Resonance Properties of Class I and Class II Neurons Differentially Modulated by Channel Noise

Lei Wang

1Neuroscience and Intelligent Media Institute, Communication University of China

E-mail: wanglei_nc@163.com

Abstract. Resonance properties of two different neuron types (Class I and Class II) induced by channel noise are investigated in this study. It is found that for Class I neuron, spiking activity is enhanced when certain noise intensity is presented, especially under weak current stimuli -- a typical phenomenon of stochastic resonance (SR); while for Class II neuron, in addition to perform the SR, certain noise intensity would inhibit neuronal activity under some current stimuli -- a typical phenomenon of inverse stochastic resonance (ISR). Moreover, we show that only sodium channel noise or potassium channel noise variation can achieve the similar phenomena. Consequently, the model results suggest that channel noise may exert differential roles in modulating the resonance properties of Class I and Class II neurons.

1. Introduction

Stochastic resonance (SR) is a typical phenomenon observed when certain noise inputs can enhance the weak-signal processing ability of systems or devices [1]. During the past decades, SR has been widely found in neural systems. It was revealed that additive current noise with certain intensity can help single neurons [2-3] and neuronal networks detect subthreshold signals [4-8].

In addition to SR, inverse stochastic resonance (ISR) has recently been found theoretically and experimentally in some neural systems. Generally, ISR refers to the occurrence of a minimum in firing rate which occurs for certain noise intensity [9-10]. For instance, Tuckwell and Jost [11-13] have suggested that current noise with weak intensity would inhibit the generation of repetitive spiking of neurons. Moreover, certain intensities of conductance noise [14] and color noise [15] have also been shown to inhibit rhythmic neuronal activity.

Besides the above noise sources, channel noise intrinsically exist in biological neurons has been well recognized to play significant roles in modulating neuronal activities [16-17]. The relationship between channel noise and ISR has also been investigated, e.g. [18-19]. However, these analyses were primarily on the classical or standard Hodgkin-Huxley (HH) neuron, which belongs to Class II according to previous categories [20-21], whether other classes of neurons can also demonstrate the channel noise induced ISR is still not completely clear. In view of this, this paper aims to investigate how intrinsic channel noise would modulate the resonance properties of Class I neuron, and compare to the results of Class II neuron.

2. Model and methods

Two ionic models were introduced to represent Class I and Class II neurons respectively. One model is referred from Traub and Miles [22], and the other model is referred from the classical HH neuron [23]. Neuronal membrane dynamics are described by the equations below:
\[
C_m \frac{dV}{dt} = -g_N a m^3 h (V_m - V_{Na}) - g_K n^4 (V_m - V_K) - g_L (V_m - V_L) + I
\]  
(1)

\[
\frac{dx}{dt} = \alpha_x (1 - x) - \beta_x x + \sigma \xi_x(t) \quad (x = m, n, h)
\]  
(2)

where \( V_m \) is the membrane potential, \( C_m \) is the membrane capacitance, \( I \) is the current stimulus, \( g_{Na}, g_K \) and \( g_L \) are the maximal conductance of sodium, potassium and leakage, respectively. \( V_{Na}, V_K \) and \( V_L \) are the reversal potentials, respectively; \( m \) and \( h \) represent the activation and inactivation gating variables for sodium channel, and \( n \) represents the activation gating variable for potassium channel.

