

# **Dynamical Response Properties of a Canonical Model for Type-I Membranes**

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## **Abstract**

We study a canonical model of type-I membranes subject to a correlated fluctuating input currents. We present a semi-analytical approach for calculating the response of this neuron model to time dependent inputs both in the input current and the noise amplitude using a novel sparse matrix representation of the systems Fokker-Planck operator. It turns out, that the maximum stimulation frequency which can be transmitted through this model neuron is approximately given by the stationary firing rate. Our results agree well with the behavior of a conductance-based model-neuron but are in qualitative disagreement with key response properties of leaky integrate-and-fire neurons.

## I. INTRODUCTION

Cortical neurons *in vivo* are subject to an immense synaptic bombardment which leads to rapid fluctuations in their membrane potential (MP) [5]. For analytical, as well numerical studies it is crucial to identify simple, yet biophysical realistic neuron models, which reproduce the dynamical behavior of real neurons under such conditions. Here we present the stationary and dynamical response properties of a canonical model of membranes exhibiting Type-I excitability in a biologically realistic regime. For a temporally correlated input current we expand the Fokker-Planck operator into a suitable basis set, for which the matrix representation is sparse. Subsequent diagonalization of the resulting Fokker-Planck matrix allows for a very fast and efficient computation of the firing rate, as well as the stationary density of the MP. In the second part we study dynamical responses based on linear response theory. We show that the speed of responses is closely connected to the spectral properties of the Fokker-Planck operator and identify a cut-off frequency, which is approximately given by the stationary firing rate of the model neuron. Above this cut-off frequency the response amplitude is strongly damped. We show that this behavior is shared by a conductance based model neuron and is in qualitative disagreement with results reported on the leaky integrate-and-fire (LIF) model. Our study corroborates and extends recent reports [6, 11], indicating that the LIF model is incapable of mimicking the dynamical response properties of conductance based model neurons. In addition our new method provides efficient computational tools for the analysis of dynamical neuronal responses.

## II. MODEL

In our study we use a canonical model of type-I membranes. This model undergoes a saddle node bifurcation when brought to repetitive firing. Close to the bifurcation it can be shown that the complex dynamics of a multidimensional conductance based model can be described by its normal form[15]. For a saddle-node bifurcation this is given by,  $C\dot{V} = A(V - V^*)^2 + (I - I_c)$ , which is a dynamical equation for the MP  $V$  of the neuron. The rheobase of the neuron is denoted by  $I_c$ , the constants  $A$  and  $V^*$  can be deduced from the multidimensional conductance based model (see Fig. 1). It is convenient to introduce dimensionless quantities  $\bar{V} = \tau A(V - V^*)/C$  and  $\bar{I} = A(I - I_c)\tau^2/C^2$ , where we have introduced the effective time constant  $\tau$ . The rescaled dynamics is

then given by:

$$\tau \dot{\bar{V}} = \bar{V}^2 + I \quad (1)$$

For an input current which is larger than the rheobase, i.e.  $I > 0$ , the MP has a finite “blow-up” time, which means that it needs a finite time to get from  $-\infty$  to  $+\infty$ , where the latter is identified with the emission of a spike. The normal form Eq. (1) can formally transformed into a phase oscillator, the  $\theta$ -neuron[10], by substituting  $\bar{V} = \tan(\theta/2)$ :

$$\tau \dot{\theta} = (1 - \cos \theta) + I(1 + \cos \theta) \quad (2)$$

with the angle variable  $\theta$  in the interval  $(-\pi, \pi]$ . Here, a spike is emitted each time  $\theta$  reaches the value  $\pi$ . In the following the input  $I$  will be decomposed into two parts,  $I = I_0 + \sigma z(t)$ , a mean input current  $I_0$  and a stationary fluctuating part  $\sigma z(t)$  with  $\langle z(t) \rangle = 0$  and the correlation function  $\langle z(t)z(t') \rangle \propto \exp(-(t - t')/\tau_c)$ .

