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Ideal observer of single neuron activity

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Abstract

We find that adding certain amounts of inhibitory inputs to a neuron improves its capability of accurately decoding the input information. The optimal ratio r of inhibitory to excitatory inputs for decoding the input information from an observation of the efferent interspike intervals is calculated. Surprisingly, the Fisher information could be zero for certain values of the ratio, seemingly implying that it is impossible to read out the encoded information at these values. By analyzing the maximum likelihood estimate of the input information, it is then concluded that the input information is, in fact, most easily estimated at the points where the Fisher information vanishes. © 2002 Published by Elsevier Science B.V.

Keywords: The Fisher information; Encoding; Decoding; Maximum likelihood estimate; The integrate-and-fire model

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1. Introduction

The brain is intricately wired in such a way that single neuron extensively receives both excitatory and inhibitory inputs. Traditionally, it is believed that all information is encoded in excitatory inputs and inhibitory inputs only play a passive role. The functional role of the inhibitory input is much less known than its counterpart, although in recent years there are a large body of literatures devoted to the issue, both theoretically and experimentally (see for example [11,5,14]).

Assume that neurons are ideal observer, in the sense that they are able to *optimally* decode information: they are capable of reading out the input information with the attainment of the the Cramér–Rao inequality bound (see for example [16, Chapter 2]). Suppose that $\hat{\lambda}(r)$ is an estimate of the input rate λ. We know from the Crámer–Rao

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inequality that

$$\langle(\hat{\lambda}(r) - \langle\hat{\lambda}(r)\rangle)^2\rangle \geqslant \frac{(1 + (\langle\hat{\lambda}(r)\rangle - \lambda)')^2}{I(\lambda, r)}$$

where $()'$ is the derivative with respect to λ and $I(\lambda, r)$ is the Fisher information about λ. Hence for any estimate $\hat{\lambda}(r)$ of λ, its accuracy (variance) is limited by the Crámer–Rao inequality bound:

$$\frac{(1 + (\langle\hat{\lambda}(r)\rangle - \lambda)')^2}{I(\lambda, r)}.$$

For an unbiased estimate of the stimulus, i.e. $\langle\hat{\lambda}(r)\rangle - \lambda = 0$, according to the Cramér–Rao inequality, we know that the decoding accuracy (variance) is simply limited by the inverse of the Fisher information. Hence, when the estimate of the stimulus is unbiased and attains the Cramér–Rao inequality bound which is proportional to the inverse of the Fisher information (ideal observer), we know that the larger the Fisher information is, the lower the variance of the estimate, i.e. the more accurate the estimate.

In the present paper we wish to answer the following questions. *What is the ratio between the inhibitory input and the excitatory input so that the neuron could optimally decode the input information?* By optimization, we mean at these points of the ratio where the Fisher information attains its global maximum. Remember that the ratio r between inhibitory inputs and excitatory inputs possibly ranges from zero (purely excitatory inputs) to one (exactly balanced inhibitory and excitatory inputs).

Using the Fisher information, we theoretically explore the issue that at which ratio r a neuron optimally reads out the input information. Although information theory has been successfully and extensively applied to neuroscience for the past decades, it is generally accepted that to calculate rigorously it is still very difficult and many approximated methods have been proposed [18]. Here we first develop a method to approximate the distribution density of the efferent interspike intervals of the integrate-and-fire (IF) model, which then enables us to *rigorously* carry out the calculation of the Fisher information of the IF model to an end [10,18]. Furthermore, we find that the Fisher information reaches its global maximum when there are certain amounts of inhibitory inputs, as in realistic neuron systems where certain amount of inhibitory inputs are always presented.

When the Fisher information is positive, our results above already tell us that adding inhibitory inputs could improve the neuronal capability of decoding the input information and so our aforementioned question is answered. Nevertheless, the other illuminating and surprising result found here is that the Fisher information could be zero at some values of the ratio $r > 0$ of the model. At these values of r where the Fisher information vanishes we call them singular points [17], theoretically it is impossible to estimate or decode the input information since the variance of any estimate is infinity. In statistical theory, it is conventionally assumed that the Fisher information is always greater than zero [16]. Our results in the present paper provide us with a concrete example which clearly shows that the Fisher information could be zero in physiologically plausible parameter regions. The result seems quite count-intuitive.

To gain a better understanding of the results above, we then employ the maximum likelihood estimate to decode the input rate. When the maximum likelihood estimate exists and is unique, it is asymptotically unbiased and attains the Crámer–Rao inequality bound [16, p. 444]. The maximum likelihood estimate usually gives two solutions of the input rate in the model we consider. Only when the Fisher information vanishes, there might be a unique solution. *This scenario enables us to propose a method to unambiguously read out the input information at singular points*. The conclusion above is totally different from the traditional view that *the larger the Fisher information is, the easier the estimate of the input information will be*. We refer the reader to [6] for details.

