

Energy dependence on modes of electric activities of neuron driven by multi-channel signals

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Abstract Neuron can receive electric signals or forcing currents from more than one channel, and these forcing currents could show some diversity. Based on the Hindmarsh–Rose neuron model, mixed forcing currents, which are composed of low-frequency, high-frequency and constant signals, are imposed on the neuron, and multiple modes of electric activities could be observed alternately (in turn) from the neuron. Based on the Helmholtz theorem, the Hamilton energy is calculated to discern the energy dependence on the mode selection of the electric activities of neuron. It is found that the response of electrical activities much depends on the amplitude than the frequency when mixed signals are imposed on the neuron synchronously; however, the rhythm of electrical activities could be adjusted by the frequency of the periodical signals in the mixed signal. It is confirmed that the energy is much dependent on the mode of electrical activi-

ties instead of the external forcing currents directly, and a smaller energy occurs under bursting states. The delayed response of Hamilton energy to external forcing currents confirms that neuron contributes to energy coding. These results could be helpful for further investigation on energy problems in neuronal network associated with model transition for collective behaviors.

Keywords Neuron · Hamilton energy · Bursting state · Helmholtz theorem

1 Introduction

Neurons are responsible for exchanging signals to and from the central nervous system (CNS). Neural information is encoded and transmitted as spikes in membrane electrical potential that action potentials are generated [1–11]. For example, Behdad et al. [4] designed an artificial neuronal circuit to explore the dynamics in Morris–Lecar neuron. Gonzalez-Miranda [5] reported the possible pacemaker behaviors in Morris–Lecar (ML) model. Newby et al. [6] analyzed the excitability of ML neuron driven by channel noise. Ciszak et al. [7] explained the autonomous transitions between waking and sleep states modulated by synaptic plasticity. Tang et al. [8] constructed a minimal neuron-astrocyte network model by connecting a neurons chain and an astrocytes chain, and the possible role astrocytes play in the SDs propagation was discussed. Wang et al. [9] studied the multiple responses of ML neuron driven

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by various stimuli. Ibarz et al. [11] proposed a map-based neuron model, and its dynamics was also discussed. Neurons also can produce bursting oscillation that is a relatively slow rhythmic alternation between an active phase of rapid spiking and a quiescent phase without spiking. In computational neuroscience, external forcing current and other bifurcation parameters [12–21] could be adjusted to observe the transition between modes of electric activities, for example, the Hindmarsh–Rose (HR) neuron model [10] can present quiescent, spiking, bursting and even chaotic state by increasing the external forcing current carefully. For example, Storaace et al. [12] presented detailed bifurcation analysis within HR neuron. Innocenti et al. [13] investigated the mode transition of electrical activities. Wang et al. [14] suggested that time-delayed feedback control can control the behavior of neuron. Zhang et al. [15] discussed the transition in electrical activities by system size in coupled neurons. Li et al. [16] reported the synchronization dependence on order parameter in neuronal network. Barrio et al. [17] analyzed the chaotic structure in chaotic bursting neurons. Djeundam et al. [18] investigated deterministic and stochastic bifurcations in HR neuron model. Li et al. [19] discussed the emergence of chaos in a two-dimensional discrete HR model. Furthermore, Dong et al. [20] explored the dynamical behaviors in a fractional-order HR model. Based on the mentioned neuron models, networks are designed to study the collective behaviors [22–33] and pattern formation [34–36] of neurons. For example, Djeundam et al. [22] investigated the stability of synchronous network with different coupling types. Kakmeni et al. [23] discussed the collective response of HR neuronal network driven by local nonlinear excitation. Baptista et al. [24] discerned the modulation effect of chemical and electric synapses on synchronization and information coding of neuronal network. Wu et al. [25] suggested that impulsive control scheme could be useful for realizing synchronization of neuronal network. Wei et al. [26] argued that long-range connection in random can change the collective behaviors of network. Jalili et al. [27] detected the synchronization behavior in Newman–Watts network of Hindmarsh–Rose neuron. Qin et al. [28] discovered the contribution of autapse driving to stable spatial patterns in neuronal network with diversity in time delay. Wang et al. [29] presented discussion about parameter estimation in HR neuron model based on adaptive synchronization and mixed synchronization. Yilmaz et al. [30]

confirmed that autapse driving can enhance stochastic resonance in a scale-free network, and it was also found that autapse driving can modulate the collective behavior in small-world network as a pacemaker [31]. Uzun et al. [32] presented detailed comments on scale-free connection in neuronal network. Furthermore, Qin et al. [33] discussed the potential function of autapse driving in the network and confirmed that autapse driving with positive time-delayed feedback can enhance oscillating while negative feedback can calm down the exciting neurons and even block the wave propagation in the network [34]. The collective behaviors of network could be regulated by pacemakers such as spiral wave and target waves. However, breakup of spiral waves in network can disturb the ordered spatial pattern and cause breakdown of synchronization or ordered states in network. For example, Ma and Song et al. [35,36] suggested that time series analysis could be effective to predict the occurrence of breakup of spiral wave and breakdown in spatial order of network. In experimental way, Wang et al. [37] suggested that multi-arm spiral waves could be formed and developed by adjusting the conductance of ion channels carefully.

The neurodynamics has been extensively investigated by using the presented neuron models. Indeed, the mode transition of electrical activities and emergence of action potential in neuron are associated with the energy encoding and energy metabolism [38,39]. It shows some difficulties to detect the energy consumption and supply in exact way; therefore, some researchers suggested that Hamilton energy [40,41] could be estimated in neuron and oscillator models by using Helmholtz theorem [42]. For example, Song et al. [43] confirmed that bursting and chaotic states in neuron can present lower Hamilton energy and it could indicate that paroxysmal epilepsy can release large energy before restoring normal activity. Furthermore, chaotic systems with multi-attractors can also hold lower Hamilton energy and it could decrease the requirements for electric devices [44]. In fact, neuronal activities are much complex than the presented models could produce in theoretical and numerical way. Gu et al. [45] suggested an improved neuronal model, and the parameter region is expanded to study the transition of multiple electric activities. Xu et al. [46] studied a neural network model of spontaneous up and down transitions based on our former study of a single-neuron model. Lv et al. [47,48] argued that the effect of electromagnetic induction should be considered dur-

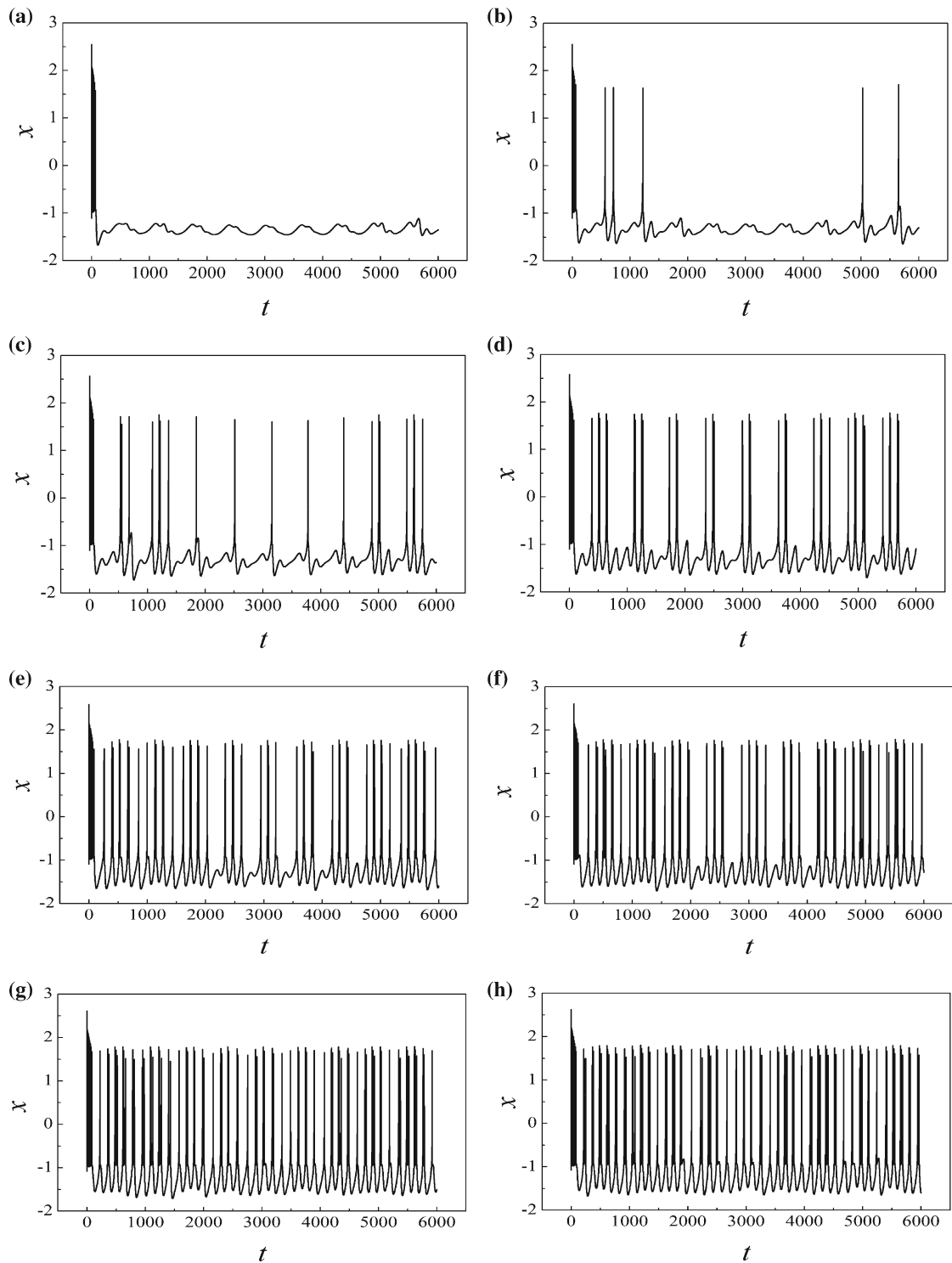
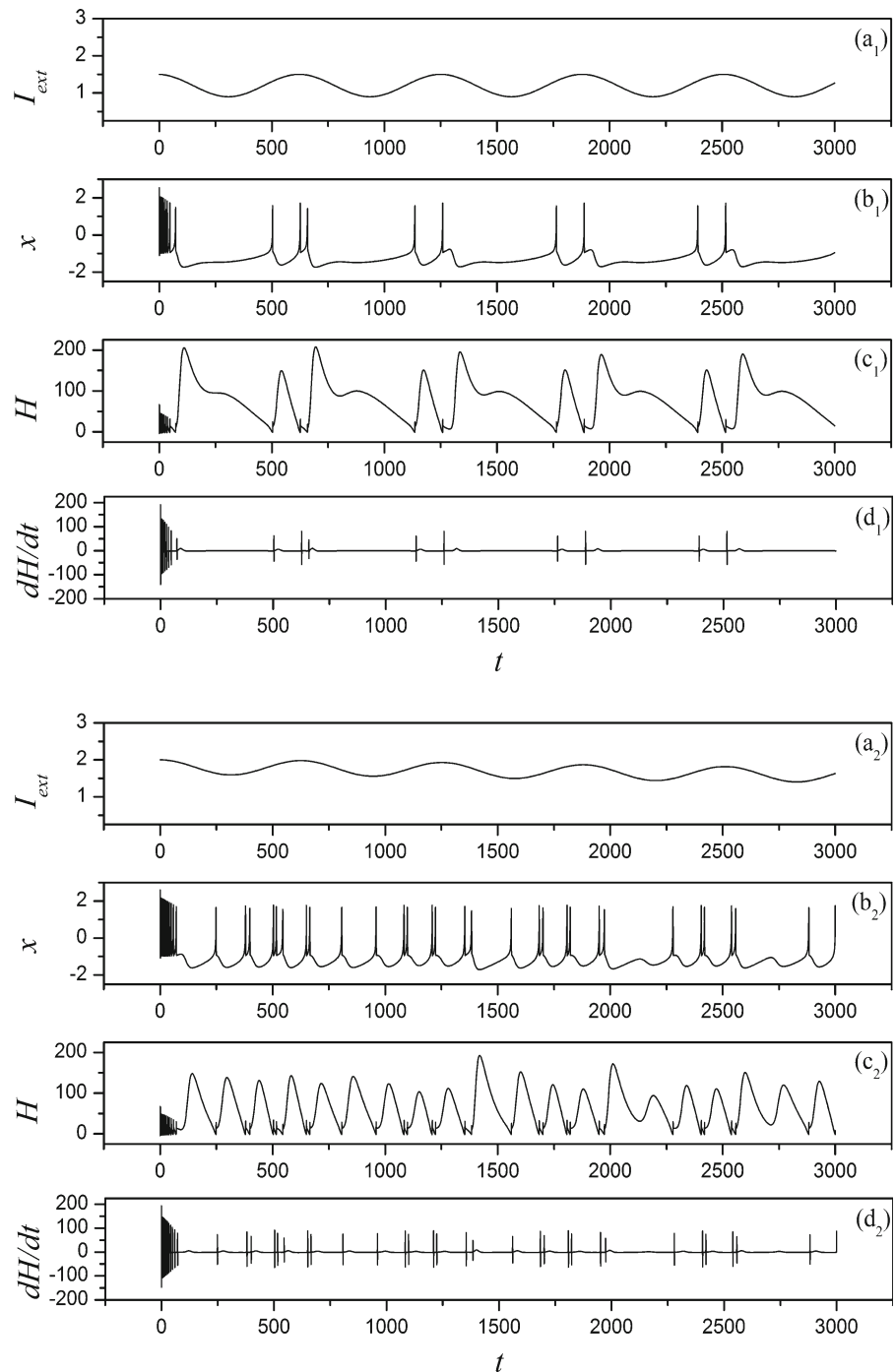


