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Characteristics of critical amplitude of a sinusoidal stimulus in a model neuron*

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The characteristics of the critical amplitude of a sinusoidal stimulus in a model neuron, Morris–Lecar model, are investigated numerically. It is important in the study of stochastic resonance to determine whether a periodic stimulus is subthreshold or not. The critical amplitude as a function of the stimulus frequency is not a constant, but a curve, which is the boundary between subthreshold and suprathreshold stimulation. It has been considered that this curve is *U*-shaped in the previous investigations, and this has been accepted as a universal phenomenon. Nevertheless, we think that it is only true for a type of neuron: namely, resonators. Actually, there exists another type of neuron, integrators, which can undergo a saddle-node on invariant circle bifurcation from the rest state to the firing state. For the latter we find that the critical amplitude increases monotonically as the frequency of sinusoidal stimulus is increased. This is shown by way of the Morris–Lecar model. As a consequence, the critical amplitude curve is studied further, and the dynamical mechanisms underlying the change in critical amplitude curve are uncovered. The results of this paper can provide a reference to choose the subthreshold periodic stimulus.

Keywords: stochastic resonance, Hopf bifurcation, saddle-node on invariant circle bifurcation, Morris–Lecar model
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1. Introduction

How do sensory neurons detect external weak excitation? It is well known that neurons operate in a noisy environment. The noise consists of environmental noise and intrinsic noise, such as ionic channel conductance fluctuations, synaptic fluctuations and thermal noise. The stochastic resonance (SR) has been argued to be a mechanism for weak signal detection and transduction.[1,2] It has been widely considered that the SR is a nonlinear phenomenon wherein the output signal-to-noise ratio (SNR) can be optimized by a particular level of noise: namely, the SNR first increases to a maximum and then decreases as the intensity of external noise increases. This is because a weak periodic stimulus entrains large-scale environmental fluctuations, with the result that the periodic component is greatly enhanced. Experimentally and theoretically, it has been shown that the ability of sensory neurons to detect external weak stimulus can be enhanced by a certain intensity of noise.[3−7] Consequently, noise may play an active role in the detection of weak signals and information processing and transduction in the neural system.

In the study of the SR phenomenon in a model neuron, however, it is important to determine if a periodic stimulus is subthreshold or not.[8] Evidently, there exists a critical amplitude for a periodic stimulus, above which the neuron will fire and below which the neuron will not. Therefore, if the amplitude of a periodic stimulus exceeds a certain critical value, the neuron will exhibit firing behaviour. Most recently, it has been shown that the critical amplitude of a sinusoidal stimulus varies with the stimulus frequency in the Hindmarsh–Rose and Hodgkin–Huxley model, and exhibits typically a *U*-shaped curve.[8−12] However,

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the dynamical mechanism underlying the U-shaped curve is unclear. Is it a universal feature?

In this study, we will answer this question. A conductance-based model, the Morris–Lecar (ML) neuron, is introduced to clarify our opinions. This paper is organized as follows. In Section 2 the ML model is described. For this model there are two types of dynamical mechanisms from the rest state to repetitive spiking, depending on the values of parameters, which is shown in Section 3. In Section 4 the critical amplitude curve of sinusoidal stimulus is investigated numerically for these two types of dynamical mechanisms, respectively. Some conclusions are drawn in Section 5.

2. Morris–Lecar model

This model was formulated by Morris and Lecar,[13] in the context of electrical activity of the barnacle muscle fibre, and it is a Fitzhugh–Nagumo/Hodgkin–Huxley hybrid. The differential equation and V-dependent functions are

$$\begin{aligned} C\frac{\mathrm{d}V}{\mathrm{d}t} =& -\bar{g}_{\mathrm{Ca}} m_\infty(V)(V-V_{\mathrm{Ca}}) \\ & -\bar{g}_{\mathrm{K}} w(V-V_{\mathrm{K}}) - \bar{g}_{\mathrm{L}}(V-V_{\mathrm{L}}) + I_{\mathrm{ext}}, \\ \frac{\mathrm{d}w}{\mathrm{d}t} =& \phi\frac{[w_\infty(V)-w]}{\tau_w(V)}, \end{aligned}$$

with steady states for the Ca^{2+} and K^+ current fractions

$$\begin{aligned} m_\infty(V) =& 0.5\{1+\tanh[(V-V_1)/V_2]\}, \\ w_\infty(V) =& 0.5\{\tanh[(V-V_3)/V_4]\}, \end{aligned}$$