The parameters  $\tau$ ,  $I_0$  and  $\sigma$  have been chosen to reflect the conditions of a cortical neuron *in vivo*. A spike takes about 1ms, to reflect this we choose  $\tau = 0.25\text{ms}$ . A rough estimate of the relaxation time of  $\theta$  for  $I_0 < 0$  is given by approximating the dynamics near the stable fixed point at  $-\sqrt{I_0}$  by an Ornstein-Uhlenbeck process, yielding,  $\tau_{\text{relax}} = \tau(2\sqrt{I_0})^{-1}$ . To meet realistic relaxation times of the MP of the order of 10ms it turns out that  $I_0$  has to be of the order  $10^{-3}$ . To then achieve realistic rates from 2Hz to 10Hz,  $\sigma$  has to be of the order  $10^{-3}$ – $10^{-2}$ . We note that the regime  $I_0 \approx 0$  is as well the regime where the normal form reflects most realistically the dynamics of the multidimensional conductance based model.

### III. SPECTRUM AND EIGENFUNCTIONS OF THE FOKKER-PLANCK OPERATOR WITH CORRELATED INPUT NOISE

We will now continue with the discussion of the case of a temporally correlated input current. To do this we add a second dynamical equation:

$$\tau_c \frac{dz(t)}{dt} = -z(t) + \sqrt{\tau} \eta(t),$$

where  $\eta(t)$  is Gaussian white noise and  $\tau_c$  the correlation time of the input. The Fokker-Planck equation which governs the dynamics of the probability density function is then:

$$\begin{aligned} \partial_t P(\theta, z, t) = & -\tau^{-1} ((1 - \cos \theta) + (I_0 + \sigma z(t))(1 + \cos \theta)) P(\theta, z, t) \\ & + \tau_c^{-1} \partial_z z P(\theta, z, t) + \frac{1}{2} \tau \tau_c^{-2} \partial_z^2 P(\theta, z, t) = \hat{L}(\theta, z) P(\theta, z, t) \end{aligned} \quad (3)$$

Here  $P(\theta, z, t)$  is now the time-dependent joint probability density of  $\theta$  and  $z$ . The boundary conditions are periodic in the  $\theta$ - and natural in the  $z$ -direction. The firing rate  $v(t)$  is the probability current through the line  $\theta = \pi$ :

$$v(t) = 2\tau^{-1} \int_{-\infty}^{\infty} P(\pi, z, t) dz \quad (4)$$

For this correlated input current it is unknown how to compute the stationary density or the firing rate analytically. It is only possible to give approximate solutions for very small or large values of  $\tau_c$  [4, 13], where compared to the white-noise Fokker-Planck operator the noise strength  $\sigma$  is effectively changed. In the following we will use a semi-analytical approach, which does not rely on any further approximations of the Fokker-Planck operator  $\hat{L}(\theta, z)$ . This is done by representing  $\hat{L}(\theta, z)$  as a sparse matrix by expanding it into the complete orthonormal basis,  $\psi_{n,m}(\theta, z) = \left(2^{m+1} \sqrt{\pi/2(\tau_c/\tau)} m!\right)^{-1/2} e^{in\theta} H_m\left(\sqrt{2(\tau_c/\tau)} z\right) e^{-z^2 \tau_c/\tau}$ , with  $n \in \mathbb{Z}$ ,  $m \in \mathbb{N}_0$ , where  $H_m(z)$  denotes the Hermite polynomial of order  $m$  [2]. Eq. (3) then yields the following eigenvalue problem:

$$\begin{aligned} \lambda a_{n,m} = & \left(-i\tau^{-1}(1+I_0)n - \tau_c^{-1}m\right) a_{n,m} + (2\tau)^{-1}i(1-I_0)n (a_{n-1,m} + a_{n+1,m}) \\ & - \frac{i n \sigma}{2\sqrt{\tau\tau_c}} \left( (m+1)a_{n,m+1} + m a_{n,m-1} + \frac{1}{2}(m+1)(a_{n-1,m-1} + a_{n+1,m-1}) \right) \\ & + \left(\sqrt{2\tau\tau_c}\right)^{-1} \sqrt{(m+1)(m+2)} a_{n,m+2} \end{aligned} \quad (5)$$

