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Optimal time scales of input fluctuations for spiking coherence and reliability in stochastic Hodgkin–Huxley neurons

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ABSTRACT

Channel noise, which is generated by the random transitions of ion channels between open and closed states, is distinguished from external sources of physiological variability such as spontaneous synaptic release and stimulus fluctuations. This inherent stochasticity in ion-channel current can lead to variability of the timing of spikes occurring both spontaneously and in response to stimuli. In this paper, we investigate how intrinsic channel noise affects the response of stochastic Hodgkin–Huxley (HH) neuron to external fluctuating inputs with different amplitudes and correlation time. It is found that there is an optimal correlation time of input fluctuations for the maximal spiking coherence, where the input current has a fluctuating rate approximately matching the inherent oscillation of stochastic HH model and plays a dominating role in the timing of spike firing. We also show that the reliability of spike timing in the model is very sensitive to the properties of the current input. An optimal time scale of input fluctuations exists to induce the most reliable firing. The channel-noise-induced unreliability can be mostly overridden by injecting a fluctuating current with an appropriate correlation time. The spiking coherence and reliability can also be regulated by the size of channel stochasticity. As the membrane area (or total channel number) of the neuron increases, the spiking coherence decreases but the spiking reliability increases.

1. Introduction

It is well-accepted that electrical information in nervous system is encoded, processed, and transmitted by trains of neuronal action potentials [1–3]. Thus, a main goal in neuroscience is to understand how neurons generate action potentials both spontaneously and in response to synaptic and other inputs. It has been shown that the rate and timing of action potentials, or spikes, are strongly affected by the interaction between external inputs and intrinsic neuronal properties [4,5]. Experimental and simulated approaches have indicated that intrinsic neuronal properties, such as their membrane currents, the distribution of ion channels, and cell morphology contribute to the electrical responses of cells [6–8].

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Neural spikes are also subject to sources of noise, which is mainly generated from random processes in ion channels and synapses [9]. Most of previous studies focus on the external sources of noise, such as synaptic noise and stimulus noise [10,11], while other investigations have focused on intrinsic noise generated by ion channels [12,13]. Advances in single-channel recording technique demonstrated that individual ion channel can switch between open and closed state in an apparently random manner [14,15]. This can generate an internal source of noise, known as channel noise, and add fluctuations to ion conductance. Channel noise, which is distinguished from external sources, has important effects on neuronal dynamics and coding. It can alter the firing threshold, spike timing, and interspike interval statistics [16–18]. Channel noise can also contribute to the overall variability in the nervous system, which in turn may pose constraints on the fidelity of the motor and sensory systems of an animal and limit the miniaturization of the brain's wiring [19].

The constructive effects of noise on neural systems have been extensively studied and many noise-induced dynamic behaviors have been found [20,21]. The most typical one is stochastic resonance (SR), where the response of a nonlinear system to a weak periodic signal can be amplified and optimized by the addition of an external noise with appropriate strength [22–24]. Without the periodic signal, coherent oscillation in a nonlinear system can be purely induced by the noise, and the regularity of this oscillation is optimal for an appropriate level of noise, which is known as coherence resonance (CR) [25]. The phenomenon of CR has been found in a variety of neural systems, from single neuron [26,27] to neural networks [28–35]. Both SR and CR are thought to be basic mechanisms that neurons employ to transmit signals among neurons.

The reliability of neural responses, which refers to the neuron's ability to generate the same spike patterns in different repetitions of the same stimulus [36], is a prerequisite for neural encoding. Reliable spiking carries information and provides a substrate for neural coding [37]. Stimuli which evoke highly reproducible spike times across trials can be encoded by the spike time, whereas stimuli resulting in imprecise spike times are encoded almost exclusively by the spike rate [38].

The properties of inputs are major factors affecting the neural spike-time reliability. Previous studies show that spike-time reliability is enhanced with stimulus amplitude increasing [38]. In the intermediate amplitude regime, the frequency content of the stimulus is an important factor determining reliability [39,40]. Spike-time reliability of a neuron is maximal for those stimuli that contain frequencies matching the intrinsic frequency of a neuron [41]. Mainen and Sejnowski investigated the reliability of spike time in neocortical pyramidal cells, and found that spike timing is highly unreliable for repeated direct current inputs, whereas fluctuating current inputs significantly improve the firing reliability [38]. Galan et al. further investigated the mechanisms for neural reliability in experiments with mitral cells in the olfactory bulb and pyramidal cells in the neocortex and in computer simulations of simple neural models [42,43]. They demonstrated an optimal time scale of the input fluctuations for maximal spike-time reliability.

The intrinsic properties of neurons can also determine the reliability. It has been found experimentally that different types of neurons are tuned to different stimuli with respect to spike-time reliability. For example, cortical interneurons show maximum reliability in response to higher-frequency sinusoidal stimuli, whereas pyramidal cells respond more reliably to lower-frequency sinusoidal inputs [44]. Schreiber et al. investigated the influence of ionic conductance of cortical neurons on spike-time reliability in response to suprathreshold rhythmic inputs [45]. It is also shown that blocking the potassium A-current can improve spike-time reliability, whereas larger persistent sodium current impairs reliability [46]. Moreover, Schneidman investigated the critical role of ion channel stochasticity in determining spike-time reliability and suggested that the inherent noise in ion channels enables neurons to act as "smart" encoders [47]. It is also suggested that a low intrinsic noise level in spike generation could enable neurons to accurately transform synaptic input into spike sequences [38].

In this paper, we investigate the effects of intrinsic noise, which results from the fluctuations of ion currents passing through the neuron's membranes, on spiking pattern of single stochastic HH neuron in response to external fluctuating inputs. The Stochastic-Shielding Approximation is applied into Markov Chains for whole-channel models of channel noise, which is computationally expensive to stimulate. We demonstrate how intrinsic properties of channel noise and external input can modulate the spiking regularity and reliability of stochastic neuron. An optimal correlation time of input fluctuations is found for the maximal spiking findings. The simulations also show that the optimal time scale is determined by the cooperation of inherent oscillations of stochastic neuron and external input. We further investigate the mechanisms underlying the existence of optimal spiking coherence and reliability.

2. Stochastic Hodgkin–Huxley neuron model

In our simulations we use a single compartment model of the Hodgkin–Huxley (HH) model with stochastic ion-channel gating. In order to improve the computational efficiency, we use the stochastic HH neuron model with the stochastic-shielding approximation proposed by Schmandt and Galan [48]. The membrane potential of a stochastic HH neuron is given by:

$$C\frac{\mathrm{d}V}{\mathrm{d}t} = -g_{Na}(V - E_{Na}) - g_K(V - E_K) - g_L(V - E_L) + I_0 \tag{1}$$

where C corresponds to the membrane capacitance with 0.01 $\mathrm{pF}/\mu\mathrm{m}^2$, g_{Na}, g_K, and $g_{leak} = 3\ \mathrm{pS}/\mu\mathrm{m}^2$ are the Na^+, K^+, and leak conductance with their respective reversal potential, $E_{Na} = 45$ mV, $E_K = -77$ mV, and $E_{leak} = -54$ mV. I_0 is the injected current, which is generated by convolving frozen white noise with an alpha function $(t/\tau \cdot \mathrm{e}^{-t/\tau})$ and rescaling to the desired variance, so that the amplitude of the fluctuations is the same for all τ.