A possible dynamical origin for contrast gain control

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Abstract

Analysis of the behavior of leaky integrate-and-fire (LIF) neuron as a function of input stimulus statistics shows that statistics-dependent gain control observed in a variety of neurons can be attributed to the intrinsic mechanism of spike generation. The average firing rate and the gain slope of the transfer function vary with the mean and the variance of the input stimulus, contributing to the tuning of the neuron to these stimulus statistics. Such tuning can be observed even in neuron with a fixed membrane time constant, as a direct consequence of the stochastic bifurcation dynamics of spike generation.

Key words: Adaptation, Transfer function, Gain control

1 Introduction

The spike-triggered average (STA), i.e., the first-order Wiener kernel, is a linear approximation to the transfer function or the receptive field of a spiking neuron. In numerous experiments, the STA kernel is found to change with the statistical properties of the input stimulus, such as its mean (for review, see [1]), the spatial and temporal contrast or variance (for review, see [2,3]).

Optimization methods have been developed to decompose linear kernel and the adaptive gain control mechanism [4]. The assumption there is that the linear kernel might have not changed, and the change in time constant of the LIF model can completely account for the change in the STA kernel. The basic fact about contrast gain control is that at low contrast, the STA kernel of a neuron is found to increase in amplitude and dilate in time [5-8]. This

makes functional sense, for at low contrast, it might be beneficial to integrate the input signals longer and increase the gain of the neuron. Yet, the exact mechanism underlying such a change is not known. Is this a network effect or a single cell effect? Does it involve changes in the intrinsic property of the neuron such as its membrane time constant or could it arise from the intrinsic mechanism of spike generation of a neuron with fixed parameters. Here, we will show theoretical analysis of a LIF model, even with a fixed set of parameters is sufficient produce the adaptive change in the STA kernel and contrast (variance) gain control due to the stochastic bifurcation dynamics of the neuron. Changes in membrane time constant in the LIF model is not a necessary condition for contrast gain control.

2   LIF model

To answer this question, we analyzed the mean activities of a LIF model as a function of stimulus statistics. The simple leaky integrate-and-fire (LIF) model [9] captures two key properties of an excitable neuron: an all-or-none firing behavior related to bifurcation, and a refractory period during which the neuron recovers its excitability. A LIF model is a RC circuit, given by,

$$dV/dt = -V/\tau_m + \mu + \sigma\xi(t), \text{ if } V(t) < V_{th}, \tag{1}$$

$$V(t^+) = V_0, \text{if } V(t^-) = V_{th}, \tag{2}$$

$\tau_m = RC$ is the time constant of the neuron with resistance R and capacitance C. Here, $V_0 = 0mV$, $V_{th} = 12mV$, $\tau_m = 10ms$, $R = 3M\Omega$, $C = 3.33nF$ and the absolute refractory period $\tau_{ref} = 4ms$. μ is the mean value of the Gaussian white noise. The constant stimulus threshold $\mu_c = V_{th}/R = 6\mu A/cm^2$.

Without loss of generality, the Gaussian white noise (GWN) $\mu + \sigma\xi(t)$ is used as input to the neuron. The statistical properties of the stimulus are characterized by its mean value μ and standard deviation σ. $\xi(t)$ is the GWN with zero mean $< \xi(t) >= 0$ and unit σ i.e. $< \xi(t_1)\xi(t_2) >= \delta(t_1 - t_2)$, where $< ... >$ represents the ensemble average over the noise distribution.

3   Results

The linear part of the model, Eq.(1) combines with nonlinear part Eq.(2) creates a saddle-node bifurcation point [10] at μ_c. When $\sigma = 0$, for only a constant sub-threshold stimulus ($\mu < \mu_c = V_{th}/R$), the membrane potential $V(t)$ will relax to a stable equilibrium, i.e., the resting state $\mu\tau$ [9]. When $\mu \geq \mu_c$, the neuron will generate a spike. Eq.(1) describes the evolution of a well-known stochastic diffusion process, also called Ornstein-Uhlenbeck process (OUP) for a GWN input with $\sigma \neq 0$. OUP is a type of transformed Brownian motion process. At time t, the probability distribution of a neuron's voltage

potential V is given by a probability density function (PDF), $P(V,t)$, that satisfies the Fokker-Planck equation [9]:

$$\frac{\partial P(V,t)}{\partial t} = \frac{1}{2}\sigma^2 \frac{\partial^2 P(V,t)}{\partial V^2} - (\mu - \frac{V}{\tau_m} \frac{\partial P(V,t)}{\partial V}),\tag{3}$$

with an absorbing boundary condition $P(V_{th},t) = 0$ [10] and satisfying the normalization condition,

$$\int\limits_{-\infty}^{V_{th}} P(V,t)dV = 1.\tag{4}$$

Note that Fokker-Planck equation has also been widely used in both single neuron and neuronal population analysis [9,11]. It has been recently used to derive the instantaneous input-output relationship of a single neuron [12] that matches well with the behavior of single neuron's input-output function. The analysis here however is focused on the relationship between statistical quantities, i.e. statistical mean firing rate and the mean and the variance of the input stimulus' statistics.