Fig. (2) shows the spectrum and the stationary density of the operator  $\hat{L}(\theta, z)$  for  $\tau_c = 10\text{ms}$  and a stationary rate of  $v = 10\text{Hz}$  calculated using the sparse matrix representation Eq. (5). The spectrum is composed of several wedges which are located at integer multiples of  $\tau_c^{-1}$ . The real part of the eigenvalues in each wedge grows approximately quadratically, as expected for a diffusion process, they determine the decay rate of the corresponding eigenfunction. Their oscillating frequency is given by the imaginary parts of the eigenvalues, which are approximately equidistant.

#### IV. LINEAR RESPONSE THEORY

The eigenfunctions and eigenvalues of the Fokker-Planck operator determine the temporal evolution of the probability density function [14]. In particular it is possible to connect them to the response properties to a time-varying stimulus in linear response theory (For details see [11]). For a periodic modulatory input the operator resulting Fokker-Planck operator  $\hat{L}_{\text{LR}}(\theta, z)$  is then

composed of two parts:

$$\hat{L}_{LR}(\theta, z) = \hat{L}(\theta, z) + \varepsilon \hat{L}_1(\theta, z) e^{i\omega t} \quad (6)$$

where  $\hat{L}_1(\theta, z)$  takes the form  $\hat{L}_1(\theta, z) = -\tau^{-1} \partial_\theta (1 + \cos \theta)$  for a modulation in the input current and  $\hat{L}_1(\theta, z) = -\tau^{-1/2} z (1 + \cos \theta)$  for a modulation in the noise amplitude. The resulting time dependent probability density function can then be written as  $P_{TD}(\theta, z, t) = P_0(\theta, z) + \tilde{P}(\theta, z, t)$  with the stationary density  $P_0(\theta, z)$  of  $\hat{L}$  and,

$$\tilde{P}(\theta, z, t) = \sum_k \frac{c_k}{i\omega - \lambda_k} P_{\lambda_k}(\theta, z) e^{i\omega t}, \quad (7)$$

where the  $c_k$  are the expansion coefficients of  $\hat{L}_1(\theta, z) P_0(\theta, z)$  in eigenfunctions  $P_k(\theta, z)$  of  $\hat{L}_0(\theta, z)$ . The time dependent firing rate is given by Eq. (4):

$$v(t) = 2\tau^{-1} \int_{-\infty}^{\infty} (P_0(\theta, z) + \tilde{P}(\theta, z, t)) dz =: v_0 + \tilde{v}(\omega) e^{i(\omega t + \varphi(\omega))}$$

The response amplitude  $\tilde{v}(\omega)$  and phase  $\varphi(\omega)$  are shown for different values of  $v_0$  in Fig. 3 for the case of a current and noise modulation. The linear response amplitude exhibits a resonance maximum at approximately  $v_0$  and then rapidly decays to zero. The corresponding phase lag drops to  $-\pi$  and shows a small dip at the resonance frequency. As cut-off frequency we choose the resonance frequency, since inputs with a larger frequency are strongly damped. It is determined by the second eigenvalue of the first wedge for a current modulation and the first eigenvalue of the second wedge for a noise modulation, which can be seen from the decomposition of  $\hat{L}_1(\theta, z) P_0(\theta, z)$  in eigenfunctions of  $\hat{L}_1(\theta, z)$ . Figure (4) shows the dependence of the cut-off frequency as a function of the correlation time  $\tau_{\text{relax}} = (\text{Re}\lambda_2)^{-1}$ , where  $\lambda_2$  is the second eigenvalue of the first wedge, for several values of the stationary firing rate  $v_0$ . The different values of the relaxation time at constant stationary rate have been calculated by varying  $I_0 < 0$  and  $\sigma$  simultaneously. With increasing values of  $\tau_{\text{relax}}$  the cut-off frequency grows and saturates at values above  $v_0$ . For realistic correlation times, however, of about 10 – 20ms it takes approximately the same values as  $v_0$ .

