Analytic expressions for rate and CV of a type I neuron driven by white Gaussian noise

Benjamin Lindner, André Longtin

Department of Physics, University of Ottawa, 150 Louis Pasteur, Ottawa, Canada KIN 6N5

Adi Bulsara

SPAWAR Systems Center, Code D363 4950 Lassing Road, A341, San Diego, CA 92152-6147, USA

October 30, 2002

Abstract

We study the one-dimensional normal form of a saddle-node system under the influence of additive Gaussian white noise and a static "bias current" input parameter, a model that can be looked upon as the simplest version of a type I neuron with stochastic input. This is in contrast with the numerous studies devoted to the noise-driven leaky integrate-and-fire neuron. We focus on the firing rate and coefficient of variation (CV) of the interspike interval density, for which scaling relations with respect to the input parameter and noise intensity are derived. Quadrature formulae for rate and CV are numerically evaluated and compared to numerical simulations of the system and to various approximation formulae obtained in different limiting cases of the model. We also show that caution must be used to extend these results to the Θ neuron model with multiplicative Gaussian white noise. The correspondence between the first passage time statistics for the saddle-node model and the Θ neuron model is indeed obtained only in the Stratonovich interpretation of the stochastic Θ neuron model, while previous results have focused only on the Ito interpretation. The correct Stratonovich interpretation yields CV's which are still relatively high, although smaller than in the Ito interpretation; it also produces certain qualitative differences, especially at larger noise intensities. Our analysis provides useful relations for assessing the distance to threshold and the level of synaptic noise in real type I neurons from their firing statistics. Extensions and limitations of our analysis for the study of noise-induced firing in higher-dimensional type I neuronal models are also discussed.

1 Introduction

The transition from quiescent to periodic firing behavior as a bias current increases leads to significant changes in the dynamics of an excitable system. This transition is characterized by the behavior of the firing frequency across this transition. It is possible to divide neurons according to this behavior into type I and type II dynamics. Type I dynamics exhibit a continuous variation in firing frequency as a bias parameter (such as an input current) is increased. Dynamically, such a transition to repetitive firing is associated with a saddle-node bifurcation. At this bifurcation, a stable and an unstable fixed point coalesce and disappear, with a stable limit cycle taking their place. In the neural modeling context, the stable fixed point is associated with the resting potential, while the unstable fixed point (and associated unstable direction(s) or "unstable manifold" in phase space) is associated with the threshold of the cell. On the other hand, type II membranes exhibit a finite non-zero frequency as repetitive firing begins. Such transitions are associated with Hopf bifurcations. Some model and experimental systems can exhibit transitions to repetitive firing via one or the other of these mechanisms, depending on system parameters.

The relevance of noise-induced firing in Type I membranes is related to the problem of "large coefficients of variation (CVs)". There has been much effort to explain the observed variability in firing rates in various experimental preparations and, in fact, much attention devoted to the occurrence of interspike interval histograms (ISIH) with high CVs defined as the ratio of ISIH standard deviation to mean (Wilbur and Rinzel, 1983; Softky and Koch, 1993; Shadlen and Newsome, 1994; Bell et al., 1995; Troyer and Miller, 1997). Gutkin and Ermentrout (1998) have shown using numerical simulations that large CVs can be obtained from type I dynamics with noise. They used the so-called one-dimensional Θ neuron model (Ermentrout, 1996) and compared results from stochastic simulations of this model with those from simulations of the two-dimensional Morris-Lecar model (Morris and Lecar, 1981; Rinzel and Ermentrout, 1989) that has inspired the elaboration of the Θ neuron model. Other researchers (Gang et al., 1993; Rappel and Strogatz, 1994) have also explored the effect of noise on saddle-node bifurcations in a generic dynamical system, while Longtin (1997) has studied the effect of noise on this bifurcation in the Hindmarsh-Rose bursting neuron model and shown how the ISIH's and other firing statistics vary with noise strength.

The origin of the high variability seen in certain experiments and in noise-driven models of type I membranes can be understood from the seminal theoretical work of Sigeti and Horsthemke (1989). They studied how noise can move the state variable across the unstable fixed point associated with a saddle-node bifurcation. Their analysis was performed on a one-dimensional dynamical system known as "the normal form of the saddle-node bifurcation". This system describes the long-lived dynamics of a (possibly higher-dimensional) system in the vicinity of this bifurcation, all other aspects of the dynamics having decayed away to zero. More precisely, their analysis was confined to the bifurcation point itself, where the saddle and the node have coalesced into a semi-stable fixed point. In other words, they focused on the normal form $\dot{x} = \beta + x^2$ with $\beta = 0$; they also considered the Adler equation $\dot{\theta} = 1 - \cos\theta$, a variant of this normal form which agrees with it to second order. In neural terms, that means that the bias current is set right at rheobase.

The analysis of Sigeti and Horsthemke (1989) described how noise pushes solutions over the saddle-node point in terms of the two first moments of the first passage time density. While those theoretical/computational studies were carried out *at* the bifurcation, our present study aims to explore the vicinity of this bifurcation, thus making it relevant to a range of experimentally plausible parameters in real neurons. The goal of our paper is to provide analytical insight into how noise, e.g. of synaptic origin, affects the transition to repetitive firing in type I membranes. We give exact and simplified approximate expressions for the mean interspike interval (ISI), for the ISI standard deviation, and for coefficient of variation (CV) defined as the ratio of standard deviation to mean; these expressions are sought as a function of the input parameters.

The paper is organized as follows. In section 2.1 we introduce our basic spike generator model, discuss its relation to the Θ neuron, and derive some scaling relations for rate and CV with respect to the input parameters. In section 3, we give exact integral expressions for the first two central moments of the interspike interval and derive simple approximations for various limit cases. The results, i.e. rate and CV as functions of constant input and noise intensity are discussed in section 4; we also compare results from different versions of the stochastic Θ model and those from our basic model. In section 5 our results are summarized and briefly discussed in a more general context.

2 The model and its basic properties

2.1 Stochastic spike generator model for a type I neuron

Every system that is close to a saddle-node bifurcation will be dominated by the quasi one-dimensional passage through the region around its fixed point or points. This holds true also for many neurons known as type I neurons and in particular for neuron models like, for instance, the Morris-Lecar model (Morris and Lecar, 1981). The influence of noise on such a system is of eminent importance for issues like spike train variability or reliability of signal transmission through neurons. Moreover, the typical spike train input received by many higher order neurons can be also approximated by a simple noise process (diffusion approximation, see, for instance, Tuckwell (1988)). The simplest choice for a random input that still permits an extensive analytical treatment, is an uncorrelated noise, i.e. a white noise[1]. We allow for a finite mean value of the noise that can be looked upon as a separate constant input.

