Behaviors of Spike Output Jitter in the Integrate-and-Fire Model

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We consider behaviors of output jitter in the simplest spiking model, the integrate-and-fire model. The full spectrum of behaviors is found: The output jitter is sensitive to the input distribution and can be a constant, diverge to infinity, or converge to zero. Exact formulas for the convergence or the divergence of output jitter are given. Our results suggest that the exponential distribution is the critical case: A faster rate of decrease in the distribution tail as compared to the exponential distribution tail ensures the convergence of output jitter, whereas slower decay in the distribution tail causes the divergence of output jitter. [S0031-9007(97)04695-4]

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In order to clarify basic issues in neuronal signal information processing [1–6], the simplest model of a spiking cell, the IF model, proposed by Lapicque in 1907 [7] is currently receiving renewed attention. Although the model has a certain number of risky simplifications, it characterizes many aspects of real neurons, and it serves as a rudimentary model to assess theoretical hypotheses on the role of randomness [8]. For an understanding of interspike interval (ISI) variability, Troyer and Miller [9], for example, discuss the dynamics of the model. They find that, when ISIs are dominated by post-spike recovery, $1/\sqrt{N}$ arguments [10] hold and spiking is regular; after the "memory" of the last spike becomes negligible, spike threshold crossing is caused by input variance around a steady state, and spiking is Poisson. With the same model, Marsalek, Koch, and Maunsell [11] consider the relationship between the time variance of a synaptic input and output spike in individual neurons. They assume that the arrival time of inputs is centered on $t = 0$ and that its standard deviation in time, henceforth called input jitter, is σ_{in}. Under the further assumption that N synapses excite a pulse generating neuron, the standard deviation in time of the spike triggered in response to the input, termed the output jitter σ_{out}, is computed. It is shown that $\sigma_{\text{out}} \ll \sigma_{\text{in}}$ which implies that, depending on other sources of temporal jitter, the temporal variability in spike times in response to an input converges towards a constant.

Most results on the IF model to date are based upon numerical simulations and such studies will certainly reveal some fundamental characteristics of the model and the neuron, but there is the possibility that it may misjudge the behaviors of the model. In the present paper we carry out a thoroughly theoretical study of the behavior of input jitter and spike output jitter. We find that there are three types of behavior of σ_{out}. One is the same as that discovered by Marsalek, Koch, and Maunsell [11] and an exact relation between input jitter and output jitter is given for inputs with a Gaussian distribution or a uniform interval distribution, respectively. The second is that σ_{out} diverges to infinity when inputs obey a Pareto interval 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 [12,13] difficult. The third is that σ_{out} remains constant for inputs with an exponential interval distribution. The mean firing time of output can either go to infinity for inputs with a Gaussian distribution or an exponential interval distribution or become a constant when inputs obey a uniform interval distribution.

The model without leakage.—We take into account the simplest model of a spiking cell—the IF model—with a capacitance C and a voltage threshold V_{thre}. Positive charges (EPSPs) or negative charges (IPSPs) are dumped onto the capacitance, depolarizing or hyperpolarizing the membrane. An output spike is produced if V_{thre} is reached and, after it, the membrane potential is reset to V_{rest}. As in [11], for simplicity the IF unit is assumed to receive only N excitatory synaptic inputs of equal weight (EPSPs) a. Each synaptic input 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 $V(0) = V_{\text{rest}}$, $I(t) = \sum_{i=1}^{N} a\delta(t - \xi_i)$ and independently identically distributed (i.i.d.) random sequence ξ_i, $i = 1, \ldots, N$. The solution of Eq. (1) is $V(t) = V_{\text{rest}} + \frac{1}{C}\sum_{i=1}^{N} aI_{\{\xi_i<t\}}$ which means that when $t = \xi_i$ the neuron receives an EPSP from the ith input. A typical family of parameters which matches slice recordings of regular spiking cells is [14] $V_{\text{rest}} = -73.6 \pm 1.5$ mV, $1/g_{\text{leak}} = 39.9 \pm 21.2$ MΩ, $C = \tau g_{\text{leak}}$, $\tau = 20.2 \pm 14.6$ ms. The absolute spike threshold V_{thre} was set 20 mV above V_{rest}, and a is a constant related to the size of a single EPSP. Recently [15], simultaneous intracellular recordings from pairs of pyramidal cells in a cortical slice revealed 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 we need about $N \sim 40$ EPSPs to trigger a spike.

