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Temperature-induced logical resonance in the Hodgkin–Huxley neuron

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Logical resonance has been demonstrated to be present in the FitzHugh–Nagumo (FHN) neuron, namely, the FHN neuron can operate as a reliable logic gate within an optimal parameter window. Here we attempt to extend the results to the more biologically realistic Hodgkin–Huxley (HH) model of neurons. In general, biological organisms have an optimal temperature at which the biological functions are most effective. In view of this, we examine if there is an optimal range of temperature where the HH neuron can work like a specific logic gate, and how temperature influences the logical resonance. Here we use the success probability P to measure the reliability of the specific logic gate. For AND logic gate, P increases with temperature T, reaches the maximum in an optimal window of T, and eventually decreases, which indicates the occurrence of the temperature-induced logical resonance phenomenon in the HH neuron. Moreover, single and double logical resonances can be induced by altering the frequency of the modulating periodic signal under the proper temperatures, suggesting the appearance of temperature-controlled transition of logical resonance. These results provide important clues for constructing neuron-based energy-efficient new-fashioned logical devices.

Keywords: stochastic resonance, logical stochastic resonance, Hodgkin–Huxley neuron, temperature

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1. Introduction

Numerous studies have demonstrated that noise can play a positive role in nonlinear systems over the past few decades. For instance, noise can be used as an effective method to amplify weak periodic signals. This phenomenon is regarded as stochastic resonance (SR), which was first proposed by Benzi and collaborators when they explored the problem of the periodically recurrent ice ages.[1] In fact, noise can also exert positive effects in the nonlinear systems even if an external weak periodic signal is absent. For example, the noise-driven nonlinear system without an external periodic signal can show resonant oscillation behaviors under moderate noise intensity, thereby significantly improving the regularity of system dynamics, which is called coherent resonance (CR).[2,3] With further research, multiple SRs or CRs have been revealed, and their positive roles in the nonlinear systems have been widely explored and confirmed.[4,5]

Noise widely exists in electronic elements. As described by Moore's law of miniaturization, further integration density of computer chips causes the aggravation of thermal fluctuations (noise)[6] and noises can seriously impair the performance of the computational devices.[7] Inspired by SR, Murali and collaborators found that noises in computational devices can be exploited constructively to improve the reliability of logical operations.[8] The response of a noise-driven bistable system to two independent aperiodic square waves (considered as two unrelated logic inputs) can be mapped into logic output, where the bistable system can be regarded as a logic gate. An optimal window of noise intensity for bistable system exists, which greatly enhances the success rate of logic operations.[8] This phenomenon is known as logical stochastic resonance (LSR) because of its similarity with SR.[8] LSR can occur even for subthreshold inputs, so it emerges as a potential option for constructing energy-efficient new-fashioned logical devices. Some efforts have been devoted to implementing this new-style LSR-based logical gate.[9–12] In the past decade, LSR has received more and more attention.[13–19]

Noise is not the only factor to induce logical resonance. Periodic force,[20–23] parameter,[24] time delay,[25–27] autapse,[28] coupling,[29,30] and chaotic signal[31,32] can be used as replacements for stochastic noise to obtain similar results with SR. The scope of the research has been extended from typical bistable systems to multi-stable systems in order to explore all types of logical operations. Meanwhile, the constructive role of noise, periodic and chaotic signals in information storage has also been widely investigated by implementing set–reset latch operation.[33–41] Our recent study has verified that the dynamical behaviors of the chaos-driven FitzHugh–Nagumo (FHN) neuron under the periodic force-modulated input signals can be interpreted as the specific logic output, and the excitable two-state FHN neuron can operate as a logic gate in the optimal range of intensity of chaotic driving force.[42]

