodic pattern in  $\Omega_{m,h,j}$  in the next result (and later in Theorem 4.2).

**Lemma 4.2.** *If a  $W_d$ -oscillation and some  $W_u$ -oscillations coexist in a periodic pattern, then  $\Delta t$  for the  $W_d$ -oscillation is equal to the  $\Delta t$  for all the  $W_u$ -oscillations.*

**Proof.** We consider  $\sigma = (\pi_1, \pi_2, \dots, \pi_N) = (W_d, W_u, \dots, W_u) \in \Omega_{1,h,0}$ , where  $W_d$  is characterized by  $(t_{down}, \Delta t_1)$  and  $W_u$  is characterized by  $(t_{up}, T_{FD}, \Delta t_2)$ .

By condition (3.4),  $\pi_N = W_u$  can be generated if and only if

$$T + t_{down} + \Delta t_1 + (h-1)(T + t_{up} + T_{FD} + \Delta t_2) + T_{FR} + t_{up} = \tau.$$

Similarly, for  $\varphi\sigma = (\pi_2, \dots, \pi_N, \pi_1)$ , we have

$$h(T + t_{up} + T_{FD} + \Delta t_2) + T_{FR} - (T_{FD} - t_{down}) = \tau.$$

The above two equations give rise to  $\Delta t_1 = \Delta t_2$ .

The same argument can be used for a periodic pattern in  $\Omega_{1,h,j}$  with  $h, j \geq 1$ . This completes the proof.  $\square$

By Lemma 4.2, we can (and shall) use  $\Delta t$  to denote the common value for a  $W_d$ -oscillation and all  $W_u$ -oscillations in a given periodic pattern. Lemmas 4.1 and 4.2 imply that by the time the inhibition wears off, the membrane potentials of a  $W_d$ -oscillation and all  $W_u$ -oscillations are essentially of the same voltage. This is in agreement with the work of [16].

Condition (3.4) immediately leads to

**Lemma 4.3.** *Assume  $\tau \in [nT, nT + T]$  for an integer  $n$ . Then  $\Omega_{0,0,1} \subseteq \Omega_\tau$  holds true when and only when  $\tau \in [nT, nT + T_{FR} - T_{FD}]$ , and the periodic pattern is (1V).*

We now consider  $\Omega_{1,0,n}$ .

**Lemma 4.4.**  *$\Omega_{1,0,n} \subseteq \Omega_\tau$  holds true when and only when  $\tau \in (nT + T_{FR} - T_{FD}, nT + T_{FR}]$ , and the periodic pattern is (1 $W_d, nV$ ).*

**Proof.** We consider  $\sigma = (\pi_1, \dots, \pi_{n+1}) = (W_d, V, \dots, V)$ . Condition (3.4) gives rise to

$$\begin{cases} nT + t_{down} + \Delta t + T_{FR} \geq \tau + T_{FD} & \text{for a } V\text{-oscillation;} \\ nT + T_{FR} + t_{down} = \tau + T_{FD} & \text{for a } W_d\text{-oscillation.} \end{cases}$$

This means that a given segment of potentials  $nV$  is followed by a  $W_d$ -oscillation if and only if  $nT + T_{FR} + t_{down} = \tau + T_{FD}$ ; and a given segment  $(W_d, (n-1)V)$  is followed by a  $V$ -oscillation if and only if  $nT + t_{down} + \Delta t + T_{FR} \geq \tau + T_{FD}$ .

For a  $W_d$ -oscillation, we have  $\Delta t \geq 0$  and  $0 < t_{down} \leq T_{FD}$ . Therefore, the above inequality and equation are consistent. When  $t_{down}$  approaches zero and  $t_{down} = T_{FD}$ , we obtain the minimum value  $\tau_{min} = nT + T_{FR} - T_{FD}$  and the maximum value  $\tau_{max} = nT + T_{FR}$  for the existence of such a periodic pattern, respectively.  $\square$

Note that the fact that the maximum value  $\tau_{max}$  of the periodic pattern of  $\Omega_{0,0,1}$  in Lemma 4.3 is equal to the minimum value  $\tau_{min}$  of the periodic pattern of  $\Omega_{1,0,n}$  suggests that a pattern transition occurs at  $\tau = nT + T_{FR} - T_{FD}$ .

**Lemma 4.5.**  $\Omega_{0,1,n} \subseteq \Omega_\tau$  holds true when and only when  $\tau \in (nT + T_{FR}, nT + T_{FR} + T_c]$ , and the periodic pattern is  $(1W_u, nV)$ .

**Proof.** We consider  $\sigma = (\pi_1, \dots, \pi_{n+1}) = (W_u, V, \dots, V)$ . Condition (3.4) gives rise to

$$\begin{cases} nT + t_{up} + T_{FD} + \Delta t + T_{FR} \geq \tau + T_{FD} & \text{for a } V\text{-oscillation;} \\ nT + T_{FR} + t_{up} = \tau & \text{for a } W_u\text{-oscillation.} \end{cases} \quad (4.7)$$

It yields  $\Delta t \geq 0$  and hence,  $0 < t_{up} \leq T_c$ . When  $t_{up}$  approaches zero or  $t_{up} = T_c$ , we obtain the minimum value  $\tau_{min} = nT + T_{FR}$  or the maximum value  $\tau_{max} = nT + T_{FR} + T_c$  for the existence of such a periodic pattern, respectively.  $\square$

Again, this shows a pattern transition from  $\Omega_{1,0,n}$  to  $\Omega_{0,1,n}$  at  $\tau = nT + T_{FR}$ .

