Adaptation of the transfer function of the Hodgkin-Huxley (HH) neuronal model [1]

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Abstract

The transfer functions of sensory neurons are known to adapt to the statistics of the input signals. It is however unclear whether such adaptation arises from the nonlinear dynamics of the neuron or emerges from the collective interaction among neurons embedded in a network. We investigated the Hodgkin-Huxley (HH) neuronal model's response to Gaussian white noise signals of different variances and found that the recovered kernel adapt its preferred temporal frequency and its energy gains according to noise variance. This adaptation is likely a consequence of the cooperative interaction between the noises and the bifurcation dynamics of the neurons.

Key words: Adaptation, Receptive field; Wiener kernel

1 Introduction

Recent neurophysiological research suggests that the stimulus-response functions of visual and auditory neurons adapt to the statistics of stimuli [1-6]. The adaptation of retinal neurons, for example, allow the visual system to operate effectively over an enormous dynamic range of lighting conditions. In blowfly, it was found that the input-output relationship of the H1 neuron adapt to the variance of the input noises [3-4]. Such adaptation has been suggested to play a role in maximizing information transmission by matching the sensitivity of the neurons to the spatial and temporal range of the stimuli and noises [7]. However, it is not clear how this adaptation comes about. Does it emerge from the interaction of a network of neurons, or does it emerge from the intrinsic dynamical mechanisms inside a neuron? Neurons communicate and compute with spikes, and the generation of spikes involves nonlinear mechanisms. Could the nonlinear dynamics of the neuron itself naturally produce a certain degree of adaptation and plasticity?

2 Methods

To investigate these issues, we apply an advanced system identification technique based on Laguerre expansion [8] to examine the transfer function of the Hodgkin-Huxley (HH) model [9] under the stimulation of Gaussian white noise (GWN) stimuli. The HH model provides an empirical description of real neuron that captures both of its spiking behavior and refractory properties.

Based on the input GWN, i.e., $x(t)$ and the output spike trains of the HH neuron, i.e., $y(t)$, we can characterize the cell's transfer function $h_\tau, h_{\tau_1,\tau_2}$ (the first and the second order kernel respectively) with memory length L as follows:

$$y(t) = h_0 + \sum_{\tau=1}^{L} h_\tau x(t-\tau) + \sum_{\tau_1=1}^{L} \sum_{\tau_2=1}^{L} h_{\tau_1,\tau_2} x(t-\tau_1) x(t-\tau_2). \tag{1}$$

where h_o is the mean firing rate, h_τ is the first order kernel and h_{τ_1,τ_2} is the second order kernel. We restricted τ to be positive so we only consider causal filters. We used GWN signals with a fixed, short correlation time (cut frequency = 500 Hz) and zero mean, so the only free statistical parameter is the standard deviation σ.

3 Results

We varied σ systematically from 1 to 20 $\mu A/cm^2$, and recorded the spike trains generated by the HH model. Fig.1(a) and (b) shows an example of the input signal (with $\sigma = 5$) and the output of the HH neuron in response to this input signal. Using 200 seconds of these input and output data, we recovered

the first and second order kernels of the HH neuron using the Laguerre expansion technique, shown in Fig.1(c) and (d). To verify the appropriateness of the method, we applied the method to recover a mathematically defined static kernel (e.g., the first kernel $K1= sin(\pi\ t/10)exp(-t/10)$, the second kernel $K2 = K1\otimes K1$) with noises of different σ. We found the static kernels recovered are invariant over a large range of σ. But for a HH neuron, the kernels recovered using different noise σ are found to change. Specifically, when we increase σ, the kernel is found to contract in time, i.e. the preferred temporal frequency of the filter increases. Fig.2(a) shows the kernels recovered for three different σ's. The amplitude of the kernel first increases and then decreases with an increase in σ, reaching a global maximum at an intermediate σ. This phenomenon is related to the reported variance or contrast adaptation in electrophysiological experiments [1,4].

To evaluate this adaptation phenomenon systematically, we compute the power spectral density (PSD) of the first order kernel for noise with different σ as shown in Fig.2(b). The preferred frequency of the kernels was computed as the peak frequency in the PSD. Fig.2(c) shows that the preferred frequency of the kernel increases gradually with an increase in σ, changing from 47 Hz to 66 Hz as σ changes from 1 to 20. The kernel frequency saturated with further increase in σ. These findings suggest that the frequency tuning of a neuron is adaptive to the variance of the noise input.