Fig. 1 Time series for sampled membrane potential are calculated when neuron is driven by mixed signal at $\varphi = 0$, $A = 0.2$, $B = 0.1$, $\omega = 0.01$, $N = 0.1$, for **a** $I_{\text{ext}} = 1.2$, **b** $I_{\text{ext}} = 1.3$, **c** $I_{\text{ext}} = 1.4$, **d** $I_{\text{ext}} = 1.5$, **e** $I_{\text{ext}} = 1.6$, **f** $I_{\text{ext}} = 1.7$, **g** $I_{\text{ext}} = 1.8$, **h** $I_{\text{ext}} = 1.9$

Fig. 2 Time series for sampled membrane potential and energy function are calculated when neuron is driven by mixed signal at $\varphi = 0$, $A = 0.2$, $B = 0.1$, $\omega = 0.01$, $N = 0.1$, for (a1, b1, c1, d1) $I_{\text{ext}} = 1.5$, (a2, b2, c2, d2) $I_{\text{ext}} = 1.7$



ing the occurrence of electric activities of neuron, so an additive variable for magnetic flux [34] is introduced into the HR neuron model, and the improved neuronal model can presented multiple modes of electric activi-

ties. As mentioned in Ref. [47], multiple modes of electrical activities could be reproduced by changing one bifurcation parameter due to the effect of electromagnetic induction. Realistic neurons can develop complex

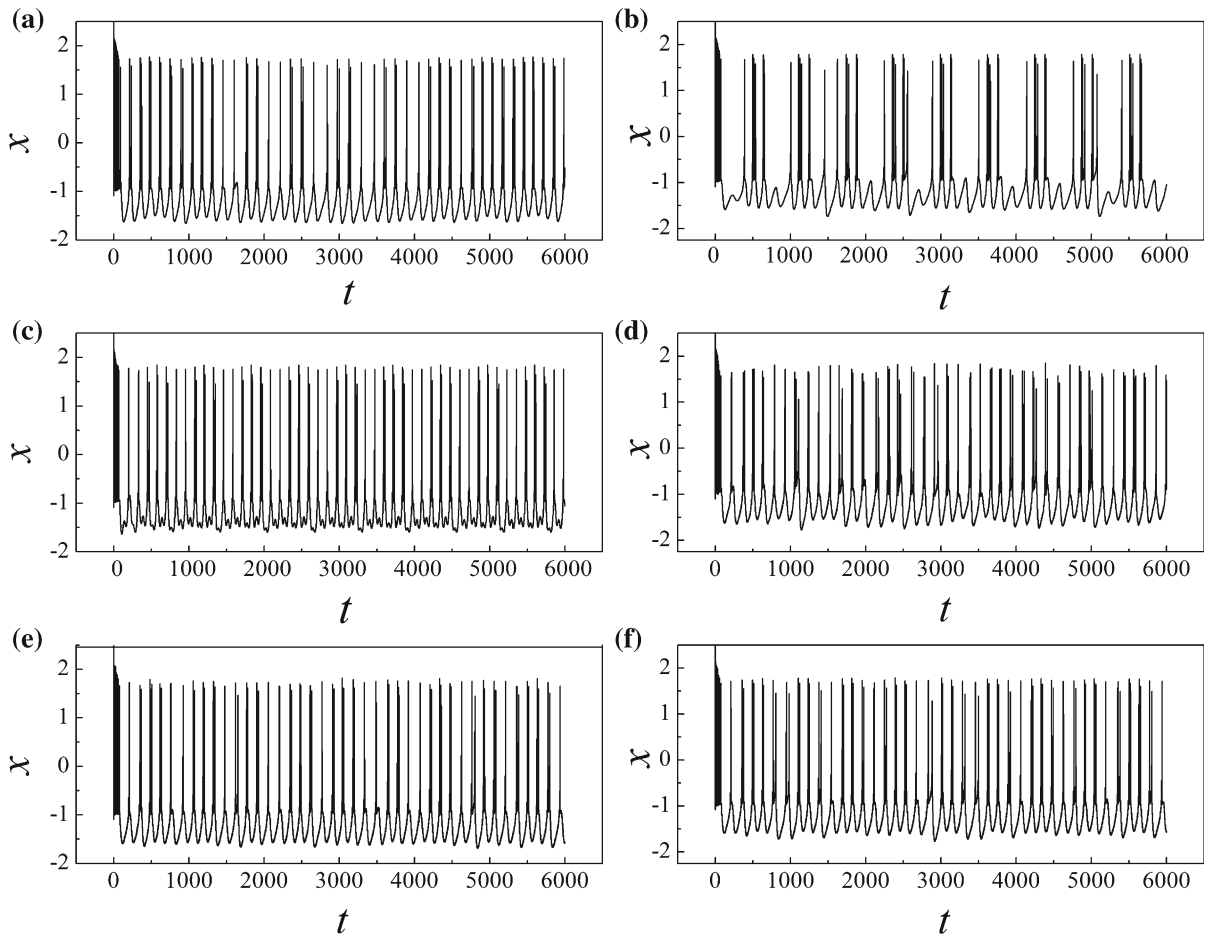


Fig. 3 Time series for sampled membrane potential are calculated when neuron is driven by mixed signal at $\varphi = 0$, $A = 0.1$, $B = 0.2$, $\omega = 0.01$, $I_{\text{ext}} = 1.7$. For **a** $N = 0.1$, **b** $N = 1$, **c** $N = 10$, **d** $N = 100$, **e** $N = 500$, **f** $N = 1000$

anatomical structure [49], and many biological, physical effect should be considered. For example, when mixed signals are imposed on neurons synchronously, how to encode and give appropriate response to these stimulus in order?

In this paper, multiple channels-driving signals, which different types of electrical stimulus are imposed on the neuron synchronously and simultaneously, are imposed on HR neuron model, the response of the electrical activities is discussed, respectively. It is interesting to find the response preferences to different external forcing currents. It could be helpful to understand the potential mechanism for signal processing of neurons when several external forcing currents are imposed on the neuron simultaneously.

