# Information transmission with renewal neurons

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### Introduction

The information theoretic approach to neuroscience has become increasingly popular, both in experimental [1, 2] and theoretical [3] studies. These studies generally make highly simplifying assumptions about the underlying noise in the system, either assuming Poissonian neurons, or rate based neurons with rate-independent Gaussian noise.

Information theory was developed to investigate the amount of information available in a system in the presence of noise [4]. Clearly the results of this theory are highly dependent on the noise model. When applying information theory to a biological system, it is therefore crucial have a noise model that is sufficiently close to the underlying noise of the system. In this study I will show that the highly simplified descriptions of the noise generally used in current models yield misleading results, and suggest a better model.

Many experimental studies show that, with repeated presentation of the same stimulus, the variance of the total number of spikes emitted varies approximately linearly with the mean spike count [5]. The correlation between consecutive interspike intervals (ISIs) is also nearly negligible. Poisson processes neatly capture these feature of the spike statistics, but they do not replicate the interspike interval (ISI) distributions of real neurons.

### Model

These features can be captured in a model neuron in which the ISIs are independently drawn from a rate dependent distribution $\rho_\nu(t)$, where $\rho_\nu$ satisfies

$$\rho_\nu(t) = \nu \rho(\nu t). \tag{1}$$

and $\nu$ is the firing rate. To ensure that the distribution yields the proper rate and is correctly normalized, one has to impose

$$\int \rho(x) dx = \int x \rho(x) dx = 1. \tag{2}$$

Under these constraints, $\rho$ can still be chosen so that the theoretical and experiment ISI distribution agree.

**Spike Counting versus Precise Timing**

For Poisson neurons one can show that an optimal estimate of the rate of the neuron can be obtained only using the total number of spikes that is fired. I will first show that this is generally not true for arbitrary renewal processes.

The maximum accuracy with which the rate can be estimated is determined using the Fisher information $I_F$. The standard deviation for the best estimator is given by $\sigma = 1/\sqrt{I_F}$.

To determine whether information about the rate is lost when one only uses the total number of spikes in a time window of duration $T$, rather than the timing of each spike, we calculate the Fisher information of the rate given the spike count, denote by $I_F(\nu|n)$, and compare this with the Fisher information given the timing of all spikes, $I_F(\nu|\{t_i\})$.

If $T$ is finite, $I_F(\nu|n)$ can, in general, not be calculated, since there is no simple expression for $p_{\nu,T}(n)$, the probability of having $n$ in a time window of duration $T$. This has to be determined numerically. On can however derive an analytical expression for $I_F(\nu|\{t_i\})$.

Here I will not derive this expression. I will just recapitulate some results. Only for a Poisson process no information is lost when the spike count is used to estimate the rate. For other Gamma processes a finite amount of information is lost, due to boundary effects at the beginning and end of the measuring interval. In all other renewal processes a finite *fraction* of the information is lost, even in the large $T$ limit.

In this $p_{\nu,T}(n)$ approaches a Gaussian distribution with mean $\nu T$ and variance $C_V^2 \nu T$. To leading order

$$I_F(\nu|n) = \frac{T}{C_V^2 \nu}. \tag{3}$$

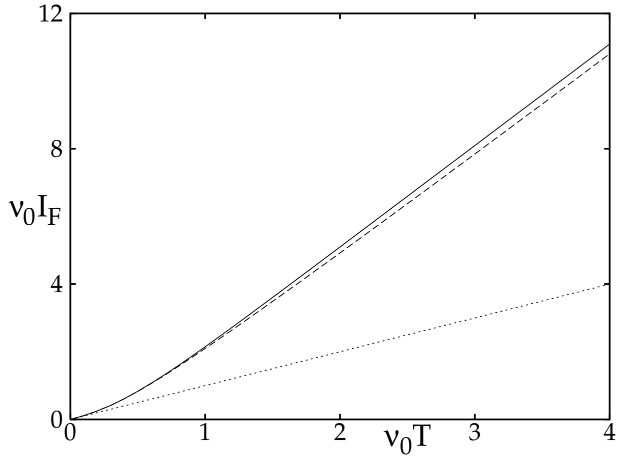


Figure 1: Fisher information $I_F$ of the rate function of time $T$ for a Poisson process (dotted line) and a Gamma Process with $C_V^2 = 1/3$ (solid line, using all spike times, dashed line, spike count only).

