

A simple stochastic model of spatially complex neurons

Roger Rodriguez^{a,*}, Petr Lánský^b

^a Centre de Physique Théorique, CNRS, Luminy Case 907, 13288 Marseille Cedex 9, France

^b Institute of Physiology, Academy of Sciences of the Czech Republic, Videnska 1083, 14220 Prague 4, Czech Republic

Abstract

A method for studying the coding properties of a multicompartmental integrate-and-fire neuron of arbitrary geometry is presented. Depolarization at each compartment evolves like a leaky integrator with an after-firing reset imposed only at the trigger zone. The frequency of firing at the steady-state regime is related to the properties of the multidimensional input. The decreasing variability of subthreshold depolarization from the dendritic tree to the trigger zone is shown for an input that is corrupted by a white noise. The role of a Poissonian noise is also investigated. The proposed method gives an estimate of the mean interspike interval that can be used to study the input–output transfer function of the system. Both types of the stochastic inputs result in broadening the transfer function with respect to the deterministic case. © 2000 Elsevier Science Ireland Ltd. All rights reserved.

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1. Introduction

The frequency of uniformly sized action potentials is one of the basic modes of signaling in the nervous system. As the stimulus intensity increases, an increase in the neuronal activity follows. The concept of rate coding, including other statistical measures such as, for example, its variability, is based on the assumption that permits the replacing of time averaging by assembly averaging. This type of coding ensures high reliability against any distortion. We have been interested, in this paper, in the derivation of the property of rate coding of neurons in dependency on their compartmental structure.

In that way, an obvious tendency in computational neuroscience is to build more and more complex neuronal models composed of a very high number of compartments, each of them including kinetics of various ionic channels (DeSchutter, 1989; Segev et al., 1989; Segev, 1992). These models aim on the closest resemblance to the reality as possible. On the other hand, the models appearing recently in physical (biophysical) journals and aiming to study the properties of the information transfer within the neurons are constructed in simpler way to gain an insight into the role of different parameters of the models and to permit, at least, some analytical calculations, and thus not to rely completely on the numerical techniques. Of course, these models do not describe reality in detail; however, their advantage is a possibility to study the input–out-

* Corresponding author.

E-mail address: rodrig@cpt.univ-mrs.fr (R. Rodriguez).

put characteristics of a model neuron (for an introduction, see Tuckwell, 1988).

Even the simple models differ in the level of complexity in which they describe the membrane voltage dynamics: starting with the perfect integrator (for example, Bulsara et al., 1994), using the most common concept of the leaky integrator (for example, Bulsara et al., 1996; Plesser and Tanaka, 1998; Shimokawa et al., 1999) and also including more complex models like Fitzhugh–Nagumo neurons (for example, Tuckwell and Rodríguez, 1998). However, all these models are of single-point type, which means that they behave as a single compartment without taking into account any spatial characteristics of real neurons.

Beside the single-point models, there were also attempts to study the input–output characteristics by introducing the spatial structure of neurons, at least in the simplest way (Rospars and Lánský, 1993; Bressloff, 1995; Lánský and Rospars, 1995). This led to the investigation of a model neuron divided into two parts and based on the following assumptions:

1. The neuron is assumed to be made of two interconnected, dendritic and trigger zone, compartments.
2. The input is present at the dendritic compartment only.
3. The potentials of the two compartments are described by leaky integrators with a reset mechanism at the trigger zone.

This two-point schema had been investigated under different modifications, and in a deterministic as well as stochastic manner. In our recent studies (Lánský and Rodríguez, 1999a,b), it has been shown that the activity described by the two-compartment model is less sensitive to abrupt changes in stimulation, which is caused by a smoothing effect of the spatial arrangement. The delayed response of the two-point model is a natural consequence of the fact that the input takes place at a compartment different from that at which the output is generated. Furthermore, the model predicts serial correlation of interspike intervals, which is a phenomenon often observed in experimental data but not reproducible in single-point models under steady-state input. Finally, the model neuron shows a lower sensitivity to the

input intensity and a larger coding range than the single-point model. Now, we wish to show at least some of these properties, on a more complex model neuron.

The general case of a multicompartmental neuronal model with a branching structure is considered in the present contribution. The input, in contrast to the previous models, may take place at any compartment. The differential equations for the mean depolarization (the deterministic model) in all compartments for subthreshold stimulation are given. The firing frequency is calculated under the deterministic scenario and estimated for the stochastic variants. The implications for the rate coding properties of the model are derived. The analytical results are verified and illustrated by simulations.

2. Multicompartmental integrate-and-fire neuronal model with branching structure

2.1. The model

First, we formally describe the multicompartmental neuronal model based on the concept of leaky integration. Using the compartmental approach, a continuously distributed cellular body and dendritic tree is decomposed into small subunits for which the electrical properties, the capacitance and resistance, are considered fixed (for example, Perkel and Mulloney, 1978; Perkel et al., 1981; Edwards and Mulloney, 1984). Furthermore, there exists only one unique compartment (a trigger zone) in which generation of an action potential can take place. As soon as the variable characterizing this compartment (its membrane potential) crosses a firing threshold, S , for the first time, the action potential is generated and the variable is instantaneously reset to the resting level, here taken as zero. The other compartments aim at description of a dendrite and, due to the lack of their reset after the firing, they are governed by linear equations. Even if the dendritic system has a rather complex structure, the whole system will have its nonlinear behavior concentrated at one variable, the trigger zone depolarization, only. The equations for the membrane

potentials of all compartments follow from the Kirchhoff laws for a system composed of parallel (r, C) circuits separated by junctional resistances R , where r is the transmembrane resistance and C is its capacitance.

