

# Adaptation of the transfer function of the Hodgkin-Huxley (HH) neuronal model <sup>1</sup>

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## Abstract

The transfer functions of visual and auditory neurons have been found to adapt to the statistics of the input signals. This adaptation has been suggested to maximize information transmission (Brenner, et al., 2000; Wainwright, 1999). However, given only the output of the neuron was monitored in these studies, it was not clear whether the adaptation arises from the nonlinear dynamics of the neuron in response to the noise statistics of stimuli, or emerges from the collective interaction in a network of neurons in which the neuron being studied was embedded. Here, we performed a simulation study to clarify this issue. Specifically, we provided stimulus of different noise variance to a Hodgkin-Huxley (HH) neuronal model and measured its output. We then applied a system identification technique based on Laguerre expansions (Marmarelis, 1993) to recover the first and second order kernels of the neurons. We found that the transfer function measured from a HH model did adapt according to the stimulus' noise statistics. The change of the frequency tuning and the power of the transfer function as a function of noise variance is likely a consequence of the cooperative interaction between the noises and the nonlinear dynamic of the neuron.

*Key words:* adaptation, receptive field; Wiener kernel; HH model

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## 1 Introduction

Recent experimental research suggest the stimulus-response function of visual and auditory neurons adapt to the statistics of stimuli (Smirnakis, et al., 1997; Fairhall, et al., 2001; Brenner, et al., 2000; Fairhall, et al., 2001; Kim and Rieke, 2001; Jenison, 2001). The adaptation of retinal neurons, for example, allow the visual system to operate effectively over an enormous dynamic range of lighting conditions (Smirnakis et al., 1997). In blowfly, it was found that the input-output relationship of the H1 neuron adapt to the variance of the input noises (Brenner, et al., 2000). 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 scales of the stimuli and noises (Wainwright, 1999). However, it is not clear how this adaptation come 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 system identification techniques to examine the transfer function of a neuronal model, i.e., the Hodgkin-Huxley (HH) model (Hodgkin and Huxley, 1952), under different kinds of stimulus statistics. The HH model is an empirical description of the time- and voltage-dependence of currents flowing across the membrane of giant axon of the squid. It captures both the spiking behavior and refractory properties of real neurons.

Specifically, we want to know how much adaptation is exhibited by a single neuron system. Techniques for identifying the transfer function of nonlinear system are fairly well developed. We used an advanced Wiener kernel method based on Laguerre expansion technique (Marmarelis, 1993) to obtain the kernels of the simulated neuron using Gaussian white noise (GWN) stimuli. It is known that when the bandwidth of the noises are high enough, the first and second kernels of a nonlinear system can be accurately recovered.

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  $h_\tau, h_{\tau_1, \tau_2}$  (first and second order wiener kernel respectively) with memory length  $L$  as following:

$$y(t) = h_0 + \sum_{\tau=1}^L h_\tau x(t - \tau) + \sum_{\tau_1=1}^L \sum_{\tau_2=2}^L h_{\tau_1, \tau_2} x(t - \tau_1) x(t - \tau_2). \quad (1)$$

where  $h_0$  is the mean firing rate,  $h_\tau$  is the first order kernel and  $h_{\tau_1, \tau_2}$  is the second order kernel. We restricted  $\tau$  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 that the only free statistical parameter is the variance  $\sigma$ .

### 3 Results

We varied  $\sigma$  (the standard deviation of the GWN) of the input systematically from 1 to 20  $\mu A/cm^2$ , and recorded the spike trains generated by the HH model. Figure 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 kernel of the HH neuron using the Laguerre expansion technique, as shown in Figure 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  $\sigma$ . We found the static kernels recovered are invariant against noise  $\sigma$ . But for a HH neuron, the kernels recovered using different noise  $\sigma$  are found to change. Specifically, when we increase  $\sigma$ , the kernel is found to contract in time, i.e. the temporal frequency tuning of the filter increases. Figure 2(a) shows the kernels recovered from GWN of three different  $\sigma$ 's.