2 Model and scheme

The dynamic equations for the Hindmarsh–Rose neuron [10]-driven by external forcing current could be described as follows

$$\begin{aligned}
 \dot{x} &= y - ax^3 + bx^2 - z + I_{\text{ext}} \\
 \dot{y} &= c - dx^2 - y \\
 \dot{z} &= r[s(x + 1.6) - z]
 \end{aligned}
 \tag{1}$$

where the variable x, y, z , represents the membrane potential, recovery variable for slow current and adaption current, respectively. I_{ext} is the external forcing current and could be composed of the periodic and constant signal, for example, it reads as follows

$$I_{\text{ext}} = I + A\cos\omega t + B\cos(N\omega t + \varphi) \quad (2)$$

where I is a constant current, A, B represents the amplitude and ω is the angular frequency of periodic forcing current, respectively. That is to say, constant and periodical forcing with frequency diversity are

imposed on the neuron synchronously and simultaneously. The parameters a, b, c, d, r, s are selected as the same values in most of the previous works, for example, $a = 1, b = 3, c = 1, d = 5, s = 4, r = 0.006$ and quiescent, spiking, bursting even chaotic state can be induced by adjusting appropriate forcing current

Fig. 4 Time series for sampled membrane potential and energy function are calculated when neuron is driven by mixed signal at $\varphi = 0, A = 0.1, B = 0.2, \omega = 0.01, I_{\text{ext}} = 1.7$. For (a₁, b₁, c₁, d₁) $N = 0.1$, (a₂, b₂, c₂, d₂) $N = 1$, (a₃, b₃, c₃, d₃) $N = 10$, (a₄, b₄, c₄, d₄) $N = 100$

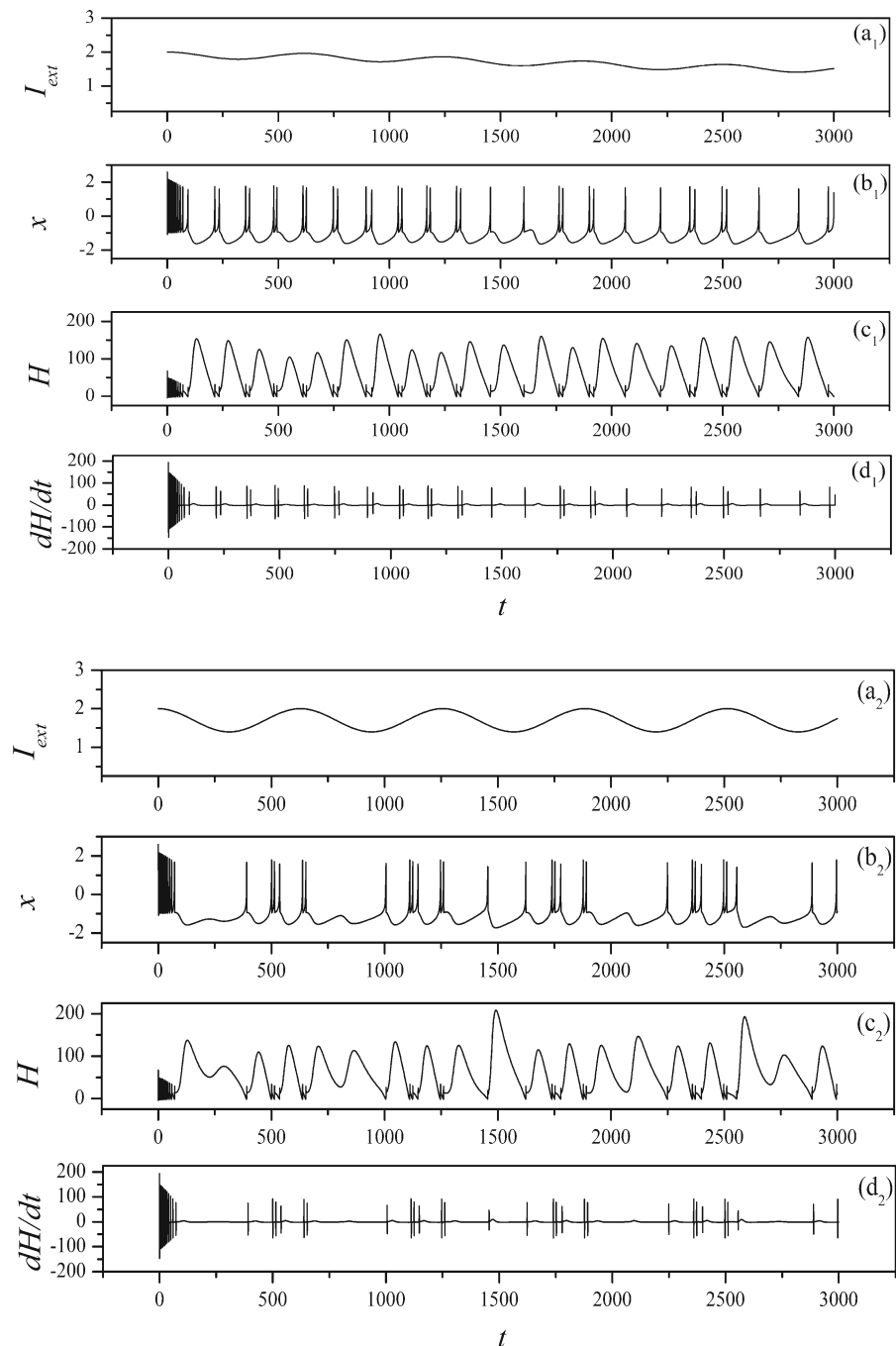
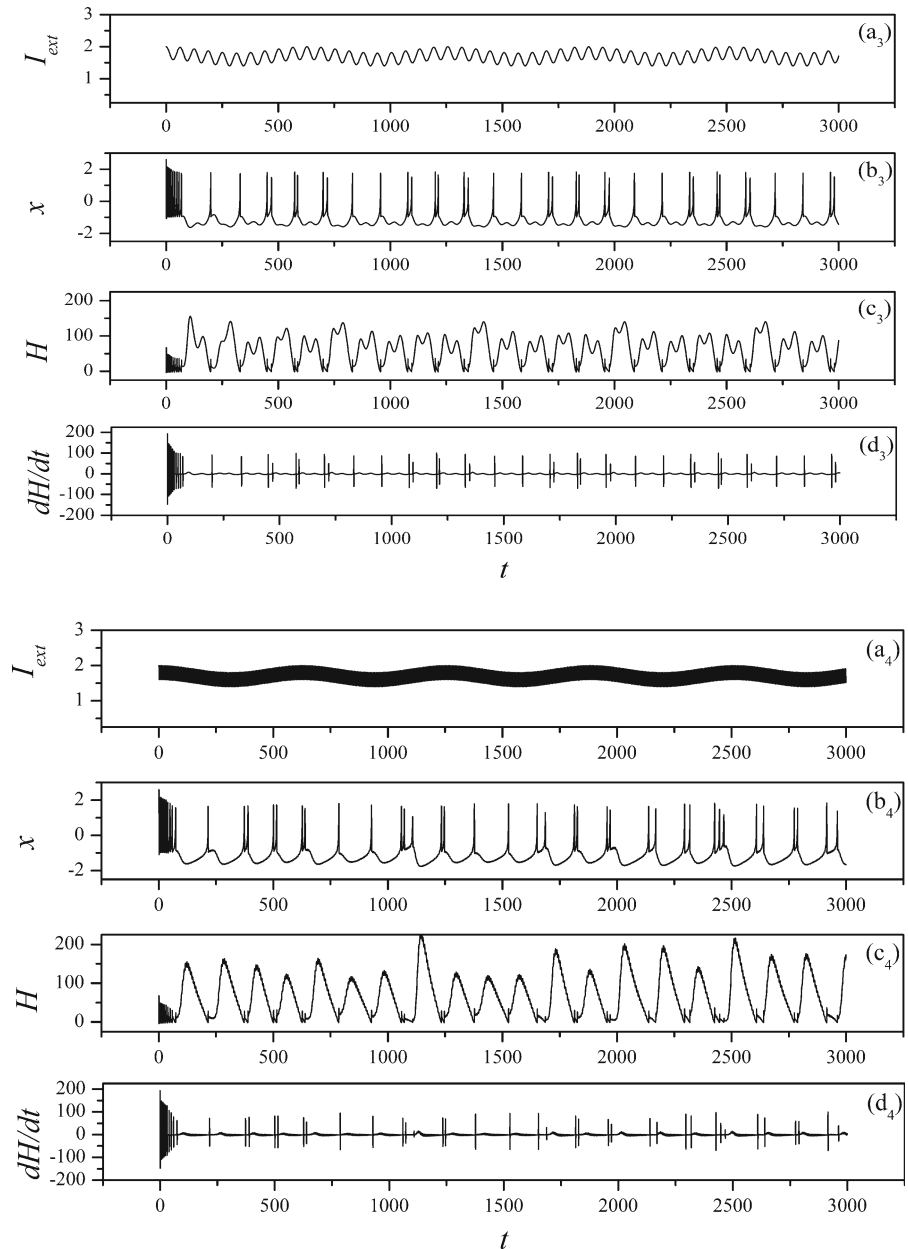


Fig. 4 continued



carefully. φ is initial phase, and N is an integer that can select a high-frequency signal. That is to say, a mixed signal forcing composed of constant, periodic signal with diversity in frequency will be imposed on the neuron, and the transition of electric activities will be detected. The occurrence of action potential and transition of electric activities depend on the energy release and supply; it is important to discern the changes of energy associated with electric modes

by applying different mixed forcing currents. Based on the Helmholtz theorem in Refs. [42, 50], the dynamical equations for neuron are regarded as a velocity vector field, and further considered by a sum of two vector fields $f(*) = f_c(*) + f_d(*)$, where $f_c(*)$ is conservative field containing the full rotation and $f_d(*)$ is dissipative containing the divergence. In the case of HR neuron model, the two sub-vector fields are described as follows

$$f_c(x, y, z) = J(x, y, z) \nabla H = \begin{pmatrix} y - z + I_{\text{ext}} \\ c - dx^2 \\ rs(x + 1.6) \end{pmatrix} \tag{3a}$$

where $J(*)$ is a skew-symmetric matrix that satisfy satisfies Jacobi's closure condition and H is the Hamilton energy function which could be defined as follows

$$f_d(x, y, z) = R(x, y, z) \nabla H = \begin{pmatrix} -ax^3 + bx^2 \\ -y \\ -rz \end{pmatrix} \tag{3b}$$

$$\nabla H^T f_c(x, y, z) = 0 \tag{4a}$$

$$\nabla H^T f_d(x, y, z) = dH/dt = \dot{H} \tag{4b}$$

Fig. 5 Time series for sampled membrane potential and energy function are calculated when neuron is driven by mixed signal at $\varphi = 0, A = 0.1, B = 0.2, N = 1, I_{\text{ext}} = 1.7$. For (a1, b1, c1, d1) $\omega = 0.01$, (a2, b2, c2, d2) $\omega = 0.1$, (a3, b3, c3, d3) $\omega = 1$

