Neuronal Models With Masked Signals

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Abstract

Suppose that a neuron receive two signals masked by random noise. We ask after neuronal transformation whether the masked signals will become more separable or more mixed. We prove that with positive correlations between input singles, the output will be more separable. The critical value at which the total probability of misclassification is zero is analytically obtained.

Key words: The integrate-and-fire model, discrimination, masked signals, exactly balanced inputs

1 Introduction

It is a long standing issue in neuroscience to understand why a neuron in the cortex fires randomly. We all believe that a neuron performs certain computation tasks, but its exact computation objective is not clear. Hence it is difficult to unveil the functional meaning of noise in neuron computation. Many hypotheses have been put forward in the literature: sparse coding, optimization entropy etc. The shortcoming of these approaches is that, for example, even if a neuron does optimize its entropy when it computes, its functional (computational) meaning is still not clear. We all know optimization its entropy implies at the neuron will operate in a state of most randomness. What is the computational advantage of the neuron at such a state? Another approach to explore the functional meaning of random firing is the stochastic resonance[7]. As we have pointed out before[4], unfortunately in the stochastic resonance literature, most, if not all, publications treat the dynamics of a neuron as a perturbation of a deterministic system, rather than a genuine stochastic system where the noise strength is proportional to the signal. Therefore, the

results of stochastic resonance are interesting and relevant to some biological systems, but certainly not to neurons in the cortex.

In the present paper, we propose a novel approach: both on the setup of the problem and on theory, to tackle the issue. Suppose that a neuron receives two set of signals. Both of them are contaminated by noise, as shown in Fig. 1. After neuron transformations, we intend to know that the signals become more mixed or more separated. This is a typical decision theory. To discriminate between two input signals is of crucial importance for a nervous system.
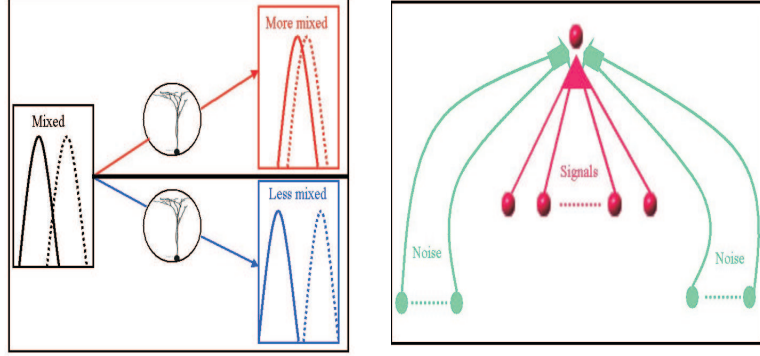

Fig. 1. Schematic plot of the issue we discussed. Right: after neuronal transformation mixed (masked) signals will become more separable or mixed? Left: input signals to a neuron model.

Due to the space limit we only present theoretical results here and refer the reader to our full paper for numerical results. We confine ourselves to the integrate-and-fire model[6]. More specifically we consider neuron models with a combination of (coherent) signal inputs and masking 'noise' inputs. We find that with a small fraction of signal inputs, the efferent spike trains of the model contain enough information to discriminate between different inputs (see below for more details).

We then explore the possible functional role of inhibitory inputs on discrimination tasks. A neuron extensively receives both excitatory and inhibitory inputs. It is clear that the excitatory input codes the input information: the stronger the stimuli are, the faster the neuron fires. Less is known about the inhibitory input, much as different, theoretical hypotheses have been put forward in the literature ranging from actually synchronizing the firing of a group of neurons [18], linearizing input-output relationship [5] and increasing neuron firing rates [4] etc. We find that adding certain amount of inhibitory inputs considerably enhances the neuronal discrimination capability if signal inputs are correlated.

The conclusion above seems quite counter intuitive. We all know that increasing inhibitory inputs to a single neuron model will result in an increase on

the variability of its efferent spike trains [4]. The histogram of firing rates will thus become more spread out and, as a consequence, the discrimination of different inputs becomes more difficult. However, this is not the case. To understand the mechanism underpinning the observed phenomena, we then go a step further to theoretically explore the model behaviour. Based upon the IF model, a theory on discrimination tasks is developed. We find that two key mechanisms for achieving a better separation of output signals, in comparison with input signals, are

(1) input signals are positively correlated and
(2) excitatory inputs and inhibitory inputs are exactly balanced.