Therefore $\sigma_\nu = C_V \sqrt{\nu/T}$, and the estimate $\nu_{est} = n/T$ is an optimal estimator for the rate if only the spike count is used. For the Fisher information in the spike timing one can show that it approaches

$$I_F(\nu|\{t_i\}) = -\nu T \int_0^\infty \rho_\nu(t) \frac{\partial^2}{\partial \nu^2} \log(\rho_\nu(t)) dt \tag{4}$$

in the large $T$ limit.

Using these results, it is straightforward to show that for Gamma processes, $\rho_\nu(t) = (\alpha\nu t)^{\alpha-1} \exp(-\alpha\nu t)/\Gamma(\alpha)$, in the large $T$ limit

$$I_F(\nu|n) = I_F(\nu|\{t_i\}) = T/\alpha\nu \tag{5}$$

Hence for Gamma processes from which one measures for a relatively long time no information is about the rate is lost by only using the spike count. This is not true for other renewal process is used.

A better fit for the ISI distribution than a Gamma process is obtained if one uses an inverted Gaussian distribution for the ISIs,

$$\rho(x) = \frac{C_V^{-1}}{\sqrt{2\pi x^3}} e^{-(x-1)^2/2C_V^2 x}. \tag{6}$$

so that $I_F(\nu|\{t_i\})$ is given by

$$I_F(\nu|\{t_i\}) = \frac{T}{\nu}\left[\frac{1}{2} + \frac{1}{C_V^2}\right]. \tag{7}$$

Thus the ratio between $\sigma_\nu(n)$ and $\sigma_\nu(\{t_i\})$, the variance of the best estimator using the spike count and all spike times respectively, satisfies

$$\frac{\sigma_\nu(n)}{\sigma_\nu(\{t_i\})} = \sqrt{1 + \frac{1}{2C_V^2}}. \tag{8}$$

Therefore, with $C_V = 1$, the approximate value for many cortical cells, the best estimate for $\nu$ decreases by about 22% in accuracy if only the spike count is considered.

**Optimal Encoder**

Now consider the best way to *encode* a stimulus with renewal neurons. Consider a situation where a neuron is used to transmit a stimulus signal $s$. assume that $s$ is drawn from a distribution $P_s$. One can than ask what is the best way to encode this stimulus. This is determined by maximizing the mutual information $I_M$ between the stimulus and the neuron's output.

Most theoretical studies that use information theory, investigate models with rate-based neurons, in which the mean rate $R$ of the neuron satisfies $R = \nu(s) + \eta$, where the Gaussian noise variable $\eta$ satisfies $<\eta>= 0$ and $<\eta^2>= \sigma^2$ with small $\sigma$, and $\nu(s)$ is a non-decreasing function of $s$. Thus the distribution $P_\nu$ of $\nu$ satisfies $P_\nu(\nu)d\nu = P_s(s)ds$. Maximizing $I_M(R,s)$, under the constraint $\int RP_\nu(\nu) = \nu_0$, one then obtain for $P_\nu$

$$P_\nu(\nu) = e^{-\nu/\nu_0}/\nu_0. \tag{9}$$

Now consider the same situation with a renewal neuron. Here the rate of the neuron is $\nu(s)$ and one has to maximize the mutual information between the spike train and $s$. Using $P_\nu(\nu)d\nu = P_s(s)ds$ the mutual information $I_M$ between the spike train and the stimulus can be written as

$$\begin{aligned} I_M &= \sum_{n=0}^{\infty}\int_0^T dt_1 \int_{t_1}^T dt_2 \ldots \int_{t_{n-1}}^T dt_n \int_0^\infty d\nu P_\nu(\nu)\rho_\nu(n,t_1,\ldots,t_n) \times \\ &\quad \left[\log\left(\rho_\nu(n,t_1,\ldots,t_n)\right) - \log\left(\int d\nu' P_\nu(\nu')\rho_{\nu'}(n,t_1,\ldots,t_n)\right)\right] \end{aligned} \tag{10}$$