**Theorem 4.1.** Periodic patterns in  $\Omega_{0,h,j}$  with  $h, j \geq 1$  and  $N := h + j \leq n + 1$  can be generated if and only if

$$\begin{cases} t_{up} = \frac{\tau - [(N-1)T + T_{FR} + (h-1)(T_{FD} + \Delta t)]}{h}, \\ 0 < t_{up} \leq T_c \quad \text{and} \quad 0 \leq \Delta t < \Delta t_{max}. \end{cases} \quad (4.8)$$

The minimum and maximum values of  $\tau$  for the existence of such periodic patterns are given by

$$\begin{cases} \tau_{min} = (N-1)T + T_{FR} + (h-1)T_2, \\ \tau_{max} = (N-1)T + T_{FR} + (h-1)T_{FD} + hT_c, \end{cases} \quad (4.9)$$

where

$$T_2 := \Delta t_{max} + T_{FD}. \quad (4.10)$$

**Proof.** We consider  $\sigma = (\pi_1, \dots, \pi_n) = (hW_u, jV) \in \Omega_{0,h,j}$ . Condition (3.4) gives rise to

$$\begin{cases} (N-1)T + h(t_{up} + T_{FD} + \Delta t) + T_{FR} \geq \tau + T_{FD} & \text{for a } V\text{-oscillation;} \\ (N-1)T + (h-1)(t_{up} + T_{FD} + \Delta t) + T_{FR} + t_{up} = \tau & \text{for a } W_u\text{-oscillation.} \end{cases}$$

It yields  $\Delta t \geq 0$  and hence  $0 < t_{up} \leq T_c$ . Re-arranging the above equation leads to (4.8).

The extreme case,  $t_{up} = 0$  and  $\Delta t = \Delta t_{max}$ , gives rise to the minimum value  $\tau_{min}$  as

$$\begin{aligned}\tau_{min} &= (N-1)T + T_{FR} + (h-1)(T_{FD} + \Delta t_{max}) \\ &= (N-1)T + T_{FR} + (h-1)T_2,\end{aligned}$$

where  $T_2$  is defined by

$$T_2 = \Delta t_{max} + T_{FD}.$$

The situation, where  $t_{up} = T_c$  and  $\Delta t = 0$ , gives rise to the maximum value as

$$\tau_{max} = (N-1)T + T_{FR} + (h-1)T_{FD} + hT_c.$$

□

**Lemma 4.6.** *If  $h$  and  $j$  have no common factor, the number of periodic patterns in  $\Omega_{0,h,j}$  is  $\binom{h+j}{h}/(h+j)$  and periodic patterns are all the possible arrangements of  $h$   $W_u$ -oscillations and  $j$   $V$ -oscillations in a ring. If  $h$  and  $j$  have a common factor  $q > 1$ , then the possible arrangements of periodic patterns in  $\Omega_{0,h/q,j/q}$  must be deducted.*

For example, all possible arrangements of 2  $W_u$ -oscillations and 4  $V$ -oscillations ( $\Omega_{0,2,4}$ ) in a ring are  $\sigma_1 = (2W_u4V)$ ,  $\sigma_2 = (1W_u1V1W_u3V)$  which is equivalent to  $(1W_u3V1W_u1V)$ , and  $\sigma_3 = (1W_u2V1W_u2V)$ . Although a periodic pattern  $\sigma_3 = (1W_u2V1W_u2V)$  is a possible arrangement of  $\Omega_{0,2,4}$ , the minimum periodic pattern of  $\sigma_3$  is the periodic pattern  $(1W_u2V)$  which belongs to the pattern set  $\Omega_{0,1,2}$ . Therefore, the number of periodic patterns in  $\Omega_{0,2,4}$  is  $[\binom{6}{2} - 3]/6 = 2$  and  $\Omega_{0,2,4} = \{(2W_u4V), (1W_u1V1W_u3V)\}$ .

**Lemma 4.7.** *If  $\Omega_{0,h,j} \subseteq \Omega_\tau$  and  $h, j$  have a common factor  $q > 1$ , then  $\Omega_{0,h/q,j/q} \subseteq \Omega_\tau$ . Furthermore, periodic patterns in both  $\Omega_{0,h,j}$  and  $\Omega_{0,h/q,j/q}$  coexist on the same interval  $\tau \in (\tau_{min}, \tau_{max})$  with  $\tau_{min}$  and  $\tau_{max}$  being given in (4.9).*

**Theorem 4.2.** *We now consider the general case where  $N$  is fixed, and  $h$  and  $j$  may vary under the constraint that  $1 \leq N := h + j \leq n$*

(i). *Periodic patterns in  $\Omega_{1,h,j}$  with  $h, j \geq 0$  and  $1 \leq N := h + j \leq n$  can be generated if and only if*

$$\begin{cases} NT + h(t_{up} + T_{FD} + \Delta t) + T_{FR} + t_{down} = \tau + T_{FD}, \\ 0 < t_{up} \leq T_c, \\ 0 < t_{down} \leq T_{FD}, \\ 0 \leq \Delta t < \Delta t_{max}. \end{cases} \quad (4.11)$$

*The minimum and maximum values of  $\tau$  for the existence of such a periodic pattern are given by*

$$\begin{aligned}\tau_{min} &= NT + T_{FR} + (h-1)T_{FD} \\ &\quad + \min_{0 \leq \Delta t \leq \Delta t_{max}} [f_1(\Delta t) + h\Delta t + hf_2(\Delta t)],\end{aligned} \quad (4.12)$$

$$\tau_{max} = NT + T_{FR} + hT_2. \quad (4.13)$$

(ii). If  $\tau$  reaches its minimum value  $\tau_{min}$  at  $\Delta t = \Delta t_{max}$ , periodic patterns can not be generated at this minimum value.

(iii). If  $\tau$  does not reach its minimum at  $\Delta t = \Delta t_{max}$ , then a pattern transition occurs at  $\tau = NT + T_{FR} + hT_2$ .

**Proof.** We consider  $\sigma = (\pi_1, \dots, \pi_N) = (W_d, hW_u, jV)$  with  $j \geq 1$ . Condition (3.4) gives rise to

$$\begin{cases} NT + t_{down} + \Delta t + h(t_{up} + T_{FD} + \Delta t) + T_{FR} \leq \tau + T_{FD} & \text{for a } V\text{-oscillation;} \\ NT + h(t_{up} + T_{FD} + \Delta t) + T_{FR} + t_{down} = \tau + T_{FD} & \text{for a } W_d\text{-oscillation.} \end{cases}$$

The above equation and inequality give rise to  $\Delta t \geq 0$  and hence  $0 < t_{up} \leq T_c$ . For a  $W_d$ -oscillation, we have  $0 < t_{down} \leq T_{FD}$ .