Without correlations, no matter how strong the inhibitory inputs are, the separability of the output signals and the input signals is identical: if the input signals are separable, so are the output signals and vise versa. With correlations, the stronger the inhibitory inputs are, the better the separation.

Theoretically the critical value of the coherent inputs at which the output histograms are separable is exactly obtained (Theorem 2) for the case of correlated and exactly balanced inputs (the most interesting case). The results enable us to assess the dependence of our conclusions on different model parameters and input signals. It is illuminating to see that the critical value is independent of model parameters including the threshold, the decay time and the EPSP and IPSP magnitude.

All the aforementioned results are obtained for the IF without reversal potentials, we further examine our conclusions for the IF model with reversal potentials. Since adding reversal potentials to a model is equivalent to increasing its decay rate (depending on input signals), we would naturally expect that the model with reversal potentials will become more effectively to distinguish different inputs. The conclusion is numerically confirmed.

During the past few years, inhibitory inputs (see for example [9,10]) and correlated inputs (see for example [15,16]) are two topics widely investigated in neuroscience. It seems it is generally accepted that they play important roles in information processing in the brain. Our results here provide a convincing and direct evidence to show that they do improve the performance of a single neuron. Such results would also be valuable on practical applications of spiking neural networks [8].

2 The Models

We begin with by modelling the inputs. The first neuron model we use here is the classical integrate-and-fire model [2,3,17]. When the membrane potential V_t is below the threshold V_{thre}, it is given by

$$dV_t = -L(V_t - V_{rest})dt + dI_{syn}(t) \tag{1}$$

where L is the decay coefficient and the synaptic input is

$$I_{syn}(t) = a\sum_{i=1}^{p} E_i(t) - b\sum_{j=1}^{q} I_j(t)$$

with $E_i(t), I_i(t)$ as Poisson processes with rate $\lambda_{i,E}$ and $\lambda_{i,I}$ respectively, $a > 0, b > 0$ are magnitude of each EPSP and IPSP, p and q are the total number of active excitatory and inhibitory synapses. Once V_t crosses V_{thre} from below a spike is generated and V_t is reset to V_{rest}, the resting potential. This model is termed as the IF model. The interspike interval of efferent spikes is

$$T = \inf\{t : V_t \geq V_{thre}\}$$

We then turn to the situation that a small amount of correlations are added to the synaptic inputs which code coherently moving dots. For the simplicity of notation we assume that the correlation coefficient between ith excitatory (inhibitory) synapse and jth excitatory (inhibitory) synapse is $c > 0$. The correlation considered here reflects the correlation of activity of different synapses, as discussed and explored in [4,19].

More specifically, synaptic inputs take the following form ($p = q$)

$$
\begin{aligned}
I_{syn}(t) &= a\sum_{i=1}^{p} E_i(t) - b\sum_{j=1}^{p} I_j(t) \\
&= a\sum_{i=1}^{p_c} E_i(t) + a\sum_{i=p_c+1}^{p} E_i(t) - b\sum_{i=1}^{p_c} I_i(t) - b\sum_{i=p_c+1}^{p} I_i(t)
\end{aligned}
$$

where $E_i(t), i = 1, \cdots, p_c$ are correlated Poisson processes with an identical rate λ_1, $E_i(t)$ is Poisson processes with a firing rate λ_i independently and identically distributed random variables from $[0, 100], i = p_c + 1, \cdots, p$, $I_i(t), i = 1, \cdots, p$ have the same property as $E_i(t)$, but with a firing rate of $r\lambda_i$ for $r \in [0, 1]$ representing the ratio between inhibitory and excitatory inputs.

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In numerical simulations[6], we further use diffusion approximations to approximate synaptic inputs [17].

$$i_{syn}(t) = ap_c\lambda_1 t + a\sum_{i=p_c+1}^{p}\lambda_i t - bp_c r\lambda_1 t - b\sum_{i=p_c+1}^{p} r\lambda_i t$$
$$+\sqrt{(a^2+b^2 r)\lambda_1 p_c(1+c(p_c-1)) + (a^2+b^2 r)\sum_{i=p_c+1}^{p}\lambda_i} \cdot B_t$$

where B_t is the standard Brownian motion, $\lambda_1 = 25$ Hz or 75 Hz.

