

Rate and CV of a type I neuron driven by white noise

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Abstract

We study a white-noise driven spike generator that includes the one-dimensional normal form of a saddle-node bifurcation (characteristic feature of type I neurons). Scaling relations and exact expressions for rate and CV of the interspike interval are derived. We show that if the model is excitable (oscillatory), the CV is confined to the range $(1/\sqrt{3}, 1)$ (to $(0, 1/\sqrt{3})$). Inclusion of finite values for threshold and reset of the spike generator (quadratic integrate-and-fire model) result in even higher CV values. In accordance with previous numerical studies, these findings provide a possible explanation for the high variability found *in vivo* for cortical neurons.

Introduction

Hodgkin (1948) divided neurons into type I and type II according to their behavior at the transition from quiescent to repetitive firing. Type I neurons are characterized by arbitrarily low firing rates as the input current approaches its critical value, a behavior associated with a saddle-node bifurcation. In contrast, type II neurons undergo a sub-critical Hopf bifurcation accompanied by the onset of firing with a finite rate.

When these neurons are in the excitable regime (i.e. beyond their transition to repetitive firing) and stimulated by noise the higher order characteristics of the neuronal dynamics show also remarkable differences. As numerically shown by Gutkin and Ermentrout (1998), simplified (Theta neuron) as well as conductance-based (Morris-Lecar) models of type I show a high interspike interval (ISI) variability irrespective of the input parameters as long as the system is excitable. The high variability becomes apparent by a large coefficient of variation (CV, ratio of standard deviation of ISI to its mean) which is close to one. In contrast to this finding, systems with a Hopf bifurcation as for instance the FitzHugh-Nagumo model can show an arbitrary low variability in the excitable regime (Pikovsky and Kurths, 1997), i.e. a CV close to zero. Also, the leaky integrate-and-fire (LIF) neuron (which is neither type I nor type II) can be tuned to show low variability in the excitable regime (Lindner et al., 2002). The large ISI variability for type I neurons offers a possible explanation for the variability found in *in vivo* recordings of cortical cells (see, e.g., Softky and Koch, 1993).

Here we study a spike generator that is obtained from the normal form of a saddle-node bifurcation and, hence, represent the most simple dynamical description of a type I neuron (Gutkin and Ermentrout, 1998). If finite start and reset values are used, this model is also known as the quadratic integrate-and-fire model (see, e.g., Hansel and Mato, 2001, 2003).

In our model a variable $x(t)$ is started at a negative value x_- and evolves then according to

$$\dot{x} = \beta + x^2 + \sqrt{2D}\xi(t). \quad (1)$$

Here β is a constant input and the last term is white Gaussian noise of intensity D . As soon as $x(t)$ reaches a certain positive value x_+ a spike is generated at this instant and the variable $x(t)$ is reset to x_- . In this way a stochastic spike train is generated with interspike intervals that correspond to passages of $x(t)$ from x_- to x_+ . In the next section we use $x_{\pm} = \pm\infty$, while the effect of finite values is discussed at the end of the paper.

The system is oscillatory for $\beta > 0$ (repetitive firing even if $D = 0$) and excitable if $\beta < 0$ (no firing if $D = 0$). Here, we focus on the stationary spike rate r and the coefficient of variation CV

$$r(\beta, D) = \frac{1}{\langle T \rangle}, \quad CV(\beta, D) = \frac{\sqrt{\langle \Delta T^2 \rangle}}{\langle T \rangle} \quad (2)$$

where $\langle T \rangle$ and $\langle \Delta T^2 \rangle = \langle T^2 - \langle T \rangle^2 \rangle$ stand for the mean and variance of the ISI, respectively.