After the usual reduction procedure from the multidimensional dynamics (Ermentrout, 1996; Gutkin and Ermentrout, 1998; Hoppensteadt and Izhikevich, 1997)), the one-dimensional normal form driven by a white noise input reads

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

Here time is measured in the typical time scale of the model. The parameter D denotes the noise intensity and the Gaussian white noise $\xi(t)$ obeys the correlation function $\langle \xi(t)\xi(t+\tau)\rangle = \delta(\tau)$. The parameter β is another input parameter; it is constant, and can also be thought of as a static or very slowly varying signal. We note that this reduction has assumed a prior approximation regarding the nature of the noise. If the noise is meant as synaptic input to a cell, this input modifies the conductances which multiply the usual "battery" terms $(V_{rev} - V)$ in the Hodgkin-Huxley formalism. This gives rise to multiplicative noise, since the state variable (the voltage) multiplies the noise (the fluctuating conductance). The reduction is assumed to take place very near the bifurcation, so that the noise can be made additive (the voltage is set to a constant in the synaptic battery terms). It is not known generally what effect this approximation has on the dynamics, except right near the bifurcation.

We shall consider in this work a simple spike generator that produces spikes whenever the variable x reaches positive infinity. After occurrence of a spike the variable is reset to minus infinity. The interspike intervals (ISI) are thus independent realizations of the passage time of variable x from minus to plus infinity. The presence of the square term and the white Gaussian noise in eq. (1) ensures that this passage time is finite (in spite of the infinite threshold and reset values) for all values of the input parameter β.

A simulation of the system can, of course, be only performed for finite initial and threshold points x_- and x_+, respectively.

---

[1] The term "white" refers to the power spectrum of the noise, which is flat, i.e. contains all frequency (as white light contains all frequencies of the visible electromagnetic spectrum). A flat spectrum in turn implies a δ correlation of the noise (Risken, 1984, see, e.g.), i.e., the process has no correlations over a finite time at all.

Starting at $x = x_-$, the dynamics eq. (1) can be numerically integrated with a sufficiently small time step Δt

$$x(t + \Delta t) = x(t) + \beta \Delta t + \sqrt{2D\Delta t}\, \xi_t \tag{2}$$

where the ξ_t values are independent Gaussian random numbers with unit variance (Risken, 1984). The rule for reset and generation of the i-th firing time t_i is

$$x(t) = x_+ \;\rightarrow\; t_i \doteq t \;\text{ and }\; x(t^+) = x_-, \tag{3}$$

i.e., the firing (spike) times are defined as the instants at which x crosses x_+; the variable x is reset to x_- right after occurrence of a spike. The points x_- and x_+ should be chosen sufficiently large and the time step sufficiently small, such that a further increase or decrease, respectively, does not change the statistics of the measured quantities of interest significantly. Three example trajectories for different values of β are shown in Fig. 1.

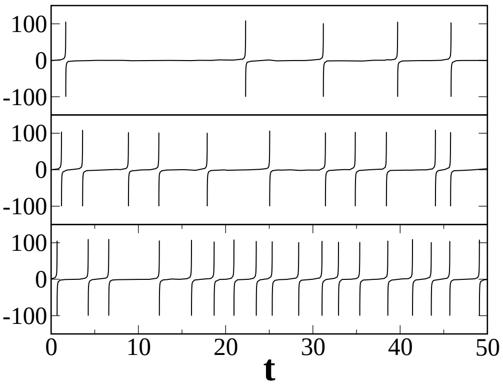

Figure 1: Trajectories of the model obtained by a simulation of the stochastic differential equation eq. (2) with threshold and reset parameters $x_\pm = \pm 100$, $D = 1$, and $\beta = -1, 0, 1$ (from top to bottom).

The sequence of firing times generated by the model $(\cdots, t_{i-1}, t_i, t_{i+1}, \cdots)$ describes a renewal point process (Cox, 1962), i.e. subsequent intervals between firing times, i.e. $T_i = t_i - t_{i-1}$ and $T_{i+1} = t_{i+1} - t_i$ are statistically independent (therefore, we omit in the following the index i). Here, we shall study two basic quantities, namely, the stationary firing rate and the coefficient of variation.

The stationary firing rate is given by the inverse of the mean interspike interval $\langle T \rangle$ (with the brackets standing for an ensemble average)

$$r(\beta, D) = \frac{1}{\langle T \rangle}. \tag{4}$$

The coefficient of variation (CV) is the relative standard deviation of the interspike interval, it is a second order quantity that measures the variability of spiking and is given by

$$CV(\beta, D) = \frac{\sqrt{\langle \Delta T^2 \rangle}}{\langle T \rangle} \tag{5}$$

where $\langle \Delta T^2 \rangle = \langle T^2 - \langle T \rangle^2 \rangle$ stands for the variance.

Before we proceed, we would like to give an instructive mechanical analogy for the dynamics eq. (1). We may associate a potential with eq. (1) the derivative of which yields the deterministic part of the r.h.s. (the constant has been chosen to be zero):

$$V(x) = -x^3/3 - \beta x \tag{6}$$

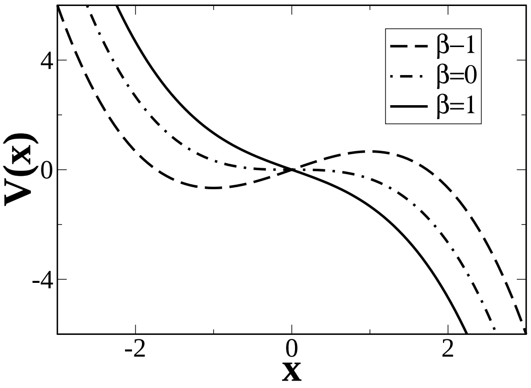

Figure 2: Potential associated with eq. (1) for different values of β.

Depending on the value of β this potential exhibits (1) for $\beta < 0$ a minimum and a maximum, (2) for $\beta = 0$ a saddle point or (3) for $\beta > 0$ no extrema at all, resulting in quite different statistics of the passage times and thus of the spike train. In Fig. 2 we show these different shapes that correspond to the following firing regimes of the type I neuron: (1) $\beta < 0$ noise-activated firing, i.e. the ISI is dominated by the noise-assisted escape from the potential minimum at $x = -\sqrt{\beta}$ over the potential barrier at $x = \sqrt{\beta}$, corresponding to the famous Kramers problem (Kramers, 1940); (2) $\beta = 0$ right at the saddle-node bifurcation, where no firing occurs without noise but the statistics of interspike intervals (first passage time of particle) is very particular (Sigeti and Horsthemke, 1989); and (3) $\beta > 0$ the oscillatory ("running") regime, where the associated potential has no minimum ("downhill motion").