In contrast to this result, the LIF model predicts a response amplitude that remains at a finite value in the limit [3]  $\omega \rightarrow \infty$  and thus predicts an instantaneous response. Fig. (4) compares the responses of both models to a step input with the response of a conductance based model neuron. Both the conductance based model and the normal-form neuron show a response which is much slower than that of the LIF neuron.

Using direct numerical simulations and asymptotic analysis Fourcaud et al [6] showed, that neuron models with a realistic spike generating mechanism exhibit a cut-off frequency in the

linear response amplitude. In this study, however, it was shown that the Wang-Buzsáki model and the  $\theta$ -neuron differ in their asymptotic behavior in the limit  $\omega \rightarrow \infty$ , where the Wang-Buzsáki model shows a  $\omega^{-1}$  decay, while the response of the  $\theta$ -neuron decays as  $\omega^{-2}$ . We would like to point out, however, that the  $\omega^{-2}$  decay of the  $\theta$ -neuron is only due to two features of the model: (1) The insensitivity to inputs at the point where a spike is emitted and (2) due to the symmetry of the dynamics, i.e.  $\dot{V}(-V) = \dot{V}(V)$ . When these conditions are lifted, a  $\theta$ -type model will also exhibit a  $\omega^{-1}$  decay for large frequencies [12]. In the presented study we concentrated on the cut-off behavior of the linear response amplitude, which takes place at frequencies comparable to the stationary rate and for which the high-frequency limit is thus not critical, as exemplified by the simulations.

## V. CONCLUSION

In conclusion, we presented the linear response theory for the firing rate of the  $\theta$ -neuron in response to both time dependent input currents and time dependent noise amplitudes. For an effective numerical treatment we derived a sparse matrix representation of the Fokker-Planck operator. Using the eigenvalues and eigenfunctions of this operator, we showed that the transmission amplitude is in both cases strongly damped for frequencies above a cut-off frequency. In a wide range of parameters this cut-off frequency is approximately at the mean firing rate. The response behavior agrees well with the dynamics of a conductance based model neuron and is different from the behavior of the LIF model. Our results indicate that the  $\theta$ -neuron, although simple, can appropriately capture essential dynamical properties of real neurons.

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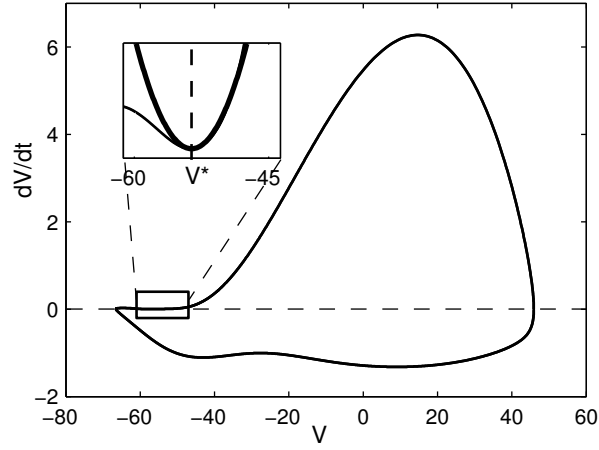


Figure 1: Near the onset of repetitive firing the dynamics of a type-I membrane is governed by its normal form. Here shown for the -Stevens model neuron.