Using the example presented in Fig. 1, we can identify the structure of the model:

- the depolarization at the trigger zone is denoted by X_{tz} ;
- the potentials of the nearest (connected to the trigger zone compartment) are denoted $\{X_{i_1}\}$, $i_1 = 1, \dots, P^1$ where P^1 is the number of these compartments; in Fig. 1, $P^1 = 3$;
- analogously, for the second level of the compartments connected to X_{i_1} , the notation $X_{i_1 i_2}$ is used, $i_2 = 1, \dots, P^2_{i_1}$. In Fig. 1, $P^2_1 = 2$, $P^2_2 = 1$, $P^2_3 = 2$ and the number of higher branches is determined similarly ($P^3_{11} = 3$, $P^3_{12} = 2$, $P^3_{21} = 1$, and so on).
- for a model with maximum number of branching levels B , the potentials at this level are denoted by $X_{i_1 \dots i_B}$; in Fig. 1, $B = 5$.

The parameters (r, C) are indexed in the same way as the compartments and, analogously, the junctional resistance between compartments $i_1 i_2 \dots i_k$ and $i_1 i_2 \dots i_{k+1}$ is denoted by $R_{i_1 \dots i_k, i_1 \dots i_{k+1}}$. They can take different values for

different compartments. The following notation for constants is used throughout the rest of the paper $\alpha_{i_1 \dots i_k} = (r_{i_1 \dots i_k} C_{i_1 \dots i_k})^{-1}$, $\alpha_{i_1 \dots i_k, i_1 \dots i_{k+1}} = (R_{i_1 \dots i_k, i_1 \dots i_{k+1}} C_{i_1 \dots i_k})^{-1}$ and the constant input vector $\tilde{I} = (I_{tz}, I_{i_1}, I_{i_1 i_2}, \dots, I_{i_1 i_2 \dots i_B})^T$. The column vector of membrane potentials in all the compartments is denoted by \tilde{X} and a system of differential equations for its components can be written as follows.

- (i) For a compartment that is neither a trigger zone nor the terminal one,

$$\begin{aligned} & + \frac{d}{dt} X_{i_1 \dots i_k} + \alpha_{i_1 \dots i_k} X_{i_1 \dots i_k} \\ & = \alpha_{i_1 \dots i_{k-1}, i_1 \dots i_k} (X_{i_1 \dots i_{k-1}} - X_{i_1 \dots i_k}) \\ & \quad - \sum_{j=1}^{P^k_{i_1 \dots i_{k-1}}} \alpha_{i_1 \dots i_k, i_1 \dots i_{k-1} j} (X_{i_1 \dots i_k} - X_{i_1 \dots i_{k-1} j}) \\ & \quad + I_{i_1 \dots i_k} \end{aligned} \quad (1)$$

- (ii) The potential at the trigger zone is governed by the equation

$$+ \frac{d}{dt} X_{tz} + \alpha X_{tz} = \sum_{j=1}^{P^1} \alpha_j (X_{tz} - X_j) + I_{tz} \quad (2)$$

where α (respectively α_j) is the reciprocal value of the trigger zone time constant (respectively junctional time constant between the trigger zone and connected compartments).

- (iii) For the K terminal compartments

$$\begin{aligned} & + \frac{d}{dt} X_{i_1 i_2 \dots i_b} + \alpha_{i_1 \dots i_b} X_{i_1 i_2 \dots i_b} \\ & = \alpha_{i_1 \dots i_{b-1}, i_1 \dots i_b} (X_{i_1 \dots i_{b-1}} - X_{i_1 i_2 \dots i_b}) + I_{i_1 i_2 \dots i_b} \\ & \quad b = b_1, \dots, b_K \end{aligned} \quad (3)$$

This system of equations will be used for determining the properties of the model.

2.2. Coding properties of the model

For long-lasting constant stimulation, a regular firing is achieved under the condition $S < X_{tz}(\infty)$, where $X_{tz}(\infty)$ is the asymptotic value of the trigger zone potential in the absence of the firing