In the experiment of Newsome and his colleagues, the input image is a collection of moving dots, say p dots. p_c out of p dots move with an identical (coherent) direction, either upward or downward and $p - p_c$ dots move with random directions. In the literature [1], p_c/p is called coherence level. We assume that an MT neuron exclusively receives information of motion directions of an input image (moving dots), i.e. the cell receives p synaptic inputs, each represents the moving direction of a dot. Denote that $N_i(t), i = 1, \cdots, p$ as a Poisson process with a rate λ_i, where λ_i takes value from $[0, 100]$Hz, i.e. $(\lambda_i/100)2\pi$ is the motion direction of the i-th random moving dot (see [1]) and the motion of each dot is coded by the firing rate of a single synaptic (Poisson) input. Hence $\lambda_i = 25$ Hz represents the input of upward motion, or the ith dot moves upward; $\lambda_i = 75$ Hz represents the downward motion.
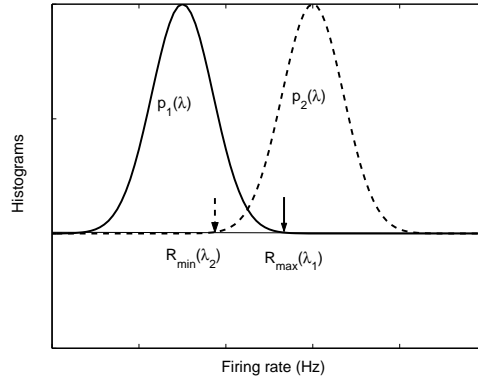
3   Theoretical Results

Fig. 2. A schematic plot of two output histograms, $R_{\min}(\lambda_2)$ and $R_{\max}(\lambda_1)$.

In this section we concentrate on theoretical results. Let Λ be the set of input frequency of the model, which is $[0, 100]$. It will become obvious that all theoretical results are independent of this choice. For a fixed $(\lambda_1 \in \Lambda, \lambda_2 \in \Lambda)$ with $\lambda_1 < \lambda_2$ we have corresponding two histograms $p_1(\lambda)$ and $p_2(\lambda)$ of output firing rates as shown in Fig. 2. Let

$$R_{\min}(\lambda_2) = \min\{\lambda : \ p_2(\lambda) > 0\}$$

and

$$R_{\max}(\lambda_1) = \max\{\lambda : \ p_1(\lambda) > 0\}$$

and denote

$$\alpha(\lambda_1, \lambda_2, c, r) = \{p_c : R_{\min}(\lambda_2) = R_{\max}(\lambda_1)\} \tag{2}$$

If it is clear from the context about the dependence of $\alpha(\lambda_1, \lambda_2, c, r)$ on c, r, we sometimes simply write $\alpha(\lambda_1, \lambda_2, c, r)$ as $\alpha(\lambda_1, \lambda_2)$. Hence for fixed (λ_1, λ_2), $\alpha(\lambda_1, \lambda_2)$ gives us the critical value of p_c: when $p_c > \alpha(\lambda_1, \lambda_2)$ the input patterns are perfectly separable in the sense that the the output firing rate histograms are not mixed with TPM=0; when $p_c < \alpha(\lambda_1, \lambda_2)$ the input patterns might not be separable with TPM> 0. Note that we consider the worst case here and in practical applications, the critical value of p_c at which the input patterns are perfectly separable, as found in the previous section, is in general lower than $\alpha(\lambda_1, \lambda_2, c, r)$. From now on, all figures are generated using the same parameters as in the previous section, if not specified otherwise.

Here is the basic idea of our approach. As pointed out before, it is not easy to directly calculate the distribution of $\langle T \rangle$. Nevertheless, the discrimination task is only involved in the most left point of $p_2(\lambda)$, i.e. $R_{\min}(\lambda_2)$, and the most right point of $p_1(\lambda)$, i.e. $R_{\max}(\lambda_1)$, provided that both p_2 and p_1 are positive only in a finite region. This is exactly the case for the model we considered here since neurons fire within a finite region.