and a transition rate,

$$\tau_w(V) = 1/\cosh[(V-V_3)/(2*V_4)].$$

Here the parameter C denotes the capacity; $\bar{g}_{\mathrm{Ca}}$, $\bar{g}_{\mathrm{K}}$ and $\bar{g}_{\mathrm{L}}$ are the maximal conductance of calcium, potassium and leak, respectively, and V_{Ca}, V_{K} and V_{L} are the corresponding reversal potentials. I_{ext} represents the external stimulus current, and ϕ denotes the change between slow and fast regions of the neuron. All conductances are in $\mathrm{mS/cm^2}$ and voltages in mV; the capacity C in $\mu\mathrm{F/cm^2}$ and currents in $\mu\mathrm{A/cm^2}$. In the ML model, I_{ext} is assumed to take $I_{\mathrm{ext}} = I_0 + I_1\sin(2\pi ft) + \xi(t)$. Therein, I_0 denotes the total synaptic inputs from the environment, varying slowly with time. Here, we take it as a control parameter of bifurcation. The term $I_1\sin(2\pi ft)$ is a subthreshold stimulus signal: that is, it is insufficient to evoke firing of the neuron by itself. Due to the aforementioned various noise sources, in general, $\xi(t)$ is chosen as Gaussian white noise.

One can see that the equation is a two-dimensional description of neuronal spiking dynamics. The first equation describes the evolution of the transmembrane potential V, and the second equation characterizes the evolution of a slow recovery variable w, which represents the open probability for the potassium channel.

3. Dynamical mechanisms in the Morris–Lecar model

From the perspective of nonlinear dynamics, a rest state of a neuron corresponds to an equilibrium attractor, and repetitive spiking to a limit cycle attractor. A neuron is excitable if it resides near a bifurcation from equilibrium to a limit cycle. Although there are numerous neuron models based on different voltage dependent ionic channels, only two major dynamical mechanisms of excitability are observed frequently in nature: that is, saddle-node on invariant circle (SNIC) bifurcation and Hopf bifurcation (HB).[14,15]

Assuming that there is only one term I_0 in I_{ext}, we investigate the dynamical behaviour of the deterministic model neuron as a function of I_0. In this paper, we focus our attention on bifurcation mechanisms from the rest state to periodic firing. Interestingly, the ML model neuron undergoes a completely different bifurcation from rest state to periodic firing under two different parameter sets. In these two parameter sets, except for V_3, V_4, $\bar{g}_{\mathrm{Ca}}$ and ϕ, the other parameters are the same: namely, $V_1 = -1.2$, $V_2 = 18$, $\bar{g}_{\mathrm{K}} = 8$, $\bar{g}_{\mathrm{L}} = 2$, $V_{\mathrm{K}} = -84$, $V_{\mathrm{L}} = -60$, $V_{\mathrm{Ca}} = 120$ and C=20.

When $V_3 = 2$, $V_4 = 30$, $\bar{g}_{\mathrm{Ca}} = 4.4$ and $\phi = 0.04$, the bifurcation diagram of membrane potential versus I_0 is as shown in Fig.1. One can see that the ML model neuron undergoes a subcritical HB from rest state to periodic firing. Namely, at $I_0 = 93.86$ the left rest state disappears via the subcritical HB, and the neuron displays periodic spiking. A saddle-node bifurcation of limit cycles occurs at $I_0 = 88.29$: that is, a stable limit cycle merges with an unstable limit cycle. In particular, on the right-hand side of periodic spiking, the dynamical mechanisms are the same as those of the left-hand side.

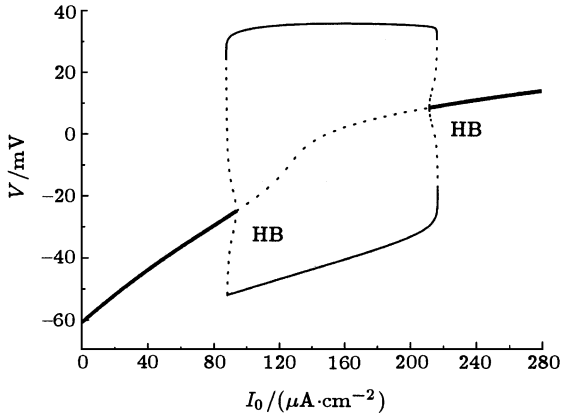


Fig.1. Bifurcation diagram of the membrane potential versus I_0. The bold solid lines represent stable focus points, and the thin lines correspond to the maximum and the minimum of membrane potential amplitude of periodic spiking. The dotted line between the two HB points is composed of unstable focus points.

