Waveform sample method of excitable sensory neuron

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(Dated: February 9, 2008)

We present a new interpretation for encoding information of the period of input signals into spike-trains in individual sensory neuronal systems. The spike-train could be described as the waveform sample of the input signal which locks sample points to wave crests with randomness. Based on simulations of the Hodgkin-Huxley (HH) neuron responding to periodic inputs, we demonstrate that the random sampling is a proper encoding method in medium frequency region since power spectra of the reconstructed spike-trains are identical to that of neural signals.

PACS numbers: 87.10.+e, 05.45.Tp

In the last decade the phenomenon of the stochastic resonance of excitable neuron has been extensively studied both experimentally [1, 2, 3, 4] and theoretically [3, 4, 5]. In these studies stochastic excitable sensory neurons or neuron models subject to periodic signals. Stochastic resonance means that the ability of neurons for responding to the weak signal is enhanced by noise. The power spectral density of action potential was used as one of common methods for estimating the sensitivity of stochastic neurons to weak input signal [6]. The power spectrum revealed the frequency information of input signal [5, 9]. However, the code for encoding and decoding in neuron is not clarified at the moment [10].

We made a study based on a popular Hodgkin-Huxley (HH) neuron model which was originally proposed to account for the property of squid giant axons [12] and has been generalized with modifications of ion conductances [13]. It describes the spiking behavior and refractory properties of real neurons and serves as a paradigm for spiking neurons based on nonlinear conductance of ion channels [12]. The dynamics of HH model is described by the following set of coupling ordinary differential equations: one for the membrane potential \( V \) and the other three for the gating variables: \( m, n, \) and \( h \); that is,

\[
\dot{V} = (I_{ion}(t) + I_{ext}(t) + I_{noise})/C_m, \quad (1a) \\
\dot{m} = (m_\infty(V) - m)/\tau_m(V), \quad (1b) \\
\dot{h} = (h_\infty(V) - h)/\tau_h(V), \quad (1c) \\
\dot{n} = (n_\infty(V) - n)/\tau_n(V), \quad (1d)
\]

where

\[
I_{ion}(t) = -g_{na}m^3h(V-V_{na})-g_kn^4(V-V_k)-g_l(V-V_l). \quad (1e)
\]

The ionic current \( I_{ion}(t) \) describes the ionic transport through the membrane, and includes the sodium (\( I_{na} \)), potassium (\( I_k \)), and leak (\( I_l \)) currents. The constants \( g_{na}, g_k, \) and \( g_l \) are the maximal conductances for ion and leakage channels, and \( V_{na}, V_k, V_l \) are the corresponding reversal potentials; \( m_\infty, h_\infty, n_\infty \) and \( \tau_m, \tau_h, \tau_n \) represent the saturation values and relaxation times of the gating variables [14]. Detailed values of parameters can be found in [12, 13]. \( I_{ext} \) is the external stimulus received by neuron. We model the noisy current as an exponentially correlated colored noise

\[
\tau_d \frac{dI_{noise}}{dt} = -I_{noise} + \sqrt{2D} \xi(t), \quad (2)
\]

where \( \xi(t) \) is Gaussian white noise, \( D \) and \( \tau_d \) is the intensity and the correlation time of the colored noise, respectively. In the following numerical simulations we took \( \tau_d = 2 \)msec. Differential equations given by Eqs. [1e], [1a]–[1d] were integrated by the forth-order Runge-Kutta method. The colored noise in Eq. [2] was solved following ideas by Fox et al. [16]. The time step was \( \Delta t = 0.02 \) msec.

We use spike-train rather than membrane potential to represent the temporal sequence of firing events of neurons. Because it is believed that most of information in neural systems is coded in the time sequence of action potential [17]. The spike-train is a binary time series with a value \( 1 \) at the time of action potential generations and \( 0 \) at other times. The spikes were defined as 20mV-level crossing from below to above values of the membrane potential \( V \).