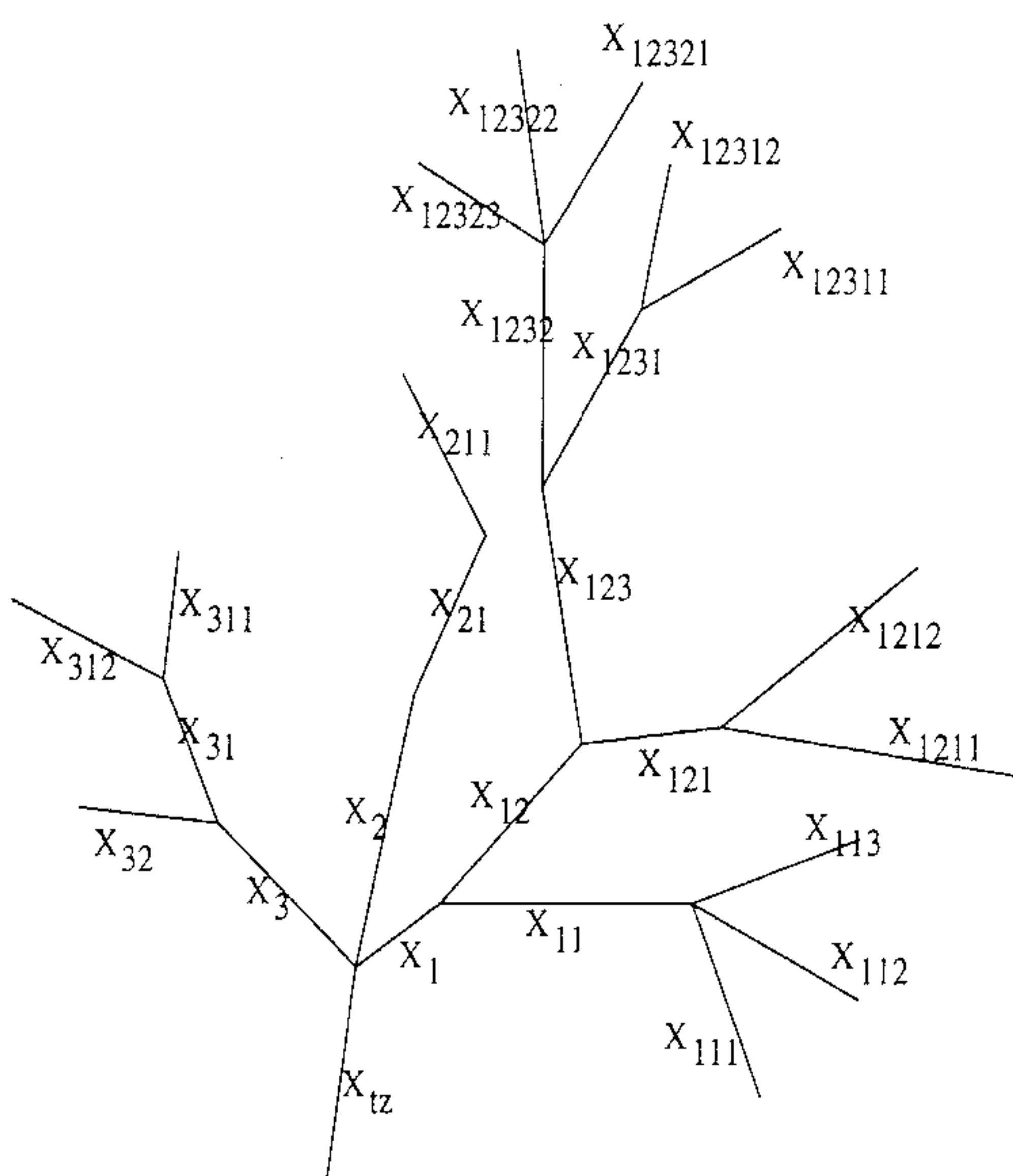


Fig. 1. Schematic representation of a neuron.

threshold. If t_j and t_{j+1} are the times of the j th and $(j+1)$ th spikes in the activity of the model neuron, the aim is to derive a relationship between the length of the interspike interval $(t_{j+1} - t_j)$ and the input \tilde{I} . To solve this problem, the system Eqs. (1)–(3) has to be investigated. Let $\tilde{X} = (X_{tz}, \hat{X}_d)^T$, where \hat{X}_d is a N_d dimensional vector of dendritic membrane potentials, similarly, let $\tilde{I} = (I_{tz}, \hat{I}_d)^T$ be the decomposition of the external inputs. Then, system Eqs. (1)–(3) takes the form $d\tilde{X}/dt = M\tilde{X} + \tilde{I}$ with the following initial conditions $X_{tz}(t_j) = 0$, $\hat{X}_d(t_j) = \hat{X}_d^j$. For all values of $t \in [t_j, t_{j+1}]$, the solution of Eqs. (1)–(3) is given by $\tilde{X}(t) = e^{M(t-t_j)}\tilde{X}(t_j) + S_{t_j}^t e^{M(t-s)}\tilde{I}ds$. In order to find the time of the next spike, under the stationary firing, namely to find t_{j+1} such that $X_{tz}(t_{j+1}) = S$, the additional condition $\hat{X}_d(t_{j+1}) = \hat{X}_d(t_j)$ has to be imposed on this solution.

Let $Q^j(t) = e^{M(t-t_j)}$ and consider the case in which an inverse matrix to M exists. Thus, we can write $\tilde{X}(t) = [Q^j(t) - 1]M^{-1}\tilde{I} + Q^j(t)\tilde{X}(t_j)$. Taking the decomposition of $Q^j(t)$ and M in accordance with the trigger zone and dendrite, we have

$$M = \begin{pmatrix} M_1 & M_2 \\ M_3 & M_4 \end{pmatrix} \quad \text{and}$$

$$Q^j(t) = \begin{pmatrix} Q_1^j(t) & Q_2^j(t) \\ Q_3^j(t) & Q_4^j(t) \end{pmatrix}$$

where M_1 (resp. $Q_1^j(t)$) is a scalar, M_4 (resp. $Q_4^j(t)$) is a $N_d \times N_d$ matrix, M_2 (resp. $Q_2^j(t)$) is a line vector and M_3 (resp. $Q_3^j(t)$) is a column vector, both with N_d components. A simple calculation gives the following two relations:

$$\begin{aligned} [Q_3^j(t_{j+1})M_2 + Q_4^j(t_{j+1})M_4 - M_4]\hat{X}_d^T(t_j) \\ = -Q_3^j(t_{j+1})I_{tz} - Q_4^j(t_{j+1})\hat{I}_d^T + \hat{I}_d^T + M_3S \\ [Q_1^j(t_{j+1})M_2 + Q_2^j(t_{j+1})M_4 - M_2]\hat{X}_d^T(t_j) \\ = -Q_1^j(t_{j+1})I_{tz} - Q_2^j(t_{j+1})\hat{I}_d^T + \hat{I}_{tz} + M_1S \end{aligned}$$