Temperature is known to be a pivotal disturbance of bio-

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logical functionalities in living systems. From the perspective of biochemical reactions, temperature drastically affects enzyme activity,[43] thereby affecting enzyme-catalyzed rates[44] and even the metabolism level of the whole organisms.[45] From the standpoint of information processing and signal transmission, temperature exerts influence on signal propagation through axons by altering the neuroplasticity of the brain and nervous system.[46] Experimental observations show that the opening time of sodium ion channels of the myocardium is influenced by temperature.[47] Furthermore, low temperatures may cause conduction failure of the action potentials, although the action potentials cannot be faithfully conducted either at fever-like temperatures.[48] An optimal temperature exists for the propagation of action potentials.[49–51] In addition, the firing dynamic of the neurons is affected by temperature and the firing frequency is reduced at low temperature. Our recent studies have shown that the successful implementation of logical operation with the FHN neuron is dependent on firing behaviors of the FHN neuron.[42] Thus some interesting issues are naturally aroused: How does the temperature affect logical resonance in the HH neuron? Is there an optimal range of temperature where the HH neuron can work like a specific logic gate?

2. Model and scheme

The temperature-controlled HH neuron model describing the membrane potential of the giant squid axon is given by the following set of equations:[52]

$$\begin{aligned} C_{\rm m}\frac{{\rm d}V}{{\rm d}t} &= g_{\rm K}n^4(V_{\rm K}-V)+g_{\rm Na}m^3h(V_{\rm Na}-V) \\ &\quad +g_{\rm L}(V_{\rm L}-V)+I, \qquad (1) \\ \frac{{\rm d}y}{{\rm d}t} &= \alpha_y(V)(1-y)-\beta_y(V)y, \quad (y=m,h,n). \qquad (2) \end{aligned}$$

Here V indicates the membrane potential, while m, n and h indicate the gating probabilities of different ionic channels, respectively. The fixed parameters in equation (1) are presented in Table 1. And the kinetic rates of ion channels are given by[52]

$$\alpha_m = \frac{0.1\phi(T)(V+40)}{1-\exp(-(V+40)/10)}, \qquad (3a)$$

$$\beta_m = 4\phi(T)\exp(-(V+65)/18), \qquad (3b)$$

$$\alpha_n = \frac{0.01\phi(T)(V+55)}{1-\exp(-(V+55)/10)}, \qquad (4a)$$

$$\beta_n = 0.125\phi(T)\exp(-(V+65)/80), \qquad (4b)$$

$$\alpha_h = 0.07\phi(T)\exp(-(V+65)/20), \qquad (5a)$$

$$\beta_h = \frac{\phi(T)}{1+\exp(-(V+35)/10)}, \qquad (5b)$$

with

$$\phi(T) = 3^{(T-6.3\ ^\circ{\rm C})/10\ ^\circ{\rm C}}. \qquad (6)$$

The above-mentioned equations (3)–(6) describe that the opening and closing rates of the ion channel at a high temperature are faster than that at a low temperature. The character I in Eq. (1) stands for external stimuli given by[42]

$$I = (s_1+s_2)B\sin(\omega t), \qquad (7)$$

where s_1 and s_2 are two unrelated aperiodic 2-level square waves. They encode two independent binary logic input signals, respectively, according to the following encoding rule: for logic input 1, s_1 and s_2 take value 3.5, or 0 for logic input 0. $B\sin(\omega t)$ denotes periodic force with amplitude B and angular frequency ω, which is used to modulate two input signals. As previously mentioned,[8,15,31] the resting and excited states of the HH neuron are interpreted as logic output 0 and 1, respectively. So the input–output associations for AND & OR logic gates are listed in Table 2.

Table 1. Parameters for the temperaturecontrolled Hodgkin–Huxley neuron model.

Symbol	Definition	Value & units
$C_{\rm m}$	specific membrane capacitance	1 μF/cm^2
$V_{\rm K}$	potassium reversal potential	−77 mV
$V_{\rm Na}$	sodium reversal potential	50 mV
$V_{\rm L}$	leakage reversal potential	−54.4 mV
$g_{\rm K}$	potassium channel conductance	36 mS/cm^2
$g_{\rm Na}$	sodium channel conductance	120 mS/cm^2
$g_{\rm L}$	leakage conductance	0.3 mS/cm^2

Table 2. The truth table for AND & OR logic operations.