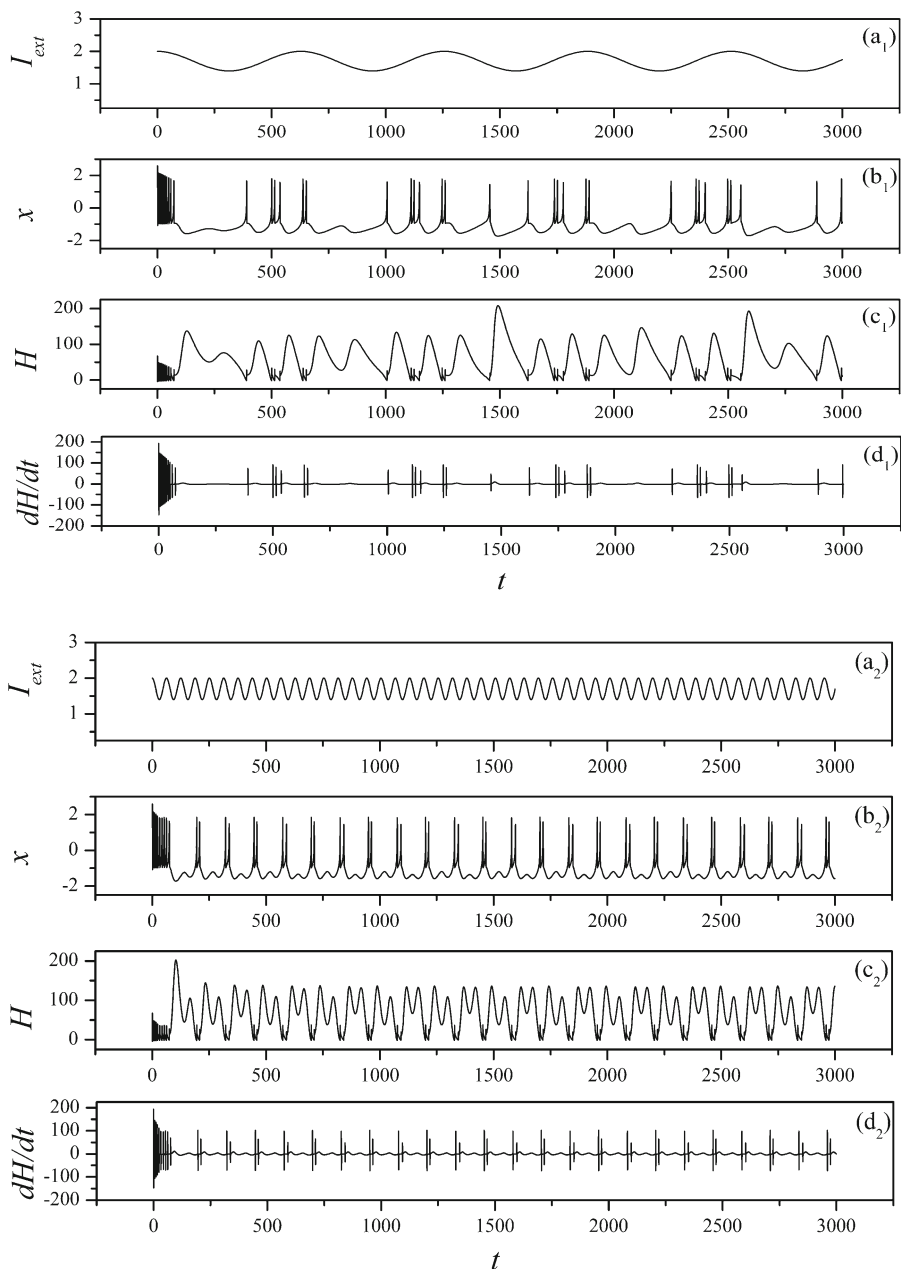
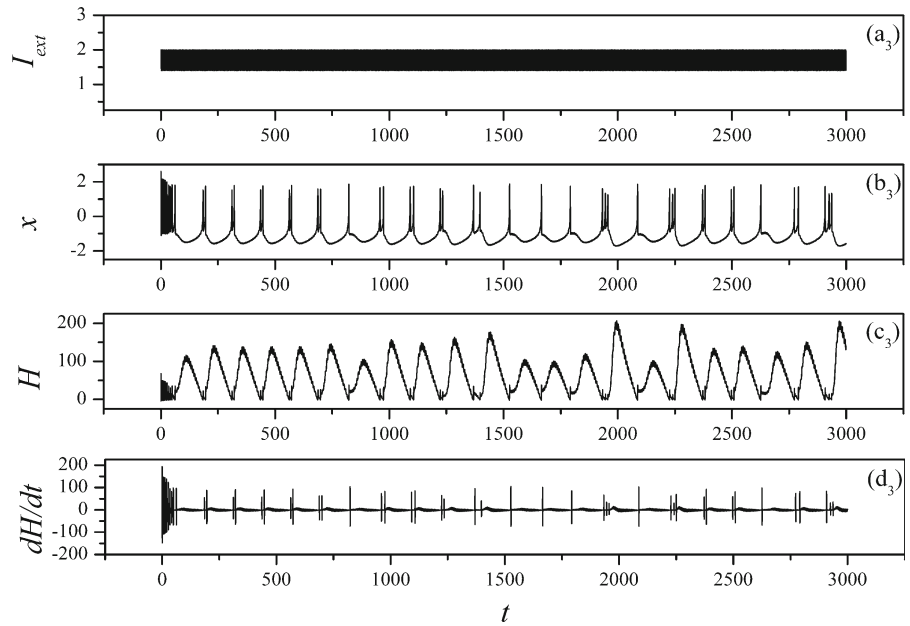


Fig. 5 continued



The Hamilton energy function H is approached by

$$H = \frac{2}{3}dx^3 - 2cx + rs(x + 1.6)^2 + (y - z + I + A \cos \omega t + B \cos(N\omega t + \varphi))^2 \tag{5}$$

And the change of Hamilton energy versus time is calculated by

$$dH/dt = [2dx^2 - 2c + 2rs(x + 1.6)](-ax^3 + bx^2) + 2[y - z + I + A \cos \omega t + B \cos(N \cos \omega t + \varphi)](rz - y) \tag{6}$$

In the following section, different external forcing currents are imposed on the neuron to investigate the response and selection of neuronal activities.

3 Numerical results and discussion

The fourth Runge–Kutta algorithm is used to calculate the time series from the HR neuron model at fixed time step $h = 0.01$; the transient period is about 6000 time units. With increasing the external forcing current $I = I_{ext} = 1.2, 1.3, 1.4, 1.5, 1.6, 1.7, 1.8, 1.9$, the electric activities of neuron can pass from spiking

to bursting states by applying weak periodic signals, and these results are calculated in Fig. 1.

The previous works confirmed that the electric mode of output series will be invariant when the external constant forcing current is fixed. Periodic forcing with small intensity can adjust the electric modes of neuronal activities, and the transition of electric mode depends on the properties of periodical signal. The competition between the low-frequency and high-frequency signals determinates the rhythm of electric activities. As a result, different modes of electrical activities can be selected by applying appropriate periodic and constant signals. Furthermore, the energy dependence on electric modes is calculated according to Eq. (5), and the results are shown in Fig. 2.

The results in Figs. 1 and 2 confirmed that the energy is much dependent on the electric mode controlled by the external forcing current. It is found that smaller energy is approached under bursting states while spiking states make neuron hold higher energy. Indeed, the diversity in frequency of mixed forcing signal also changes the electric modes of electric activities, as a result, low frequency and high frequency with different ratios are calculated under different N , and results are calculated in Fig. 3.

It is found in Fig. 3 that the electric activities of neuron show multiple modes, and the spiking and bursting states occur alternatively; furthermore, the rhythm

of the electric activities depends on the competition between the high and low frequency of external forcing currents. To discern the energy transition with the change of electric modes, the Hamilton energy is also calculated, and the detailed results are presented in Fig. 4.

The outputs for sampled membrane potentials are much dependent on the external periodical forcing,

and the discharge rhythm of electric activities of neuron could be adjusted by the high-frequency section of the mixed forcing signal. The discharge rhythm is increased with increasing the high frequency of the mixed forcing signal. The energy is dependent on the electric mode instead of the external forcing though the electric mode can be changed by the external forcing current. Furthermore, the angular frequency has been

Fig. 6 Time series for sampled membrane potential and energy function are calculated when neuron is driven by mixed signal at $\varphi = 0$, $A = 0.1$, $N = 1$, $\omega = 0.01$, $I_{\text{ext}} = 1.7$. For (a1, b1, c1, d1) $B = 0.2$, (a2, b2, c2, d2) $B = 0.5$, (a3, b3, c3, d3) $B = 0.8$, (a4, b4, c4, d4) $B = 1.0$