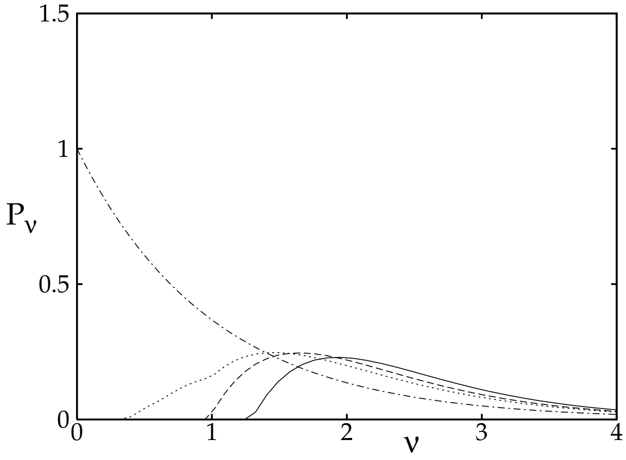


Figure 2: The rate distribution $P_\nu$ for $T = 0.5$ (solid line), $T = 1.0$ (dashed line) and $T = 2.0$ (dotted line). For comparison the rate-based solution is also shown (dashed dotted line).

where $\rho_\nu(n, t_1, \ldots, t_n)$ is the probability distribution of having $n$ spikes between times $t = 0$ and $t = T$, occurring at times $t = t_1 i, t_2 > t_1$, etc., for a rate $\nu$. If this is maximized one obtains an optimal rate distribution that depends on $T$. Figure 2 shows this distribution for a Poisson process with $\nu_0 = 1$. For $T$ of order 1 the Poisson neurons show a bimodal rate distribution. The distribution has two components, a delta function around $\nu = 0$ and a higher rate component that that extends from approximately $\nu = 1/T$. Qualitatively similar behavior is obtained for Gamma processes and presumably for other renewal processes.

Thus by accounting for the spike variability by describing the neurons as renewal processes one automatically obtains an optimal code in which the neuronal activity is sparse, with no output for weak stimuli and a vigorous response for stronger inputs.

**Discussion** If one describes the activity of these neurons by rate dependent renewal processes many of the features of the spike statistics can be captured with reasonable accuracy. It is hoped that using information theory on such models gives a good description of the bottle-necks in transmission that the cortex tries to overcome. I have shown that the properties of such models can differ significantly from those in simpler models with either Poisson or rate-based neurons. The fact that in general information is lost in renewal processes if only the total spike count is used to determine rate has important consequences for experimental data analysis. Experimental studies have tried to determine on what time scale the firing rate changes, some time after stimulus onset [1]. This question was addressed by binning the spikes in bins of varying width, and determining for which width information starts to be lost. An (unstated) assumption in this procedure is that, as long as the rate stays constant, no information is lost with binning. In general this is not true. Thus these studies only determine a lower limit on the time scale on which the rate varies.

Olshausen and Fields have used an optimal coding scheme for natural images In their model they used rate-based neurons, and had impose an extra constrained of a sparse representation to replicate the receptive field properties of V1 simple cells. For a renewal neuron that optimally encodes a one dimensional stimulus I found that the encoding is automatically sparse. This suggests that a model of V1 with renewal neuron that optimally encodes natural stimuli does not need an extra constraint of sparseness to mimic the properties of V1 cells. This would change our view of the role of a sparse representation.

## References


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