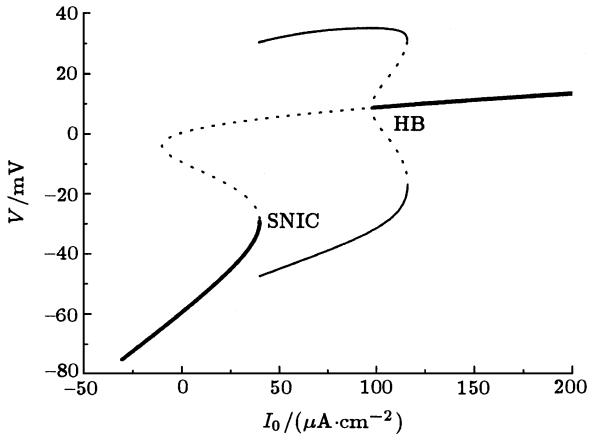


Fig.2. Bifurcation diagram of the membrane potential versus I_0. The left bold line consists of stable nodes, while the right bold line is of stable focus points. The meaning of thin lines is the same as in Fig.1.

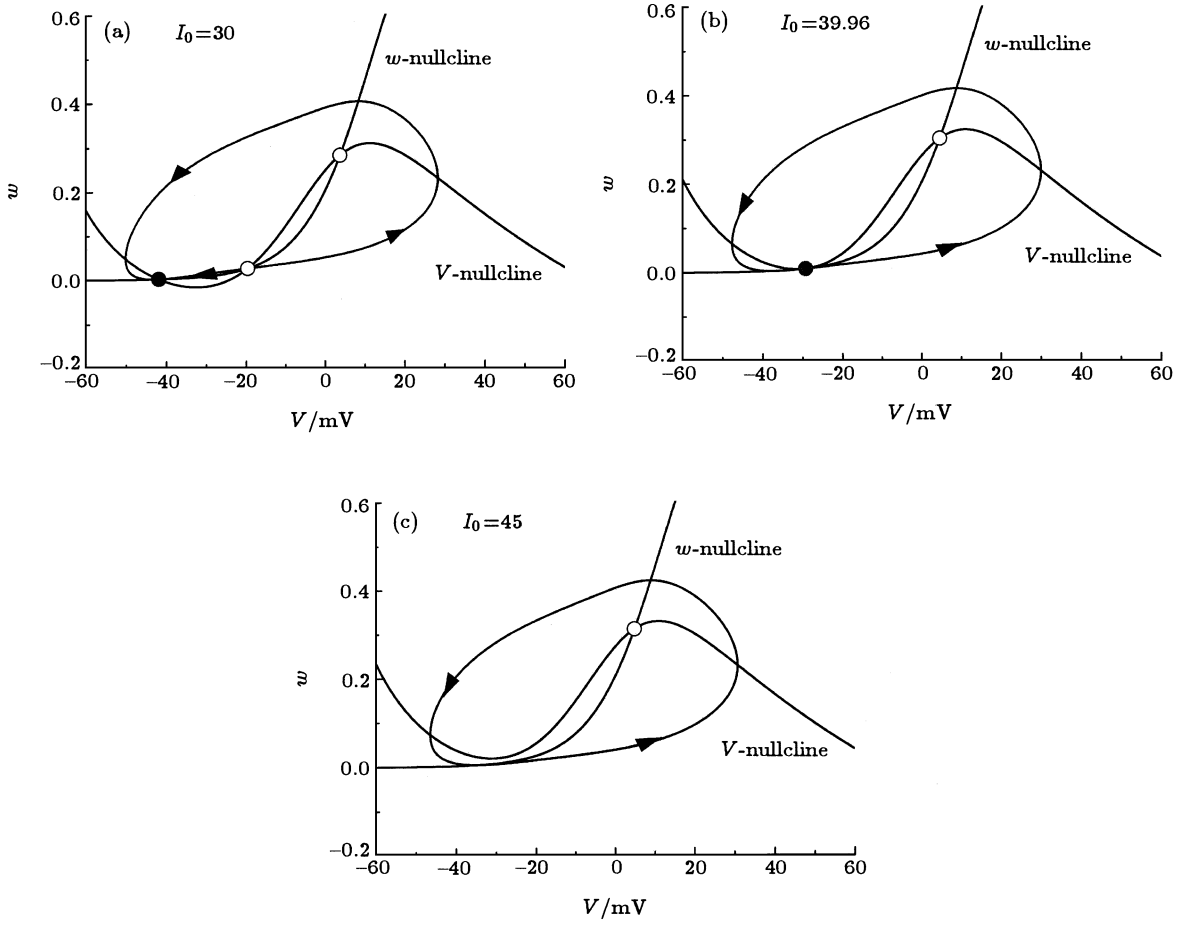


Fig.3. Nullclines in the phase plane of $w - V$ of the neuron near the SNIC bifurcation. The open circles are the unstable focus points except for the middle open circle in (a) being a saddle. The solid circle in (a) is a stable node, and the grey circle in (b) a saddle-node. (a) The unstable invariant manifold is also drawn before the bifurcation corresponding to $I_0 = 30$. (b) At $I_0 = 39.96$ the saddle merges with the node, and the SNIC bifurcation occurs. (c) The saddle-node disappears via the SNIC bifurcation, and a limit cycle corresponding to the periodic spiking is shown when $I_0 = 45$.

When $V_3 = 12$, $V_4 = 17.4$, $\bar{g}_{Ca} = 4$ and $\phi = 1/15$, the bifurcation diagram of the membrane potential versus I_0 is as shown in Fig.2. Clearly, the ML model neuron transits a SNIC bifurcation at $I_0 = 39.96$, and the state of the neuron changes from rest state to periodic spiking. A subcritical HB occurs at $I_0 = 97.79$, and a saddle-node bifurcation of limit cycles at $I_0 = 116.1$. Now, let us investigate the locations of V-nullcline and the w-nullcline in the phase plane of $V - w$ before and after the SNIC bifurcation, as seen in Figs.3(a)–3(c). It is known that the