2.2 Relation to the Θ neuron model

The dynamics eq. (1) can be transformed to the so-called Θ neuron model by the new variable (Ermentrout, 1996)

$$\Theta = 2 \arctan(x) \tag{7}$$

resulting in a stochastic differential equation with multiplicative white noise (i.e., the prefactor of the noise term depends on the state variable)

$$\dot{\Theta} = (1 - \cos(\Theta)) + (1 + \cos(\Theta))(\beta + \sqrt{2D}\xi(t)). \tag{8}$$

For this phase oscillator model, threshold and reset values are at finite values, namely at $-\pi$ and π, respectively. The Θ model with a white noise input current, however, must be treated with caution. A stochastic differential equation with multiplicative noise is not uniquely determined - it has to be supplemented by an interpretation (so called Ito-Stratonovich dilemma, see, e.g., Gardiner, 1985). This seems to be paradoxical since the original dynamics eq. (1), which is driven by additive noise, is non-ambiguous. The resolution of this paradox is given by the fact that the Stratonovich interpretation is the only interpretation that permits the usual transformation of variables (Gardiner, 1985, p. 100). Since eq. (8) results from such a transformation (namely, eq. (7)), we have to interpret eq. (8) in Stratonovich's sense. This is also plausible for another reason: driving currents in real neurons are never white noise but will have a finite correlation time; white noise that is thought of as the limit of a "colored" noise with negligible correlation time leads to the Stratonovich interpretation of a dynamics with multiplicative noise (see, e.g., Risken, 1984, chapter 3.3.3).

In the following, we wish to use a simple Euler integration algorithm (see, e.g., Risken, 1984) which assumes the Ito interpretation. Thus we must first express our Stratonovich stochastic differential equation into its corresponding Ito form. This correspondence preserves the physics of the problem. This Ito equivalent stochastic differential equation eq. (8) has an additional drift term $-D\sin(\Theta)(1 + \cos(\Theta))$. The integration scheme analog to eq. (2) then reads

$$\Theta(t + \Delta t) = \Theta(t) + [(1 - \cos(\Theta(t))) + (1 + \cos(\Theta(t))(\beta - D\sin(\Theta(t)))]\Delta t + \sqrt{2D\Delta t}(1 + \cos(\Theta(t))\xi_t \tag{9}$$

where ξ_t are again Gaussian distributed random numbers with unit variance. Note that in (Gutkin and Ermentrout, 1998) the drift term is apparently missing and hence the dynamics has been interpreted in the sense of Ito. This leads to the following integration scheme

$$\Theta(t + \Delta t) = \Theta(t) + [(1 - \cos(\Theta(t))) + \beta(1 + \cos(\Theta(t))]\Delta t + \sqrt{2D\Delta t}(1 + \cos(\Theta(t))\xi_i, \tag{10}$$

which is also the one that could be expected from a straightforward (although inexact) inclusion of Gaussian white noise in the Θ neuron dynamics.

Clearly, the difference between eq. (10) and eq. (9) vanishes in the weak noise limit since the additional Stratonovich drift in eq. (9) is proportional to noise intensity D. We will show that simulation of the Stratonovich version indeed yields the same statistics of interspike intervals as the original dynamics eq. (1) whereas the Ito interpretation eq. (10) of the Θ neuron model which was used by Gutkin and Ermentrout (1998) leads to different results in particular at moderate to large noise intensity.

2.3 Scaling relations

We return now to the original model eq. (1). Therein we have two free parameters β and D. If we properly rescale x and t it is possible to obtain the same nonlinearities as in eq. (1), except for a new combination of the parameters β and D (threshold and reset values do not change in any case since they remain at plus and minus infinity, respectively). This gives us scaling relations for rate and CV with respect to the input parameters D and β. Moreover, we can eliminate one of the parameters, although we still have to distinguish between the three different firing regimes. For $\beta = 0$ which has been treated by Sigeti (1988), i.e., for

$$\dot{x} = x^2 + \sqrt{2D}\xi(t). \tag{11}$$

we choose the new variable and time as

$$y = x/a, \quad \tilde{t} = at \tag{12}$$

with a arbitrary but positive. This leads to[2]

$$\dot{y} = y^2 + \sqrt{2D/a^3}\xi(\tilde{t}). \tag{13}$$

With $a = D^{1/3}$ we can eliminate the noise intensity (Sigeti, 1988). Of course, the moments of ISI will be still rescaled according to eq. (12), however, the CV which is the *relative* standard deviation of the ISI, remains the same for all values of D

$$CV(\beta = 0, D) = CV(\beta = 0, D/a^3) \;\; \Rightarrow \;\; CV(\beta = 0, D_1) = CV(\beta = 0, D_2). \tag{14}$$

---

[2] Note that $\xi(t/a) = \sqrt{a}\xi(t)$ which can be seen by considering the correlation function: $\langle \xi(t/a)\xi(t'/a)\rangle = \delta([t - t']/a) = a\delta(t - t') = \langle \sqrt{a}\xi(t)\sqrt{a}\xi(t')\rangle$.

The elimination of noise intensity is also possible for $\beta \neq 0$. (This fact was also suggested independently by E. Izhikevich, personal communication). With respect to the approximations we shall derive, it is, however, more convenient to set $a = \sqrt{|\beta|}$. This yields the following dynamics

$$\dot{y} = \frac{\beta}{|\beta|} + y^2 + \sqrt{2D/|\beta|^{3/2}}\xi(\tilde{t}) = \begin{cases} +1 + y^2 + \sqrt{2D/|\beta|^{3/2}}\xi(\tilde{t}) & , \quad \beta > 0 \\ -1 + y^2 + \sqrt{2D/|\beta|^{3/2}}\xi(\tilde{t}) & , \quad \beta < 0 \end{cases} \tag{15}$$

i.e., we obtain the same dynamics with rescaled noise intensity and an input which is either plus or minus one. Thus, to understand the dynamics of the model, it suffices to consider the three cases where $\beta = \pm 1$ or 0.

Obviously, the new time scale rescales also the moments of the passage time by $\langle \tilde{T}^n \rangle = |\beta|^{\frac{n}{2}} \langle T^n \rangle$. Using this and the above relations, we find the following scaling relations for rate and CV ($\beta \neq 0$)

$$r(\beta, D) = \sqrt{|\beta|} r(\pm 1, |\beta|^{-3/2} D) \tag{16}$$

$$\langle \Delta T^2 \rangle(\beta, D) = |\beta|^{-1} \langle \Delta T^2 \rangle(\pm 1, |\beta|^{-3/2} D) \tag{17}$$

$$CV(\beta, D) = CV(\pm 1, |\beta|^{-3/2} D) \tag{18}$$

where the sign on the right hand side coincides with that of β.

From the first equation it can be inferred that for positive input ($\beta > 0$) and vanishing noise the rate scales like $r \sim \sqrt{\beta}$. In the presence of noise an increase in β diminishes the effective noise intensity.

The third equation is even more important. The range of possible CV's does not depend on β as long as its sign is fixed. Plotting the CV as a function of noise intensity results always in the same curve apart from a stretching by $|\beta|^{-3/2}$ in the argument. Furthermore, we see from eq. (18) that the CV in the large noise limit corresponds to the CV at finite D but vanishing input, i.e.

$$\begin{aligned} \lim_{D \to \infty} CV(\beta, D) &= \lim_{D \to \infty} CV(\pm 1, |\beta|^{-3/2} D) \\ &= \lim_{\beta \to 0} CV(\pm 1, |\beta|^{-3/2} D) = CV(0, D) \end{aligned} \tag{19}$$

By similar arguments, asymptotic scaling relations for strong noise (or equivalently weak input β) can be derived, given by

$$r(\pm 1, D) \approx A_1 D^{1/3} + B_1 \beta D^{-1/3} , \quad D \to \infty \tag{20}$$

$$CV(\pm 1, D) \approx A_2 + B_2 \beta D^{-2/3} , \quad D \to \infty. \tag{21}$$

In these formulas A_1, A_2, B_1 and B_2 denote numerical constants, that will be given below. Small noise intensity will require higher order terms in β (rate and CV in eq. 20 and eq. (21) diverge for $D \to 0$ what is not expected from the biological point of view) and thus the linearity with respect to input depends strongly on the noise level.