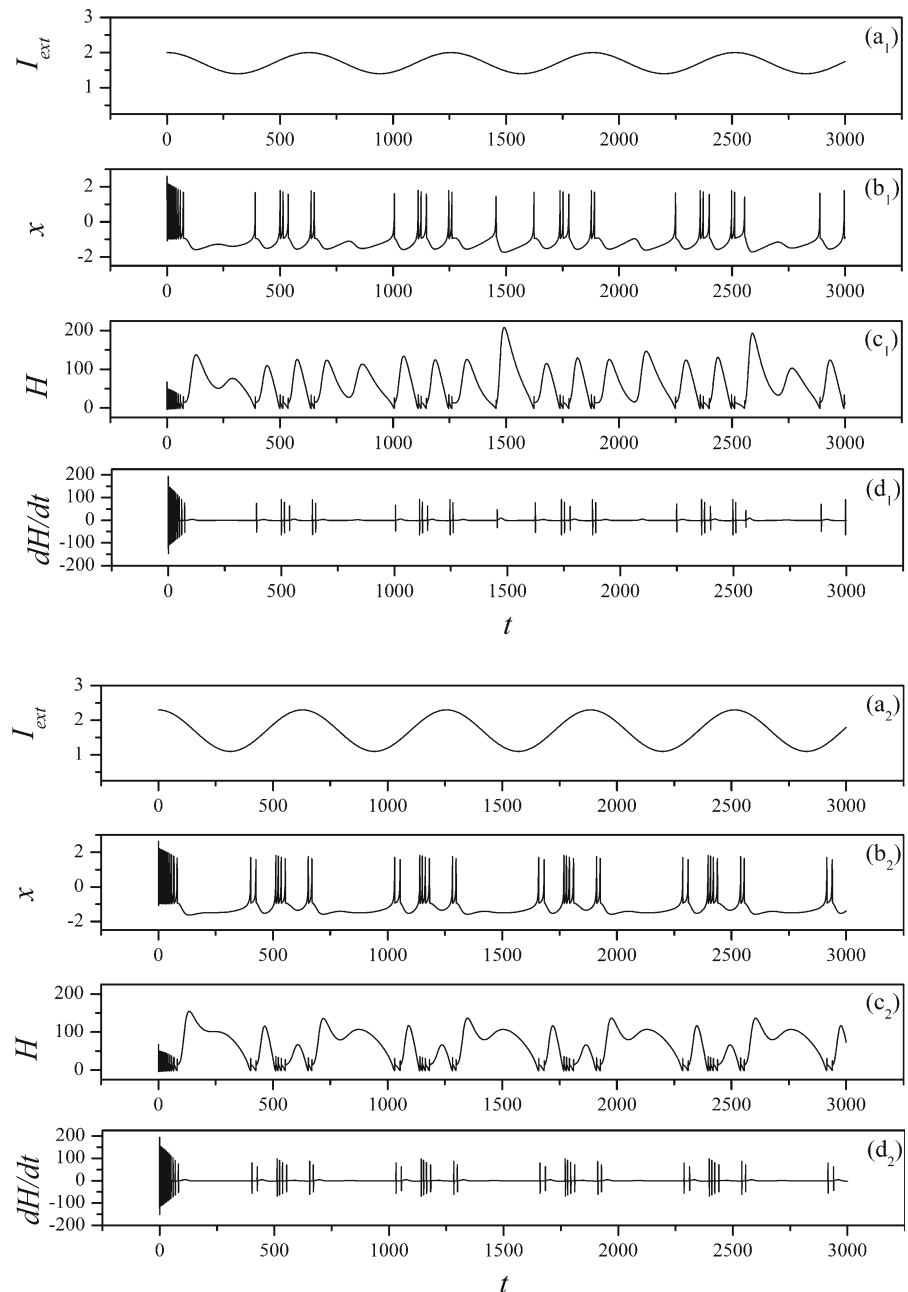
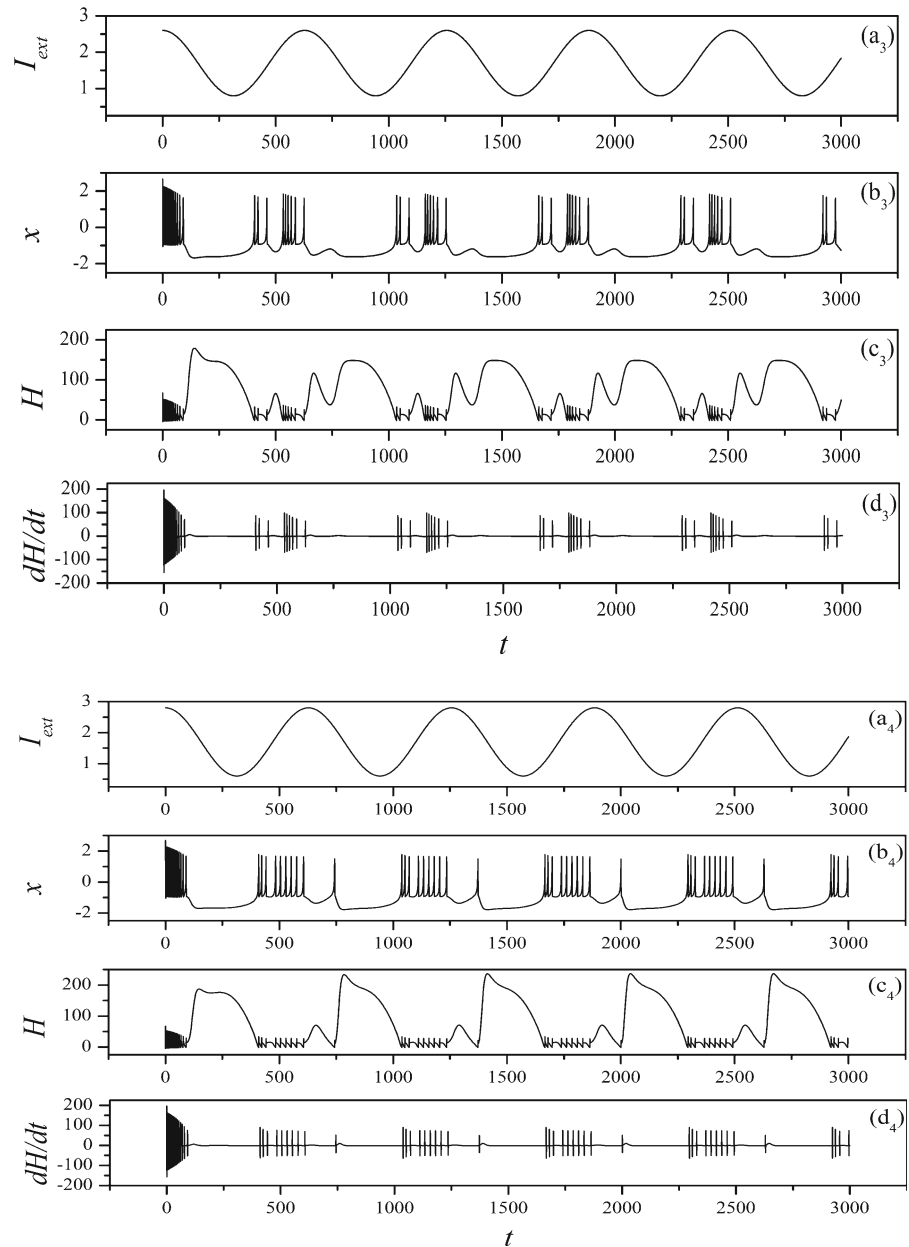


Fig. 6 continued



increased to study the mode transition and changes of energy by applying mixed signal on the neuron, and the results are shown in Fig. 5.

The results in Fig. 5 confirmed that the selection of angular frequency in the mixed signal still can affect the mode of electric activities, the discharge frequency and even energy transition though the periodic forcing is under low amplitude. Interestingly, multiple modes of electric activities occur alternatively with chang-

ing the external mixed forcing current instead of sole mode of electric activities. Furthermore, the amplitude of periodic forcing current in the mixed signal is adjusted to detect the transition of mode and energy during the driving by external signals. For example, the same frequency is used in the periodic forcing at $A = 0.1$, $\omega = 0.01$, $I_{ext} = 1.7$, $\varphi = 0$; the amplitude B is increased from 0.2 to 1.0; it is found that the outputs for membrane potentials show multiple modes in

the electric activities that spiking discharge is accompanied by bursting state. Similar results are confirmed under fixed amplitude B by increasing the amplitude A in the periodic signal. For detailed description and estimation, the energy is calculated in Figs. 6 and 7.

The results in Figs. 6 and 7 confirmed that electrical activities of neuron can switch from different modes and distinct transition between modes occur

with increasing the amplitude of periodic forcing current in the mixed signals. The Hamilton energy also changes with fluctuation when the mode of electrical activities is switched alternatively. The potential mechanism could be that combination of different periodic forcing signals injects mixed signal via multiple channels, and thus, the modes of electrical activities are adjusted synchronously; as a result, the modes of elec-

Fig. 7 Time series for sampled membrane potential and energy function are calculated when neuron is driven by mixed signal at $\varphi = 0$, $B = 0.1$, $N = 1$, $\omega = 0.01$, $I_{\text{ext}} = 1.7$. For (a1, b1, c1, d1) $A = 0.2$, (a2, b2, c2, d2) $A = 0.4$, (a3, b3, c3, d3) $A = 0.8$, (a4, b4, c4, d4) $A = 1.0$