Define $\xi = \inf\{t : V(t) > V_{\text{thre}}\}$. We first consider the case of N (fixed but large) EPSPs arriving at a neuron and generating an output spike, and so $\xi = \max\{\xi_1, \ldots, \xi_N\}$.

The output jitter is given by $\sigma_{\text{out}}^2 = \langle(\xi - \langle\xi\rangle)^2\rangle$. As it is always true that neurons can be excited by activation of a small subset of their synaptic inputs, it is then more interesting to consider the case of an output spike produced when only $N - k$ (for any given $k > 0$) EPSPs arrive. In this case—a neuron with redundant inputs—ξ is the kth largest of $\xi_i, i = 1, \ldots, N$. Similar results for $k > 0$ and $k = 0$ (the largest maximum) are obtained. We present a brief description of the results for $k > 0$ as well.

The model with leakage.—It is well known that depolarizations do not persist forever, but that perturbations of membrane voltage tend to decay toward the resting potential. The IF Model with leakage can be expressed in the following way [16]:

$$C\dot{V} = -g_{\text{leak}}V + I(t)\,. \tag{2}$$

The solution of Eq. (2) is

$$V(t) = V_{\text{rest}} + \frac{1}{C}\sum_{i=1}^{N}\exp[(\xi_i - t)/\tau]aI_{\{\xi_i<t\}}\,. \tag{3}$$

Note that, in this case, the actual number N of EPSPs which can cause a spike depends on each realization of $\xi_i, i = 1, 2, \ldots$, and cannot be determined in advance.

We discuss the case $k = 0$ first and then the case $k > 0$.

Behaviors of extreme values.—For most commonly encountered random variable sequences, the distribution of their extreme value (the maximum of the sequence) takes the following form [17]:

$$P\big(a_N(\xi - b_N) \le x\big) \to G(x) \tag{4}$$

for constants a_N, b_N. According to different forms of the distribution $G(x)$, the input distributions can be further divided into three types. Type-I input distributions: $G(x) = \exp(-e^{-x}), -\infty < x < \infty$. The Gaussian distribution is a special case with $a_N = (2\ln N)^{1/2}$ and $b_N = (2\ln N)^{1/2} - 1/2(2\ln N)^{-1/2}(\ln\ln N + \ln 4\pi)$. Type-II input distributions: $G(x) = 0$ if $x \le 0$ and $G(x) = \exp(-x^{-\alpha})$ for some $\alpha > 0$ if $x > 0$. The Pareto distribution with distribution function $F(x) = 1 - Kx^{-\alpha}, x \ge K^{1/\alpha}, K > 0, \alpha > 0$ is an example of this type of behavior with $a_N = (KN)^{-1/\alpha}, b_N = 0$. For simplicity of notation we take $K = 1$ in the following discussion. Type-III input distributions: $G(x) = \exp[-(-x)^\alpha]$ for some $\alpha > 0, x \le 0$, and $G(x) = 1$ if $x > 0$. The uniform distribution on $[0, 1]$ is of this type with $\alpha = 1$, $a_N = N$, and $b_N = 1$.

Various necessary and sufficient conditions are known—involving the "tail behavior" $1 - F(x)$ as x increases—for each type of limit, where $F(x)$ is the distribution function of ξ_1. Here is an example. Let $x_F = \sup\{x : F(x) < 1\}$. Then $\xi_i, i = 1, \ldots, N$ belongs to each of the three types if and only if the following applies: Type-I, there exists some strictly positive function $g(t)$ such that $\lim_{t\to x_F}[1 - F\big(t + xg(t)\big)]/[1 - F(t)] = e^{-x}$ for all x; type-II, $x_F = \infty$ and $\lim_{t\to\infty}[1 - F(tx)]/[1 - F(t)] = x^{-\alpha}, \alpha > 0$, for each $x > 0$; type-III, $x_F < \infty$ and $\lim_{h\to 0}[1 - F(x_F - xh)]/[1 - F(x_F - h)] = x^\alpha, \alpha > 0$, for each $x > 0$.