3 Exact and approximate expressions for spike rate and CV

3.1 Exact formulae for the first two central moments of the interspike interval distribution

The hierarchy of quadrature expressions for the moments of the passage time problem in an arbitrary potential are known for a long time (Pontryagin et al., 1933). The standard expressions for mean and variance of the first passage time Gardiner (1985) can be somewhat simplified (Lindner, 2002) yielding

$$\langle T \rangle = \left(\frac{9}{D}\right)^{1/3} \int_{-\infty}^{\infty} dx\, e^{-\alpha x - x^3} \int_{-\infty}^{x} dy\, e^{\alpha y + y^3} \tag{22}$$

$$\langle \Delta T^2 \rangle = \left(\frac{9}{D}\right)^{2/3} \int_{-\infty}^{\infty} dx\, e^{-\alpha x - x^3} \int_{x}^{\infty} dy\, e^{-\alpha y - y^3} \left[\int_{-\infty}^{x} dz\, e^{\alpha z + z^3}\right]^2 \tag{23}$$

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

These integrals may be evaluated numerically by standard procedures[3]. There are, however, a number of cases where the integrals can be carried out analytically which gives us some additional control over the accuracy of our numerical integration.

First of all, the mean first passage time, i.e. the mean ISI can be expressed by an infinite sum (Colet et al., 1989) as follows[4]

$$\langle T \rangle = \left(\frac{1}{3D}\right)^{1/3} \sqrt{\frac{\pi}{3}} \sum_{n=0}^{\infty} (-1)^n \frac{2^{(2n+1)/3}}{n!} \Gamma\left(\frac{2n+1}{6}\right) \left(\beta \sqrt[3]{\frac{3}{D^2}}\right)^n \tag{24}$$

Here $\Gamma(\cdot)$ denotes the Gamma function (Abramowitz and Stegun, 1970). It should be mentioned that this formula is especially useful for large noise intensities, whereas in the weak noise limit many terms are required to achieve convergence.

---

[3] The infinite integration boundaries have to replaced by finite ones that are chosen sufficiently large such that a further increase does not change the results to within the desired accuracy.

[4] Note that there are write errors in eqs. (3.6) and (3.7) of (Colet et al., 1989)

Furthermore, for $\beta = 0$ both mean and variance of the ISI can be calculated analytically (see Sigeti, 1988; Sigeti and Horsthemke, 1989). The result is nice and simple and reads

$$\langle T(\beta = 0)\rangle = [\Gamma(1/3)]^2 \left(\frac{1}{3D}\right)^{1/3}. \tag{25}$$

$$\langle \Delta T^2(\beta = 0)\rangle = \frac{1}{3}[\Gamma(1/3)]^4 \left(\frac{1}{3D}\right)^{2/3} = \frac{1}{3}\langle T\rangle^2. \tag{26}$$

The latter equality in eq. (26) implies that, for $\beta = 0$, the ratio of variance and mean square of the ISI (and hence also the CV) is a constant and independent of noise intensity in accordance with eq. (14). Rate and CV of the type I neuron read in this case

$$r(\beta = 0, D) = \frac{1}{[\Gamma(1/3)]^2}(3D)^{1/3} = 0.201 D^{1/3}, \qquad CV(\beta = 0, D) = 1/\sqrt{3} \tag{27}$$

Since the integral and sum formulas above are not very transparent we shall derive some simplifications that apply in different limit cases: 1) weak noise and positive input ($\beta > 0$, oscillatory regime), i.e. limit cycle dynamics weakly perturbed by noise, 2) weak noise and negative input ($\beta < 0$, excitable regime), i.e. excitations are rare and an escape rate description applies, and 3) weak input or strong noise limit.

3.2 Rate and CV in the oscillatory regime at weak noise

For a strictly monotonously decreasing potential (as in our problem for $\beta > 0$), general approximation formulae for the mean and the variance of the passage time to linear order in D were given by Arecchi and Politi (1980) and yield in our case

$$\begin{aligned} \langle T\rangle(-\infty \to \infty) &\approx \pi/\sqrt{\beta}, & (28)\\ \langle \Delta T^2\rangle(-\infty \to \infty) &\approx \frac{3D\pi}{4\beta^{5/2}}. & (29) \end{aligned}$$

There is no linear contribution in D to the mean ISI; the value $\pi/\sqrt{\beta}$ is clearly the deterministic passage time along the entire x-axis. This time as well as the variance of the passage time both decrease with increasing β.

For rate and CV we find

$$r \approx \sqrt{\beta}/\pi, \qquad CV = \sqrt{\frac{3D}{4\pi}}\beta^{-3/4} \quad \text{for} \quad \beta \gg D^{2/3}. \tag{30}$$

This scaling behavior (independence of mean ISI of D, variance of ISI going as $\sqrt{D}$) resembles that of a perfect integrate-and-fire (PIF) neuron driven by white noise (see, for instance, Bulsara et al., 1994). Indeed, for weak noise and positive input, one may even approximate the PDF of the interspike interval by an inverse Gaussian (i.e. the ISI probability density function for a perfect integrate-and-fire neuron) - an approach that works rather well and will be presented elsewhere.

3.3 Rate in the excitable regime and weak noise

For $\beta < 0$ and weak noise, the passage from minus to plus infinity is dominated by the escape from the potential minimum at $x_- = -\sqrt{\beta}$ over the barrier at $x_+ = \sqrt{\beta}$. A standard saddle point approximation of the integral in eq. (22) yields an exponential firing rate (Colet et al., 1989)

$$r = \frac{\sqrt{|\beta|}}{\pi} \exp\left[-\frac{4|\beta|^{3/2}}{3D}\right] \quad \text{for} \quad D \ll |\beta|^{3/2} \tag{31}$$

which is the Kramers escape rate for the potential eq. (6) in the overdamped case (Kramers, 1940). A similar approximation of the variance in eq. (23) gives the square of the mean ISI, i.e. such an approach yields a CV of unity equivalent to the rare-event statistics of a Poisson process.

3.4 Rate and CV in the case of weak input or strong noise

If the input β is weak in amplitude or equivalently the noise intensity is sufficiently strong ($|\beta| \ll D^{2/3}$), we expect that rate and CV deviate only linearly from the simple expressions in eq. (27).