Analytical results

Using scaling arguments for the dynamics eq. (1), we can derive the following relations between the quantities of interest at different input parameters (Lindner et al., 2003)

$$r(\beta, D) = \sqrt{|\beta|} r(\pm 1, |\beta|^{-3/2} D) \quad (3)$$

$$CV(\beta, D) = CV(\pm 1, |\beta|^{-3/2} D) \quad (4)$$

where the sign on the right hand side coincides with that of β . These relations reveal that for an understanding of the dynamics, the study of the three distinct cases, $\beta = \pm 1$ or 0, suffices since all other cases can be mapped onto those. Furthermore, from eq. (4) it becomes evident that the range of possible CV values does not depend on the input parameter β as long as its sign is fixed. For instance, plotting the CV as a function of noise intensity D for different negative values of β amounts to a “stretching” in the argument of the CV curve.

The rate and CV are determined by the mean and variance of the ISI which are given by (Lindner et al., 2003)

$$\langle T \rangle = \left(\frac{9}{D} \right)^{1/3} \int_{-\infty}^{\infty} dx e^{-\alpha x - x^3} \int_{-\infty}^x dy e^{\alpha y + y^3} \quad (5)$$

$$\langle \Delta T^2 \rangle = \left(\frac{9}{D} \right)^{2/3} \int_{-\infty}^{\infty} dx e^{-\alpha x - x^3} \int_x^{\infty} dy e^{-\alpha y - y^3} \left[\int_{-\infty}^x dz e^{\alpha z + z^3} \right]^2 \quad (6)$$

$$\alpha = \left(\frac{3}{D^2} \right)^{1/3} \beta$$

Various approximations of these integral expressions can be found in (Lindner et al., 2003). For $\beta > 0$ (oscillatory regime) and at weak noise, for instance, one obtains

$$r \approx \sqrt{\beta}/\pi, \quad CV = \sqrt{\frac{3D}{4\pi}} \beta^{-3/4} \quad \text{for } \beta \gg D^{2/3}, \quad (7)$$

while for weak input ($|\beta| \ll 1$) (i.e., in either firing regimes) and strong noise we find

$$r \approx 0.201 D^{1/3} + 0.147 D^{-1/3} \beta, \quad CV \approx 0.578 + 0.250 \cdot D^{-2/3} \beta. \quad (8)$$

Finally, we would like to point out that the model may be easily transformed to the Theta neuron model (Gutkin and Ermentrout, 1998). For white-noise stimulation, however, caution must be used since the resulting stochastic differential equation involves multiplicative noise and is therefore ambiguous (the so called Ito-Stratonovich dilemma). As shown by Lindner et al. (2003), only the Stratonovich interpretation of the Theta model yields the same ISI statistics as the original model eq. (1). The Ito interpretation (Gutkin and Ermentrout, 1998) shows distinct features like a noise independent spike rate for $\beta = 1$ and a generally higher CV than the original dynamics (for details, see Lindner et al., 2003).

Results and conclusions

Rate and CV as functions of noise intensity and constant input are shown in Figs. 1 and 2, respectively. We have verified our analytical results by means of computer simulations (see Lindner et al., 2003, for details) and found excellent agreement.

The rate increases monotonously with growing noise for all β with differing behavior in the weak noise limit (i.e., saturation for $\beta > 0$ and exponential increase for $\beta < 0$). The CV shows a different behavior depending on the sign of β . For $\beta = -1$ it drops from the Poissonian limit ($CV = 1$ for $D \rightarrow 0$, rare spiking) to $1/\sqrt{3} \approx 0.58$, i.e. the same CV as obtained for $\beta = 0$. According to the scaling relation eq. (4), the CV for any negative value is restricted to this range ($1/\sqrt{3}, 1$) and it always decreases with increasing noise. In contrast, the CV for $\beta > 0$ always increases and is restricted to the range $(0, 1/\sqrt{3})$. Hence, in the oscillatory regime additional noise increases variability, while in the excitable regime, remarkably, variability is reduced by increasing the input noise.