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The curve in Fig. 1(a) represented precisely the phase of sinusoidal signals used in different trials, but intensity was not included. When the sine signal is strong, $A_1 = 2.0 \mu A/cm^2$, and noise is absent, the spike-trains in Fig. 1(b) was activated. There is a spike in each period of signal. And the spikes fire precisely at a specific phase of sine signal during every positive half-cycle. There is a common delay between spikes and corresponding wave crests, which does not affect the temporal structure of the spike-train and the correlation between the input signal and the spike-train. According to the phase locking of firing to sinusoidal signal, we simplified the description of the correlation between the input signal and the spike-train as that every wave crest of the pure tone sine wave activates a spike. In the second trial, we added noise into the HH neuron which received the sinusoidal signal used upper. The intensity of noisy current was $D = 5.0$. The spike-train recorded from the simulation was shown in Fig. 1(c). Notice that most of the spikes deviated from the positions contrasting to that in the above spike-train and few spikes disappeared randomly. The size of deviation is random and small. In the third trial, we decrease the amplitude of periodic signal to $A_1 = 1.0 \mu A/cm^2$, and remained the intensity of noise as $D = 5.0$. The spike-train computed from the trial was illustrated by Fig. 1(d). Under this condition, the number of spikes had a sharp decrease compared with the spike-train activated by strong signal shown in Fig. 1(c). It is random that whether a wave crest activates a spike. The spikes in the spike-train also deviate from the positions of the wave crests. Although randomness entered the spike-train when noise was presence, the phase locking was affected slightly by noise.

Pure tone stimulations have been used in many studies of neuronal response. Subsequently, we considered the signal which is a sum of two sinusoidal functions with different frequencies:

$$I_{ext} = A_1 \sin(2\pi f_1 t) + A_2 \sin(2\pi f_2 t).$$

We took the frequencies of two sinusoidal functions as $f_1 = 0.05kHz$ and $f_2 = 0.065kHz$, respectively. In Fig. 2, the waveform of the combined signal and the spike-trains activated by it were illustrated. In Fig. 2(b), during a period of the input signal, from 600 msec to 800 msec, three spikes fired and locked to the three highest wave crests. When noise was added to the neuron, the number of spikes increased. Some spikes fired randomly at the small neighborhoods of weaker wave crests. The stronger a positive half-wave is, the larger probability it gives rise to a spike. According to the correlations between the input signal and the spike-train, we propose an interpretation of the encoding mechanism. The phase locking phenomena suggest that the response to periodic signal can be considered as a waveform sample: when a sensory neuron receives the periodic signal, it samples the input signal through the nonlinear response and the signal was sampled as the action potential. The sampling method has the following properties. (i) Sample points appear in the
neighboring of the wave crest of input signals. (ii) It is unnecessary that every wave crest is sampled. The probability that a wave crest is sampled depends on the strength of it. (iii) The position of the sampling points distribute randomly in the neighborhood of the wave crest of signals. (iv) The values of the sampling points do not depend on the signals which are sampled. All samples have the same value.

To demonstrate the waveform of the spike train method, we used it to recover the basic characteristics of neural signals. The power spectra of the spike train was used to evaluate the frequency information of neural signals and assess the coherence of the spiking activity with the signal frequency, which has been used extensively in the studies of stochastic resonance as mentioned above. We computed the power spectral density from simulating the process that an individual HH neuron responded to periodic signals and the Monte-Carlo (MC) simulations of the waveform sample method. The power spectra were computed from 200 averages of the power spectrum for the time series of the spike train with length 2. The power spectrum of the spike train was shown in Fig. 4(a). In the power spectrum, the main feature due to the periodic signal is the narrow peak at the fundamental frequency riding on a broad noise background. Additionally, the harmonic of the fundamental frequency exists in the power spectrum. This result agrees excellently with the experiment in Ref. 1. The power spectrum quantifies the information content of the spike train without invoking any specific encoding mechanism. The peak of power spectral density located at the fundamental frequency proves that the information of the period of the signal must be encoded in the spike train by the individual HH sensory neuron. As an example, we consider a simple rule of the waveform sample. The probability that a wave crest gives a sample point is proportional to the amplitude of signal:

$$P_i = I_i / I_c,$$

(5)

where $I_i = A_1$ is the amplitude of the pure tone sinusoidal signal, $I_c$ is constant which is larger than $A_1$. The positions of sample points were subjected to Gaussian distribution:

$$p(s_i) = \frac{1}{\sqrt{2\pi}\sigma} \exp\left(-\frac{(s_i - t_i)^2}{2\sigma^2}\right),$$