To find this linear expansion for the firing rate, we keep only the first two terms in the sum formula of the mean ISI eq. (24) and expand the rate with respect to β. This yields after some manipulations

$$\begin{aligned} r(\beta \ll 1, D) &\approx \frac{(3D)^{1/3}}{[\Gamma(1/3)]^2} + \frac{9}{8}\frac{3^{1/6}}{\pi^3}[\Gamma(2/3)]^4 \, D^{-1/3} \, \beta \\ &= 0.201 \, D^{1/3} + 0.147 \, D^{-1/3} \, \beta \end{aligned} \tag{32}$$

For the CV, the numerical constant, namely the derivative of the CV with respect to β, can be only performed numerically. We find that this derivative is well approximated by $1/4D^{-2/3}$, i.e.

$$\begin{aligned} CV(\beta \ll 1, D) &\approx \frac{1}{\sqrt{3}} + \frac{1}{4}D^{-2/3} \, \beta \\ &= 0.578 + 0.250 \cdot D^{-2/3} \, \beta \end{aligned} \tag{33}$$

Clearly, eq. (32) and eq. (33) can be not only used in case of a weak input but also regarded as large noise asymptotic.

4 Results

In the next two sections we discuss rate and coefficient of variation as functions of the noise intensity and of the constant input. In all figures, lines for $\beta \neq 0$ were obtained by numerical evaluation of the quadrature formulae[5] eq. (22) and eq. (23) and insertion into eq. (4) and eq. (5); for $\beta = 0$ formula eq. (27) was used. Symbols indicate results of numerical simulations of the dynamics using reset and absorption points $x_{\pm} = \pm 500$, an Euler scheme with $\Delta t = 10^{-3}$ or $\Delta t = 10^{-4}$ (latter at large noise intensity). Depending on parameters, up to 10^5 spikes were used for estimation of the statistics of the interspike interval. In the left panels of all figures we compare the numerically evaluated quadrature results and the numerical simulations - they are in all cases in excellent agreement with each other as it should be. In the right panels the quadrature results are compared to the various approximations obtained in the previous section.

In the third section we compare rate and CV with simulation results of the Θ neuron using either the Stratonovich or Ito interpretation and compare the results to those of Gutkin and Ermentrout (1998).

4.1 Rate and CV as functions of noise intensity

The rate depicted in Fig. 3 behaves at large noise intensity rather independently of the value of β; it is seen to increase in proportion to $D^{1/3}$ according to eq. (27). The effect of β becomes apparent at small noise intensity, where the rate (1) saturates if $\beta > 0$ (solid line) at the value given by eq. (30), (2) increases like for large noise with a power law for $\beta = 0$ according to eq. (27), or (3) increases following an exponential dependence on inverse noise intensity (Kramers law eq. (31)) for $\beta < 0$.

The approximation eq. (31) for $\beta < 0$ is valid only for rather small noise intensity. In contrast, the result from linearization around $\beta = 0$ (eq. (32)) fits pretty well for moderate to large noise intensity and for both $\beta = 1$ or -1. In fact, one may interpolate between the weak and strong noise approximations without making an appreciable error.

The coefficient of variation tends in the strong noise limit to $1/\sqrt{3}$ as predicted by eq. (19). In the weak noise limit it decreases either to zero ($\beta > 0$) corresponding to a perfectly regular firing for the oscillatory system in the absence of noise or tends to one ($\beta < 0$), indicating rare spiking with Poisson statistics. The exceptional case $\beta = 0$ leads to $CV = 1/\sqrt{3}$ for all noise intensities. Note that any finite value of β will lead to one of the other limits if the noise is

---

[5] The sum formula eq. (24) showed excellent agreement with the quadrature result, but is not discussed in the following

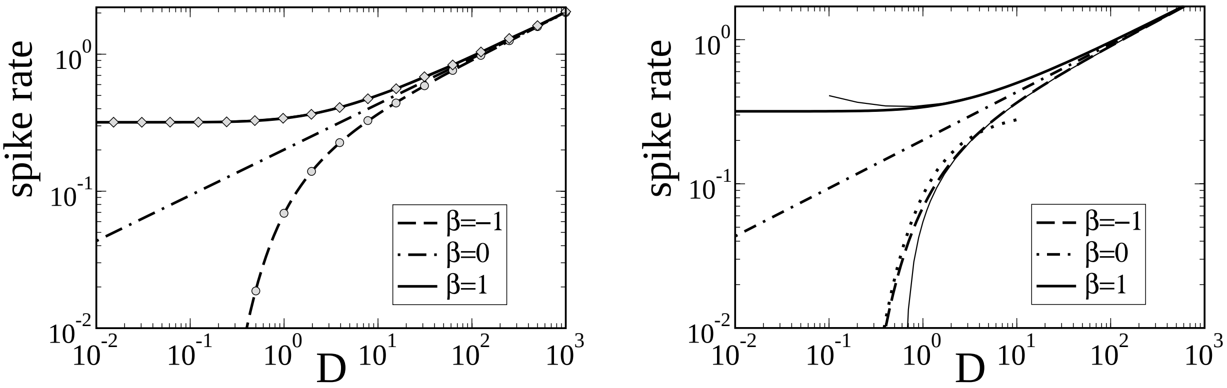

Figure 3: Spike rate of neuron vs. noise intensity for the three distinct cases $\beta = \pm 1$ or 0. Left: quadrature results compared to simulations (symbols). Right: quadrature results compared to Kramers rate eq. (31) (dotted line, only for $\beta = -1$), and linearization approximation eq. (32) (thin solid lines).

sufficiently weak. Indeed for vanishing noise, $\beta = 0$ can be looked upon as a threshold value, as we will see also later on.

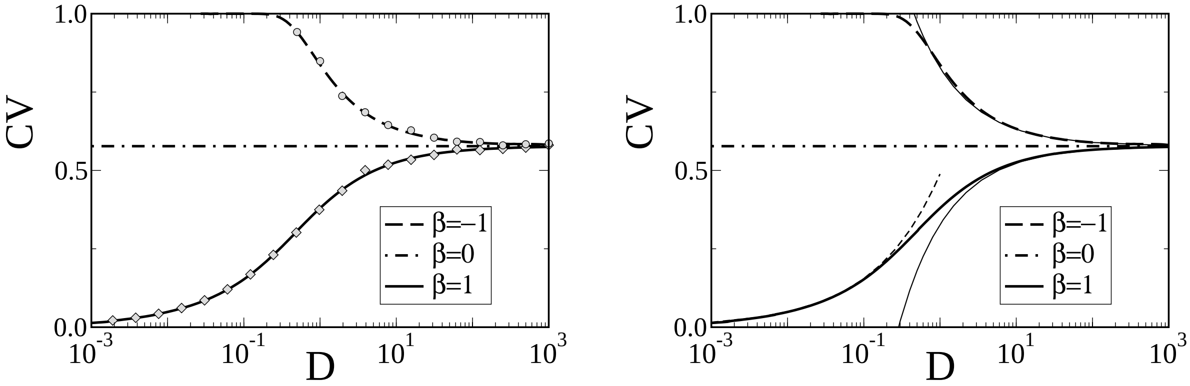

Figure 4: Coefficient of variation vs. noise intensity for the three distinct cases $\beta = \pm 1$ or 0. Left: quadrature results compared to simulations (symbols). Right: quadrature results compared to weak noise expansion for $\beta > 0$, i.e., eq. (30) (thin dashed), and linearization approximation eq. (33) (thin solid lines).