Rate and CV as functions of the constant stimulus β are shown in Fig. 2. The rate

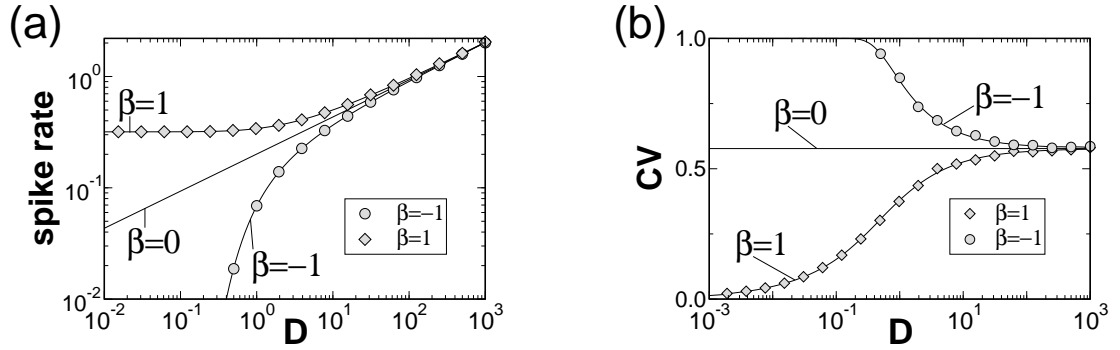


Figure 1: Spike rate (a) and CV (b) vs. noise intensity for three values of β as indicated. Quadrature results (thin lines) compared to simulations (symbols, see legend).

increases and the CV decreases monotonously with increasing input as can be expected. While for strong noise the CV shows a linear behavior (this was numerically found by Gutkin and Ermentrout (1998)), at small noise a remarkable threshold like behavior of the CV around $\beta = 0$ is obtained.

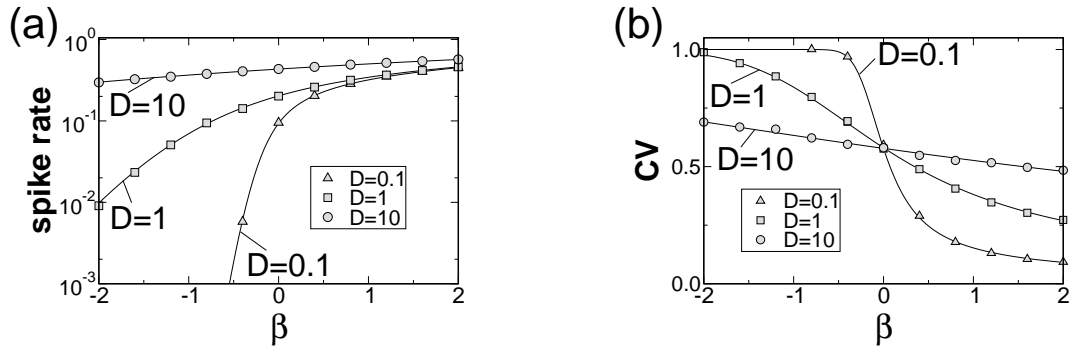


Figure 2: Spike rate (a) and CV (b) vs. constant input for three values of the noise intensity as indicated. Quadrature results (thin lines) compared to simulations (symbols, see legend).

To see which of these features remain when we use finite boundaries, we compare in Fig. 3 rate and CV as functions of the noise intensity for $x_{\pm} = \pm 2$ (for the quadrature formulas, see Lindner et al., 2003) to the above results for infinite boundaries. For finite values of x_{\pm} , we find both higher rates and larger CVs for all values of β and D . Differences to the infinite boundary case are most pronounced at strong noise for both rate and CV. The main qualitative changes are that the rate grows with a different exponent at high noise and that the CV grows for large noise unbounded for all values of β . In the excitable case, the CV passes through a minimum as a function of D , indicating an optimal noise intensity for most regular spiking right at the minimum of the CV. This effect is known as coherence resonance (Pikovsky and Kurths, 1997); it is clearly absent for infinite boundaries.