In stationary conditions, the flux of realizations crossing the threshold, or the mean firing spike rate r, satisfies the following relation:

$$r = \frac{1}{2}\sigma^2 \frac{\partial^2 P}{\partial V^2}\,|_{V_{th}} = \left[(\mu - \frac{V}{\tau_m})\frac{\partial P}{\partial V} - \frac{1}{2}\sigma^2 \frac{\partial^2 P}{\partial V^2}\right]_{V_0}.\tag{5}$$

Then the time-independent stationary firing rate r can be derived from the above equations as [9],

$$r = 1/\tau_{ref} + \sqrt{\pi}\tau_m \int\limits_a^b exp(x^2)[1 - erf(x)]dx,\tag{6}$$

with $a = \frac{\tau_m(\mu - V_{th}/R)}{\sigma\sqrt{\tau_m}}$, $b = \frac{\tau_m\mu}{\sigma\sqrt{\tau_m}}$, where r, τ_{ref} and τ_m are the mean firing rate, the absolute refractory period, neuronal time constant, respectively. $erf(x)$ is the error function. The analytical input-output relations of r as a function of σ and μ are plotted in Fig.1(a),(b). The firing rate r increases roughly sigmoidally with μ for small σ, but linearly with μ for larger σ (Fig.1a). The critical point where $r \geq 0$ shifts to the left with an increase in σ, implying the bifurcation point has moved to the left. In addition, the exact location of the bifurcation point becomes ambiguous for large σ. The noise induced shifting of the bifurcation point may be the critical factor underlying adaptation of the kernels of the neuron. Moreover, the $r - \mu$ curve has a steeper slope for smaller σ, indicating that the neuron is more sensitive to low stimulus than to a high contrast one, consistent with experimental observation on the change in kernel function.

For a fixed μ, the firing rate r increases with σ, and saturates at large σ, showing a tuning phenomenon (see Fig.1b) to σ as well as μ. This suggests that the stimulus variance can influence spiking behavior. To establish the relationship between the transfer function and the stimulus parameters analytically, we perform the following transformation. In the linear approximation, we can write the input signal $s(t)$ and output mean firing rate $r(t)$ of the neuron as [7,13]:

$$r(s_0 + \delta s) = r_0(s_0) + \delta s \int\limits_0^\infty h(\tau; s_0)d\tau, \tag{7}$$

where h is the first order kernel. The local slope of the input-output curve, which is called the static incremental sensitivity, is the integral of the first order kernel [7],

$$\rho = \frac{dr}{d\mu} = \int\limits_0^\infty h(\tau; \mu)d\tau. \tag{8}$$

Combining Eqs.(8) and (12), we can express the incremental sensitivity in terms of σ and μ, see Fig.1(c) and (d). interestingly, $\mu < \mu_c = 6$, the incremental sensitivity exhibits a global maximum as a function of standard deviation σ (see Fig.1c). This indicates that the transfer function is tuned to the stimulus' statistics. For $\mu \geq \mu_c = 6$, the incremental sensitivity decreases gradually as a function of σ. $\mu_c = 6$ serves as a boundary, which divides the system's motion into two different dynamical behaviors.

Fig.1(d) shows the incremental sensitivity (gain slope) as a function of μ for different σ. For very small μ, e.g., for $\sigma = 0.1$, the curve shows a very sharp peak near the constant stimulus bifurcation point, $\mu_c = 6$. As σ increases, the corresponding peak shifts to the left and becomes more ambiguous. This corresponds to the fact that for the bifurcation point of the system becomes less distinct and shifts to a smaller value at large σ, which is consistent with the findings in Fig.1a. The decrease of the threshold will make the neuron become more sensitive to input signal, while the ambiguity in the location of the threshold increases the stochasticity in generating the spikes. There exists an optimal value of σ, in which the increase in sensitivity and the increase in stochasticity will have an optimal tradeoff in maximizing the signal to noise ratio. The change of effective bifurcation point with σ is a cooperation between the stimulus statistics and the nonlinear threshold dynamics of the neuron. This cooperation drives the system to fire spikes more quasi-regularly, and produces the maximal gain in the transfer function curves, producing a tuning phenomenon to σ. This may be the origin of the changes in the amplitude and the power of the STA kernels observed in experiments. (Noted that the peak position and the shape of the curve will change when we change the value of the parameters, such as $\tau_m = RC$, v_{th}, but the basic phenomenon is same according to our analysis.)