The approximation eq. (30) is shown in Fig. 4 as a dashed line. The "square-root" law describes the true CV up to $D \approx 0.2$ rather well. For a general (positive) value of β the approximation is valid for noise intensities that yield a CV below 0.25. This can be precisely formulated as a condition between D and β

$$\beta > \left(\frac{12D}{\pi}\right)^{2/3}. \tag{34}$$

The linearization result shown by thin solid lines in Fig. 4 seems to have an even larger range of validity. For $\beta = -1$ one may use the weak-input approximation eq. (33) as a good estimate as long as the CV is below 0.9. For $\beta = 1$, the approximation coincides with the exact result in line thickness for CVs between 0.5 and $1/\sqrt{3}$. Via the scaling relation eq. (18) these estimates can be generalized to arbitrary negative (positive) values of β, respectively since a change in input rescales only the noise intensity but not the range of CV.

4.2 Rate and CV as functions of the constant input

Since β plays the role of an input, the dependencies of rate and CV upon this parameter are of most interest. We show these dependencies for different noise intensities, i.e. $D = 0.1, 1$, or 10 in Fig.5 (rate) and Fig.6 (CV).

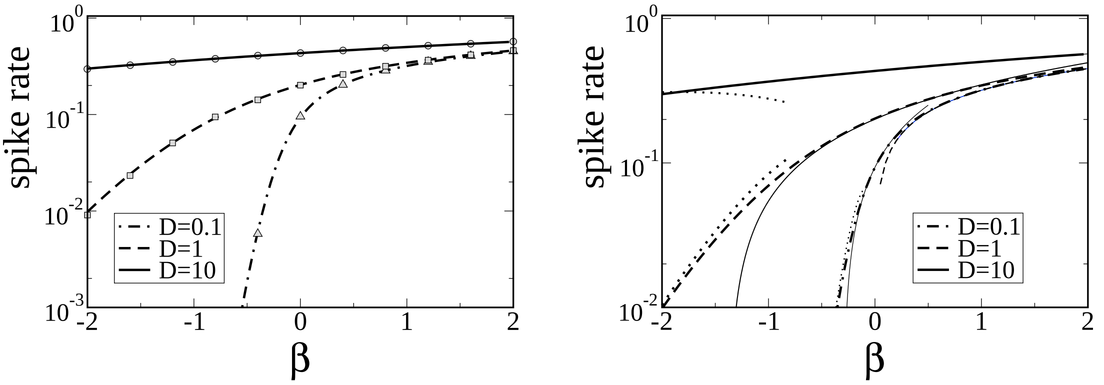

Figure 5: Spike rate of neuron vs. input β for three different noise intensities. Left: quadrature results compared to simulations (symbols). Right: quadrature results compared to Kramers rate eq. (31) (dotted), linearization approximation eq. (32) (thin solid lines), and the deterministic rate eq. (30) (thin dashed, only for $D = 0.1$).

For strong noise, the dependence of the rate on input is rather weak. This can be readily understood: the linear part of the potential governed by β is of minor importance at large noise, and a potential barrier at negative β is “not seen”. The passage through this region is biased diffusion (governed mainly by the cubic part of the potential that is independent of β).

Decreasing noise results in an increasing dependence of the rate on input, and for negative β the rate can become arbitrary low. In the limit of vanishing noise the rate can likewise attain arbitrary low values for *positive* input - this is one of the characteristic features of type I neurons (Ermentrout, 1996).

The approximation eq. (31) is shown by dashed lines. While it well describes the data for $D = 0.1$ it becomes worse with increasing noise intensity over the range of β shown in Fig. 6. On the contrary, the linearization result agrees best at large noise intensity - indeed there is no visible difference between the quadrature result and the approximation for $D = 10$. At

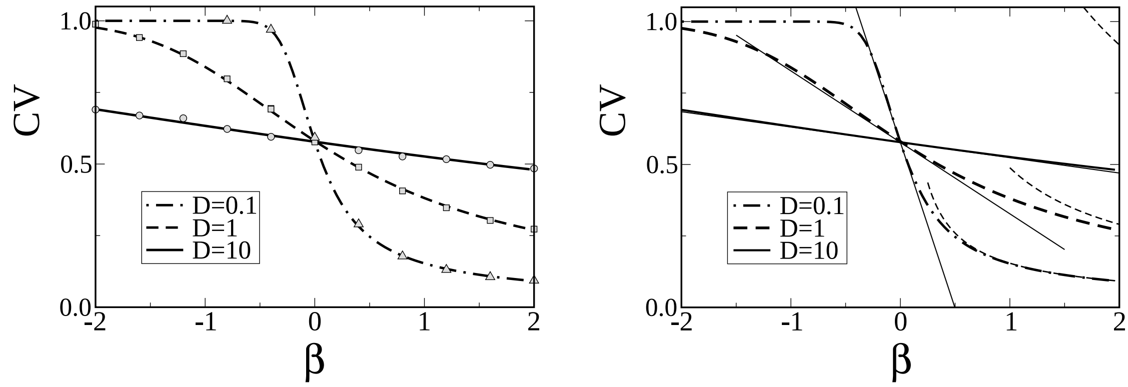

Figure 6: Coefficient of variation vs. input β for three different noise intensities. Left: quadrature results compared to simulations (symbols). Right: quadrature results compared to weak noise expansion for $\beta > 0$, i.e., eq. (30) (thin dashed), and linearization approximation eq. (33) (thin solid lines). The latter coincides with the quadrature result within line thickness for $D = 10$.

moderate noise intensity ($D = 1$) the linear behavior is restricted to a much smaller range of β. For small noise intensity and increasing β, the rate switches very fast from almost zero to a saturation value - a rather nonlinear behavior that is not well described (or only in a very small range around $\beta = 0$) by the linearization approximation eq. (32).

The shape of the CV vs. β curve is almost linear for strong noise (Fig. 6, solid line) as already mentioned by Gutkin and Ermentrout (1998). Since the quadrature formulae contain always β/D, a linearization of rate and CV with respect to β is valid for a larger range of β if D is large. Indeed, noise does not only linearize the transfer function (i.e., rate vs input parameter) but also all other statistical quantities with respect to variations of β. The linear dependence is, however, changed into a threshold-like dependence for small noise. With a look at the different small noise limits of the CV for $\beta < 0, \beta > 0$, no other behavior than this threshold behavior is indeed possible.

The approximation according to eq. (30) is shown by thin dashed lines in Fig. 6. It can be used only for the small noise level $D = 0.1$ where the CV is below 0.25 and is far off for larger noise intensities.

4.3 Comparison to simulations of the Θ neuron model

In section 2.2 we have already derived that the Stratonovich interpretation of the white noise driven Θ neuron model eq. (8) is completely equivalent to our basic model eq. (1). That means if we simulate using the scheme eq. (9) we should exactly obtain the same rate and CV as for the original model. On the contrary, the Ito interpretation of eq. (8) and the corresponding integration scheme eq. (10) should result in different rate and CV, in particular, at larger noise intensity. Here we ask whether these differences are serious or not. We will compare also to results by Gutkin and Ermentrout

(1998) who have apparently used the Ito scheme eq. (10) that does not exactly correspond to the original dynamics.