Solving this system with respect to $\hat{X}_d(t_j)$, we obtain the following N_d dimensional vector equation:

$$\begin{aligned} [Q_1^j(t_{j+1})M_2 + Q_2^j(t_{j+1})M_4 - M_2] \\ [Q_3^j(t_{j+1})M_2 + Q_4^j(t_{j+1})M_4 - M_4]^{-1} \end{aligned}$$

$$\begin{aligned} (-Q_3^j(t_{j+1})I_{tz} - Q_4^j(t_{j+1})\hat{I}_d^T + \hat{I}_d^T + M_3S) \\ = -Q_1^j(t_{j+1})I_{tz} - Q_2^j(t_{j+1})\hat{I}_d^T + \hat{I}_{tz} + M_1S \end{aligned} \quad (4)$$

which gives a closed relationship between interspike interval $(t_{j+1} - t_j)$ and the external input. We used a direct implementation of Eq. (4) as well as a numerical integration of system Eqs. (1)–(3). Both methods were compared and, in the examples presented later, they gave very similar results. Deriving the frequency of the spiking activity in the regular (stationary) regime from interspike intervals, for various external inputs, the rate coding properties of our model neuron can be deduced from this transfer function.

2.3. Examples

2.3.1. Example (a)

Previously, the relations between spiking frequency and different inputs were derived for a simple neuronal model composed of only two compartments with a single input at the dendrite, $\tilde{I} = (0, I_d)^T$, (Bressloff and Taylor, 1994; Lánský and Rodriguez, 1999a,b). This result can be directly obtained from Eq. (4). To simplify, let us assume that both compartments have the same time constants. In such a case,

$$M = \begin{pmatrix} -(z + \alpha_r) & \alpha_r \\ \alpha_r & -(z + \alpha_r) \end{pmatrix}$$

where α_r and α are the inverse junctional and transmembrane time constants. We denote

$$\begin{aligned} Q^j(t) = e^{\lambda_1(t-t_j)}[(M - \lambda_2)/(\lambda_1 - \lambda_2)] \\ + e^{\lambda_2(t-t_j)}[(M - \lambda_1)/(\lambda_2 - \lambda_1)], \quad \text{where } \lambda_1 \\ \text{and } \lambda_2 \text{ are the (negative) eigenvalues of } M; \lambda_1 = \\ -\alpha, \lambda_2 = -\alpha - 2\alpha_r. \text{ Then,} \end{aligned}$$

$$Q_3^j(t_{j+1}) = Q_2^j(t_{j+1}) = (e^{\lambda_1(t_{j+1}-t_j)} - e^{\lambda_2(t_{j+1}-t_j)})/2$$

$$Q_4^j(t_{j+1}) = Q_1^j(t_{j+1}) = (e^{\lambda_1(t_{j+1}-t_j)} - e^{\lambda_2(t_{j+1}-t_j)})/2$$

and Eq. (4) gives

$$\begin{aligned}
& [z_r Q_1^i(t_{j+1}) - (z + z_r) Q_2^i(t_{j+1}) - z_r] \\
& [-I_d Q_1^i(t_{j+1}) - I_d + z_r S] = \\
& [z_r Q_2^i(t_{j+1}) - (z + z_r) Q_1^i(t_{j+1}) + (z + z_r)] \\
& [-I_d Q_2^i(t_{j+1}) - (z + z_r) S]
\end{aligned}$$

This can be written in the form

$$\begin{aligned}
& S z (z + 2z_r) [1 - Q_1^i(t_{j+1})] \\
& + z_r I_d [Q_2^i(t_{j+1}) - Q_1^i(t_{j+1}) + 1] \\
& [Q_2^i(t_{j+1}) + Q_1^i(t_{j+1}) - 1] = 0.
\end{aligned}$$

This relationship can be obtained from the results presented by Bressloff and Taylor (1994), and is identical with formula (35) of Lánský and Rodríguez (1999a).

2.3.2. Example (b)

As a second example, let us take a model with four compartments: a trigger zone in series with a dendritic compartment that is connected to a couple of two parallel compartments, $\tilde{X} = (X_{tz}, X_1, X_{11}, X_{12})$. The system Eqs. (1)–(3) takes the form

$$\begin{aligned}
\frac{dX_{tz}}{dt} &= -(z + z_1)X_{tz} + z_1 X_1 + I_{tz} \\
\frac{dX_1}{dt} &= -(z + z_{1,11} + z_{1,12} + z_1)X_1 + z_{1,11}X_{11} \\
&\quad + z_{1,12}X_{12} + z_1 X_{tz} + I_1 \\
\frac{dX_{11}}{dt} &= -(z + z_{1,11})X_{11} + z_{1,11}X_1 + I_{11} \\
\frac{dX_{12}}{dt} &= -(z + z_{1,12})X_{12} + z_{1,12}X_1 + I_{12}
\end{aligned}$$

assuming z identical for all compartments. Fig. 2 shows the frequencies of spike emission as obtained from Eq. (4) (points) and from numerical simulation of Eqs. (1)–(3) (lines) (using a Euler method with step $dt = 0.01$ ms), for inputs applied only on the most distal compartments (dendrite 1 and dendrite 2), namely $I_{tz} = I_1 = 0$, $I_{11}, I_{12} \in [-5, 20]$ mV/s. The threshold value $S = 2$ mV and the time constants have been chosen of the order of 10 ms. The values of parameters are $z = 0.1$ ms⁻¹, $z_{1,11} = z_{1,12} = 1/16$ ms⁻¹, $z_1 = 0.9z_{1,11}$