Fig.2(b), also revealed that the peak of the PSD for noise with $\sigma = 3$ is much higher than that for $\sigma = 2$, and 10, suggesting that more spectral energy is allowed to pass through for input noise of $\sigma = 3$. That is, for some optimal stimulus statistics, the spike activities of the neuron become more coherent and resonant with the the driven stimulus. The system absorbs the energy of the environment to maximize its response to stimulus, resulting in a largest gain in the transfer function for $\sigma = 3$ (see Fig2.(d)). The total energy of the transfer function is given by,

$$E = \sum_{f=0}^{L-1}(PSD(f))/L, \tag{2}$$

where f is the index of frequency and L is the length of the PSD. Fig.2(d) shows the energy E of the first order kernel is maximal at $\sigma^2 = 9$. This phenomenon is called a coherence resonance (CR) [10].

When the noise level is low, the system is inert. Spikes will occasionally occur because the noise disturbance can drive the system through the spiking threshold. When the noise level is high, the neuron is mainly in the spiking state. The cooperation of the noise and the excitable dynamics of the system drives the system to fire spikes quasi-regularly. At too high a noise level, the quasi-regular spiking activity of the neuron is disrupted by the large stochastic nature of the noise, resulting in a decrease in the coherence of the system. At a tradeoff point, with an intermediate stimulus statistics, the neuronal dynamics is driven optimally by absorbing the energy of the environment maximally,

with a maximum sensitivity to signals. In coherent resonance, the noise levels effectively put the system into different states, changing the neurons' frequency tuning as well as the gain of its transfer function.

4   Discussion

These observations suggest that the transfer function of HH neuron is not static but dynamic. The time scale of the transfer function varies with the statistics of the stimuli. The variance of the stimulus puts the neuron into different coherent states, reflecting different degrees of synergistic interaction between the stimulus and the nonlinear dynamics of the system. The neuron's transfer function varies with the coherent state: the preferred frequency increases with σ and the gain of the transfer function reaches a maximum at $\sigma = 3$ for the standard HH model. It is expected a different set of model parameters will give a different range of frequency tuning variation as well as a different σ for the maximum cooperation with the nonlinear dynamics of the neuron.

The observed adaptation in the input-output relationship in various neurophysiological experiments [1-6] is therefore likely due, in part, to the adaptation of the transfer function of the single neuron to the different noise levels. The first and second order kernels recovered from the HH neuron, however, are significantly dilated in time scale than the adaptation found in monkey cortical neurons [11] or blowflies [3,4]. The difference in neuronal parameters may be a factor. Furthermore, given the neuron measured is part of the network with many layers of neurons lying between it and the photoreceptors on the retina, network delay and interaction would likely produce a low-pass effect, dilating the effective kernel of the measured neuron.

Our simulation suggests that synergistic cooperation between the statistics of the noises with the nonlinear dynamics of the neuron is an important and maybe crucial contributing factor to the adaptation of the neuronal transfer function to the stimulus statistics.