Specific parameters for Class I neuron are: \( C_m = 0.2 \mu F/cm^2, g_{Na} = 20 \, mS/cm^2, g_K = 6 \, mS/cm^2, g_L = 0.01 \, mS/cm^2, V_{Na} = 50 \, mV, V_K = -90 \, mV, V_L = -65 \, mV \)

\[
a_m = 0.32(V_m + 50) / (1 - \exp(-(V_m + 50) / 4))
\]  
(3)

\[
\beta_m = -0.28(V_m + 23) / (1 - \exp((V_m + 23) / 5))
\]  
(4)

\[
\alpha_n = 0.128 \exp(-(V_m + 46) / 18)
\]  
(5)

\[
\beta_n = 4 / (1 + \exp(-(V_m + 23) / 5))
\]  
(6)

\[
\alpha_s = 0.032(V_m + 48) / (1 - \exp(-(V_m + 48) / 5))
\]  
(7)

\[
\beta_s = 0.5 \exp(-(V_m + 53) / 40)
\]  
(8)

Specific parameters for Class II neuron are: \( C_m = 1 \mu F/cm^2, g_{Na} = 120 \, mS/cm^2, g_K = 36 \, mS/cm^2, g_L = 0.3 \, mS/cm^2, V_{Na} = 50 \, mV, V_K = -77 \, mV, V_L = -54.4 \, mV \)

\[
a_m = 0.1(V_m + 40) / (1 - \exp(-(V_m + 40) / 10))
\]  
(9)

\[
\beta_m = 4 \exp(-(V_m + 65) / 18)
\]  
(10)

\[
\alpha_n = 0.07 \exp(-(V_m + 65) / 20)
\]  
(11)

\[
\beta_n = 1 / (1 + \exp(-(V_m + 35) / 10))
\]  
(12)

\[
\alpha_s = 0.01(V_m + 55) / (1 - \exp(-(V_m + 55) / 10))
\]  
(13)

\[
\beta_s = 0.125 \exp(-(V_m + 53) / 80)
\]  
(14)

The effect of channel noise is employed by adding a noise term on the variation of gating variables (see \( \xi_x \) in equation (2)). Here \( \sigma \) denotes the relative noise intensity, larger value of \( \sigma \) means stronger effect of channel noise. Similar to previous reports, in which the noise input applied to neurons was usually adopted the Gaussian white noise [2,14,24], \( \xi_x \) in equation (2) is also generated by Gaussian processes with zero mean and the following covariance functions [25].

\[
\mathbb{E} \{ \xi_x(t_1) \xi_x(t_2) \} = \frac{\alpha_x (1 - x) + \beta_x x}{N_{Na}} \delta(t_1 - t_2) \quad (x = m, h)
\]  
(15)

\[
\mathbb{E} \{ \xi_x(t_1) \xi_x(t_2) \} = \frac{\alpha_n (1 - x) + \beta_n x}{N_K} \delta(t_1 - t_2) \quad (x = n)
\]  
(16)

where \( \delta \) is the Dirac delta function, \( N_{Na} \) and \( N_K \) denote the total number of sodium and potassium channels respectively on a given membrane area. We choose \( N_{Na} = \rho_{Na} S \) and \( N_K = \rho_K S \), here \( \rho_{Na} \) and \( \rho_K \) are the channel densities of sodium and potassium, respectively. \( \rho_{Na} = 10 \, \mu m^{-2} \) and \( \rho_K = 3 \, \mu m^{-2} \) for Class I neuron; \( \rho_{Na} = 60 \, \mu m^{-2} \) and \( \rho_K = 18 \, \mu m^{-2} \) for Class II neuron. \( S \) means the total membrane area, and its value is \( 10 \, \mu m^2 \).

Simulations were performed by adopting the MATLAB software, and the fourth-order Runge-Kutta algorithm is employed to calculate the membrane potentials of each neuron in equation (1-2) with time step of 0.01 ms.
3. Results
Basic frequency-stimulus (f-I) curves of Class I and Class II neurons are demonstrated in Figure 1, in which it is clear that Class I neuron fires slowly in response to weak stimuli, and displays a continuous f-I curve; while Class II neuron exhibits a discontinuous f-I curve for their inability to produce spikes below certain threshold intensities. These results are much similar to previous descriptions [20-21].

Figure 1. Frequency-stimulus (f-I) curves of Class I and Class II neurons.