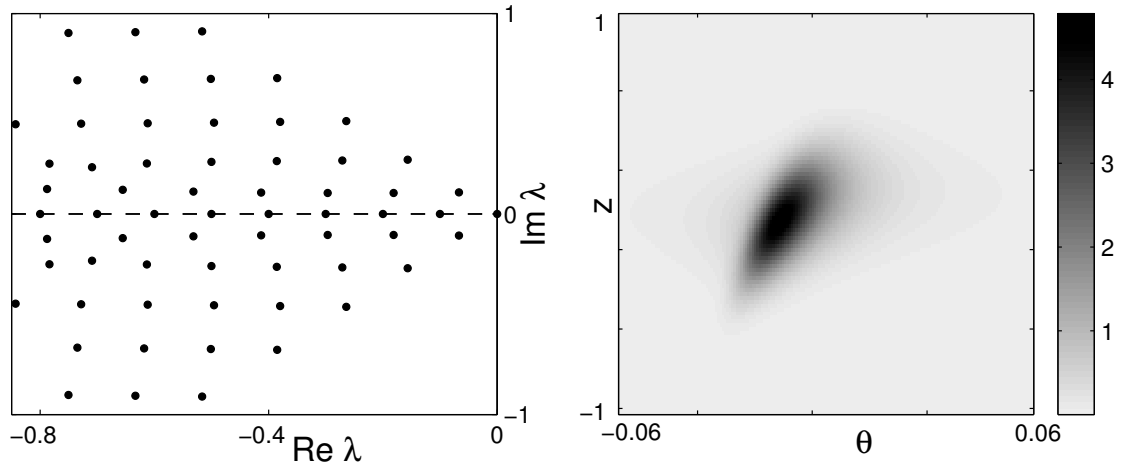


Figure 2: Eigenvalues of the operator  $\hat{L}$  (left) and the stationary density (right) for  $\tau_c = 10\text{ms}$  and  $\nu = 10\text{Hz}$  ( $I_0 = 0$ ,  $\sigma = 2.85 \cdot 10^{-3}$ ). For the numerical diagonalization the basis has been restricted to  $N = 5000$  and  $M = 60$ . The first 63 eigenvalues are shown.