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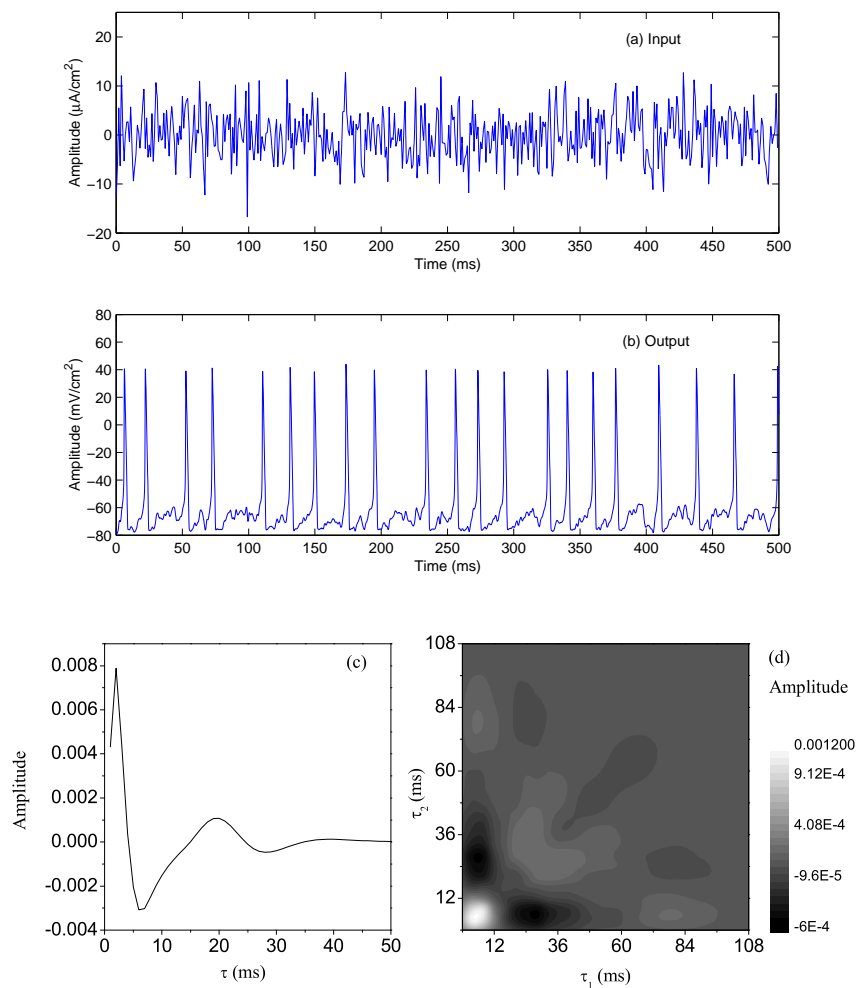
Fig. 1. (a) Input GWN with $\sigma = 5$. (b) The spike trains of the HH neuron in response to this stimulus. (c) The first order kernel of HH neuron recovered. (d) The second order kernel of the HH neuron.
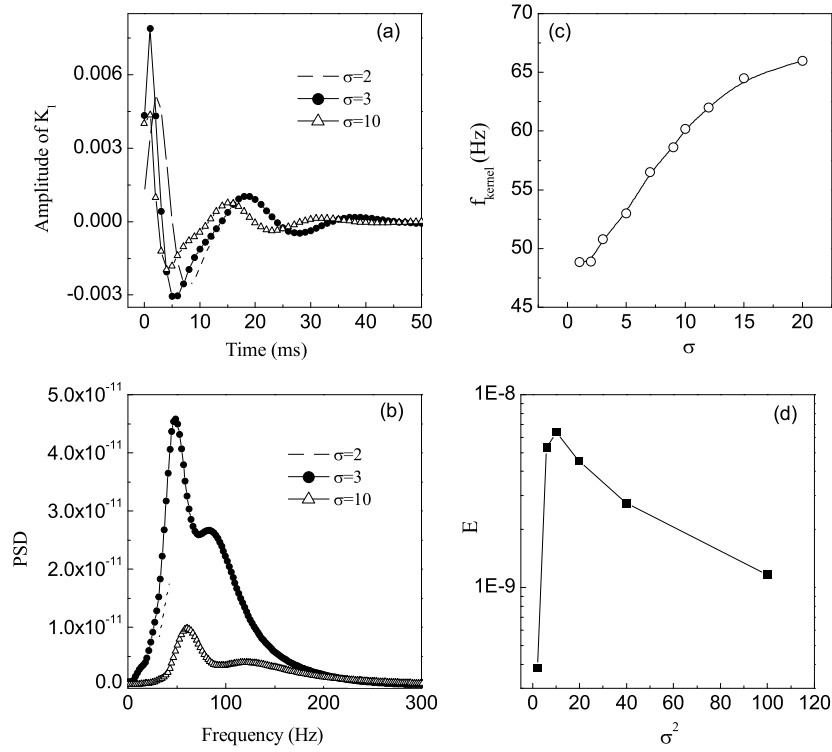
Fig. 2. (a) The first order kernels of the HH neuron for noises with $\mu = 0$; $\sigma = 2, 3, 10$, respectively. (b) The power spectra densities of the first order kernels for the three sets of noises. (c) The preferred frequency of the first order kernel as a function of σ. (d) The energy E of the first order kernel as a function of σ^2 .