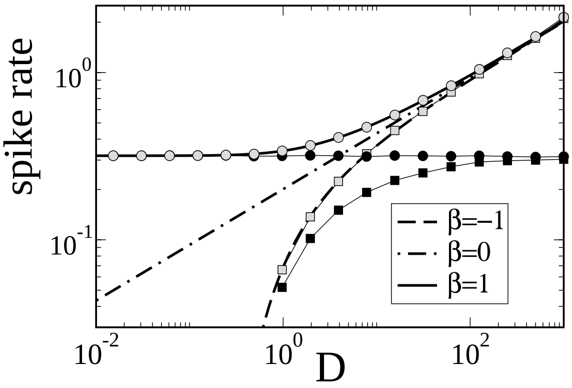

Figure 7: Firing rate as a function of noise intensity. Theory for the saddle-node system shown by solid lines for different values of β as indicated; simulation results for the Θ model in Stratonovich interpretation according to the integration scheme eq. (9) (grey symbols) and in Ito interpretation according to eq. (10) for $\beta = 1$ (dark circles) and for $\beta = -1$ (dark squares).

In Fig. 7 the firing rate is shown as a function of the noise intensity for $\beta = \pm 1$ and $\beta = 0$. The quadrature result for the original dynamics eq. (1) is compared to simulation results using the two integration schemes eq. (9) and eq. (10). While the Stratonovich scheme exactly matches the analytical curves and thereby confirms our expectation, the rate obtained by simulating the Ito scheme is below the true rate for moderate to large noise intensities and saturates in the strong noise limit. Most remarkably, for $\beta = 1$ the rate does not seem to depend on noise intensity at all, in marked contrast to the $D^{1/3}$ increase of the true rate for strong noise. As expected, both schemes yield the same function in the weak noise limit where the Stratonovich drift (proportional to noise intensity) becomes negligible.

Fig. 8 shows the CV as a function of noise intensity for the three standard values of β. Here the differences between Ito and Stratonovich interpretations of the Θ neuron model are more important. The latter yields again perfect agreement with the theoretical result for the original dynamics. The Ito scheme, in contrast, shows strong deviations for moderate to large noise intensity. The CV for the oscillatory regime ($\beta = 1$) is no longer restricted to $(0, 1/\sqrt{3})$. For both positive and negative β, the CV is always above the true CV.

Increasing noise even leads to a growth of the CV, such that for $\beta = -1$ a minimum in the CV versus noise intensity curve is seen. Such a minimum is a signature of coherence resonance (Pikovsky and Kurths, 1997) - many excitable (as opposed to periodically firing) systems exhibit their most regular spiking (as indicated by a minimal CV) if driven by a noise with finite "optimal" intensity. This effect is *clearly absent* for the original dynamics eq. (1). This qualitative difference between the Ito and Stratonovich interpretations, in the form of the existence of such a minimum, might be irrelevant in real type I neurons since the reduction from the multidimensional system to the one-dimensional normal form becomes somewhat doubtful in the strong noise limit.

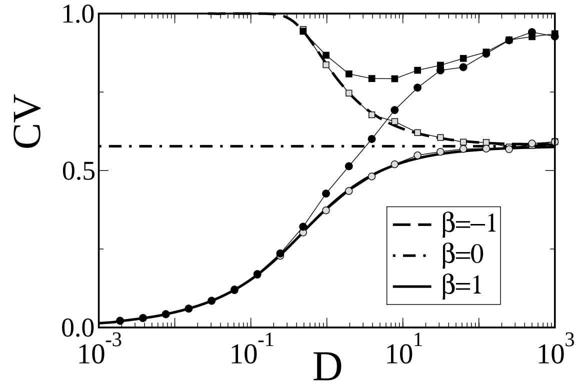

Figure 8: Coefficient of variation as a function of noise intensity. Theory for the saddle-node system shown by solid lines for different values of β as indicated; simulation results for the Θ model in Stratonovich interpretation according to the integration scheme eq. (9) (grey symbols) and in Ito interpretation according to eq. (10) for $\beta = 1$ (dark circles) and for $\beta = -1$ (dark squares).

Gutkin and Ermentrout (1998) showed by means of numerical simulations that the Θ neuron exhibits (at least for $\beta < 0$) always a high CV close to one. They started as we did with the normal form, derived the equation for the Θ neuron, but interpreted this equation apparently in Ito's sense (i.e., integrated eq. (10)). Although their conclusions are qualitatively correct, we would like to point out a quantitative discrepancy resulting from using the Ito scheme.

In Fig. 6c of (Gutkin and Ermentrout, 1998) the CV is shown as a function of the mean interval, a representation of the data that is independent of the definition of noise intensity (they use a parameter σ that is related to the noise intensity D by $\sigma = \sqrt{2D}$). For a mean ISI ranging from 1 up to 10000, they find a CV between 0.75 and 1.1 with a minimal CV at a small mean ISI (between 1 and 10). Data are pretty noisy, and Gutkin and Ermentrout (1998) do not mention the apparent minimum of the CV. We may use our data from Fig. 7 and Fig. 8 and also plot a CV vs. mean ISI curve; this is shown in Fig. 9. Simulating the Ito version of the Θ model, we recover indeed a high CV and a minimum at a low mean interval[6]. In contrast, for the original model of a saddle-node system (theoretical curve, solid line in Fig. 8) as well as for

---

[6] We note two discrepancies with the data of Gutkin and Ermentrout (1998): (1) we cannot plot a CV for an interval below $\langle T\rangle = 3.14$ since the rate is limited by the inverse of this value (cf. Fig. 7), whereas in (Gutkin and Ermentrout, 1998) there is one data point for $\langle T\rangle = 1.5$;

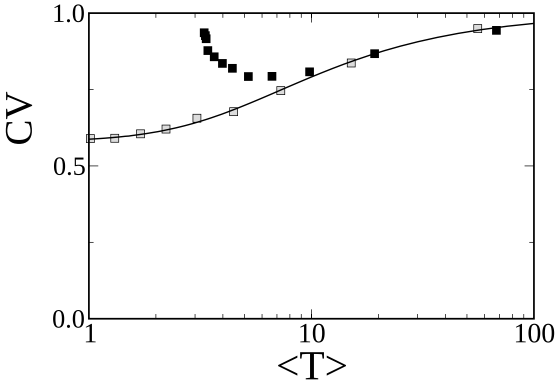

Figure 9: Coefficient of variation as a function of the mean ISI. Variation of the mean ISI is as in (Gutkin and Ermentrout, 1998) achieved by changing the noise intensity while keeping fixed $\beta = -1$. Theory for the saddle-node system shown by solid line; simulation results for the Θ model in Stratonovich interpretation according to the integration scheme eq. (9) (grey) and in Ito interpretation according to eq. (10) (black).

simulation results from the Θ model interpreted in Stratonovich's sense we obtain no minimum in the CV and observe generally a considerable lower CV at small mean intervals. The lower limit is given by the large noise limit of the CV, i.e. in the excitable regime we have $CV > 1/\sqrt{3}$. In the Stratonovich interpretation of the model as well as in the original dynamics we can have arbitrary low mean interspike intervals, i.e. arbitrary high firing rate.