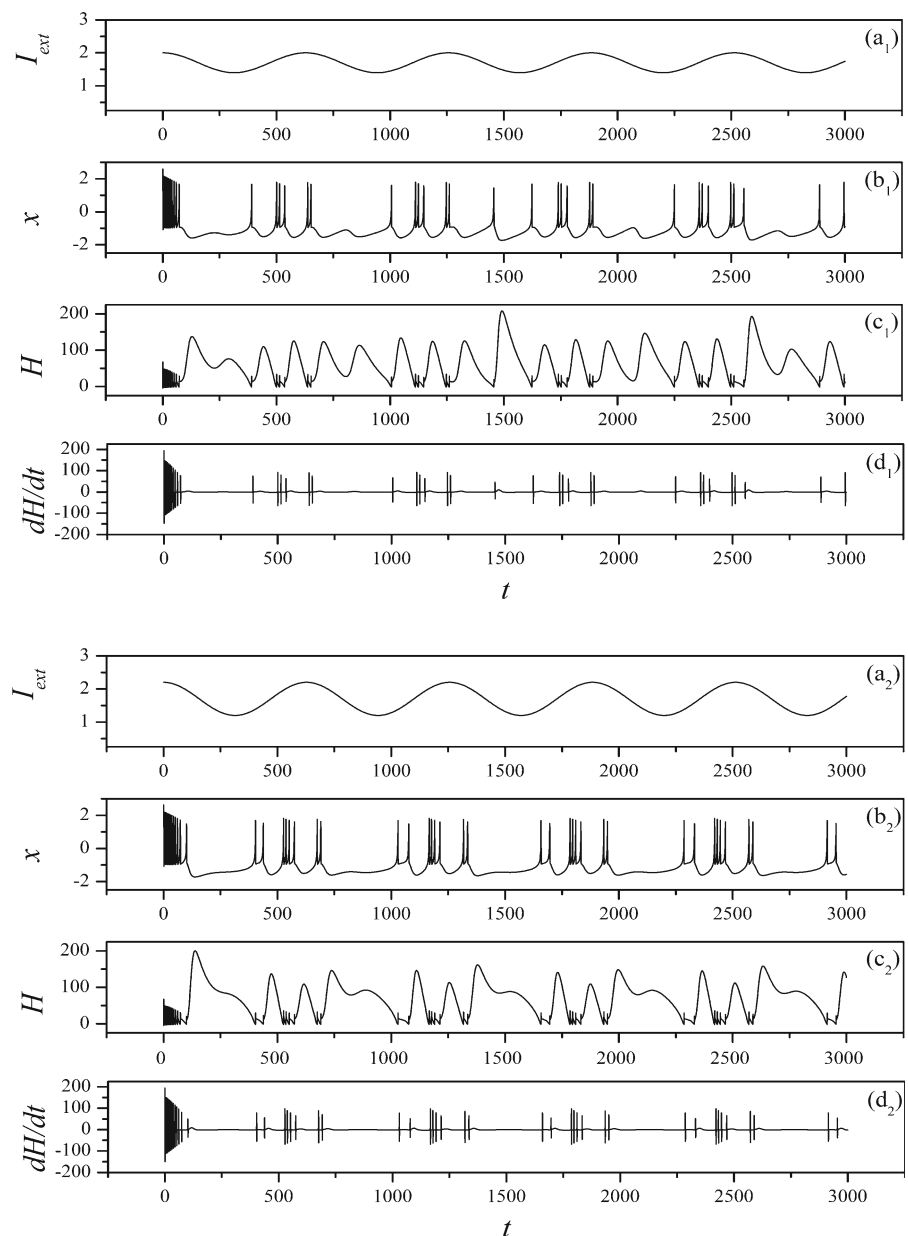
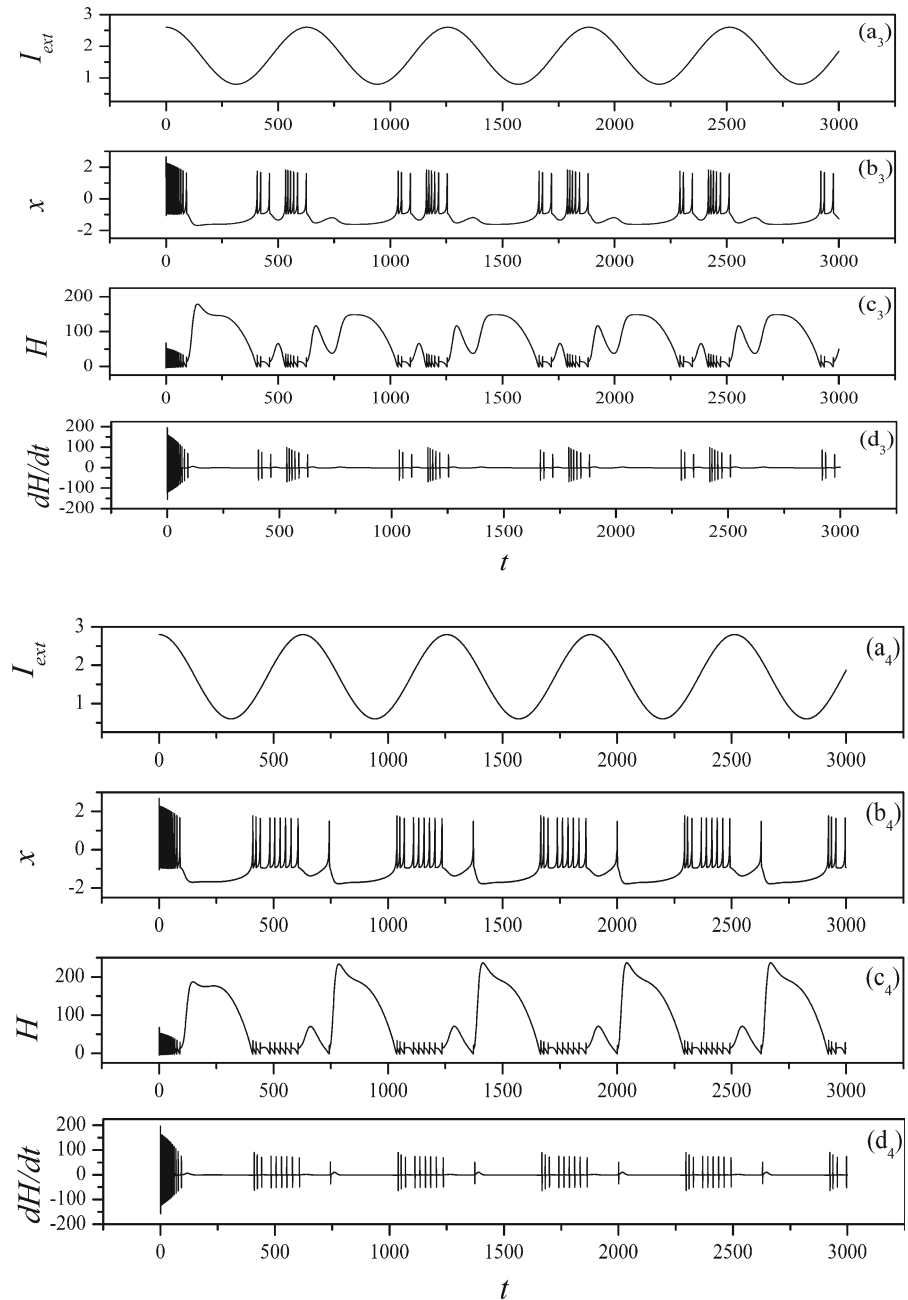


Fig. 7 continued



tric activities show variety and periodicity. It is interesting to find that transition of energy shows certain delay with changing the amplitude of external forcing current, but the energy mainly depends on the modes selection of electrical activities because neuron can encode the energy by itself. In fact, the previous investigation discussed the case for frequency multiplication

that periodical forcing of the mixed signal is changed without additive phase diversity ($\varphi = 0$). In the following, it is interesting to investigate the case for $\varphi \neq 0$.

The results in Fig. 8 found that multiple modes of electrical activities could also be observed in the time series for membrane potentials. The electrical mode is also dependent on the frequency ratio N between

the high frequency and low frequency in the mixed signal, and the energy function also changed with the mode transition of electrical activities. Furthermore, the initial phase diversity is set as $\varphi = \pi$, and results are calculated in Figs. 9 and 10.

It is found in Fig. 9 that the modes of electrical activities can also be adjusted and switched when the intensity of forcing current with low frequency is increased, and the electrical activities can alter between spiking and bursting, bursting and spiking states as

Fig. 8 Time series for sampled membrane potential and energy function are calculated when neuron is driven by mixed signal at $\varphi = \pi/2$, $A = 0.1$, $B = 0.2$, $\omega = 0.01$, $I_{\text{ext}} = 1.6$. For (a1, b1, c1, d1) $N = 0.1$, (a2, b2, c2, d2) $N = 1$, (a3, b3, c3, d3) $N = 10$, (a4, b4, c4, d4) $N = 100$

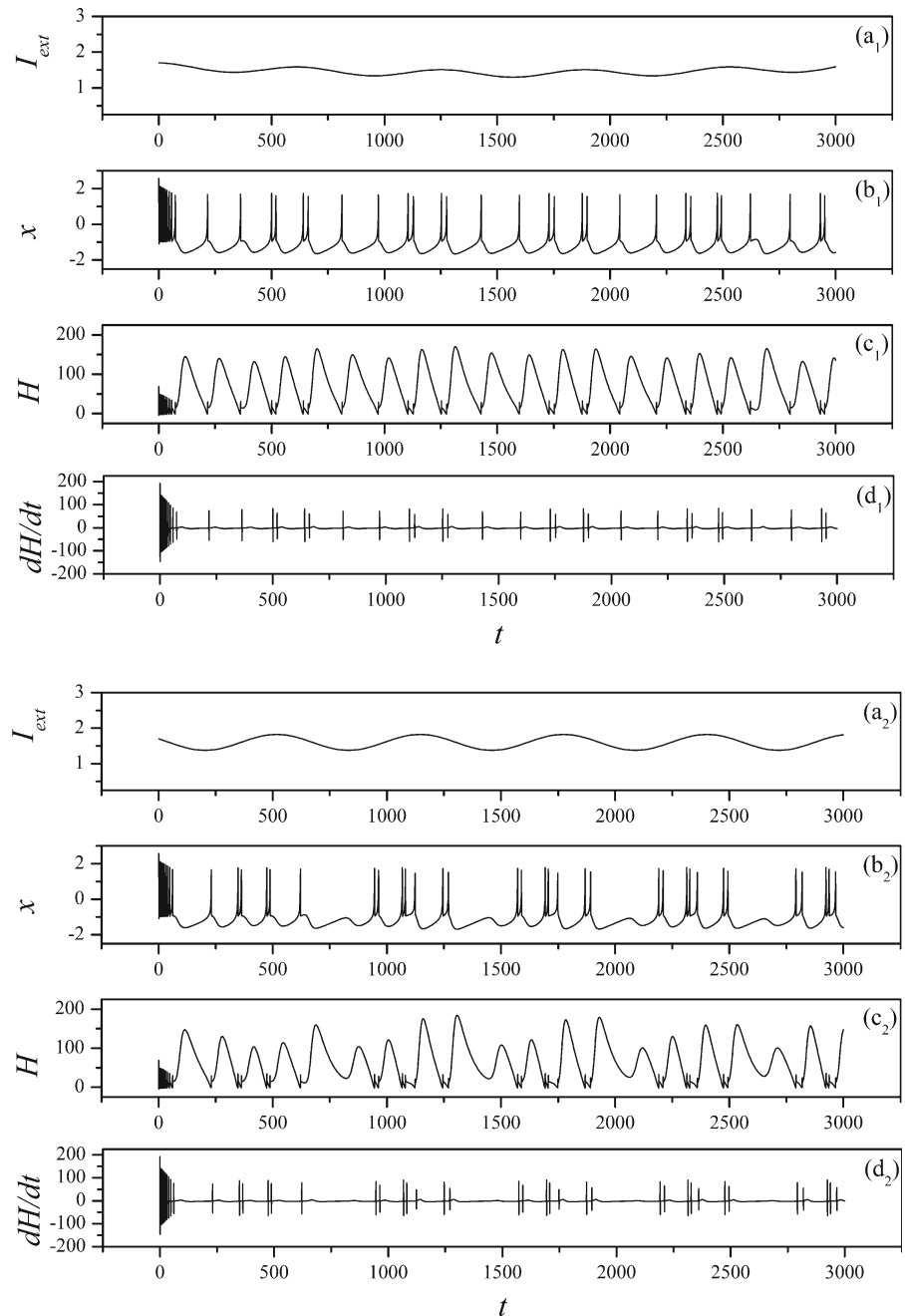
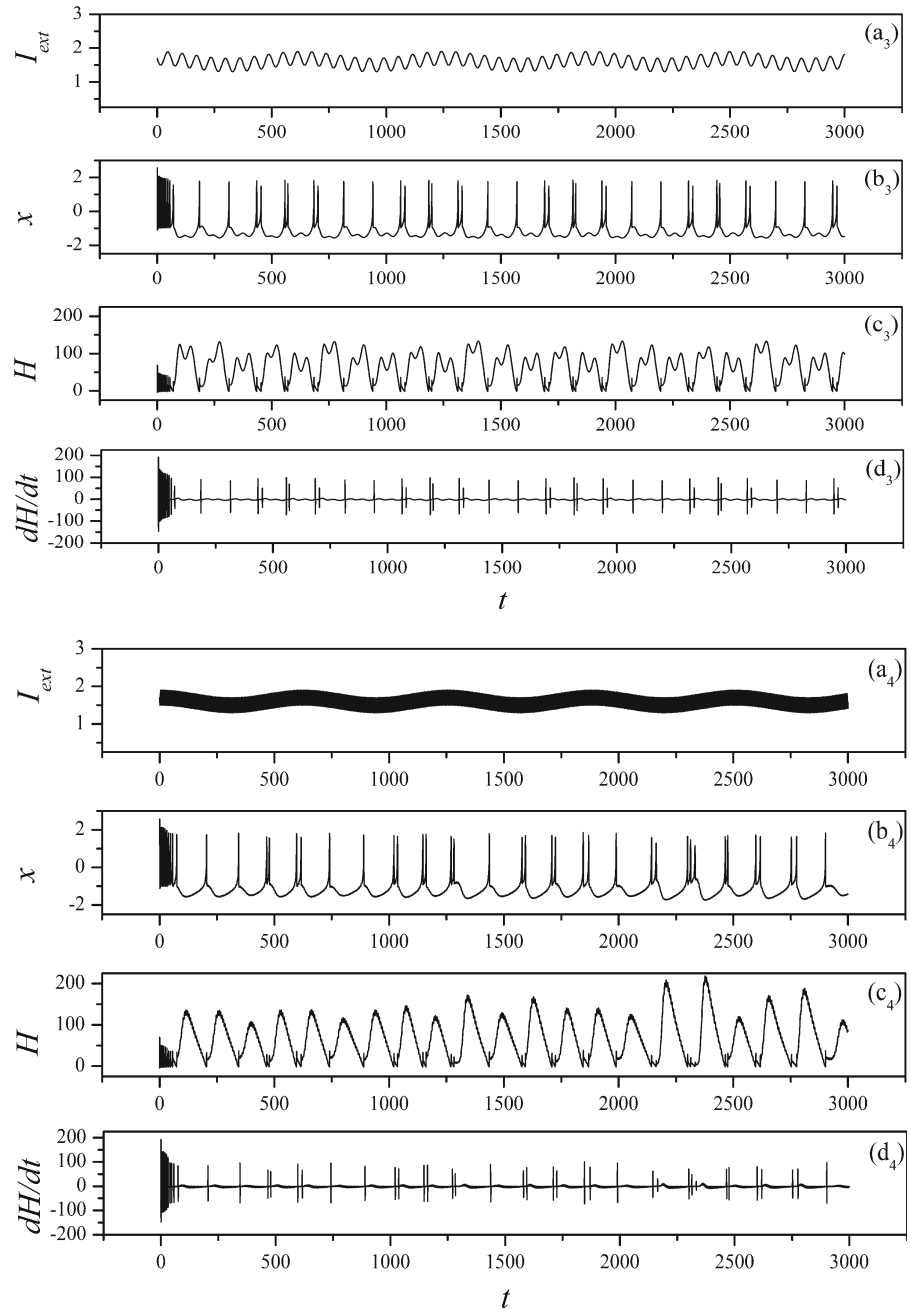