If  $j = 0$ , we also have the above equation and the condition  $\Delta t \geq 0$  because of the  $W_d$ -oscillation. Hence  $0 < t_{up} \leq T_c$  and  $0 < t_{down} \leq T_{FD}$ .

The minimum value of  $\tau$  for the existence of periodic patterns in  $\Omega_{1,h,j}$  is given by

$$\tau_{min} = NT + T_{FR} + (h-1)T_{FD} + \min_{0 \leq \Delta t \leq \Delta t_{max}} [f_1(\Delta t) + h\Delta t + hf_2(\Delta t)].$$

The extreme case,  $t_{down} = T_{FD}$  and  $\Delta t = \Delta t_{max}$  for the  $W_d$ -oscillation, and  $t_{up} = 0$  for the  $W_u$ -oscillations, gives rise to the maximum value  $\tau_{max}$  as

$$\tau_{max} = NT + T_{FR} + h[\Delta t_{max} + T_{FD}] = NT + T_{FR} + hT_2.$$

However, if  $\tau$  reaches the minimum value  $\tau_{min}$  at  $\Delta t = \Delta t_{max}$ , then  $\tau_{min} = \tau_{max}$ . This implies that the periodic pattern of  $\Omega_{1,h,j}$  can not be generated.

If periodic patterns of  $\Omega_{1,h,j}$  exist, the fact that the maximum value  $\tau_{max}$  of  $\Omega_{1,h,j}$  is equal to either the minimum value  $\tau_{min}$  of  $\Omega_{0,h+1,j}$  in Theorem 4.1 for  $j \geq 1$  or the minimum value  $\tau_{min}$  of  $\Omega_{0,1,0}$  in Theorem 4.3 for  $j = 0$ , suggests that a pattern transition occurs at  $\tau = (h+j)T + T_{FR} + hT_2$ .  $\square$

As a result of pattern transitions described above, we have the following:

**Lemma 4.8.** *Any periodic pattern in  $\Omega_\tau$  contains at most one  $W_d$ -oscillation. In other words, if  $\Omega_{m,h,j} \subseteq \Omega_\tau$ , then  $m = 0$  or  $m = 1$ .*

**Lemma 4.9.** *The number of periodic patterns in  $\Omega_{1,h,j}$  is  $\binom{h+j}{h}$  and periodic patterns are all possible arrangements of one  $W_d$ -oscillation,  $h$   $W_u$ -oscillations and  $j$   $V$ -oscillations in a ring.*

We now apply Theorem 4.2 in the case where  $h = 0, 1, 2$ .

For  $h = 0$ ,  $\tau_{min}$  and  $\tau_{max}$  are given by

$$\begin{cases} \tau_{min} = NT + T_{FR} - T_{FD}, \\ \tau_{max} = NT + T_{FR}. \end{cases} \quad (4.14)$$

This is the result of Lemma 4.4.

For  $h = 1$ ,  $\tau_{min}$  and  $\tau_{max}$  are given by

$$\begin{cases} \tau_{min} = NT + T_{FR} + T_1, \\ \tau_{max} = NT + T_{FR} + T_2, \end{cases} \quad (4.15)$$

where  $T_1$  is defined by

$$T_1 := \min_{0 \leq \Delta t \leq \Delta t_{max}} [f_1(\Delta t) + f_2(\Delta t) + \Delta t]. \quad (4.16)$$

If  $\tau$  reaches its minimum value  $\tau_{min}$  at  $\Delta t = 0$ , then  $T_1 = T_c$  and periodic patterns in  $\Omega_{0,1,n}$  transit to periodic patterns in  $\Omega_{1,1,n-1}$  at  $T = NT + T_{FR} + T_c$  for  $\tau \in (nT, nT + T)$ . Otherwise, periodic patterns in  $\Omega_{0,1,n}$  coexist with periodic patterns in  $\Omega_{1,1,n-1}$  on the subinterval  $\tau \in (nT + T_{FR} + T_1, nT + T_{FR} + T_c)$  if  $T_c < T_2$  or on the subinterval  $\tau \in (nT + T_{FR} + T_1, nT + T_{FR} + T_2)$  if  $T_c \geq T_2$ .

For  $h = 2$ ,  $\tau_{min}$  and  $\tau_{max}$  are given by

$$\begin{cases} \tau_{min} = NT + T_{FR} + T_3, \\ \tau_{max} = NT + T_{FR} + T_4, \quad \text{where } T_4 := 2T_2, \end{cases} \quad (4.17)$$

where  $T_3$  is defined by

$$T_3 := T_{FD} + \min_{0 \leq \Delta t \leq \Delta t_{max}} [f_1(\Delta t) + 2f_2(\Delta t) + 2\Delta t]. \quad (4.18)$$

We assume  $T_4 < T_{A\vartheta}$ . If  $\tau$  reaches its minimum value  $\tau_{min}$  at  $\Delta t = 0$ ,  $T_3 = T_{FD} + 2T_c$  and periodic patterns in  $\Omega_{0,2,n-1}$  transit to periodic patterns in  $\Omega_{1,2,n-2}$  at  $T = NT + T_{FR} + T_{FD} + 2T_c$  for  $\tau \in (nT, nT + T)$ . Otherwise,  $T_3 < T_{FD} + 2T_c$  and periodic patterns in  $\Omega_{0,2,n-1}$  coexist with periodic patterns in  $\Omega_{1,2,n-2}$  on the subinterval  $\tau \in ((n+1)T + T_{FR} + T_3, (n+1)T + T_{FR} + T_{FD} + 2T_c)$  if  $T_{FD} + 2T_c < T_4$  or on the subinterval  $\tau \in ((n+1)T + T_{FR} + T_3, (n+1)T + T_{FR} + T_4)$  if  $T_{FD} + 2T_c \geq T_4$ .