In order to evaluate the adaptation of the frequency tuning systematically, we compute the power spectral density (PSD) of the first order kernel for different noise standard deviation  $\sigma$  as shown in Figure 2(b). For each PSD, we computed the natural frequency of the kernels as the peak frequency in the PSD. Figure 2(c) shows that the natural frequency of the kernel increases almost linearly with an increase in  $\sigma$ , changing from 47 Hz to 67 Hz as  $\sigma$  changes from 1 to 20. These findings suggest that the frequency tuning of a neuron is adaptive to the variance of the noise input.

From Figure 2(b), we also noticed that the power spectral density peak for  $\sigma = 3$  is much higher than the power spectral density peak for  $\sigma = 2$ , and 10, suggesting that more spectral energy is allowed to pass through for input noise of  $\sigma = 3$ . In Physics, it is known that a particular noise level would allow the system to function in the most efficient or minimum energy manner. This efficiency is measured by a quantity called coherence which is given by (Lee, 1998):

$$\beta = \frac{H}{\Delta f} \quad (2)$$

where  $H$  is the maximum height in the PSD and  $\Delta f$  is the half height bandwidth in frequency in the PSD of the kernel.

Figure 2(d) shows a plot of  $\beta$  as a function of  $\sigma$ , which peaks at  $\sigma = 3$ , implying noise of  $\sigma = 3$  put the system into the most coherent state. At this state, the synergistic cooperation between the noise and the neuron's dynamic

is maximum, allowing the neuron to absorb the energy of the environment maximally and to process information with the minimum energy or maximum sensitivity. This phenomenon is called coherence resonance (Pikovsky and Kurths, 1997; Lee, 1998). For lower noise level, the system is inert; for higher noise level, the system is disrupted by the noise and is not very responsive to the signal. The noise levels in effect put the system into different coherent states which change the frequency tuning as well as the power of a neuron's 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 is changed when the noise statistics of the stimuli varies. The noise level (defined by  $\sigma$ ) can put the neuron into different coherent states – different degree of synergistic interaction between the noise and the nonlinear dynamics of the system. The neuron's transfer function varies with the coherent state: the optimal frequency the neuron selective to is found to increase with  $\sigma$  and the power of the transfer function is maximum when  $\sigma = 3$  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  $\sigma$  for maximum cooperation with the nonlinear dynamics of the neuron.

The observed adaptation in the input-output relationship in various neurophysiological experiments (Smirnakis, et al., 1997; Fairhall, et al., 2001; Kim and Rieke, 2001) is 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 faster in time scale than the adaptation found in monkey cortical neurons (Romero et al. 2002) or in fish or flowflies (Smirnakis, et al., 1997; Brenner et al 2000). The difference in neuronal parameters is likely 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 cooperation between the statistics of the noises with the nonlinear dynamics of the neuron is part of the causes for the adaptation of the neuronal transfer function to the statistics of the input stimuli.

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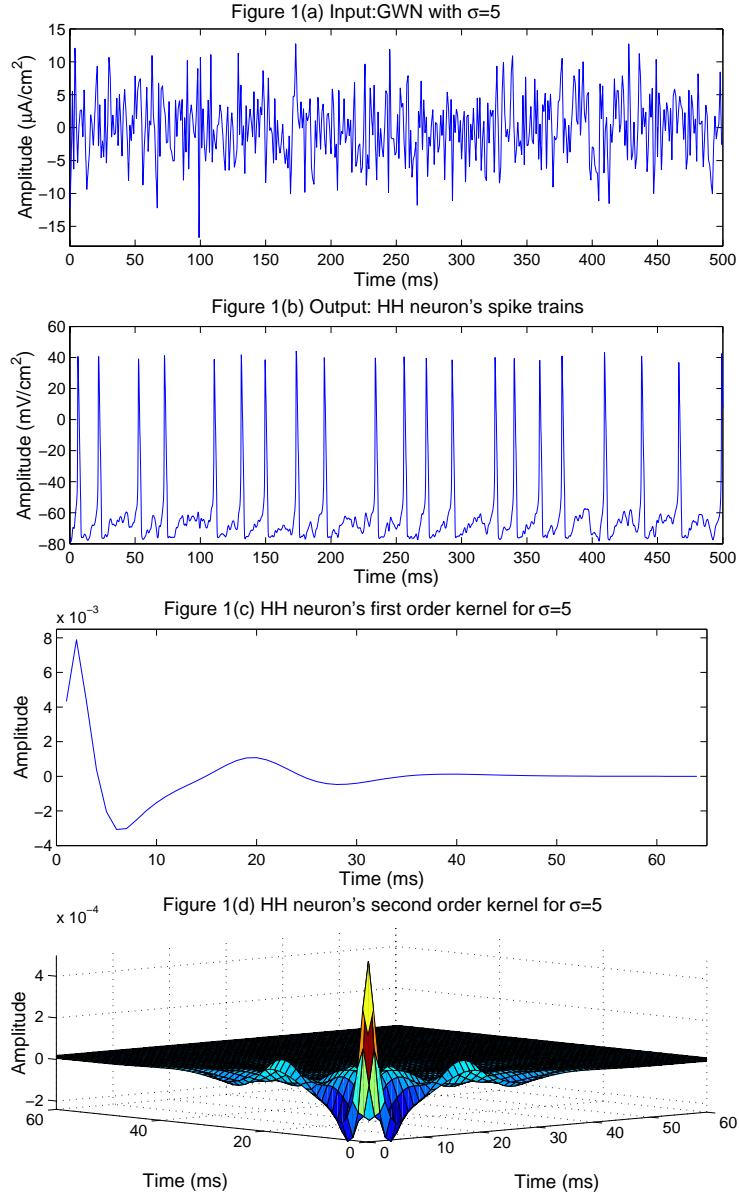