(s_1, s_2)	Logic input sets	States of neuron		Logic outputs	
		AND	OR	AND	OR
(0, 0)	(0, 0)	resting	resting	0	0
(0, 3.5)/(3.5, 0)	(0, 1)/(1, 0)	resting	excited	0	1
(3.5, 3.5)	(1, 1)	excited	excited	1	1

The reliability of the logic gate is very important for logic operations. Here we use the success probability P to measure the reliability of the specific logic gate. P is defined as the ratio of the number of successful runs (n) to the total number of runs (N), i.e., $P = n/N$. In a run, for all possible logic input combinations, the logic output obtained is always correct according to the truth table (Table 2), then this run is regarded as a successful one. Because of the delay effect, the input signal s_1 and s_2 are required to keep unchanged during the time interval (defined as 200 time units), and the unsuccessful logic operation can be tolerated if it occurs during the transient process (defined as the first 10% of this time interval). In addition, the total number of runs N is required to be big enough. In this study, N is set to 1000. We use the Euler' algorithm

to obtain the dynamics of temperature-controlled HH neuron model, with a fixed time step $\Delta t = 0.001$ time units. The initial values are chosen randomly in the reasonable ranges. In fact, control runs with smaller Δt or greater N reveal no significant difference in results.

3. Results

As shown in Fig. 1, s_1 and s_2 are two dependent aperiodic 2-level square waves (Figs. 1(a) and 1(b)), and sum of s_1 and s_2 is a aperiodic 3-level square wave (blue line) (Fig. 1(c)). According to the encoding rule listed in Table 2, when $s_1 + s_2$ takes value 0 or 3.5, the state of the HH neuron for the AND logic gate is expected to be in the resting state (i.e., the logic output is 0); when $s_1 + s_2$ takes value 7, the state of the HH neuron is expected to be in the excited state (i.e., the logic output is 1). For low temperature (such as $T = 6.3$ °C), when $s_1 + s_2$ takes value 3.5, the HH neuron lies in the excited state (i.e., the logic output is 1) (Fig. 1(c)). In this case, the right AND logic result cannot be obtained. For high temperatures (such as $T = 18$ °C), the HH neuron is not evoked for all possible values of $s_1 + s_2$ (Fig. 1(e)). The desired AND logic result cannot be obtained either. However, for moderate temperature (such as $T = 10$ °C), the consistent AND logic output is always available for all possible values of $s_1 + s_2$ (i.e., all possible logic input combinations) (Fig. 1(d)). Similarly, appropriate temperature can yield consistent OR logic output (Fig. 1(f)), while inappropriate temperature can lead to failure of OR logic operation (Fig. 1(g)). Therefore, we conclude that there are optimal ranges of temperature in which the HH neuron operates like a reliable AND/OR logic gate.