**Theorem 4.3.** *The periodic pattern  $(1W_u)$  for  $\sigma = (kW_u)$  with  $2 \leq k \leq n+1$  can be generated if and only if*

$$\begin{cases} t_{up} = \frac{\tau - [(k-1)T + T_{FR} + (k-1)T_{FD} + (k-1)\Delta t]}{k}, \\ 0 < t_{up} < T_{A\vartheta}. \end{cases} \quad (4.19)$$

*The minimum and maximum values of  $\tau$  for the existence of such periodic patterns are given by*

$$\begin{cases} \tau_{min} = (k-1)T + T_{FR} + (k-1)T_2, \\ \tau_{max} = (k-1)T + T_{FR} + (k-1)T_{FD} + kT_{A\vartheta} + (k-1)\Delta t_{min}. \end{cases} \quad (4.20)$$

**Proof.** We consider  $\sigma = (\pi_1, \dots, \pi_k) = (W_u, \dots, W_u)$  with  $W_u$  being characterized by  $(t_{up}, T_{FD}, \Delta t)$ . Condition (3.4) gives rise to

$$(k-1)T + (k-1)(t_{up} + T_{FD} + \Delta t) + T_{FR} + t_{up} = \tau.$$

Re-arranging the above formula yields equation (4.19) and  $t_{up}$  must satisfy  $0 < t_{up} < T_{A\vartheta}$ .

The extreme case,  $t_{up} = 0$  and  $\Delta t = \Delta t_{max}$ , gives rise to the minimum value  $\tau_{min}$

$$\tau_{min} = (k-1)T + T_{FR} + (k-1)T_2.$$

The situation where  $t_{up}$  approaches  $T_{A\vartheta}$  and  $\Delta t$  approaches the minimum value  $\Delta t_{min}$  yields

$$\tau_{max} = (k-1)T + T_{FR} + (k-1)T_{FD} + kT_{A\vartheta} + (k-1)\Delta t_{min}.$$

□

We now summarize our discussions about periodic patterns of recurrent inhibitory loops in the case where  $T_{FD} < T_{FR}$  and  $\Delta t_{max} \leq T_{FR} - T_{FD}$ . For a given  $\tau \in [nT, nT + T)$ , the coexistence of periodic patterns in pattern subsets  $\Omega_{0,0,1}$ ,  $\Omega_{0,1,0}$ ,  $\Omega_{0,h,j}$  ( $h, j \geq 1$ ),  $\Omega_{1,h,j}$  ( $h, j \geq 0$  and  $h + j \geq 1$ ) leads to multistability. The necessary and sufficient conditions of the existence of periodic patterns in  $\Omega_{0,h,j}$ ,  $\Omega_{1,h,j}$  and  $\Omega_{0,1,0}$  are given by Theorems 4.1, 4.2, 4.3. The most important feature of periodic patterns is the transition from one pattern subset to another at some transition values of time delay  $\tau$ :  $nT + T_{FR} - T_{FD}$ ,  $nT + T_{FR}$ ,  $nT + T_{FR} + T_2$  and  $nT + T_{FR} + T_4$ . The pattern transition plays an important role in the coexistence of multiple periodic patterns for the recurrent inhibitory loop. The coexistence of two types of  $W$ -oscillations in one periodic pattern increases substantially the number of periodic patterns in some subintervals.

## 5. Realization and illustration

In the previous section, we obtained general results of periodic patterns for a given  $\tau/T \geq 1$  when  $T_{FR} > T_{FD}$  and  $\Delta t_{max} \leq T_{FR} - T_{FD}$ . In this section, we shall use a special case to illustrate how these general results can be applied. The specified parameter values are

$$E = 1.0, \quad I_0 = 1.45, \quad a = 2.25, \quad \vartheta = 1, \quad T_{Re} = 0.25, \quad T_F = 0.2, \quad T_{FD} = 0.25.$$

We have  $T_{FR} = T_F + T_{Re} = 0.45$ . Then

$$\begin{aligned} V_A &= E(1 - e^{-T_{Re}}) = 0.2212, \quad T_{A\vartheta} = \log \left[ \frac{I_0 - V_A}{I_0 - \vartheta} \right] = 1.00455, \\ T &= T_{FR} + T_{A\vartheta} = 1.45455, \quad T_c = \log \left[ \frac{I_0 - V_A}{(I_0 - V_A - a)e^{T_{FD}} + a} \right] = 0.1851T, \\ \Delta t_{max} &= \log \left[ \frac{(I_0 - V_A - a)e^{-T_{FD}} + a}{I_0 - V_A} \right] = 0.1160T, \\ \Delta t_{min} &= -T_{FD} + \log \left[ e^{-T_{A\vartheta}} + \frac{a(e^{T_{FD}} - 1)}{I_0 - V_A} \right] = -0.2549T, \end{aligned}$$

and

$$T_1 = T_c, \quad T_2 = \Delta t_{max} + T_{FD} = 0.2879T, \quad T_3 = 0.5404T, \quad T_4 = 0.5758T.$$

It is easy to check that the conditions  $T_{FD} < T_{FR}$  and  $\Delta t_{max} < T_{FR} - T_{FD}$  are both satisfied.

We first discuss periodic patterns when  $\tau/T$  is a positive integer. The pattern subsets and the number of periodic patterns are listed in Table 1 when  $\tau = nT$  and  $1 \leq n \leq 8$ . The number 8 with \* indicates that there are two  $(1W_u)$  periodic patterns: one for  $\sigma = (5W_u)$  and one for  $\sigma = (6W_u)$ . For example,  $n = 6T$ , there are six periodic patterns:  $(1V)$ ,  $(1W_u)$ ,  $(1W_u1V)$ ,  $(3W_u3V)$ ,  $(2W_u2V1W_u1V)$  and  $(2W_u1V1W_u2V)$ , and  $\Omega_{6T} = \Omega_{0,1,0} \cup \Omega_{0,0,1} \cup \Omega_{0,1,1} \cup \Omega_{0,3,3}$ .