Behaviors of jitter without leakage.—Previous results tell us that the output jitter takes the form

$$\sigma_{\text{out}} = \sqrt{\langle(\xi - b_N)^2\rangle - (\langle\xi\rangle - b_N)^2}$$
$$= \sqrt{\int x^2 dG(x) - \left(\int x dG(x)\right)^2}\Big/a_N\,.$$

In particular the output jitter of type-I is thus

$$\sigma_{\text{out}} = \sqrt{\int_{-\infty}^{\infty} x^2\exp(-e^{-x})e^{-x}dx - \left(\int_{-\infty}^{\infty} x\exp(-e^{-x})e^{-x}dx\right)^2}\Big/a_N = 1.28/a_N\,.$$

Under the condition that $\xi_i, i = 1, 2, \ldots$, are i.i.d. random variables and normally distributed we have the following equation: $\sigma_{\text{out}} = 1.28/\sqrt{2\ln N}$. The mean of ξ, the average time for the neuron to fire is $b_N \sim \sqrt{2\ln N}$. The relation between the mean and jitter is plotted in Fig. 1. As observed by Marsalek, Koch, and Maunsell [11], the firing time is delayed to b_N and the jitter becomes sharper. The relation between input jitter and output jitter is $\sigma_{\text{out}}/\sigma_{\text{in}} = 1.28/\sqrt{2\ln N}$ as shown in the inset of Fig. 1. Note that the constant 1.28 is universal for type-I distributions.

The behavior of output spike jitter in the case of the uniform distribution is

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

which shrinks to zero faster than the case of Gaussian distribution. In contrast to the Gaussian distribution case (see Fig. 2), the firing time becomes exact at $t = 1$. The relation between input jitter and output jitter is (see [11]) $\sigma_{\text{out}}/\sigma_{\text{in}} = 2\sqrt{3}/N$.

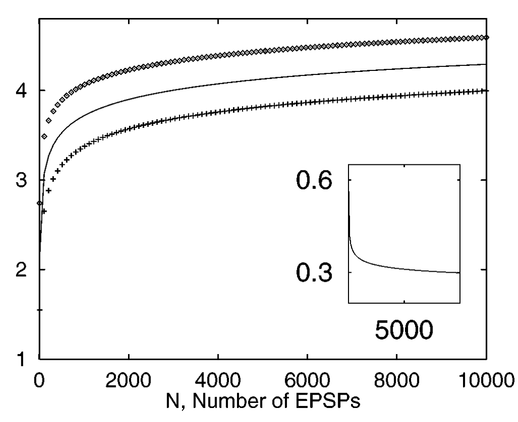

FIG. 1. Behavior of mean and jitter for inputs obeying a Gaussian distribution. The average firing time (line), mean + jitter ($\diamond$), and mean jitter ($+$) of an output spike vs N, the number of EPSPs received by the neuron. At $N = 100$ we find that mean = 2.366 and jitter = 0.422 [11]. Jitter tends to zero at a rate of $1/\sqrt{2\ln N}$, and is replotted in the inset.

In contrast to type-I and type-II behaviors, the variance for type-III behaviors tends to infinity with N; it is given by

$$\sigma_{\text{out}} = N^{1/3}\sqrt{\int_0^\infty 3x^{-2}\exp(-x^{-3})dx - \left(\int_0^\infty 3x^{-3}\exp(-x^{-3})dx\right)^2}$$

but with $\sigma_{\text{in}} = \sqrt{7}/4$. Let

$$c_1 = 4\sqrt{\int_0^\infty 3x^{-2}\exp(-x^{-3})dx - \left(\int_0^\infty 3x^{-3}\exp(-x^{-3})dx\right)^2}\bigg/\sqrt{7}\,.$$

The relation between input jitter and output jitter is given by (see Fig. 3) $\sigma_{\text{out}}/\sigma_{\text{in}} = N^{1/3}c_1$.