5 Discussion and conclusions

We have considered a simple spike generator model that involves the one-dimensional normal form of a saddle-node bifurcation and may hence be used to represent a type I neuron. The model seems to be computational simpler than the equivalent Θ neuron currently often used in neurocomputational research. Using the spike generator with saddle-node bifurcation helps, moreover, avoiding the pitfalls associated with using multiplicative white noise as in the Θ model.

A second advantage of the saddle-node spike generator is that we were able to adopt many useful analytic results for the passage time problem from the statistical physics literature on a related problem. We discussed the remarkable scaling behavior of the model, that allows to reduce the number of parameters in the problem. We gave the exact quadrature

---

(2) the CV we have found in our simulation for $\beta = -1$ is always between 0.8 and 1, whereas in (Gutkin and Ermentrout, 1998) this range is slightly larger ($CV \in (0.75, 1.1)$). Either differences can be explained by insufficient statistics in (Gutkin and Ermentrout, 1998) and possibly (since there seems to be also a systematic deviation) by a too large time step in the integration procedure. Especially at low mean ISI's (high noise intensities) we had to use time steps down to $\Delta t = 10^{-4}$ to achieve independence of the data w.r.t. time step.

expressions for mean and variance of the ISI and a simple sum formula for the mean ISI. Furthermore, we derived expressions for simple limiting cases for rate and CV of the model. All results may be useful also for problems involving networks of type I neurons.

For the problem of high variability of spike trains of cortical neurons one of our conclusions is especially relevant: given a negative input ($\beta < 0$), the CV is restricted to the interval $(1/\sqrt{3}, 1)$, it can never be lower than the high noise limit CV of the model. This stands in marked contrast to the leaky integrate-and-fire model, that can in this regime attain arbitrary low values of the CV if the input parameter is tuned to a certain small negative value (Lindner, 2002; Lindner et al., 2002). Although Gutkin and Ermentrout (1998) overestimated the CV with their simulation results, their main conclusion remains valid: type I neurons stimulated by white Gaussian noise show a high variability for arbitrary but negative input. Future work will consider a comparison of our results with a two-(or higher-) dimensional dynamics of an ionic model of a type I neuron, such as Morris-Lecar. We will also consider the theoretical analysis of the phase resetting curves and the response of the stochastic saddle-node neuron model studied here to periodic and broadband input.

6 Acknowledgments

This research was supported by NSERC Canada and a PREA award from the Government of Ontario. We also wish to thank Christophe Langevin for preliminary numerical calculations of first passage times in the Θ neuron model.

References

M. Abramowitz and I. A. Stegun. *Handbook of Mathematical Functions.* Dover, New York, 1970.

F. T. Arecchi and A. Politi. Transient fluctuations in the decay of an unstable state. *Phys. Rev. Lett.*, 45:1219, 1980.

A. Bell, Z. Mainen, M. Tsodyks, and T. Sejnowski. "Balancing" of conductances may explain irregular cortical spiking. *Tech Report INC-9502, Institute for Neural Computation, Univ. of California, San Diego*, 1995.

A. Bulsara, S. B. Lowen, and C. D. Rees. Cooperative behavior in the periodically modulated Wiener process: Noise-induced complexity in a model neuron. *Phys. Rev. E*, 49:4989, 1994.

P. Colet, M. San Miguel, J. Casademunt, and J. M. Sancho. Relaxation from a marginal state in optical bistability. *Phys. Rev. A*, 39:149, 1989.

D. R. Cox. *Renewal Theory.* Methuen, London, 1962.

G. B. Ermentrout. Type I membranes, phase resetting curves, and synchrony. *Neural. Comp.*, 8:979, 1996.

H. Gang, T. Ditzinger, C. Z. Ning, and H. Haken. Stochastic resonance without external periodic force. *Phys. Rev. Lett.*, 71:807, 1993.

C. W. Gardiner. *Handbook of Stochastic Methods.* Springer-Verlag, Berlin, 1985.

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.*, 10:1040, 1998.

F. C. Hoppensteadt and E. M. Izhikevich. *Weakly Connected Neural Networks.* Springer-Verlag, New York, 1997.

H. A. Kramers. Brownian motion in a field of force and the diffusion model of chemical reactions. *Physica*, 7:284, 1940.

B. Lindner. *Coherence and Stochastic Resonance in Nonlinear Dynamical Systems.* Logos-Verlag, Berlin, 2002.

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. Longtin. Autonomous stochastic resonance in bursting neurons. *Phys. Rev. E*, 55:868, 1997.

C. Morris and H. Lecar. Voltage oscillations in the barnacle giant muscle fiber. *Biophys. J.*, 35:193, 1981.

A. Pikovsky and J. Kurths. Coherence resonance in a noise-driven excitable system. *Phys. Rev. Lett.*, 78:775, 1997.

L. Pontryagin, A. Andronov, and A. Witt. *Zh. Eksp. Teor. Fiz.*, 3:172, 1933. Reprinted in *Noise in Nonlinear Dynamics*, 1989, ed. by F. Moss and P. V. E. McClintock (Cambridge University Press, Cambridge), Vol. 1, p. 329.

W. J. Rappel and S. H. Strogatz. Stochastic resonance in an autonomous system with a nonuniform limit cycle. *Phys. Rev. E*, 50:3249, 1994.

J. Rinzel and B. Ermentrout. Analysis of neural excitability and oscillations. In C. Koch and I. Segev, editors, *Methods in Neuronal Modeling*, page 251. MIT Press, Cambridge, Mass., 1989.

H. Risken. *The Fokker-Planck Equation.* Springer, Berlin, 1984.

M. N. Shadlen and W. T. Newsome. Noise, neural codes and cortical organization. *Curr. Op. Neurobiol.*, 4:569, 1994.

D. Sigeti. *Universal Results for the Effect of Noise on Dynamical Systems.* PhD thesis, University of Texas at Austin, 1988.

D. Sigeti and W. Horsthemke. Pseudo-regular oscillations induced by external noise. *J. Stat. Phys.*, 54:1217, 1989.

W. R. Softky and C. Koch. The highly irregular firing of cortical cells is inconsistent with temporal integration of random epsp's. *J. Neuronsci.*, 13:334, 1993.

T. Troyer and K. Miller. Physiological gain leads to high isi variability in a simple model of a cortical regular spiking cell. *Neur. Comp.*, 9:971, 1997.

H. C. Tuckwell. *Introduction to Theoretical Neurobiology.* Cambridge University Press, Cambridge, 1988.

W. Wilbur and J. Rinzel. A theoretical basis for large coefficient of variation and bimodality in neuronal interspike interval distributions. *J. Theor. Biol.*, 105:345, 1983.