**Table 1.** Pattern subsets and the number of periodic patterns when  $\tau = nT$ . In the case marked by \*, there are two  $(1W_u)$  periodic patterns: one for  $\sigma = (5W_u)$  and one for  $\sigma = (6W_u)$ .

$\tau$	Pattern Set	No.	$\tau$	Pattern Set	No.
$T$	$\Omega_{0,0,1}$	1	$5T$	$\Omega_{0,1,0} \cup \Omega_{0,0,1} \cup \Omega_{0,3,2}$	4
$2T$	$\Omega_{0,1,0} \cup \Omega_{0,0,1}$	2	$6T$	$\Omega_{0,1,0} \cup \Omega_{0,0,1} \cup \Omega_{0,1,1} \cup \Omega_{0,3,3}$	6
$3T$	$\Omega_{0,1,0} \cup \Omega_{0,0,1}$	2	$7T$	$\Omega_{0,1,0} \cup \Omega_{0,0,1} \cup \Omega_{0,3,4}$	8*
$4T$	$\Omega_{0,1,0} \cup \Omega_{0,0,1} \cup \Omega_{0,3,1}$	3	$8T$	$\Omega_{0,1,0} \cup \Omega_{0,0,1} \cup \Omega_{0,3,5} \cup \Omega_{0,6,1}$	10

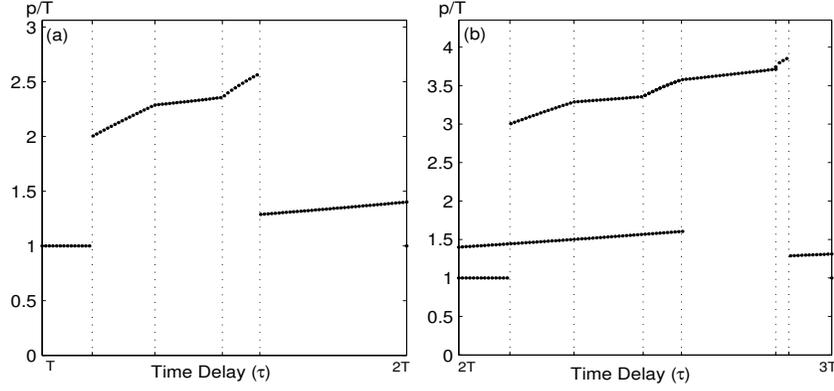
We now discuss the case where  $\tau \in (nT, nT + T)$  with a positive integer  $n$ . Figure 5 shows six coexisting periodic patterns as an example when  $\tau \in [3T + T_{FR} + T_3, 3.8515T)$ . Table 2 lists pattern subsets and periodic patterns in the interval  $\tau \in [T, 2T)$ . A plot of  $p/T$  versus  $\tau$  for  $\tau \in [T, 2T]$  is shown in Figure 4 (a), where  $p$  is the minimum period of periodic patterns and  $T$  is the intrinsic spiking period of the excitatory neuron. Four dotted lines in Figure 4 (a) are critical values  $T + T_{FR} - T_{FD}$ ,  $T + T_{FR}$ ,  $T + T_{FR} + T_1$  and  $T + T_{FR} + T_2$ , which separate the interval  $[T, 2T)$  into five characteristic subintervals. Line segments, from the bottom to the top, correspond to pattern subsets  $\Omega_{0,0,1}$ ,  $\Omega_{0,1,0}$ ,  $\Omega_{1,0,1}$ ,  $\Omega_{0,1,1}$  and  $\Omega_{1,1,0}$ . The corresponding periodic patterns in these subintervals are  $(1V)$ ,  $(1W_d1V)$ ,  $(1W_u1V)$ ,  $(1W_d1W_u)$  and  $(1W_u)$  with  $\sigma = (2W_u)$ . The periodic pattern  $(1V)$  transits to the pattern  $(1W_d1V)$  at  $\tau = T + T_{FR} - T_{FD}$ , then the pattern  $(1W_d1V)$  transits to the pattern  $(1W_u1V)$  at  $T + T_{FR}$ , and then the pattern  $(1W_u1V)$  transits to the pattern  $(1W_d1W_u)$  at  $T + T_{FR} + T_1$ , finally the pattern  $(1W_d1W_u)$  transits to the pattern  $(1W_u)$  with  $\sigma = (2W_u)$  at  $\tau = T + T_{FR} + T_2$ .

**Table 2.** Pattern subsets and periodic patterns when  $\tau \in [T, 2T)$ .

$\tau$	Pattern subsets	Periodic patterns
$[T, T + T_{FR} - T_{FD}]$	$\Omega_{0,0,1}$	$(1V)$
$(T + T_{FR} - T_{FD}, T + T_{FR}]$	$\Omega_{1,0,1}$	$(1W_d1V)$
$(T + T_{FR}, T + T_{FR} + T_1]$	$\Omega_{0,1,1}$	$(1W_u1V)$
$(T + T_{FR} + T_1, T + T_{FR} + T_2]$	$\Omega_{1,1,0}$	$(1W_d1W_u)$
$(T + T_{FR} + T_2, 2T)$	$\Omega_{0,1,0}$	$(1W_u)$

Table 3 and Table 4 list pattern subsets, periodic patterns and the number of periodic patterns in the interval  $\tau \in [2T, 3T)$  and  $\tau \in [3T, 4T)$  respectively.