intersections of these two nullclines are fixed points. In Fig.3(a) the unstable invariant manifold of the saddle is also drawn. It is evident that Fig.3 gives the detailed change in the relative positions of V-nullcline and the w-nullcline near the SNIC bifurcation.

Thus it can be seen that the ML model neuron is a self-excitable system under the aforementioned two sets of parameters. Namely, for a constant stimulus I_0, the neuron can exhibit a limit cycle oscillation of periodic spiking.

4. Critical amplitude of sinusoidal stimulus

Through different bifurcation mechanisms from rest state to periodic firing, the ML model neuron will exhibit different responses to a pulse stimulus.

If a quiescent neuron resides before HB, its membrane potential exhibits a damped subthreshold oscillation subject to a pulse stimulus. For the case of the SNIC bifurcation, however, the membrane potential shows exponential convergence to the rest state. Figure 4 shows different responses to the pulse stimulus for these two bifurcation cases.

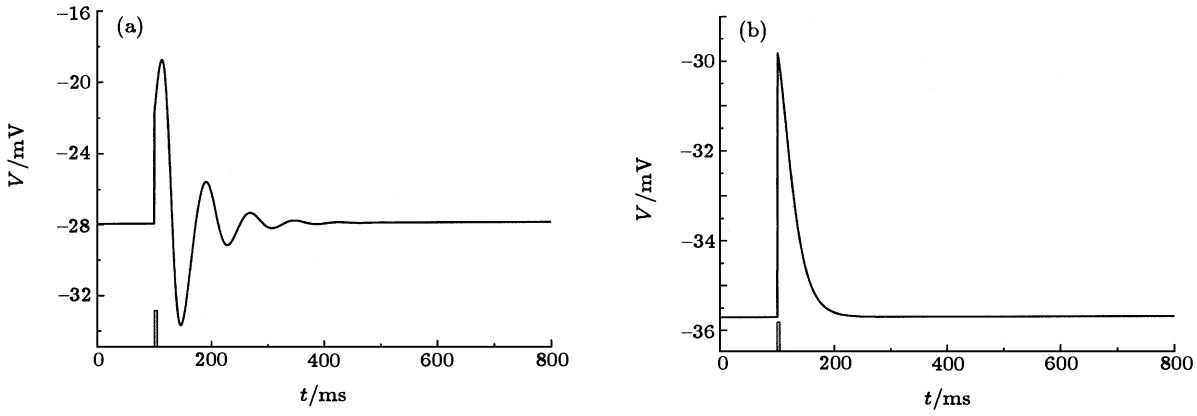


Fig.4. Distinct responses of a quiescent neuron to a pulse stimulus for the two different bifurcation mechanisms from rest state to periodic firing. At the time instant of 100th millisecond (ms), a pulse stimulus is applied, and its duration is 2 ms. The grey bars at the time instant of 100th ms is a schematic diagram of the pulse stimulus in panels (a) and (b): (a) $I_0 = 86$ before HB; (b) $I_0 = 37$ before SNIC bifurcation.