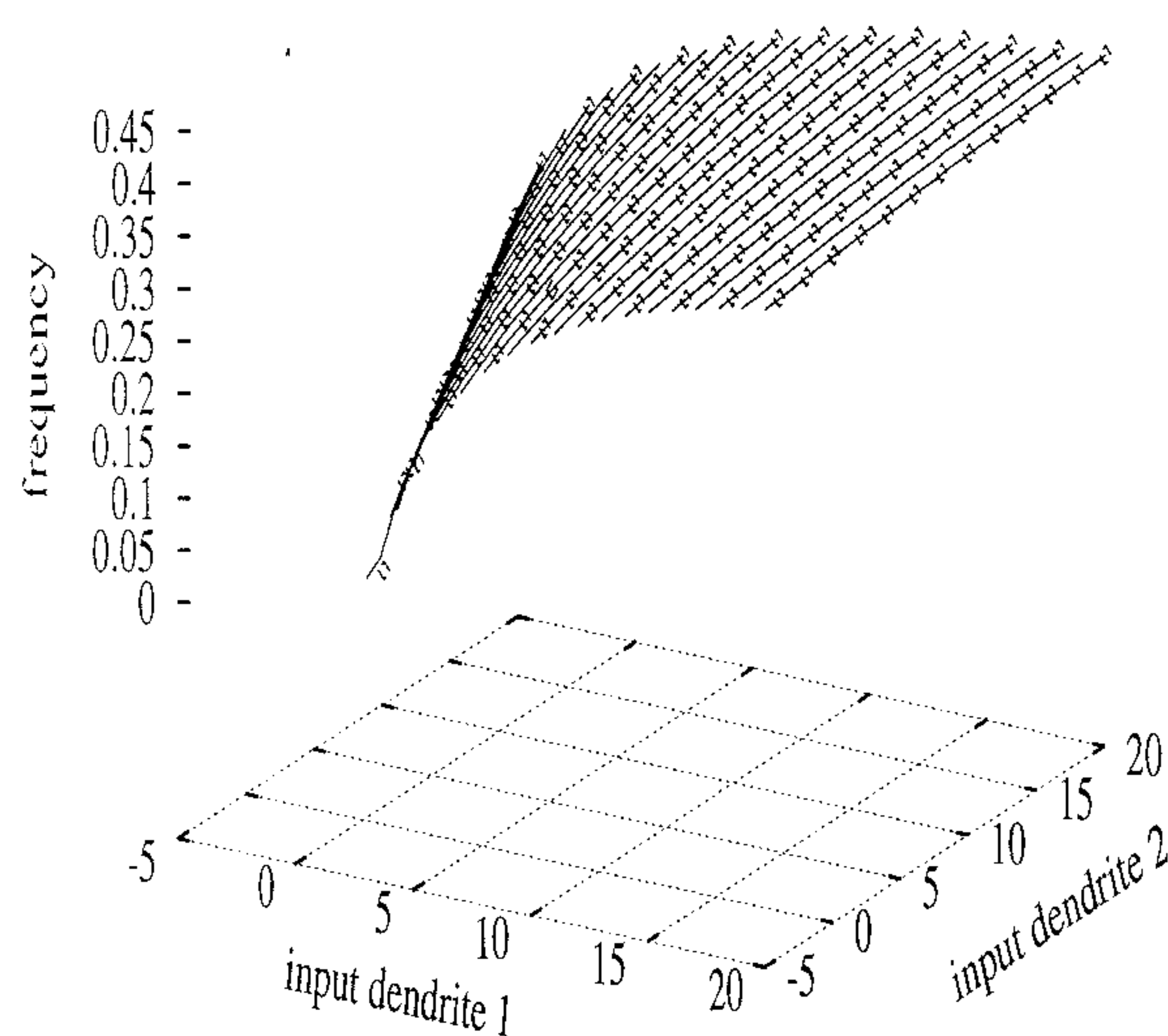


Fig. 2. Transfer function for inputs on two distal compartments

ms⁻¹, indicating a small variation of junctional time constants along compartments.

2.3.3. Example (c)

Let us consider a model with N compartments in series, $\tilde{X} = (X_{tz}, X_1, X_{11}, X_{111}, \dots, X_{1\dots1})$, with an input applied to the most distal compartment whose depolarization is $X_{1\dots1}$.

Fig. 3 shows how the transfer functions change in dependency on the number of compartments (the threshold S is kept fixed). The curves were obtained as solutions of Eq. (4) and verified by numerical integration. It follows from Fig. 3 that increasing, in this model, the number of compartments is accompanied by an increase of minimum signal intensity necessary to evoke a response.