Noise-induced spiking behaviors of Class I and Class II neurons are shown in Figure 2. It is apparent that Class I neuron is much robust to noise input, with little variation in the spiking activities, even though the noise intensity is large (σ = 20). On the contrary, Class II neuron is much sensitive to noise input, showing rather large variations in the spiking activities, even though the noise intensity is small (σ = 1).

It should be pointed out that due to the different ion dynamics in each model neurons, we use different ranges of channel noise, to obtain their overall variation trends.

Figure 3 demonstrates the resonance properties of Class I and Class II neurons. For Class I neuron, certain noise intensity would significantly enhance its responsiveness to subthreshold stimulus (I = 0.01 μA/cm²), and this increase trend persists even under relative larger suprathreshold stimulus (I = 0.05/0.40 μA/cm²). For Class II neuron, certain noise intensity would also enhance its excitability to subthreshold stimulus (I = 6.0 μA/cm²); while under stimulus near the excitation threshold, certain noise intensity would obviously inhibit its responsiveness (I = 6.5 μA/cm²). Moreover, under larger suprathreshold stimulus (I = 10 μA/cm²), noise input has little influence on neuronal activities. This group of results suggests that certain channel noise can induce the typical SR in Class I neuron; while
for Class II neuron, channel noise can not only induce the typical SR, but also induce the ISR under some current injections.

![Figure 3](image)

**Figure 3.** Channel noise induced SR (left) and ISR (right) in Class I and Class II neurons.

Contour diagrams which show the two-parameter dependence of resonance behaviors of Class I and Class II neurons are illustrated in Figure. 4. It is evident that excitability of Class I neuron is enhanced with the increase of noise intensity, while excitability of Class II neuron is inhibited by noise input under some current stimuli.

![Figure 4](image)

**Figure 4.** Two-parameter dependence of resonance behaviors in Class I and Class II neurons. Contour plots showing the SR (left) and ISR (right) are dependent on the noise intensity and stimulus amplitude.

As in the two neuron models we analyzed, there are two main kinds of ion channels: inward sodium channel and outward potassium channel. To explore how these two different ion channels contribute to the modulation of neuronal resonance properties, we separately vary noise intensity in one ion channel, and keep the other unchanged.

Model results presented in Figure. 5(A&C) show that sodium channel noise and potassium channel noise play opposite roles in modulating the resonance behaviors of Class I neuron. Specifically, increase of sodium channel noise would enhance neuronal activities, similar to the results in Figure. 4 (left); while increase of potassium channel noise would suppress neuronal activities.

Results for Class II neuron are demonstrated in Figure. 5(B&D), it is clear that increase of sodium channel noise and potassium channel noise both can induce similar variations of resonance behaviors with the results in Figure. 4 (right).
Figure 5. Two-parameter dependence of resonance behaviors in Class I and Class II neurons. Contour plots showing the SR (A&C) and ISR (B&D) are dependent on the noise intensity and stimulus amplitude, in which A&B represent sodium channel noise, while C&D represent potassium channel noise.

4. Conclusions
In summary, we have performed a numerical investigation on the effect of channel noise in modulating the neuronal resonance behaviors. By employing two different types of neuron (Class I and Class II) as bases, we show that spiking activity of Class I neuron is enhanced when channel noise with certain intensity is added, and this enhancement is particularly evident under weak current stimuli; spiking activity of Class II neuron is also enhanced by channel noise under a certain range of current stimuli, but for current stimuli near the excitation threshold, neuronal spiking activity is inhibited. In addition, we further demonstrate that variations of only sodium channel noise or potassium channel noise can achieve the similar phenomena. It should be mentioned that we have only investigated the influence of channel noise on the variation of resonance properties in two single model neurons, and did not consider any synaptic connections with other neurons. However, in the brain, neurons are organized in modules or networks to function, thus future investigations can analyze potential differences between networks composed of Class I neurons and Class II neurons.

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