In fact, if a neuron undergoes a HB from rest state to firing state, the neuron is a resonate-and-fire neuron and is termed a resonator. In contrast, if a neuron undergoes a SNIC bifurcation, the neuron is an integrate-and-fire neuron and is called an integrator. The type of bifurcation of the rest state determines the most important neuro-computational feature of the neuron.[14] Thus, it is important to distinguish integrators from resonators when studying spiking neurons.[15]

Firstly, let us consider the case that the ML model neuron is a resonator. It can be seen from Fig.1 that at $I_0 = 86$ the neuron corresponds to a rest state, which is a stable focus. That is, the neuronal system linearized around its fixed point has a pair of conjugate complex eigenvalues with negative real parts. This is the very reason that the response of a quiescent neuron to a pulse stimulus exhibits a damped subthreshold oscillation. The frequency of the damped oscillation is about 12.8Hz; moreover, it increases monotonically with the increase of I_0 before the HB. Such a damped oscillation is considered as intrinsic and has a significant effect on the response of the model neuron to sinusoidal stimulus.[1] When the frequency of sinusoidal stimulus is close to that of the damped oscillation, a nonlinear resonance occurs between them. As a result, the sinusoidal stimulus transfers effectively energy to the neuron to evoke the firing of spikes. In this way, a sinusoidal stimulus with smaller amplitude can evoke

the neuron to fire. This results in the existence of a sensitive frequency range of 8–18Hz, over which the critical amplitude of sinusoidal stimulus is even lower than that of constant stimulus.

As seen in Fig.5(a), the critical amplitude curve takes the minimum at f=11.6Hz, which is the optimal frequency for which firing can be evoked with minimum effort, that is, the smallest amplitude of sinusoidal stimulus. It is evident that the optimal frequency is close to 12.8Hz, the frequency of damped subthreshold oscillation. At the same time, one can see that the critical amplitude as a function of the frequency of sinusoidal stimulus depicts a U-shaped curve.

The existence of the sensitive frequency range implies that the subthreshold oscillation of the neuron provides itself with an effect of frequency selection to sinusoidal stimulus via resonance. As reported in Refs.[1, 2, 11], the ability of the neurons to detect weak stimulus will be significantly improved even in the presence of a small level of noise when the stimulus frequency falls in the frequency sensitivity range of 8–18Hz. Namely, the SNR has a large value in the sensitive range. As a consequence, the frequency sensitivity is of functional importance for information processing of the nervous system. Furthermore, the phenomenon of frequency sensitivity in weak signal detection has been examined experimentally.[16]

In Fig. 5(a), there is a local maximum about $f = 36$, which is about three times that of 11.6. This may be because the two frequencies are unmatchable between the aforementioned damped subthreshold oscillation and the sinusoidal stimulus.

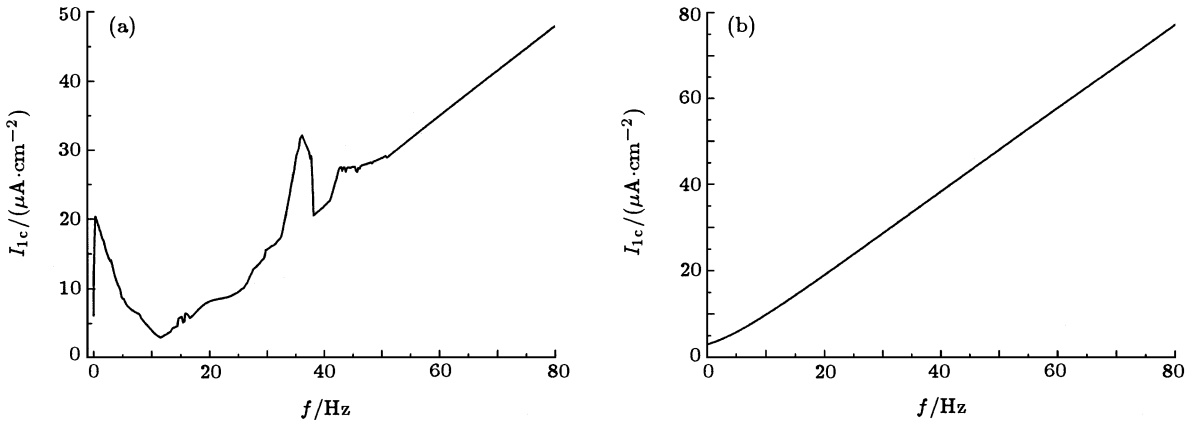


Fig.5. Critical amplitude of sinusoidal stimulus: (a) corresponding to the case of resonator at $I_0 = 86$; (b) corresponding to the case of integrator at $I_0 = 37$.