A plot of  $p/T$  versus  $\tau$  for  $\tau \in [2T, 3T]$  is shown in Figure 4 (b), where  $p$  is the minimum period of periodic patterns. Six dotted lines in Figure 4 (b) are critical values  $2T + T_{FR} - T_{FD}$ ,  $2T + T_{FR}$ ,  $2T + T_{FR} + T_1$ ,  $2T + T_{FR} + T_2$ ,  $2T + T_{FR} + T_3$



**Figure 4.** Plots of  $p/T$  versus  $\tau$  for  $\tau \in [T, 2T]$  ((a)) and  $\tau \in [2T, 3T]$  ((b)), where  $p$  is the minimum period of a given pattern in the specific interval and  $T$  is the intrinsic spiking period of the excitatory neuron. (a) Values of time delay  $\tau$  for four dotted lines are  $T + T_{FR} - T_{FD}$ ,  $T + T_{FR}$ ,  $T + T_{FR} + T_1$  and  $T + T_{FR} + T_2$ , respectively. Line segments, from the bottom to the top, correspond to pattern subsets  $\Omega_{0,0,1}$ ,  $\Omega_{0,1,0}$ ,  $\Omega_{1,0,1}$ ,  $\Omega_{0,1,1}$  and  $\Omega_{1,1,0}$ . (b) Values of time delay  $\tau$  for six dotted lines are  $2T + T_{FR} - T_{FD}$ ,  $2T + T_{FR}$ ,  $2T + T_{FR} + T_1$ ,  $2T + T_{FR} + T_2$ ,  $2T + T_{FR} + T_3$  and  $2T + T_{FR} + T_4$ , respectively. Line segments, from the bottom to the top, correspond to pattern subsets  $\Omega_{0,0,1}$ ,  $\Omega_{0,1,0}$  for  $\sigma = (3W_u)$ ,  $\Omega_{0,1,0}$  for  $\sigma = (3W_u)$ ,  $\Omega_{1,0,2}$ ,  $\Omega_{0,1,2}$ ,  $\Omega_{1,1,1}$ ,  $\Omega_{0,2,1}$  and  $\Omega_{1,2,0}$ .

**Table 3.** Pattern subsets and periodic patterns when  $\tau \in (2T, 3T)$ , where  $R_1 = 0.6076T$ ,  $R_2 = T_{FR} + T_{FD} + 2T_c = 0.8515T$  and ‘No.’ stands for ‘the number of periodic patterns’.

$\tau$	Pattern subsets	Periodic patterns	No.
$[2T, 2T + T_{FR} - T_{FD}]$	$\Omega_{0,1,0} \cup \Omega_{0,0,1}$	$(1V); (1W_u)$	2
$(2T + T_{FR} - T_{FD}, 2T + T_{FR}]$	$\Omega_{0,1,0} \cup \Omega_{1,0,2}$	$(1W_u); (1W_d2V)$	2
$(2T + T_{FR}, 2T + T_{FR} + T_1]$	$\Omega_{0,1,0} \cup \Omega_{0,1,2}$	$(1W_u); (1W_u2V)$	2
$(2T + T_{FR} + T_1, 2T + T_{FR} + T_2]$	$\Omega_{0,1,0} \cup \Omega_{1,1,1}$	$(1W_u); (1W_d1W_u1V),$ $(1W_u1W_d1V)$	3
$(2T + T_{FR} + T_2, 2T + R_1]$	$\Omega_{0,1,0} \cup \Omega_{0,2,1}$	$(1W_u); (2W_u1V)$	2
$(2T + R_1, 2T + T_{FR} + T_3]$	$\Omega_{0,2,1}$	$(2W_u1V)$	1
$(2T + T_{FR} + T_3, 2T + R_2)$	$\Omega_{0,2,1} \cup \Omega_{1,2,0}$	$(2W_u1V); (1W_d2W_u)$	2
$(2T + R_2, 2T + T_{FR} + T_4]$	$\Omega_{1,2,0}$	$(1W_d2W_u)$	1
$(2T + T_{FR} + T_4, 3T)$	$\Omega_{0,1,0}$	$(1W_u)$	1

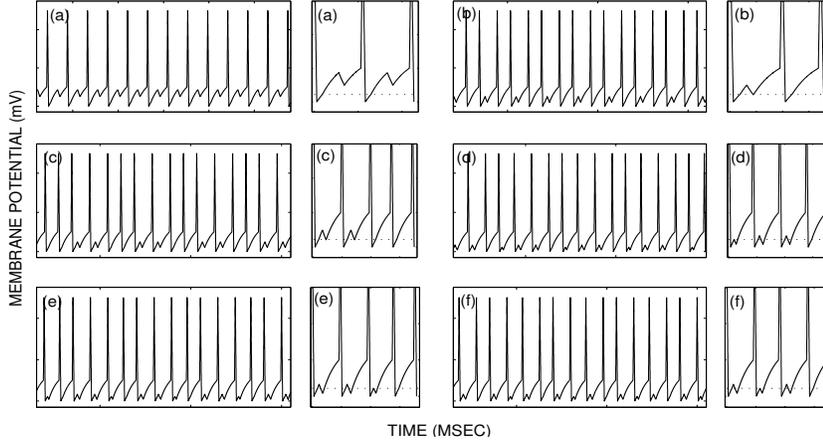
and  $2T + T_{FR} + T_4$  which separate the interval  $[2T, 3T)$  into seven characteristic subintervals. Line segments, from the bottom to the top, correspond to pattern subsets  $\Omega_{0,0,1}$ ,  $\Omega_{0,1,0}$  for  $\sigma = (3W_u)$ ,  $\Omega_{0,1,0}$  for  $\sigma = (2W_u)$ ,  $\Omega_{1,0,2}$ ,  $\Omega_{0,1,2}$ ,  $\Omega_{1,1,1}$ ,  $\Omega_{0,2,1}$  and  $\Omega_{1,2,0}$ . The periodic pattern  $(2W_u1V)$  coexists with the periodic pattern  $(1W_d2W_u)$  in the subinterval  $\tau \in [2T + T_{FR} + T_3, 2T + T_{FR} + T_{FD} + 2T_c)$ . Pattern transitions occur at critical values  $2T + T_{FR} - T_{FD}$ ,  $2T + T_{FR}$ ,  $2T + T_{FR} + T_1$ ,  $2T + T_{FR} + T_2$  and  $2T + T_{FR} + T_4$ . Multistability arises except in the subinterval  $(2T + R_1, 2T + T_{FR} + T_3] \cup (2T + R_2, 3T)$ .