3. The stochastic system

3.1. White noise perturbations and the filtering process

Let us now consider the model neuron under the action of constant deterministic inputs that are corrupted by white noise perturbations. For

subthreshold behavior, the deterministic system Eqs. (1)–(3) turns out to be a $N_d + 1$ dimensional Ornstein–Uhlenbeck process given by the stochastic differential equation

$$d\tilde{X}_t = (M\tilde{X}_t + \tilde{I}_0) dt + \tilde{\sigma} dW_t, \quad \tilde{X}_0 = \tilde{X}(0) \quad (5)$$

where \tilde{I}_0 is constant input and W_t is a standard Wiener process with amplitudes $\tilde{\sigma} = (\sigma_{I_2}, \sigma_{I_1}, \dots, \sigma_{I_1 I_2 \dots I_B})$ specific for different compartments. The mean behavior of the system of Eq. (5) is the same as the behavior of the deterministic system Eqs. (1)–(3). We will derive the second-order moments of \tilde{X}_t in order to investigate the coding characteristics of the model neuron. Denoting $K(t)$ the covariance matrix of the process \tilde{X}_t , $K(t) = E\{[\tilde{X}_t - E(\tilde{X}_t)][\tilde{X}_t - E(\tilde{X}_t)]^T\}$, it satisfies the differential equation $dK(t)/dt = MK(t) + K(t)M^T + \tilde{\sigma}\tilde{\sigma}^T$ with initial value $K_0 = E\{[\tilde{X}_0 - E(\tilde{X}_0)][\tilde{X}_0 - E(\tilde{X}_0)]^T\}$, (Arnold, 1974). The solution of this equation is

$$K(t) = e^{Mt} K_0 e^{Mt} + \int_0^t e^{M(t-s)} \tilde{\sigma} \tilde{\sigma}^T e^{M(t-s)} ds \quad (6)$$

As an example of application of this formula, we consider the last model of Section 2.3.3 (N compartments in series). For the elements of $K(t)$

$$K_{ij}(t) = [Q(t)K_0Q(t)]_{ij} + \sigma^2 \int_0^t Q_{iN}(t-s) Q_{Nj}(t-s) ds \quad (7)$$

where $Q(t) = \sum_k e^{\lambda_k t} \Pi_{j \neq k} [(M - \lambda_j)/(\lambda_k - \lambda_j)]$ and λ_i , $i = 1, \dots, N$ are the (negative) eigenvalues of the (symmetric) $N \times N$ matrix M . Integration in Eq. (7) can be performed, and the limiting value of $K_{mm}(t)$ as $t \rightarrow \infty$, which is the asymptotic value of the variance of the depolarization of the m th compartment, is obtained as:

$$\text{Var}(X_m(\infty)) = -\sigma^2 \left(\sum_{k=1}^N \frac{(L_{Nm}^k)^2}{2\lambda_k} + \sum_{(i,j)(i \neq j)} \frac{L_{Nm}^i L_{Nm}^j}{(\lambda_i + \lambda_j)} \right) \quad (8)$$