Secondly, let us investigate another case: i.e., the ML model neuron is an integrator. At $I_0 = 37$ the dynamical state of the neuron is a stable node, neurophysiologically, corresponding to a rest state, as seen in Fig.2. The eigenvalues of the neuronal system linearized at its fixed point are two negative real numbers. Consequently, it is inevitable that the membrane potential of the neuron exponentially decays to the rest state subject to a pulse stimulus. The critical amplitude of sinusoidal stimulus increases monotonically with the stimulus frequency, as shown in Fig.5(b). One can see that there is no resonant frequency for the case of integrator. Moreover, the critical amplitude of sinusoidal stimulus is larger than that of constant stimulus. It is completely different from the case of resonator. Furthermore, the critical amplitude increases almost linearly when the frequency of sinusoidal stimulus is higher than 40Hz. This is because the response of the neuron lags more and more behind the sinusoidal stimulus as the stimulus frequency increases continuously. Therefore, a larger amplitude is needed to drive the neuron from the rest state to firing state. This point is similar to the case of the bistable system;[8] however, the ML model is self-excitable: in other words, the neuron can exhibit periodic spiking under the constant stimulus I_0 across the SNIC bifurcation. The monotonically increasing curve of critical amplitude implies that an integrator is more sensitive to a sinusoidal stimulus of low frequency.

Whether the ML model is a resonator or an integrator, however, there is a common feature: that is, in the high frequency band the critical amplitude of sinusoidal stimulus increases almost linearly with the stimulus frequency. The occurrence of such a feature is because in the high band the response of the neuron is more and more slower than the sinusoidal stimulus, and then the higher energy is needed to drive the neuron transiting from rest state to firing state.

As stated above, the ML model neuron can undergo a HB or a SNIC bifurcation from rest state to firing state depending on the values of the parameters. Nevertheless, it is these two different types of bifurcations that cause the critical amplitude curve of sinusoidal stimulus to be widely divergent.

As a matter of fact, for resonators it is a common feature that the critical amplitude of sinusoidal stimulus versus its frequency exhibits the U-shaped structure. This type of neuron model includes the FitzHugh–Nagumo model, Hodgkin–Huxley model, Hindmarsh–Rose model and Chay model,[17] and so on. They all transit a HB (including subcritical and supercritical) from rest state to firing state. In contrast, the critical amplitude increases monotonically with the stimulus frequency for integrators, which undergo a SNIC bifurcation from rest state to firing state. For example, the Connor model[18] is an integrator. In this study, whether the ML model is a resonator or an integrator depends on the values of parameters. In real neurons, actually, some thalamic neurons are resonators, and various cortical neurons are integrators.

5. Conclusions

To summarize, in this paper we have investigated the difference in the critical amplitude curve of sinusoidal stimulus for the two different dynamical mechanisms from rest state to firing state in the ML neuron. At the same time, we have pointed out that the U-shaped critical amplitude is not a universal phenomenon, and this is true when a neuron is a resonator: namely, the rest state of the neuron disappears via a HB. In contrast, the critical amplitude increases monotonically with the frequency of sinusoidal stimulus when a neuron is an integrator; in the meantime, the rest state of the neuron disappears via an SNIC bifurcation. The common feature for these two types of neurons, that the critical amplitude increases almost linearly with the frequency of sinusoidal stimulus in the high frequency band, has been shown. Since it is the first task to determine the critical amplitude of a periodic stimulus in the study of the SR, the importance of the critical amplitude goes without saying. If a neuron is a resonator, the critical amplitude curve exhibits a U-shaped structure. This implies that the damped subthreshold oscillation makes the neuron respond easily to a preferred frequency stimulus via resonance. For the case of a neuron being an integrator, however, the monotonically increasing curve of critical amplitude suggests that the neuron is more sensitive to a sinusoidal stimulus of low frequency. The results of this paper can provide a reference to choose the subthreshold periodic stimulus.

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