Multistability occurs everywhere on the interval  $\tau \in [3T, 4T]$ . Figure 5 shows six coexisting periodic patterns when  $\tau \in [3T + T_{FR} + T_3, 3T + T_{FR} + T_{FD} + 2T_c)$ :  $(1W_u)$  with  $\sigma = (3W_u)$ ,  $(1W_u1V)$ ,  $(2W_u2V)$ ,  $(1W_d2W_u1V)$ ,  $(2W_u1W_d1V)$  and  $(1W_u1W_d1W_u1V)$ . For each periodic pattern, the right-hand side is the blow-up

**Table 4.** Pattern subsets, periodic patterns and the number of periodic patterns when  $\tau \in [3T, 4T)$ , where  $R = 3T + T_{FR}$ ,  $R_2 = T_{FD} + 2T_c$ .

$\tau$	Pattern subsets	Patterns	No.
$[3T, R - T_{FD}]$	$\Omega_{0,0,1} \cup \Omega_{0,1,0}$	$(1V), (1W_u)$	2
$(R - T_{FD}, R]$	$\Omega_{0,1,0} \cup \Omega_{1,0,3}$	$(1W_u), (1W_d3V)$	2
$(R, R + T_1]$	$\Omega_{0,1,0} \cup \Omega_{0,1,3}$	$(1W_u), (1W_u3V)$	2
$(R + T_1, R + T_2]$	$\Omega_{0,1,0} \cup \Omega_{1,1,2}$	$(1W_u), (1W_d1W_u2V)$ $(1W_u1W_d2V), (1W_d1V1W_u1V)$	4
$(R + T_2, R + T_3]$	$\Omega_{0,1,0} \cup \Omega_{0,1,1} \cup \Omega_{0,2,2}$	$(1W_u), (1W_u1V), (2W_u2V)$	3
$(R + T_3, R + R_2]$	$\Omega_{0,1,0} \cup \Omega_{0,1,1}$ $\cup \Omega_{0,2,2} \cup \Omega_{1,2,1}$	$(1W_u), (1W_u1V), (2W_u2V),$ $(1W_d2W_u1V), (2W_u1W_d1V),$ $(1W_u1W_d1W_u1V)$	6
$(R + R_2, R + T_4]$	$\Omega_{0,1,0} \cup \Omega_{1,2,1}$	$(1W_d2W_u1V), (2W_u1W_d1V),$ $(1W_u), (1W_u1W_d1W_u1V)$	4
$(R + T_4, 4T)$	$\Omega_{0,1,0} \cup \Omega_{0,3,1}$	$(1W_u), (3W_u1V)$	2

of the solutions in a given period (not delay  $\tau$ ) to clearly illustrate the patterns of solutions.

**Figure 5.** Six periodic solutions when  $\tau \in (3T + T_{FR} + T_3, 3T + T_{FR} + T_{FD} + 2T_c)$ : (a)  $(1W_u)$  with  $\sigma = (3W_u)$ , (b)  $(1W_u1V)$ , (c)  $(2W_u2V)$ , (d)  $(1W_d2W_u1V)$ , (e)  $(2W_u1W_d1V)$  and (f)  $(1W_u1W_d1W_u1V)$ . For each periodic pattern, the right-hand side is the blow-up of the solutions in a given period (not delay  $\tau$ ) to clearly illustrate the patterns of solutions.

## 6. Conclusions

In this first of a series of papers, we provided a rigorous and systematic qualitative study of the coexistence and transition of periodic patterns in delayed recurrent inhibitory loops. We focused on the case of short feedback duration, and we showed

that there can only be one inhibitory feedback delivered between two consecutive firing times and this feedback can generate three basic oscillations ( $V, W_d, W_u$ ). In a future study, we will consider the case of long feedback duration when we shall show that there is an additional basic oscillation much more complicated than illustrated here.

Our approach is the segmentation of the trajectory into a sequence of symbols as the three possible oscillation patterns, and analytically derive the feedback-induced action on a minimal segment of length larger than or equal to the delay. We derived a set of equations or inequalities (3.4) to determine which types of periodic patterns can be generated by recurrent inhibitory loops for a given time delay. We proved that the periodic pattern set  $\Omega_{m,h,j}$ , composed of  $m$   $W_d$ -oscillations,  $h$   $W_u$ -oscillations and  $j$   $V$ -oscillations, can be one of the following forms:  $\Omega_{0,0,1}$ ,  $\Omega_{0,1,0}$ ,  $\Omega_{0,h,j}$  ( $h, j \geq 1$ ) and  $\Omega_{1,h,j}$  ( $h, j \geq 0$  and  $h + j \geq 1$ ). Pattern transition occurs at critical values of time delay,  $T_{FR} - T_{FD}$ ,  $T_{FR}$ ,  $T_{FR} + T_1$ ,  $T_{FR} + T_2$  and  $T_{FR} + T_4$ . Pattern transitions play an important role in determining the coexistence of multiple stable patterns. We calculated the domain  $\tau \in (\tau_{min}, \tau_{max})$  for the existence of periodic patterns of  $\Omega_{m,h,j}$ . A detailed case study illustrated that multistability always occurs.

The work is based on [17], a number of developments have already been made based on this thesis. In particular, extensions of some of the ideas were made to couple network of small number of neurons [19, 30]. Naturally the number of stable periodic patterns can be further increased when the number of neurons is increased. This gives the potential that the delayed feedback can become an effective mechanism to enhance the network's capacity in terms of storing and retrieving a large number of local attractors. Unfortunately, in these extensions involving coupling and the explicit incorporation of the inhibitory neuron, much technical details were involved and we hope this work focused on a single neuron may provide better and clear insights into the fundamental issue how feedback delay is linked to symbolic dynamics.