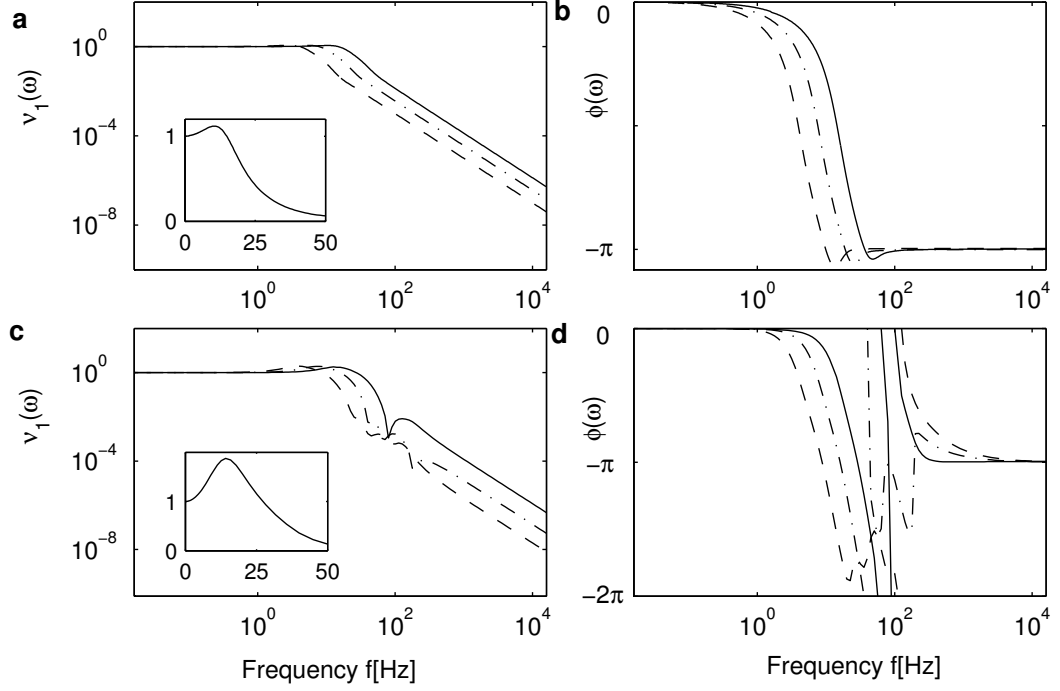


Figure 3: Response amplitude (a,c) and phase (b,d) for different values of  $v_0$  (dashed: 2 Hz, dash-dotted: 5 Hz, solid: 10 Hz) and  $\tau_c = 10\text{ms}$  and modulatory input current (top) and noise amplitude (bottom). In both cases the amplitude exhibits a maximum at approximately  $v_0$  and decays rapidly  $\propto \omega^{-2}$  for larger values of  $\omega$  (inset for  $v_0 = 10\text{Hz}$ ). The relative phase lag drops from zero to  $-\pi$  and shows a small dip at the resonance frequency for the current modulation and a number of resonances for the noise modulation, which are, however, strongly damped. (Parameters for all plots are  $I_0 = 0$  and  $\sigma = 2 \cdot 10^{-4}$  (2 Hz),  $\sigma = 8.9 \cdot 10^{-4}$  (5 Hz),  $\sigma = 2.85 \cdot 10^3$  (10 Hz))

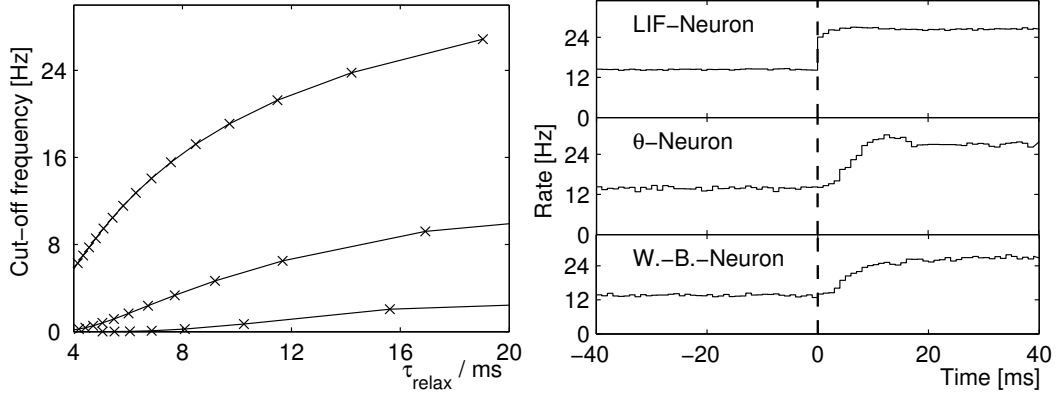


Figure 4: Left: Dependency of the cut-off frequency for different values of the stationary firing rate  $v_0$  (top: 20Hz, middle: 10Hz, bottom: 5Hz) as a function of the relaxation time  $\tau_{\text{relax}}$  of the MP. For realistic correlation times  $\tau_{\text{relax}} \approx 10\text{ms}$  it is approximately of the same value as the stationary rate  $v_0$ . Right: Comparison between the response of LIF model (top), the  $\theta$ -neuron (middle) and the Wang-Buzsáki conductance-based neuron model to a step in the mean input current ( $I_1 \rightarrow I_2$ ). All models are approximately at the onset of repetitive firing, comparable to neurons in vivo and receive an additional correlated input current with  $\tau_c = 10\text{ms}$ . While the LIF neuron responds almost instantaneously, the response of the normal-form as well as the response of the Wang-Buzsáki neuron are much slower. (Parameters for the LIF model (for the model definition see [3]):  $I_1 = 19.5$ ,  $I_2 = 21.0$ ,  $\sigma = 3$ ; parameters for the  $\theta$ -neuron:  $I_1 = -2 \cdot 10^{-4}$ ,  $I_2 = 4.4 \cdot 10^{-4}$ ,  $\sigma = 7.3 \cdot 10^{-3}$ ; parameters for the W.B.-model (for the model definition see [17]):  $I_1 = -0.2\text{nA}$ ,  $I_2 = 0.26\text{nA}$ ,  $\sigma = 5\text{nA}$ )