Fig. 8 continued



well. Furthermore, the intensity of high-frequency signal A is increased, and the results are calculated in Fig. 10.

It is found that the electrical activities can switch between spiking and bursting states during the period of increasing in the intensity of external forcing currents, while the electrical activities decrease to quiescent states or weak oscillation during the period of

decreasing the intensity of external forcing currents. The change of Hamilton energy follows the variation of electrical activities and also the changes of external forcing currents but with certain delay. From the physical view, external forcing current just inputs energy into the system; however, the Hamilton energy cannot follow up the changes of external forcing current synchronously. The mechanism could be that neuron can

Fig. 9 Time series for sampled membrane potential and energy function are calculated when neuron is driven by mixed signal at $\varphi = \pi$, $N = 0.1$, $B = 0.1$, $\omega = 0.1$, $I_{\text{ext}} = 1.6$. For (a₁, b₁, c₁, d₁) $A = 0.2$, (a₂, b₂, c₂, d₂) $A = 0.3$, (a₃, b₃, c₃, d₃) $A = 0.4$, (a₄, b₄, c₄, d₄) $A = 0.5$

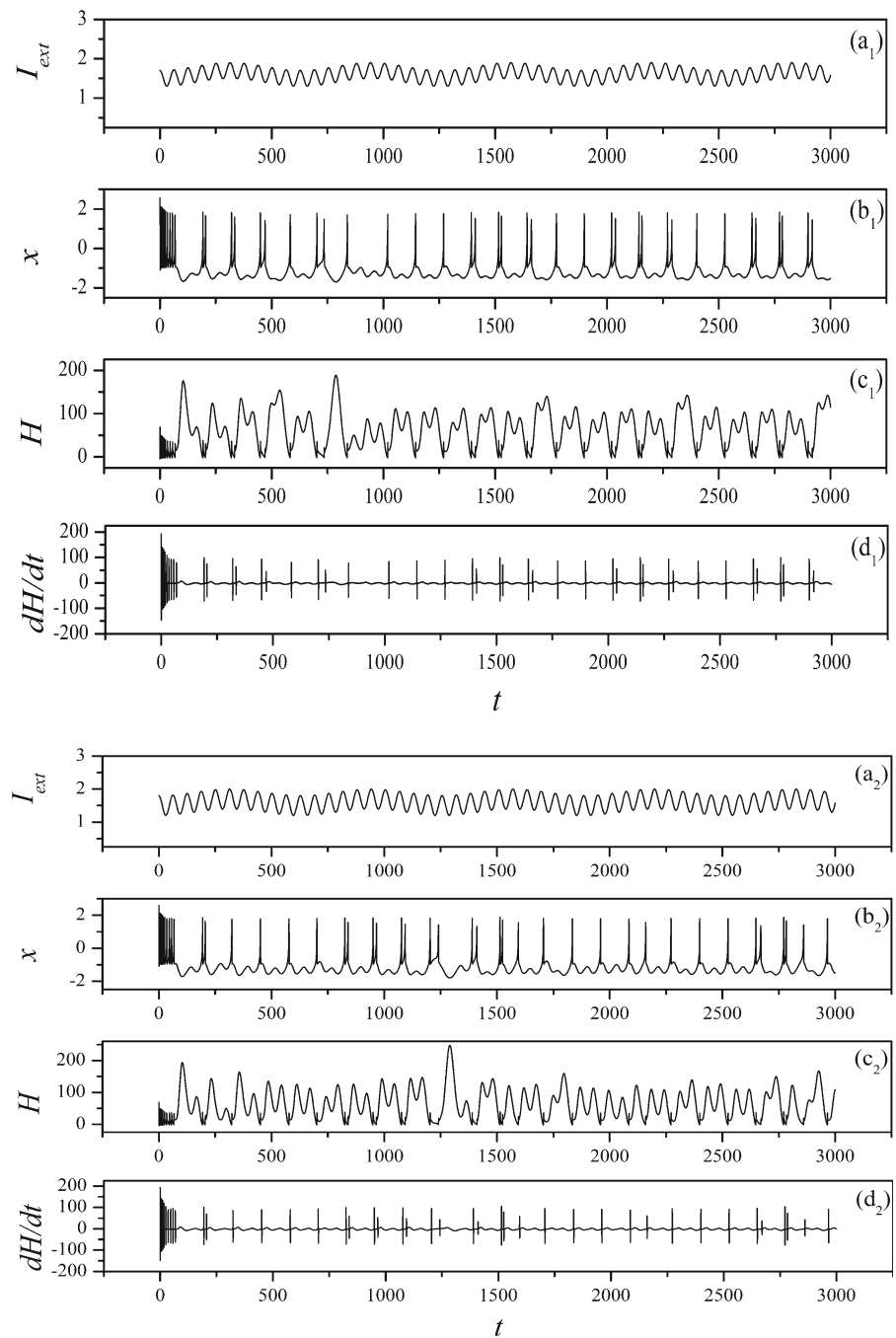


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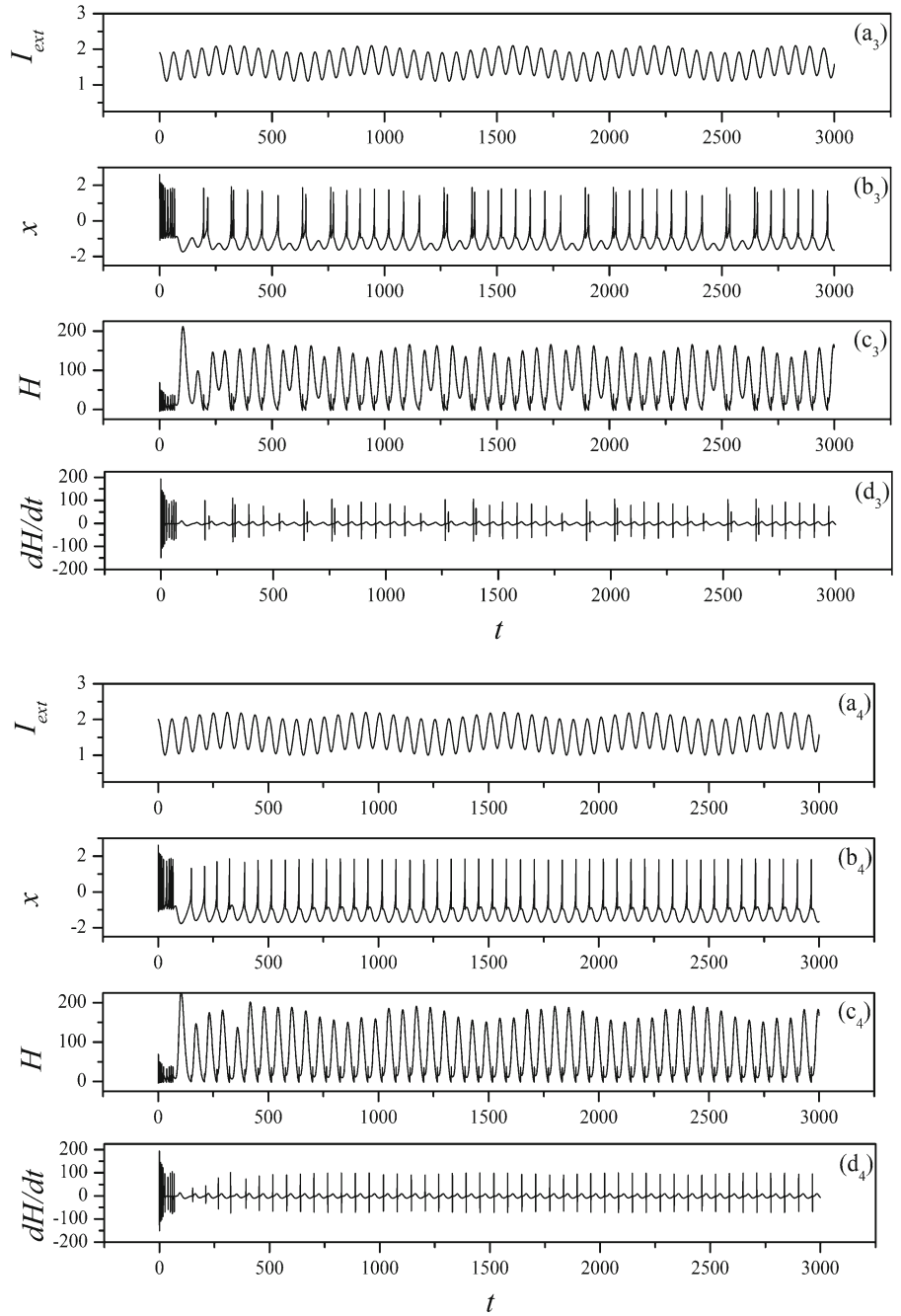