Fig. 1. (a) Input GWN with  $\sigma = 5$ , (b) the spike trains of the HH neuron, (c) The first order kernel of HH neuron for GWN with  $\sigma = 5$ , (d) The second order kernel of the HH neuron for GWN with  $\sigma = 5$ .

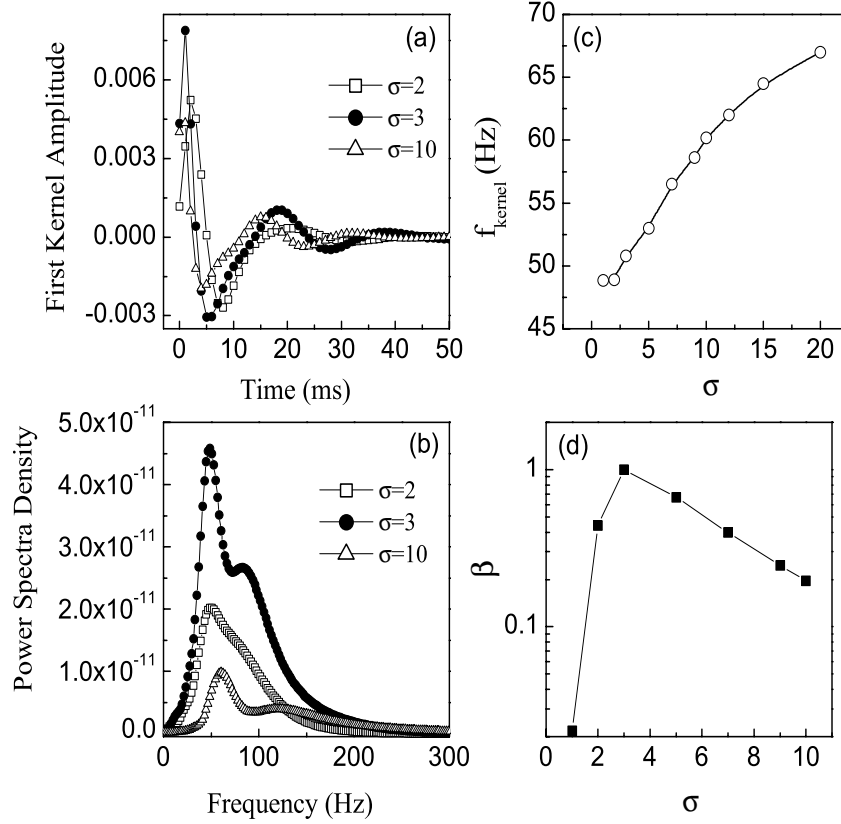


Fig. 2. (a) The first kernels of the HH neuron for noises with  $\sigma = 2, 3, 10$ , respectively. (b) The power spectra densities of the first kernels for noises with  $\sigma = 2, 3, 10$ , respectively. (c) The nature frequency of the first kernel versus  $\sigma$ . (d) The coherence of the first kernel versus  $\sigma$ .