## References

- [1] C. Börgers and N. Kopell, *Synchronization in networks of excitatory and inhibitory neurons with sparse, random connectivity*, Neural Comput, 2003, 15, 509–538.
- [2] A. Bose, N. Kopell and D. Terman, *Almost Synchronous Solutions for Pairs of Neurons Coupled by Excitation*, Physica D, 2000, 140, 69–94.
- [3] C.C. Chow, J.A. White, J. Ritt and N. Kopell, *Frequency control in synchronized networks of inhibitory neurons*, Neural Comput, 1998A, 5, 407–420.
- [4] C.C. Chow, *Phase-locking in weakly heterogeneous neuronal networks*, Physica D, 1998B, 118, 343–370.
- [5] R. Clewley, H.G. Rotstein and N. Kopell, *A Computational tool for the reduction of nonlinear ODE systems possessing multiple scales*, Multiscale Model. Simul., 2005, 4, 732–759.
- [6] S.M. Crook, G.B. Ermentrout and J.M. Bower, *Spike frequency adaptation affects the synchronization properties of networks of cortical oscillator*, Neural Comp., 1998, 10, 837–854.

- [7] G.B. Ermentrout and N. Kopell, *Fine structure of neural spiking and synchronization in the presence of conduction delays*, Proc. Nat. Acad. Sci., 1998, 95, 1259–1264.
- [8] U. Ernst, K. Pawelzik and T. Geisel, *Synchronization induced by temporal delays in pulse-coupled oscillators*, Phys. Rev. Lett., 1995, 74, 1570–1573.
- [9] J. Foss, A. Longtin, B. Mensour and J. Milton, *Multistability and delayed recurrent loops*, Phys. Rev. Lett., 1996, 76, 708–711.
- [10] J. Foss, F. Moss and J. Milton, *Noise, multistability and delayed recurrent loops*, Phys. Rev. E, 1997, 55, 4536–4543.
- [11] J. Foss and J. Milton, *Multistability in recurrent neural loops arising from delay*, J. of Neurophysiol, 2000, 84(2), 975–985.
- [12] W. Gerstner, *Time structure of the activity in neural network models*, Phys. Rev. E, 1995, 51, 738–758.
- [13] J.J. Hopfield, *Neurons with graded response have collective computational properties like those of two-state neurons*, Proc. Natl. Acad. Sci., 1984, 81, 3088–3092.
- [14] N. Kopell and G.B. Ermentrout, M.A. Whittington and R.D. Traub, *Gamma rhythms and beta rhythms have different synchronization properties*, Proc. Nat. Acad. Sci., 2000, 97, 1867–1872.
- [15] N. Kopell and G.B. Ermentrout, *Mechanisms of phase-locking and frequency control in pairs of coupled neural oscillators*, Handbook on Dynamical Systems: Toward applications. Ed. B. Fiedler, Elsevier, 2002, 2, 3–54.
- [16] N. Kopell, D. Pervouchine, H.G. Rotstein, T. Netoff, M. Whittington and T. Gloveli, *Multiple rhythms and switches in the nervous system*, Proceedings of The Second International Symposium on the Frontiers of Applied Mathematics, Conference in Honor of the 90th Birthday of C.C. Lin, Beijing, 2006. Din-Yu Hsieh, Meirong Zhang Weitao Sun. eds., World Scientific Publishing Co., 2007, 1-18.
- [17] J. Ma, *Multitability in Neural Networks with Delayed Feedback: Theory and Applications*, PhD Dissertation, York University, 2008.
- [18] J. Ma and J. Wu, *Multistability in spiking neuron models of delayed recurrent neural loops*, Neural Computation, 2007, 19, 2124–2148.
- [19] J. Ma and J. Wu, *Patterns, memory and periodicity in two-neuron delayed recurrent inhibitory loops*, Math. Model. Nat. Phenom., 2010, 5(2), 67–99.
- [20] M.C. Mackey and U. an der Heiden, *The dynamics of recurrent inhibition*, J. Math. Biol., 1984, 19, 211–225.
- [21] C.M. Marcus and R.M. Westervelt, *Stability of analog neural networks with delay*, Physical Review A, 1989, 39, 347–359.
- [22] J. Milton, *Dynamics of small neural populations*, CRM Monograph Series 7, American Mathematical Society, Providence, RI, 1996.
- [23] J. Milton and Epilepsy, *Multistability in a Dynamic Disease in Self-organized Biological Dynamics and Nonlinear Control* (J. Walleced ed. ), Cambridge University Press, Cambridge, MA., 2000, 374–386.

- 
- [24] J. Milton, J. Wu, S.A. Campbell and J. Bélair, *Outgrowing Neurological Diseases: Microcircuits, Conduction Delay and Childhood Absence Epilepsy*, In Computational Neurology and Psychiatry (P. Érdi, B. Sen Bhattacharya and A.L. Cochran, Eds), Springer, New York, 2017.
- [25] M. Morita, *Associative memory with non-monotone dynamics*, Neural Network, 1993, 6, 115–123.
- [26] D. Terman, N. Kopell and A. Bose, *Dynamics of two mutually coupled slow inhibitory neurons*, Physica D, 1998, 117, 241–275.
- [27] X.J. Wang and J. Rinzel, *Alternating and synchronous rhythms in reciprocally inhibitory model neurons*, Neural Comput., 1992, 4, 84–97.
- [28] J. Wu, *Introduction to Neural Dynamics and Signal Transmission Delay*, vol. 6 of de Gruyter Series in Nonlinear Analysis and Applications, Walter de Gruyter, Berlin, New York, 2001.
- [29] J. Wu, S.A. Campbell and J. Bélair, *Time-delayed neural networks: stability and oscillations*, Encyclopedia of Computational Neuroscience, SpringerReference (www.springerreference.com). D. Jieger and R. Jung, eds. Springer-Verlag Berlin Heidelberg, 2013.
- [30] S. Zou, Y. Chen, J. Ma and J. Wu, *Delay for the capacity-simplicity dilemma in associative memory attractor networks*, Neural Networks, 2012, 29, 37–51.