A comparison of type-I and type-II distributions may give us the following impression. The Gaussian distribution, with a density $\exp(-x^2/2)$, decreases to zero exponentially and so the maximum of a sequence goes to infinity very slowly and its variance tends toward zero, whereas the Pareto distribution, with a density $\alpha x^{-\alpha-1}$, goes to zero geometrically (slow) and hence the maximum will become more spread out. However, output jitter is capable of additional behaviors, as we will discover in the following.

From a neuronal system, it is generally believed that ξ_1 will be exponentially distributed and so its tail will go to zero exponentially. This suggests that we may expect a reduction in output jitter compared to input jitter. The reduction a_N depends on the concrete distribution and a universal constant 1.28. However, for the exponential distribution ξ_1 we have $a_N = 1, b_N = \ln N$, and thus the equation, $\sigma_{\text{out}}/\sigma_{\text{in}} = 1.28$, holds. The time taken to fire increases as $b_N = \ln N$, and the output jitter stays at a constant, output jitter is independent of N (see Figs. 3 and 4).

Now we are in a position to analyze the relationship between output jitter and input distribution. The exponential distribution is the critical case: A quickly decreasing distribution tail, such as the Gaussian distribution, ensures that the output jitter converges to zero, whereas a slow decay, such as the Pareto distribution, causes divergence of the output jitter (see Fig. 3). The critical case is when the timing of EPSPs received by a neuron is exponentially distributed; a perturbation of input distribution will change its ability to process information.

Behaviors of jitter with leakage.—Suppose that in the case of no leakage we need N_0 EPSPs to trigger a spike of a neuron. Then, if leakage is introduced, more EPSPs are needed to accumulate enough charge to produce a spike. Let us initially estimate how many EPSPs will be needed to trigger a spike in the case of leakage. We first confine ourselves to the Gaussian distribution.

From the discussion above, we see that $\xi \sim \sqrt{2\ln N}$. Taking the expectation of both sides of Eq. (3), we have $\langle V(\xi)\rangle = V_{\text{rest}} + \langle e^{\xi_1/\tau}\rangle aN/C\exp(\sqrt{2\ln N}/\tau)$. Let $(\langle V(t)\rangle - V_{\text{rest}})C/a = N_0$ then N_1 is given in $N_0 = \exp(1/2\tau^2)N_1/\exp(\sqrt{2\ln N_1}/\tau)$. On average, N_1 EPSPs can trigger a spike, and so σ_{out} takes a value at $N = N_1 > N_0$ in Fig. 1.

In the more general case where N_1 is a random number that depends on the realization of ξ_i, similar behavior to that discussed above is expected. This is partly confirmed by numerical simulations [11].

A neuron with redundant inputs.—As we mentioned above, results for the case $k > 0$ is similar to that for

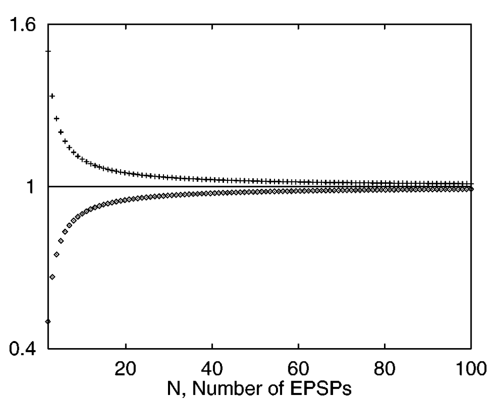

FIG. 2. Behavior of mean and output jitter for inputs obeying a uniform distribution. The average firing time (line), mean + jitter (+), and mean jitter (◇) of output spike vs N, the number of EPSPs received by the neuron, when the timing of input EPSPs is uniformly distributed.