2. Models

For two given quantities $V_{\text{thre}} > V_{\text{rest}}$ and when $v_t < V_{\text{thre}}$, the membrane potential v_t satisfies the following dynamics:

$$\begin{aligned} dv_t &= -\frac{v_t - V_{\text{rest}}}{\gamma}\,dt + dI_{\text{syn}}(t), \\ v_0 &= V_{\text{rest}}. \end{aligned} \tag{1}$$

$I_{\text{syn}}(t)$ is the synaptic input given by

$$I_{\text{syn}}(t) = \mu t + \sigma B_t \tag{2}$$

with constants $\mu \geqslant 0$, $\sigma \geqslant 0$ and the standard Brownian motion B_t. Once v_t is greater than V_{thre}, it is reset to V_{rest}. More specifically, we define $\mu = a\lambda(1-r)$, $\sigma^2 = a^2\lambda(1+r)$ where a is the magnitude of excitatory postsynaptic potentials (EPSPs) and inhibitory postsynaptic potentials (IPSPs), $\lambda = \lambda_E N_E$ is the input rate with N_E being the number of active synapses and λ_E the firing rate of each synapse, r is the ratio between inhibitory inputs and excitatory inputs. In particular, when $r = 0$ the neuron exclusively receives excitatory inputs; when $r = 1$ the inhibitory and excitatory input is exactly balanced. Here for the simplicity of notation, we assume that the EPSP and IPSP size are equal. We refer the reader to [15] for a more complete and biologically oriented formulation of synaptic inputs. The model defined by Eq. (1) is called the integrate-and-fire model [2–4,7–9,12,13,15].

In the sequel, we define $T(\lambda, r, \gamma) = \inf\{t\colon v_t \geqslant V_{\text{thre}}\}$ as the firing time (interspike intervals) for $r \in [0, 1]$.

3. Fisher information and interspike interval distributions

Suppose that a function H has a unique minimum at x_0 and a stochastic differential equation is defined by $dx_t = -H'(x_t)\,dt + \sigma dB_t$. The function H is called the potential of the dynamics x_t. Then the mean of the first hitting time T of the process x_t from $V_{\text{thre}} > x_0$ is approximately given by

$$\langle T \rangle = \frac{\sqrt{\pi}\sigma}{[H'(V_{\text{thre}})]\sqrt{(H''(x_0))^{\delta}}} \exp\left(\frac{2[H(V_{\text{thre}}) - H(x_0)]}{\sigma^2}\right) \tag{3}$$

and furthermore,

$$T \sim p(t) = \frac{1}{\langle T\rangle}\exp\left(-\frac{t}{\langle T\rangle}\right), \tag{4}$$

where $\delta > 0$ is a parameter. We refer the reader to [1] for a detailed proof of Eqs. (3) and (4). Eq. (3) together with Eq. (4) tell us that T is exponentially distributed, i.e. the efferent spike trains of the IF model are a Poisson process with a rate $1/\langle T\rangle$. The dependence of $1/\langle T\rangle$ on the function H and model parameters V_{thre}, σ, etc. is described by Eq. (3). In the next section, we will apply Eqs. (3) and (4) to the IF model.

Suppose that $\langle T\rangle$ depends on a parameter λ. The Fisher information with respect to λ [16] is defined by

$$I(\lambda) = \frac{[(\langle T\rangle)']^2}{[\langle T\rangle]^2}, \tag{5}$$

where $(\langle T\rangle)'$ is the derivative with respect to the parameter λ.

In fact, from Eq. (5) *it is readily seen that the Fisher information is zero whenever* $(\langle T\rangle)'$ *is zero*. In other words, when $\langle T\rangle$ reaches its maximum or minimum points, the Fisher information vanishes. This also suggests that singular points are very common when we consider a nonlinear model.

We then apply the results above to the integrate-and-fire model and the Fisher information is exactly calculated. We conclude that adding certain amount of inhibitory inputs improve the performance of a neuron on decoding the input information. Nevertheless, with inhibitory inputs, the Fisher information is zero at some points of r, the ratio between inhibitory to excitatory inputs. Employing the maximum likelihood estimate we explore the underpinning mechanisms. We refer the reader to [6] for details.

4. Discussion

With a fixed excitatory input to a neuron, we ask how strong the inhibitory input to the neuron is required so that it could optimally decode the input information based upon an observation of the efferent spike trains. We find that usually certain amounts of inhibitory inputs are needed to ensure that the Fisher information attains its global maximum. Although it is well known that the inhibitory input is present in real neuron systems and a number of functional roles of it have been put forward in recent years [5], it seems that we are the first to address the issue in terms of the Fisher information. The conclusions obtained here are useful when we design spiking neural networks for engineering applications as well.

A somewhat surprising result is that the Fisher information is zero at some points of the ratio. Using the maximum likelihood estimate, we find that at singular points there is a unique solution. We then articulate that at the singular point, we could most easily estimate the input rate. In summary let us define

$$\mathcal{R}_0 = \{r\colon I(\lambda, r, \gamma) = 0, r \neq 0, 1\},$$

$$\mathcal{R}_m = \{r\colon I(\lambda, r, \gamma) \text{ attains its local maximum, } r \neq 0, 1\}.$$

Inhibitory inputs ensure that $\mathscr{R}_0 \cup \mathscr{R}_m$ is not an empty set. Parameters inside $\mathscr{R}_0$ are more easily to be estimated than those inside $\mathscr{R}_m$.

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