The question remains which kind of boundary conditions are more suitable to reproduce

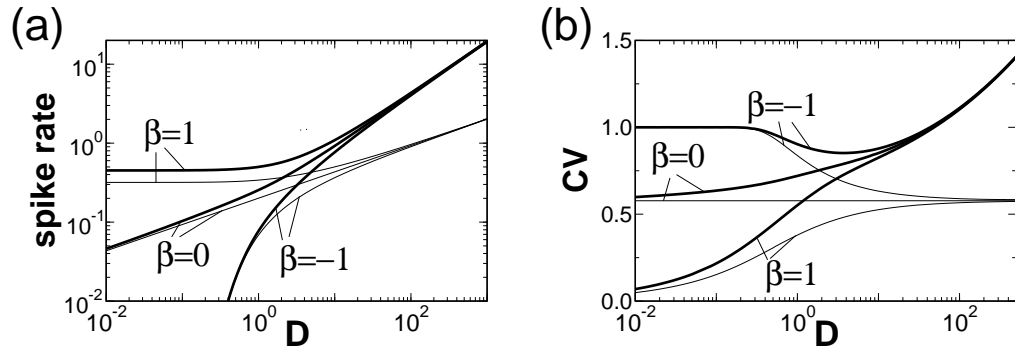


Figure 3: Rate (a) and CV (b) vs. noise intensity for three values of β as indicated. Thin (thick) lines are for $x_{\pm} = \pm\infty$ ($x_{\pm} = \pm 2$).

the behavior of more complex neuron models and, of course, of real type I neurons. Preliminary results on the white-noise driven Morris-Lecar model (not shown) indicate that the drop in CV versus noise intensity is present also in this model as long as the model generates spikes (for too strong input, the system's output is just noisy and does not show clear spiking). On the other hand, Hansel and Mato (2003) have fitted the parameters of a deterministic quadratic integrate-and-fire neuron (i.e. the above model with finite values of x_{\pm}) to the f-I curve of the multi-dimensional Wang-Buzsaki model. In this case, finite values of x_{\pm} are most likely also suitable and important in the case of noisy stimuli. Thus, the relevance of the finiteness of boundaries depends apparently on the model and, of course, on the range of noise intensities, considered.

The spike generator we have studied is simple to simulate on a computer, obeys scaling relations that allow for reduction of parameter redundancy, and helps to avoid the pitfalls associated with noisy stimulation in other models. The model offers an alternative to the more often used LIF model, especially for network simulations. It provides a more realistic description of type I neurons than the LIF model.

In accordance to the conclusions drawn by Gutkin and Ermentrout (1998), we may state that the high variability seen in *in vivo* spike trains of cortical neurons might be related to the simple facts, that these neurons are of type I and that they receive noise-like input, i.e. massive spike train input from other neurons. The results shown above indicate that for excitable type I neurons high CVs have to be expected in a fairly large range of stimulus parameters.

References

- B. S. Gutkin and G. B. Ermentrout. Dynamics of membrane excitability determine interspike interval variability: A link between spike generation mechanisms and cortical spike train statistics. *Neural Comp.*, 10:1047, 1998.

- D. Hansel and G. Mato. Existence and stability of persistent states in large neuronal networks. *Phys. Rev. Lett.*, 86:4175, 2001.
- D. Hansel and G. Mato. Asynchronous states and the emergence of synchrony in large networks of interacting excitatory and inhibitory neurons. *Neur. Comp.*, 15:1, 2003.
- A. Hodgkin. The local electric changes associated with repetitive action in a medullated axon. *J. Physiol.*, 107:165, 1948.
- B. Lindner, A. Longtin, and A. Bulsara. Analytic expressions for rate and CV of a type I neuron driven by white Gaussian noise. *Neural. Comp.*, 2003, accepted for publication.
- B. Lindner, L. Schimansky-Geier, and A. Longtin. Maximizing spike train coherence or incoherence in the leaky integrate-and-fire model. *Phys. Rev. E*, 66:031916, 2002.
- A. Pikovsky and J. Kurths. Coherence resonance in a noise-driven excitable system. *Phys. Rev. Lett.*, 78:775, 1997.
- W. R. Softky and C. Koch. The highly irregular firing of cortical cells is inconsistent with temporal integration of random EPSPs. *J. Neurosci.*, 13:334, 1993.