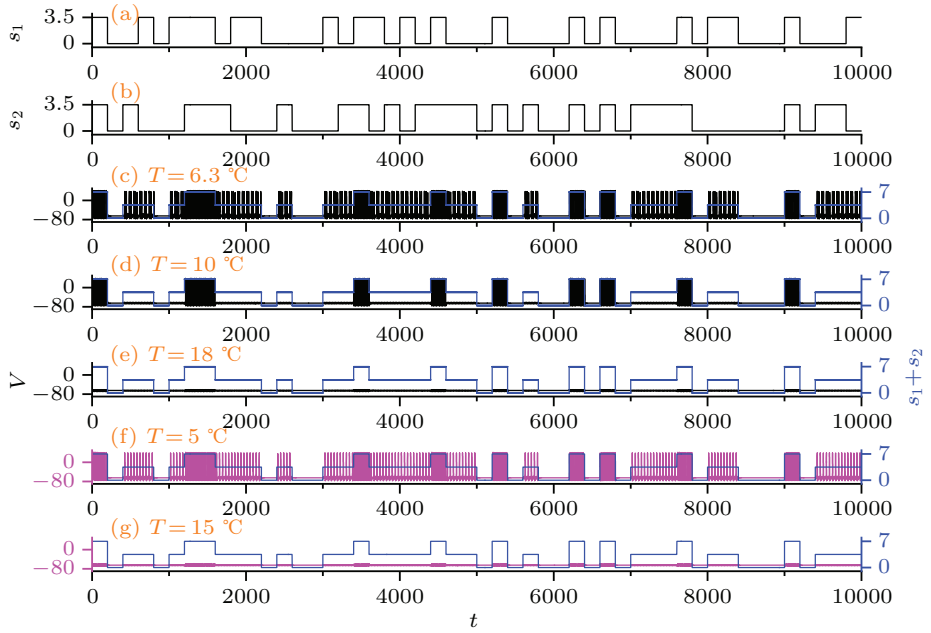


Fig. 1. Sampled time series of input signals s_1, s_2, $s_1 + s_2$, and membrane potential V of the HH neuron under representative temperatures. Appropriate temperatures can yield consistent (d) AND or (f) OR logic output for all possible logic input combinations. $B = 0.5$, $\log_{10}(\omega) = -0.5$.

In order to further obtain the optimal window of temperature, dependence of success probability P(AND) and P(OR) on temperature T are plotted for different amplitudes B of periodic force (Fig. 2). It is evident that there are optimal ranges of temperature in which the reliability of AND & OR logic gates can be maximized (Figs. 2(a) and 2(b)). Namely, temperature-induced logical resonance phenomenon can occur in the HH neuron model. When frequency is fixed (such as $\log_{10}(\omega) = -0.5$), with the increase of amplitude B, the optimal window of temperature shifts toward higher temperature for the AND & OR logic gates (Figs. 3(a) and 3(b)) and gradually broaden for the OR logic gate (Fig. 3(b)). Moreover, the position and width of the optimal window of temperature are also affected by the frequency (Figs. 4 and 5) when the amplitude is fixed.

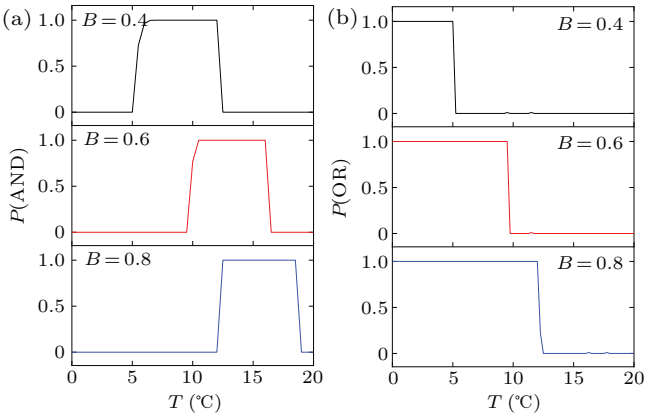


Fig. 2. Dependence of (a) P(AND) and (b) P(OR) on temperature T for different amplitudes B. There are the optimal ranges of temperature where success probabilities of obtaining AND & OR logic results are always equal to 1. In other words, temperature-induced logical resonance phenomenon occurs in the HH neuron model. $\log_{10}(\omega) = -0.5$.