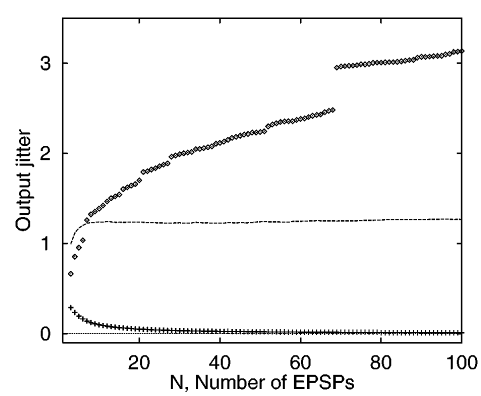

FIG. 3. The output jitter vs N, the number of EPSPs received by the neuron, when input timing is distributed as the Pareto distribution (◇) with $\alpha = 10/3$, the exponential distribution (line), and the uniform distribution (+). The exponential distribution is the critical case: If the tail of the input distribution decays to zero faster than the exponential (e.g., the uniform distribution), then output jitter converges to zero, whereas a slower decay (e.g., the Pareto distribution) causes divergence of output jitter.

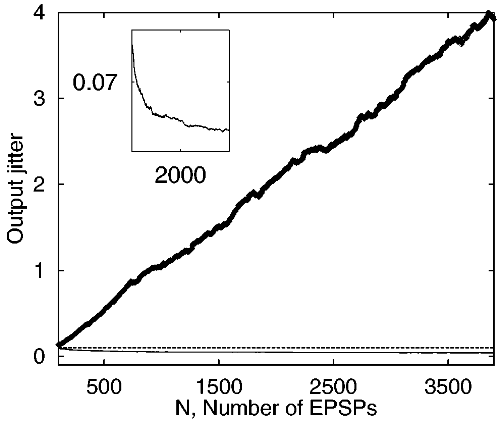

FIG. 4. Numerical results of output jitters of different distributions vs the number of total inputs N. We use $k = 100$, i.e., the number of EPSPs required to produce a spike is $N - 100$ and $\alpha = 1$ in the Pareto distribution. The Gaussian input distribution (line, replotted in the inset), Pareto input distribution (thick line), and exponential input distribution (dots) are shown.

$k = 0$. In fact, we have the following conclusion (see Theorem 2.2.2 in [17]):

$$P(a_N(\xi - b_N) \leq x) \rightarrow G(x) \sum_{s=0}^{k} \frac{(-\ln G(x))^s}{s!}, \quad (5)$$

where a_N, b_N, and function $G(x)$ are given before, dependent on the distribution, and ξ is the kth maximum of $\xi_1, \ldots, \xi_N$. Note that the behavior of output jitter (increasing, decreasing, or remaining a constant) is exclusively determined by the constant a_N, and we thus conclude that all of the results presented are qualitatively true for $k > 0$: A faster decrease in the tail than the exponential distribution will ensure the convergence of the output jitter; a slower decrease will cause the divergence of the output jitter, and the exponential distribution is the critical case. In Fig. 4 (see also Fig. 3) we present numerical results for $k = 100$ for the Gaussian distribution, Pareto distribution, and the exponential distribution.

In an attempt to fully understand the exact relationship between output jitter and input jitter, we carry out an analytical analysis on the IF model. Our results show that there are different behaviors for the output jitter. It is known that the magnitude of EPSPs is expected to vary greatly, depending on their location on the dendritic tree [18], quantal fluctuations, etc. Neuronal behaviors are greatly different as well. For example, in the vasopressin system, neurons fire without correlation among themselves, but in the oxytocin system neurons are strongly organized to fire together [19]. Our results in this paper encompass the whole spectrum of behaviors of output jitter and provide a justification for further tests on assumptions of information processing in a single neuron. The possibility that the brain might use higher order statistics has been pointed out from a theoretical viewpoint [20]. The results in this paper indicate that neurons can either amplify or diminish higher order statistics of input signals.

There remain many problems for further investigations. For example, it is interesting to consider in more detail the model with leakage, rather than in an average sense as we did here. For the model itself, we have not included inhibitory postsynaptic potentials. For a given distribution, these considerations will change the behaviors of output jitter quantitatively, but not qualitatively, as partly shown in numerical simulations [11].

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