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Output Jitter Diverges To Infinity, Converges To Zero Or Remains Constant

Jianfeng Feng† Brunello Tirozzi‡ David Brown†
†Biomathematics Laboratory, The Babraham Institute,
Cambridge CB2 4AT, UK
‡Physics Department, Rome University "La Sapienza", Italy

Abstract. In the integrate-and-fire(I&F) model, the behaviour of output jitter (standard deviation of output inter-spike interval) is sensitive to the distribution of input timing. Output jitter can converge to zero, diverge to infinity or remain constant as the number of inputs increases indefinitely. The exponential distribution is the critical case: a faster decreasing rate in the tail of the distribution than the exponential distribution (e.g. Gaussian distribution) ensures convergence of output jitter; whereas a slower decreasing rate causes divergence of output jitter(e.g. Pareto distribution). Both numerical and rigorously theoretical results are presented. Exact formulae for output jitter are given.

1. Introduction

In the simplest spiking model of a single neuron, the I&F model[9], Marsalek, Koch and Maunsell [7] consider the relationship between the temporal variance of synaptic input and output spikes in individual neurons. Under the assumption that the arrival time of inputs is Gauss or uniform, that its standard deviation in time is σ_{in}(input jitter), and that N synapsesare sufficient to excite a pulse, the standard deviation in time σ_{out}(output jitter) of the intervals between spikes triggered in response to the input is computed. It is shown that $\sigma_{out} \ll \sigma_{in}$ which implies that, depending on other sources of temporal jitter, the temporal variability in spike times responding to an input converges toward zero. They then conclude that layers of pulse-generating neurons can preserve the temporal jitter of spike times and that this jitter will converge to zero and argue that their work provides an explanation of some puzzling observations regarding the preservation of highly accurate spike timing in cortical networks.

In the present paper we carry out a thorough theoretical study of the behaviour of output jitter in relation to the characteristics of the input. We find that there are three kinds of behaviour of σ_{out}/σ_{in}:

- one is the same as that discovered by Marsalek, Koch and Maunsell [7] and an exact relationship between input jitter and output jitter is given(normal distribution, uniform distribution, truncated exponential distribution);

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- another is that σ_{out}/σ_{in} diverges to infinity(Pareto distribution) which indicates that each consecutive layer of spiking neurons will introduce more and more temporal jitter, compromising the ability of higher level neurons to sharply respond to a sensory input and rendering synfire assemblies [1] difficult;
- the other is that σ_{out}/σ_{in} is a constant(exponential distribution).

The mean firing timing of output can either tend to infinity(normal distribution, exponential distribution) or become a constant(uniform distribution, truncated exponential distribution).

This is a short report of our full papers [2, 3] published elsewhere and in which the I&F model with leakage is also considered.

2. The I&F Models

We begin with the simplest model of a spiking cell. This I&F model consists of a capacitance, C, and a voltage threshold, V_{thre}. Each synaptic input dumps positive or negative charge onto the capacitance, de- or hyperpolarizing the membrane. Once V_{thre} is reached, an output spike is generated and the membrane potential is reset to V_{rest}. As in [7], for simplicity, the I&F unit is assumed to only receive inputs from N excitatory synaptic inputs of equal weight(EPSPs) a, each of which can be activated independently of the others. More precisely the voltage $V(t)$ of a neuron satisfies

$$C\dot{V} = I(t) \tag{1}$$

with $V(0) = V_{rest}$, $I(t) = \sum_{i=1}^{N} a\delta(t - \xi_i)$ and i.i.d. random sequence $\xi_i, i = 1, \cdots, N$. The solution of eqn (1) is

$$V(t) = V_{rest} + \frac{1}{C}\sum_{i=1}^{N} aI_{\{\xi_i < t\}}$$

which means when $t > \xi_i$ the neuron receives an EPSP from the i-th input, where I_A is the indicator function. A typical family of parameters which match to slice recordings of regular spiking cells are [8] $V_{rest} = -73.6 \pm 1.5mV$, $1/g_{leak} = 39.9 \pm 21.2M\Omega$, $C = \tau g_{leak}$, $\tau = 20.2 \pm 14.6msec$. The absolute spike threshold V_{thre} was set $20mV$ above V_{rest}, a is a constant related to the size of a single EPSP. Simultaneous intracellular recordings from pairs of pyramidal cells in cortical slice reveals a range of single-axon EPSPs from 0.05 mV to greater than 2 mV with a mean of 0.55 mV, which implies that to trigger a spike about $N \sim 40$ EPSPs are needed.

Define $\xi = \inf\{t : V(t) > V_{thre}\}$. Again as in [7] we suppose that when N(fixed but large) EPSPs arrive, an output spike is generated and so $\xi = \max\{\xi_1, \cdots, \xi_N\}$. The output jitter is given by $\sigma_{out}^2 = E(\xi - E\xi)^2$.