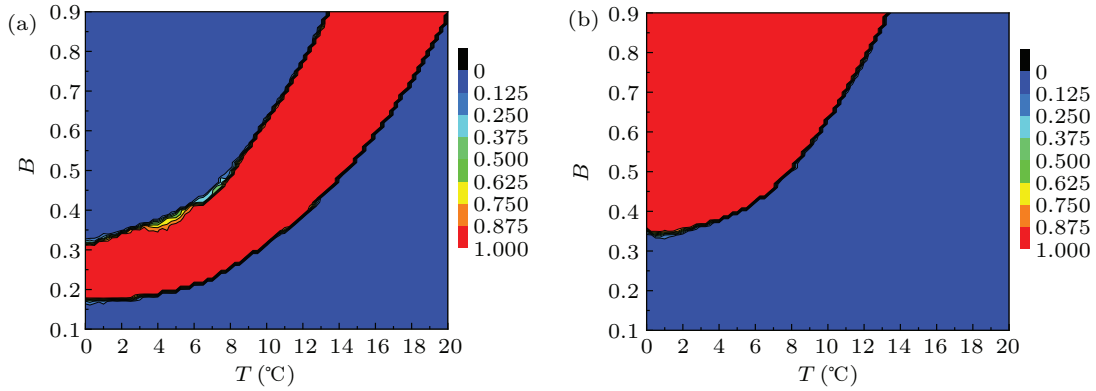


Fig. 3. Contour plots of success probability (a) P(AND) and (b) P(OR) in B–T plane. The red region indicates the occurrence of logical resonance. $\log_{10}(\omega) = -0.5$.

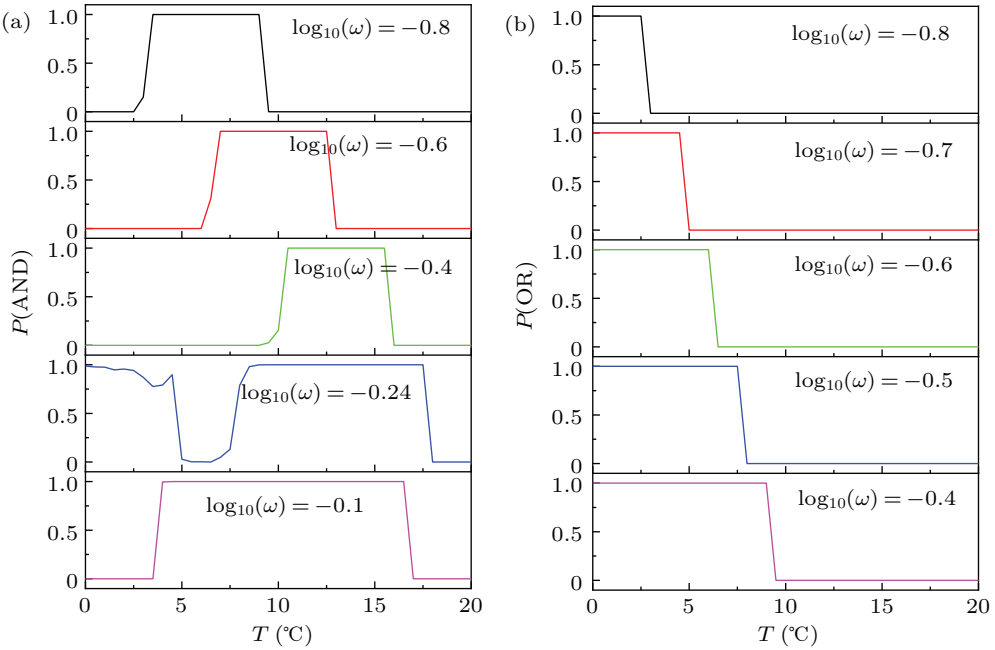


Fig. 4. Dependence of (a) P(AND) and (b) P(OR) on temperature T for different frequencies $\log_{10}(\omega)$. There are the optimal ranges of temperature where success probabilities of obtaining AND & OR logic results are always equal to 1. In other words, temperature-induced logical resonance phenomenon occurs in the HH neuron model. $B = 0.5$.