The fact that incremental sensitivity is maximized by a certain σ is important. It demonstrates that the neuron system's transfer function is not invariant but adapt to encode the input signal effectively. This can be seen as a gain control mechanism, resulting from the cooperation between the stimulus statics and the bifurcation dynamics of the neuron.

4   Discussion

Neuronal adaptation to the statistics of the stimulus is a phenomenon often observed in experiments. The global statistics of the stimulus may modify the transfer function of the neuron for encoding the precise structure of the signal. From this perspective the transfer function or the receptive field is not be a property of the neuron itself, but an emergent property arise from the interaction between the neuron and its sensory environment [13,14]. In analyzing the steady state response to a long-running stimulus with stationary statistics in a LIF model, we found that when the statistical mean of the stimulus input is less than the stimulus threshold, the gain of the system varies as a function of σ, exhibiting a maximum at an intermediate σ, displaying a variance tuning gain control phenomenon. This gain control enhances the neuron's response to weak stimulus, particularly to those stimulus with the statistics that matched with the statistics that the neuron prefers. The design of a simple threshold in spike generation plays an instrumental role as the resonance between the statistics and the threshold dynamics determines the preferred class of stimuli of the neuron. The noise level in effect puts the system into different coherent states, changing the frequency tuning as well as the gain of a neuron's transfer function. This signal statistics dependent mechanism of gain control depends only on the nonlinear dynamics of spike generation, hence is likely the cause of the adaptation of the transfer function observed in neurophysiological experiments [1-3, 5-8]. Given the LIF neuron captures the basic characteristics of almost all excitable neurons, this intelligent adaptation behavior may be ubiquitous characteristics of all spiking neurons.

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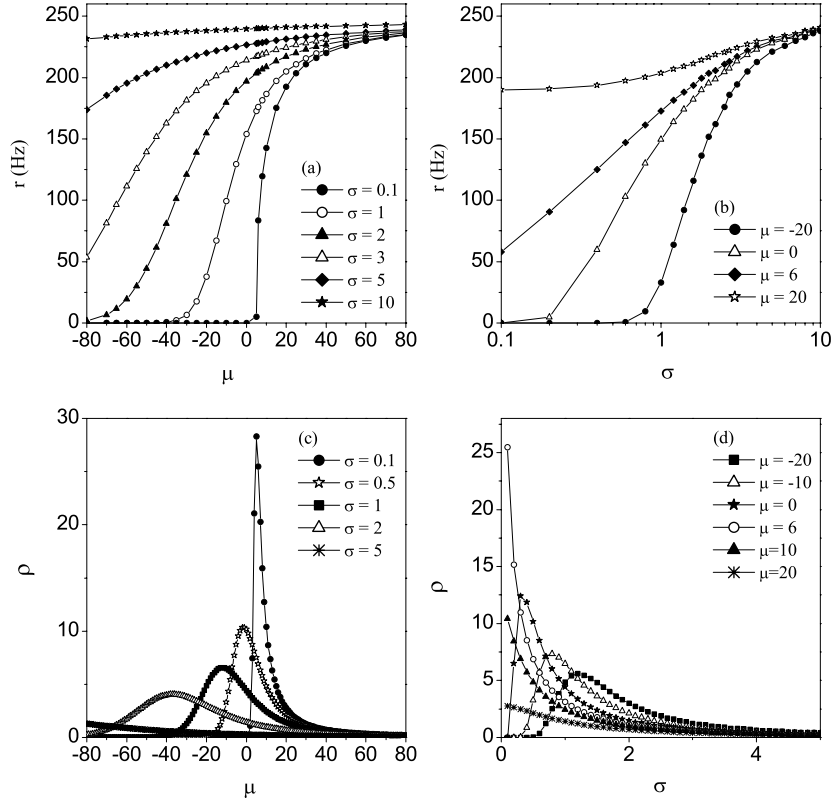[14] W. Bialek and A. Zee., Coding and computation with neural spike trains. *J.Stat.Phys.* 59 (1990) 103-115.

Fig. 1. (a) The mean firing rate as a function of σ for various μ. (b) The mean firing rate as a function of μ for various σ. (c) The static incremental sensitivity, ρ, represented by the integral of the first order kernel, as a function of σ for various μ. (d) The static incremental sensitivity, ρ, as a function of μ for various σ .