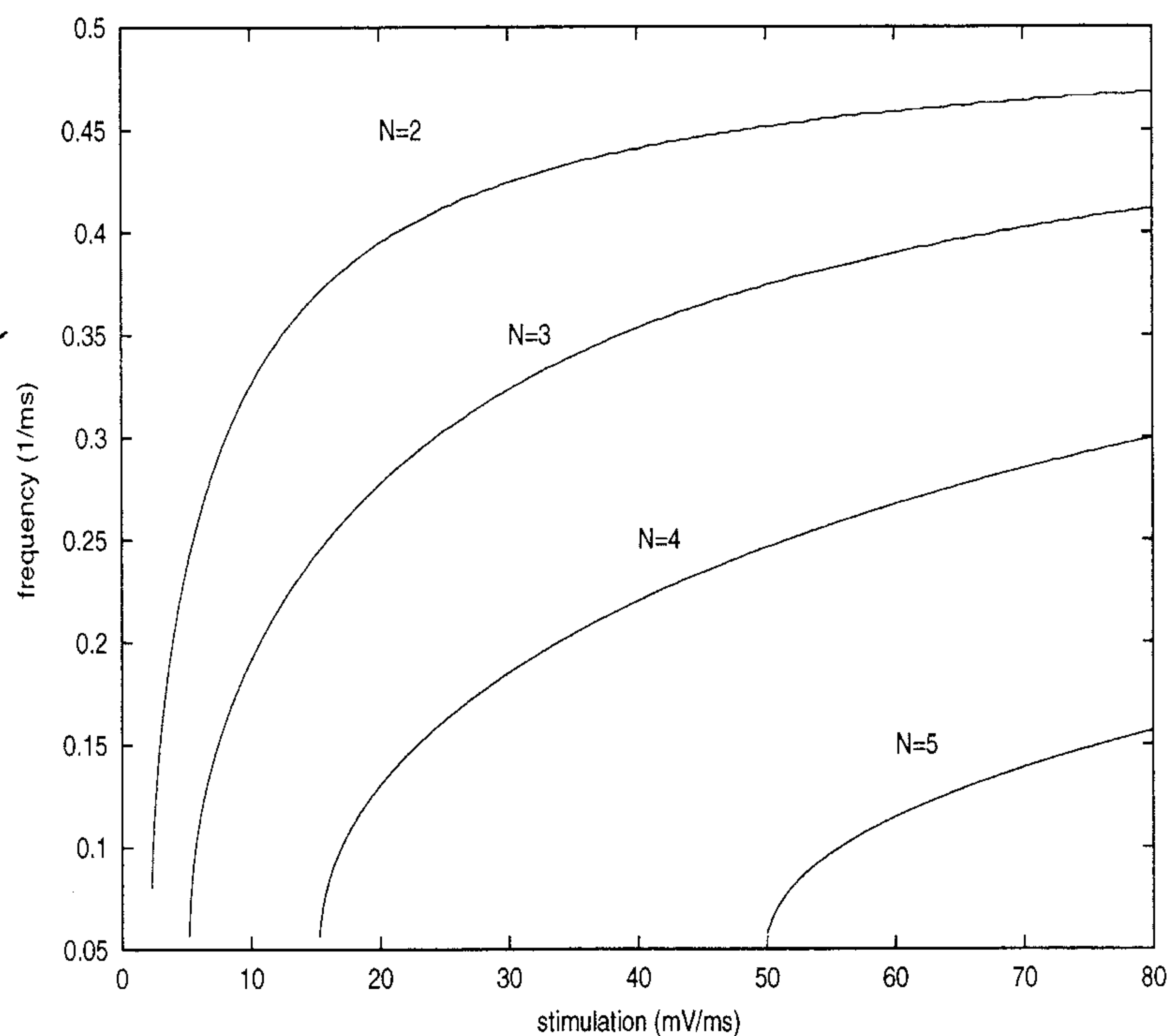


Fig. 3. Transfer function for a model with N compartments in series. The reciprocals of time constants α_j between compartments j and $j+1$ are such that $\alpha_{j+1} = (1/1.01)\alpha_j$ with $\alpha_1 = 0.2 \text{ ms}^{-1}$; the firing threshold S and constant z are the same as in Fig 2.

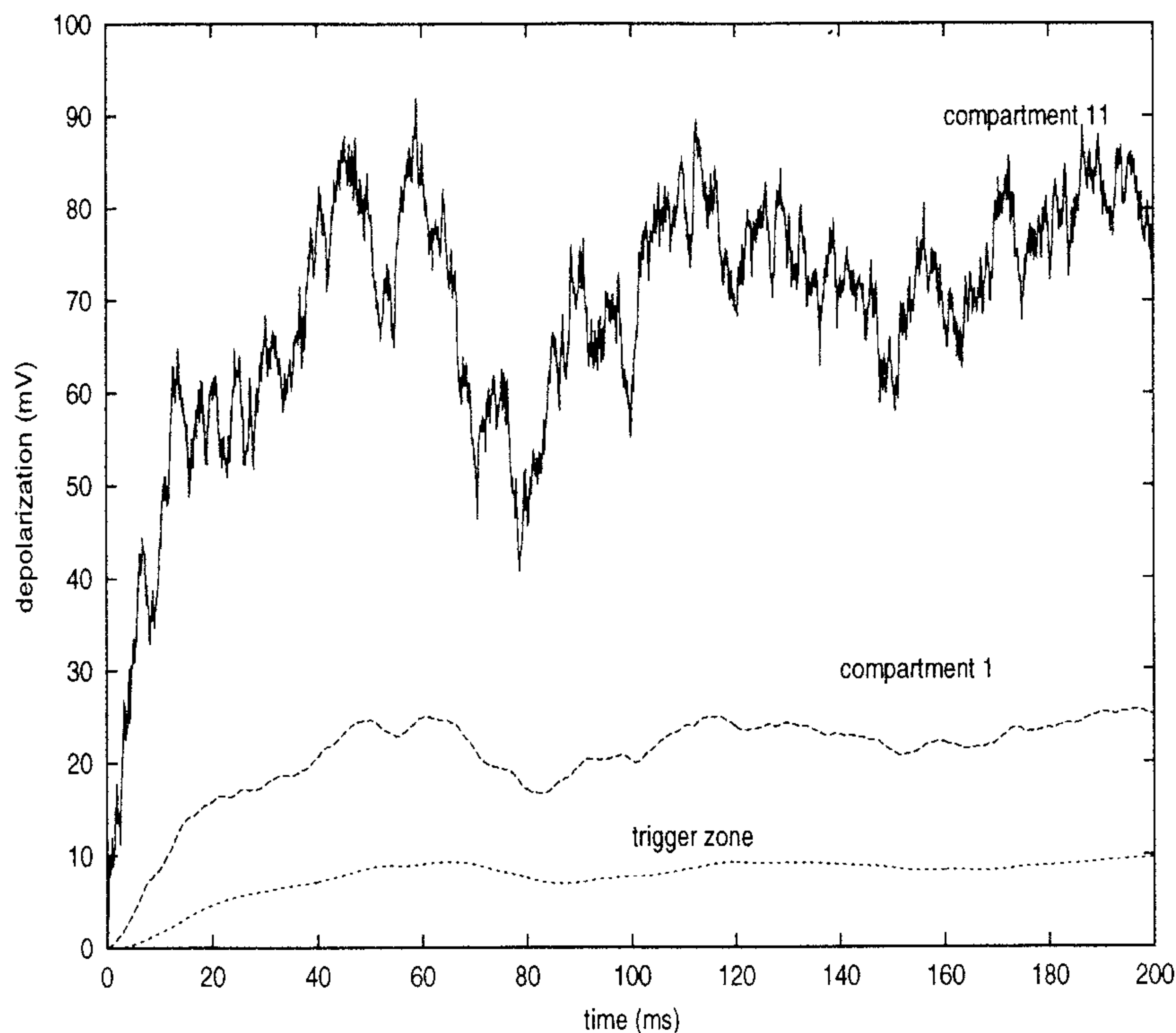


Fig. 4. Trajectories of depolarizations in the stochastic model. The parameters are $\sigma_{11} = 5.0 \text{ mV } \sqrt{\text{ms}}$, $\alpha = 0.1 \text{ ms}^{-1}$, $\alpha_r = 1/16 \text{ ms}^{-1}$, $I_d = 10 \text{ mV ms}^{-1}$.