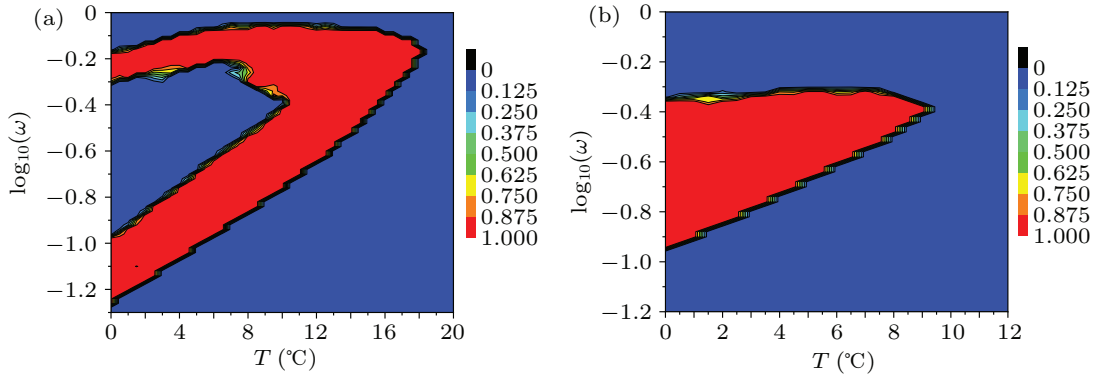


Fig. 5. Contour plots of success probability P in $\log_{10}(\omega)$–T plane. The red region indicates the occurrence of logical resonance. $B = 0.5$.

Logical resonance can also be obtained in the HH neuron by altering the amplitude or frequency of periodic force $B\sin(\omega t)$ if the temperature is appropriate (Figs. 3 and 5). Furthermore, the temperature can induce transition of logical resonance (Fig. 5(a)). That is to say, the temperature-controlled transition of logical resonance can occur in the HH neuron. For example, the temperature-controlled transition of logical resonance from double to single can be observed clearly with the increase of temperature (Fig. 6).

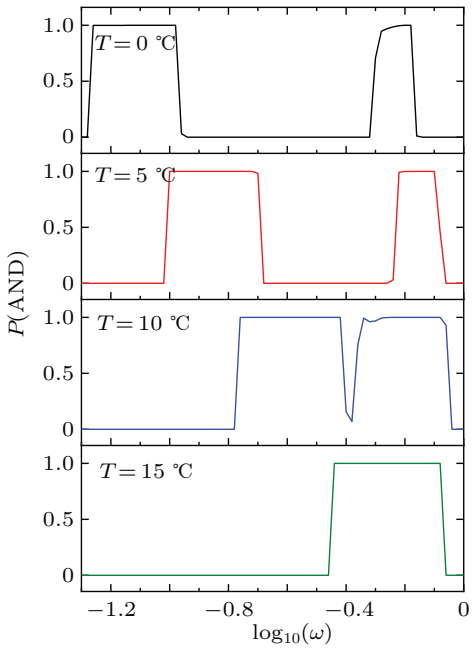


Fig. 6. Dependence of P on frequency $\log_{10}(\omega)$ for different temperatures T for AND logical operation. Clearly, the curves of P versus $\log_{10}(\omega)$ show resonant behaviors, which indicates the occurrence of logical resonance induced by regulating frequency of periodic force. In addition, from top to bottom, temperature-controlled transition of logical resonance (double-to-single) can be observed clearly with increasing temperature.

Finally, the potential mechanism for temperature-induced logical resonance is given based on phase portrait of the forced temperature-sensitive HH neuron model. Temperature alters the excitability of temperature-sensitive neurons. As illustrated in Fig. 7, increasing temperature makes it more difficult for neurons to enter a firing or excitable state. Under low temperature (such as $T = 6.3$ °C), when $s_1 + s_2$ is 0 (i.e., logic input set is (0, 0)), external stimuli I (including input signals s_1, s_2 and modulating periodic force $B\sin(\omega t)$) still has enough energy to evoke spikes (Fig. 7(a)). So the logic output of the system is 1 in this case. In consequence, the AND logic operation becomes unreliable. But with high temperature (such as $T = 18$ °C), even if $s_1 + s_2$ is 7 (i.e., logic input set is (1, 1)), external stimuli I has no enough energy to evoke spikes (Fig. 7(c)) thereby the logic output of the system is always 0. In that case, reliable AND logical operation cannot be implemented. Under an appropriate temperature (Fig. 7(b)), the responses of forced temperature-sensitive HH neurons to the input signals s_1 and s_2 could always be consistent with the logic input–output associations for specified logic gates. Moreover, the same mechanism can be used to interpret OR logical operation (Figs. 7(d)–7(f)).