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3. Results

In Fig. 1 numerical examples are presented. We choose three distributions: the uniform distribution, exponential distribution and Pareto distribution with distribution function $F(x) = 1 - x^{-3}, x > 1$ in our numerical simulations. It is readily seen that the tail of Pareto distribution decreases towards zero (in power) more slowly than the exponential distribution (see Fig. 2 (a)); the tail of the uniform distribution, (0 as soon as $x > 1$) tends to zero faster than the exponential distribution. Our numerical examples (see Fig. 1) show that the output jitter of the exponential distribution remains a constant, the output jitter of the Pareto distribution goes to infinity and the output jitter of the uniform distribution tends to zero. On each integer point($N = 3, \cdots, 1000$)) we average 10 000 times to estimate output jitter.

Now we turn to theoretical estimation of output jitter. For most commonly encountered random variable sequences, the distributions of their extreme value(maximum of the sequence) take the following form[5]

$$P(a_N(\xi - b_N) \leq x) \to G(x) \tag{2}$$

for constants a_N, b_N depending on specific distributions. According to different forms of the distribution $G(x)$ they can be further divided into three types(Type I, Type II, and Type III).

Results of extreme values in statistics (i.e. eqn (2)) tell us that the output jitter takes the form

$$\sigma_{out} = \sqrt{\langle(\xi - b_N)^2\rangle - (\langle\xi\rangle - b_N)^2} = \frac{1}{a_N}\sqrt{\int x^2 dG(x) - (\int x dG(x))^2} \tag{3}$$

In particular the output jitter of Type I(Gauss or exponential) is thus

$$\sigma_{out} = \frac{1}{a_N}\sqrt{\int_{-\infty}^{\infty} x^2 \exp(-e^{-x})e^{-x}dx - (\int_{-\infty}^{\infty} x \exp(-e^{-x})e^{-x}dx)^2} = \frac{1.277}{a_N} \tag{4}$$

Under the condition that $\xi_i, i = 1, 2, \cdots$, are i.i.d. random variables and normally distributed we have the following equation

$$\sigma_{out} = \frac{1.277}{\sqrt{2\log N}}$$

The mean of ξ, the average time for the neuron to fire, is $b_N \sim \sqrt{2\log N}$. As observed by Maresalek, Koch and Maunsell [7] the firing time is delayed to b_N and the jitter becomes sharper. The relationship between input jitter and output jitter is

$$\frac{\sigma_{out}}{\sigma_{in}} = \frac{1.277}{\sqrt{2\log N}} \tag{5}$$

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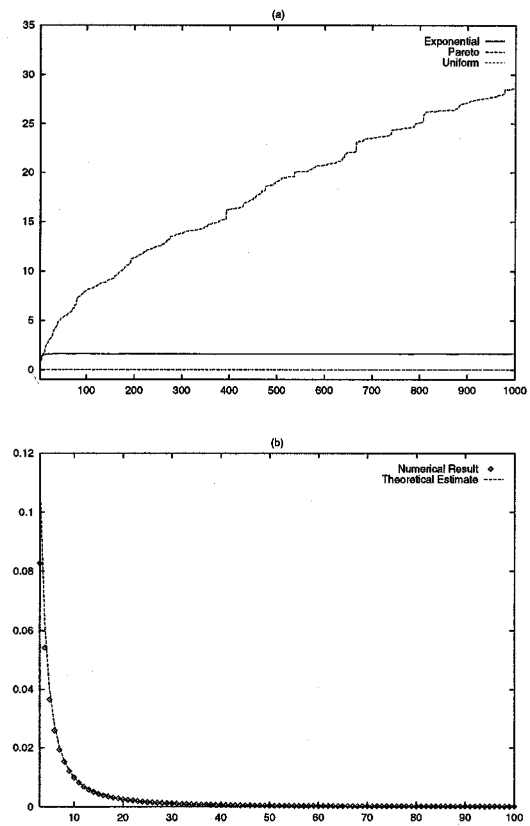

Figure 1: Square of Output jitter (σ^2_{out}) of different distributions vs number of inputs. The exponential distribution is the critical case. (a) Output jitter is sensitive to the input timing distribution. For the exponential distributed inputs, the output jitter is a constant, for the Pareto distribution, the output jitter diverges to infinity and for the uniform distribution the output jitter converges to zero(replotted in (b)). (b) Output jitter of the uniform distribution vs number of inputs. Numerical results and theoretical estimate(see eqn 6) fit perfectly well.