Fig. 10 Time series for sampled membrane potential and energy function are calculated when neuron is driven by mixed signal at $\varphi = \pi$, $N = 0.1$, $A = 0.1$, $\omega = 0.1$, $I_{\text{ext}} = 1.6$. For (a₁, b₁, c₁, d₁) $B = 0.4$, (a₂, b₂, c₂, d₂) $B = 0.6$, (a₃, b₃, c₃, d₃) $B = 0.8$, (a₄, b₄, c₄, d₄) $B = 1.0$

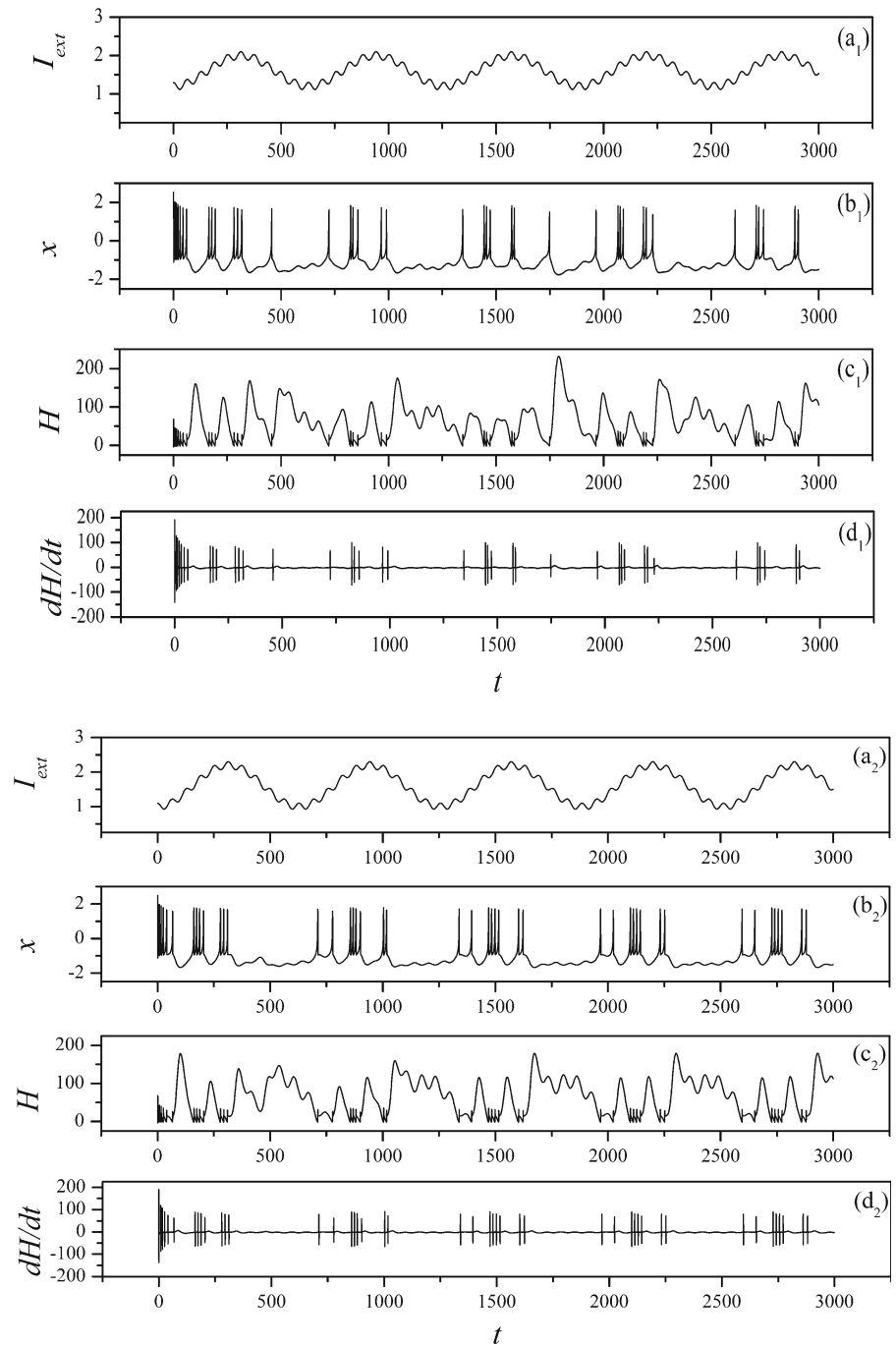
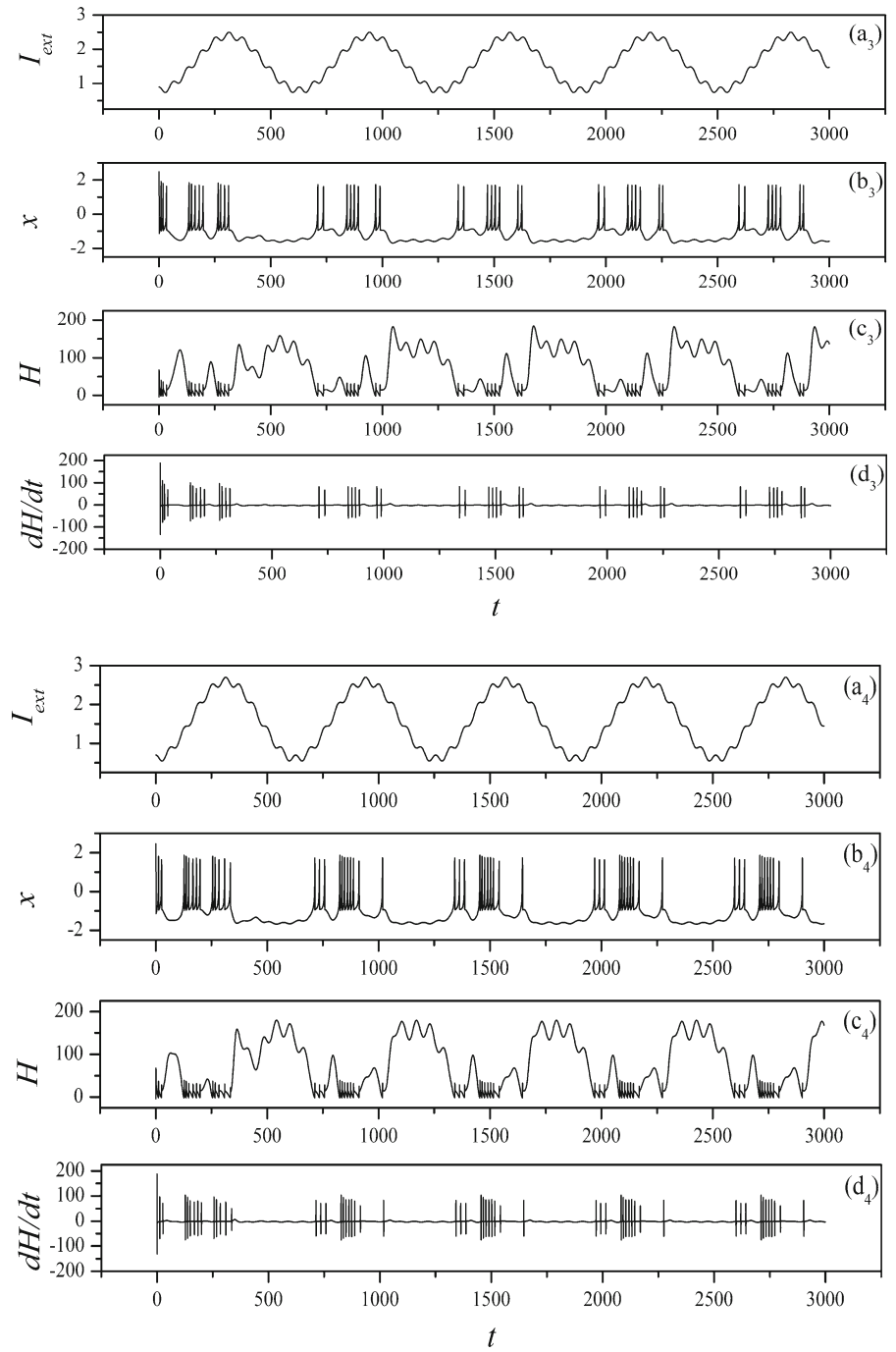


Fig. 10 continued



encode the energy; thus, the Hamilton energy mainly depends on the electrical activities instead of the external forcing directly.

4 Conclusions

Mixed forcing currents are imposed on HR neuronal model, and the response of electrical activities is investigated in presence of multi-channels stimuli synchronously. Constant signal, low-frequency and high-frequency signals are imposed on the neuron simultaneously, and multiple modes of electrical activities are observed in the time series for membrane potentials. It is found that mode transition of electrical activities depends on the amplitude and angular frequency of periodical signals. Particularly, the ratio between high frequency and low frequency can determinate the mode transition of electrical activities. The changes of Hamilton energy depend on the mode transition of electrical activities and the external forcing currents. During the transition from spiking to bursting state, Hamilton energy is decreased greatly, while Hamilton energy is increased when electrical activities are switched from bursting to spiking states. The occurrence of multiple modes in electrical activities could be associated with multi-channel inputting when the effect of electromagnetic induction is left out.

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