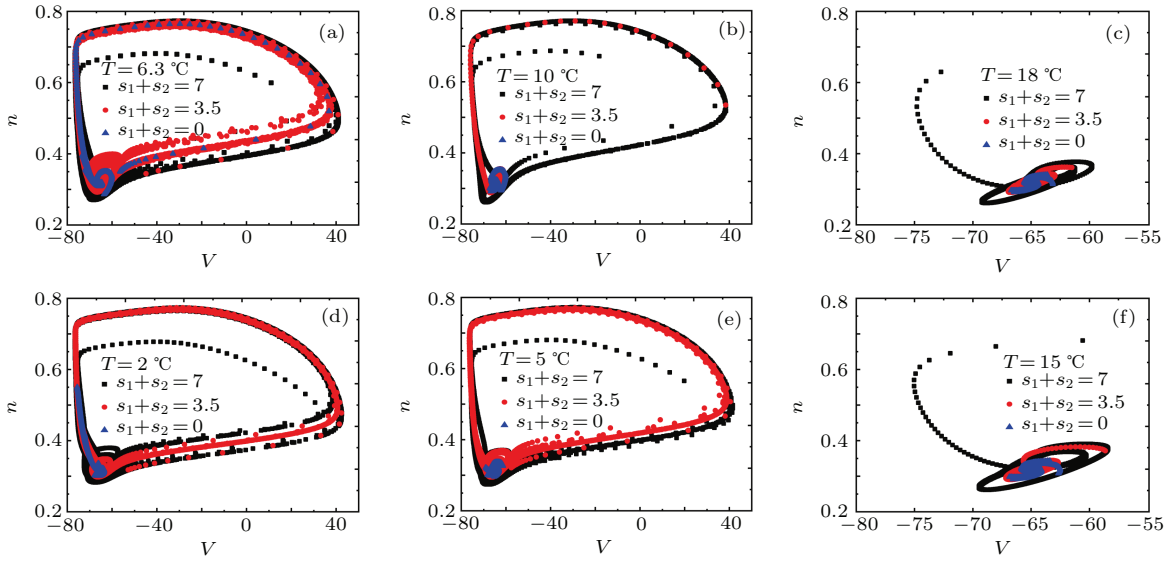


Fig. 7. Phase portrait of the forced temperature-sensitive HH neuron model for (a)–(c) AND & (d)–(f) OR logic gates. $B = 0.5$, $\log_{10}(\omega) = -0.5$.

4. Conclusions

In this study we attempt to interpret the response of the Hodgkin–Huxley (HH) neuron to external input signals as the desired logic results according to a well-defined rule. We have investigated the role of temperature in the logical resonance of HH neurons. As an indicator of the reliability of the logic gate, the success probability P increases with the increase of temperature T, reaches the maximum in the optimal window of T, and eventually decreases, which indicates the existence of temperature-induced logical resonance in the HH neuron. In addition, P also displays resonant behavior as the frequency or amplitude of the modulating periodic signal increases. That is to say, periodic force-induced logical resonance can happen in the HH neuron. Interestingly, single and double logical resonances can be induced by altering frequency under the proper temperatures. Thus, the transition between single and double logical resonances can be controlled by regulating temperature. Taken together, there is temperature-induced logical resonance and temperature-controlled transition of logical resonance in the Hodgkin–Huxley neuron. These results provide important clues for constructing neuron-based energy-efficient new-fashioned logical devices.

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