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The behaviour of output spike jitter of the uniform distribution is

$$\sigma_{out} = \frac{1}{N}\sqrt{\int_{-\infty}^{0} x^2 \exp(x)dx - (\int_{-\infty}^{0} x \exp(x)dx)^2} = \frac{1}{N} \tag{6}$$

which shrinks to zero faster than the case of Gaussian distribution. Different from the normal distribution case the firing time converges to $t = 1$. The relationship between input jitter and output jitter is (see [7])

$$\frac{\sigma_{out}}{\sigma_{in}} = \frac{2\sqrt{3}}{N} \tag{7}$$

The most different behaviour is observed for Type II random variables(Pareto). In this case we see that the variance tends to infinity given by

$$\sigma_{out} = N^{1/3}\sqrt{\int_{0}^{\infty} 3x^{-2} \exp(-x^{-3})dx - (\int_{0}^{\infty} 3x^{-3} \exp(-x^{-3})dx)^2}$$

but with

$$\sigma_{in} = \sqrt{7}/4$$

Let $c_1 = 4\sqrt{\int_0^\infty 3x^{-2} \exp(-x^{-3})dx - (\int_0^\infty 3x^{-3} \exp(-x^{-3})dx)^2}/\sqrt{7}$ the relationship between input jitter and output jitter is given by

$$\frac{\sigma_{out}}{\sigma_{in}} = N^{1/3}c_1$$

Now we are in the position to analyze the relationship between output jitter and input distribution. The exponential distribution is the critical case, for which output jitter is a constant: a faster decreasing distribution tail like the truncated exponential distribution ensures that the output jitter converges to zero; whereas a slower decay like the Pareto distribution causes the divergence of the output jitter(see Fig. 2). The critical case is when the timing of EPSPs received by a neuron is subjected to the exponential distribution: a perturbation of input distribution changes its ability to process information.

4. Discussion

In an attempt to fully understand the exact relationship between the output jitter and input jitter, we carry out an analytical analysis of the I&F model. Our results tell us that there are different behaviours for the output jitter. We summarize our results in table 1(see [3]). It is known that the magnitude of EPSPs is expected to vary greatly, depending on their location on the dendritic tree[4], quantal fluctuations and so on. Our results in this paper provide the whole spectrum of behaviours of output jitter which provides a justification for

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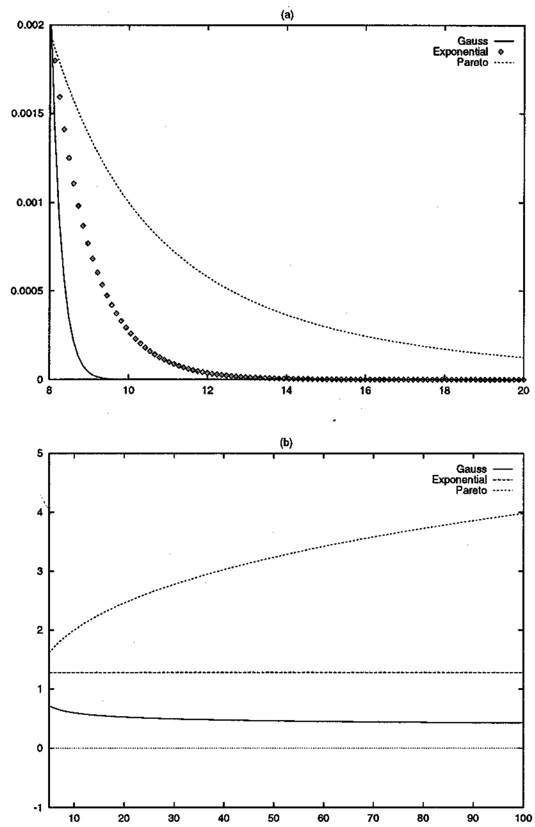

Figure 2: (a) Distribution tails of the Gaussian distribution, exponential distribution and Pareto distribution. (b) Output jitters of the Gaussian distribution, exponential distribution and Pareto distribution. The exponential distribution is the critical case(constant).

Distribution	**Output jitter/Input jitter**	**Mean firing time**
Gauss	converges towards zero	tends to infinity
Pareto	diverges to infinity	diverges to infinity[1]
Uniform	converges towards zero	tends to a constant
Exponential	becomes a constant	goes to infinity
Truncated Exponential	converges towards zero	tends to a constant

Table 1: A summary of results

further tests on assumptions of information processing in single neuron. The possibility that the brain might use higher order statistics has been pointed out from a theoretical view point [6]. Results in this paper indicate that neurons can be either a natural action amplifying or diminishing device of higher order statistics of input signals.

There remain many problems for further investigations. For example, it is interesting to consider the model with leakage in more detail, rather than in an average sense as we did in [3]. For the model itself, we have not included inhibitory postsynaptic potentials(IPSPs) and furthermore a spike is not generated when all available EPSPs are emitted, it is triggered when a fraction of them arrive. For a given distribution these considerations will change the behaviour of output jitter quantitatively, but not qualitatively, as shown in numerical simulations[7].

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