(6)

where $t_i$ is the position of the $i$th wave crest, $s_i$ is the position of sample point that locks in the neighborhood of $t_i$. We made MC simulations using the rule described by Eqs. 5 and 6 with $I_c = 2.0 \mu A/cm^2$ and $\sigma = 2.0\musec$. The power spectrum obtained from the MC simulations was compared with that of the HH neuron in Fig. 4(b). Although the background noise in the power spectra are different, the frequency structure of HH neuron has been recovered virtually. The difference between background noise in Fig. 4(b) and that in Fig. 4(a) is due to the simple rule of waveform sample which does not involve the dynamics of HH neuron.

Then we consider the combined signal described by Eq. 4. The parameters were taken as $A_2 = 1.0 \mu A/cm^2$, $f_1 = 0.05 k\nu Hz$, and $f_2 = 0.065 k\nu Hz$ in simulations. Under this condition, the HH neuron can be activated by the combined current without the assistance of noise. In the power spectrum, as illustrated by Fig. 4(a), the fundamental frequencies give two high and narrow peaks which were marked by the labels using their positions in frequency domain. Also lots of additional frequency components arise and some of which are as strong as fundamental frequencies. The frequency structure exhibited in this power spectrum was given by the precisely phase locking spike train shown above in Fig. 2(b). When noise was present, we simulated the process that HH neuron responds to the combined signal. In the case of noise intensity was taken as $D = 10.0$, the power spectrum was computed and shown in Fig. 4(b). The frequency structure has a survivability change compared with Fig. 4(a). The fundamental frequencies $f_1$ and $f_2$ give the highest peaks in the power spectrum. Most of the additional frequency components disappear. The surviving additional components locate at $f_2 - f_1$, $2f_1$ and $f_1 + f_2$ with weak strength. Noise affects the frequency structure of the output spike train of sensory HH neuron and plays an optimized role in distinguishing the fundamental frequency components in...
The present work is the further investigation of the stochastic process theory of firing events, where the frequency structure of power spectra were described elegantly. We obtained the subtler correlation between the spike-train and the input signal, and proposed a waveform sample method as an intuitive interpretation of the encoding mechanism. The waveform sample method is different from the conventional sample method used for processing signals, such as the even interval sample used for discrete Fourier transform, which does not give rise to the additional frequency components in power spectra. If the frequency of the signal received by neuron is low, the neuron will fire more than once in a period of signal. On the other hand, the dynamics of HH neuron can not lock the spike to every wave crest of the signal in the high frequency region because of the refractory properties. Although it is not a proper encoding method of neurons in low and high frequency regions, it can also convey the frequency information into the sample points in all these frequency regions. Additionally, the waveform sample method suggests a method for reconstructing the spike-train and proposes a chance to utilize the neural encoded mode without invoking neuronal models.

The power spectrum of the waveform sample of the combined periodic signal, the sample rule described by Eqs. (4) and (5) was used again. The symbol $I_i$ was the height of the $i$th wave crest of the combined periodic signal. We took the parameters as $I_e = 2.0 \mu A/cm^2$ and $\sigma = 3.0$ms. The power spectrum of the waveform sample was shown in Fig. 4(c), and it got the primary characters of the frequency structure of the Fig. 4(b). The result demonstrates that the randomness in the waveform sample method captures the effect of noise in sensory neuron. The sample rule used in the MC simulation was too simple and crude to depict the neural process exactly, but the main characteristics of spike-trains of the HH model have been obtained from the waveform sample. The waveform sample method captures the nature of the encoding mechanism that sensory neuron responds to periodic signals.

FIG. 4: (a) The power spectrum recorded from the simulation of HH neuron responding to the periodic signal described by Eq. (4) without noise. The parameters were taken as $f_1 = 0.056kH\ddot{z}$, $f_2 = 0.065kH\ddot{z}$ and $A_2 = 1.0\mu A/cm^2$. (b) The power spectrum produced by stochastic HH neuron ($D = 10.0$) responding to the combined signal. (c) The power spectrum obtained from the MC simulation of waveform sample.