Theorem 1 *Let $\lambda_{max} = max\{\lambda \in \Lambda\} = 100$ Hz, we have*

$$\alpha(\lambda_1, \lambda_2) = \left\{ p_c : \int_0^{V_{thre}L} g\left(\frac{y - a[p_c\lambda_1 + (p - p_c)\lambda_{\max}](1 - r)}{a\sqrt{[\lambda_1 p_c(1 + c(p_c - 1)) + (p - p_c)\lambda_{\max}](1 + r)}} \right) dy \right.$$
$$= \frac{\sqrt{[\lambda_1 p_c(1 + c(p_c - 1)) + (p - p_c)\lambda_{\max}]}}{\sqrt{[\lambda_2 p_c(1 + c(p_c - 1))]}} \tag{3}$$
$$\left. \cdot \int_0^{V_{thre}L} g\left(\frac{y - a(p_c\lambda_2)(1 - r)}{a\sqrt{[\lambda_2 p_c(1 + c(p_c - 1))](1 + r)}} \right) dy \right\}$$

Theorem 2 *When $c = 0$ we have*

$$\alpha(\lambda_1, \lambda_2, 0, r) = \frac{p\lambda_{\max}}{\lambda_2 - \lambda_1 + \lambda_{\max}}$$

independent of r. When $c > 0$ we have

$$\alpha(\lambda_1, \lambda_2, c, r_2) < \alpha(\lambda_1, \lambda_2, c, r_1) < \alpha(\lambda_1, \lambda_2, 0, r) \tag{4}$$

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where $1 \geq r_2 > r_1 > 0$ and furthermore

$$\alpha(\lambda_1, \lambda_2, c, 1) = \frac{\sqrt{[(\lambda_2 - \lambda_1)(1-c) + \lambda_{max}]^2 + 4p\lambda_{\max}c(\lambda_2 - \lambda_1)}}{2c(\lambda_2 - \lambda_1)} - \frac{(\lambda_2 - \lambda_1)(1-c) - \lambda_{\max}}{2c(\lambda_2 - \lambda_1)} \quad (5)$$

It is certainly interesting to compare the input histograms with output histograms. As before, let Λ be the set of input frequency of the model. For a fixed $(\lambda_1 \in \Lambda, \lambda_2 \in \Lambda)$ with $\lambda_1 < \lambda_2$ we have corresponding two histograms $p_1^i(\lambda)$ and $p_2^i(\lambda)$ of input firing rates, i.e. $p_1^i(\lambda)$ is the histogram of $p_c\lambda_1 + \sum_{i=1}^{p-p_c} \xi_i$ and $p_2^i(\lambda)$ is the histogram of $p_c\lambda_2 + \sum_{i=1}^{p-p_c} \xi_i$. Define

$$R_{\min}^i(\lambda_2) = \min\{\lambda, p_2^i(\lambda) > 0\}$$

and

$$R_{\max}^i(\lambda_1) = \max\{\lambda, p_1^i(\lambda) > 0\}$$

Then the relationship between $R_{\min}^i(\lambda_2) - R_{\max}^i(\lambda_1)$ and $R_{\min}(\lambda_2) - R_{\max}(\lambda_1)$ characterizes the input-output relationship of neuron signal transformations.

We first want to assess that whether $R_{\min}(\lambda_2) - R_{\max}(\lambda_1) > 0$ even when $R_{\min}^i(\lambda_2) - R_{\max}^i(\lambda_1) < 0$, i.e. the input signal is mixed, but the output signal is separated.

Theorem 3 *If $c > 0$ we have*

$$R_{\min}(\lambda_2) - R_{\max}(\lambda_1) > 0 \qquad when \qquad R_{\min}^i(\lambda_2) - R_{\max}^i(\lambda_1) = 0$$

Theorem 3 reveals one of the interesting properties of neuronal transformation. Under the assumption that input signals are correlated, the output signals will be separated even the input signals are mixed. As aforementioned, we believe that the fundamental requirement for a nervous system is to tell one signal from the other. Theorem 3 tells us that after the transformation of the IF neuron, the input signals could be more easily separable.

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