where L_{Nm}^k are elements of $L^k = \Pi_{j \neq k} [(M - \lambda_j) / (\lambda_k - \lambda_j)]$. The asymptotic covariances can be obtained in the same way. It follows from Fig. 4, in which the behavior of the depolarization in this model is illustrated ($N=3$, $\tilde{X} = (X_{tz}, X_1, X_{11})^T$ and $\tilde{\sigma} = (0, 0, \sigma_{11})^T$), that a decrease of stochastic fluctuations occurs from the dendritic part to the trigger zone. This decrease of variability along three compartments can be analyzed by using Eq. (8). Of course, this effect occurs also for the two-compartment model for which the formulas are simpler and thus presented here. In that case,

$$M = \begin{pmatrix} -(z + \alpha_r) & \alpha_r \\ \alpha_r & -(z + \alpha_r) \end{pmatrix}$$

with eigenvalues $\lambda_1 = -z$, $\lambda_2 = -z - 2\alpha_r$, where α and α_r correspond to the reciprocals of time constants for transmembrane current and for current between the trigger zone and the other (dendritic) compartment. We have

$$\text{Var}(X_{tz}(\infty)) = -\frac{\sigma^2}{4} \left(\frac{1}{2\lambda_1} + \frac{1}{2\lambda_2} - \frac{2}{(\lambda_1 + \lambda_2)} \right)$$

and

$$\text{Var}(X_1(\infty)) = -\frac{\sigma^2}{4} \left(\frac{1}{2\lambda_1} + \frac{1}{2\lambda_2} + \frac{2}{(\lambda_1 + \lambda_2)} \right)$$

The decreasing variability from the dendrite to the trigger zone follows clearly from these formulas; these results were obtained by another method by Lánský and Rodríguez (1999a).

The filtering of white noise from distal to proximal compartment is a rather natural mechanism due to the passive transfer of current between neighboring compartments. These analytical results concern two-compartment systems. However, Eq. (8) may be a useful tool to analyze this filtering for models with N compartments in series. The most general case, with arbitrary branching structure, can be handled directly using Eq. (6).

3.2. Poissonian inputs and mean transfer functions

The continuous trajectories of the membrane depolarization are the main characteristic of the already described multicompartmental model. The reason is that the model does not consider the soma of the neuron as its specific part, where the contributions to the membrane depolarization are not so frequent (not so many synaptic endings are located there as on the dendrite) but of substantial size. While the input at the dendrite causes small changes of the membrane potential, and thus the system is well characterized by the white noise, it would be natural to expect that the incoming signal located at the soma and near the soma has discontinuous effect on the depolarization. This leads to the investigation of a model neuron where the stochastic part also includes Poissonian inputs. Let us consider the following system:

$$d\tilde{X}_t = (M\tilde{X}_t + \tilde{I}_0) dt + d\tilde{\zeta} \quad (9)$$

where \tilde{I}_0 is constant input, $\tilde{\zeta} = (\zeta_{t_z}, \zeta_{i_1}, \zeta_{i_1 i_2}, \zeta_{i_1 i_2 i_3}, \dots, \zeta_{i_1 i_2 \dots i_B})^T$ is a multidimensional stochastic process with components of the form $\zeta_j = \sigma_j W_j + a_j N_j^+ + b_j N_j^-$. Here, σ_j is the amplitude of the white noise part with W_j as Brownian motion acting on the j th compartment, and N_j^+ (resp. N_j^-) are (independent) Poisson processes with intensities λ_j^+ (resp. λ_j^-) that drive synapses on this compartment for which excitatory and inhibitory postsynaptic potentials have their amplitudes a_j (resp. b_j). For this neuronal model, one can derive a relation between estimate of the mean interspike interval and the constant input \tilde{I}_0 . This can be done by using Eq. (4), with \tilde{I} identified as $\tilde{I} = \tilde{I}_0 + \tilde{K}$, where $K_j = a_j \lambda_j^+ + b_j \lambda_j^-$. The transfer functions deduced in this way were compared with those obtained by simulation of system of Eq. (9). Here, only a simple example is presented, in which the neuron is composed of three compartments in series, $\tilde{X} = (X_{t_z}, X_1, X_{11})^T$, with constant plus white noise input acting on X_{11} and Poissonian impulses impinging on X_1 . Using the same notation for the parameters as before, the stochastic system of Eq. (9) is

$$dX_{11} = [-(\alpha + \alpha_{1,11})X_{11} + \alpha_{1,11}X_1 + I_{11}] dt + \sigma_{11} dW$$

$$dX_1 = [-(\alpha + \alpha_{1,11} + \alpha_1)X_1 + \alpha_{1,11}X_{11} + \alpha_1 X_{t_z}] dt + a_1 dN_1^+ + b_1 dN_1^-$$

$$dX_{t_z} = [-(\alpha + \alpha_1)X_{t_z} + \alpha_1 X_1] dt$$

The input–output functions for this system are plotted in Fig. 5, where a comparison with the single-compartment model (with the same time constant α^{-1}) is also shown (curve on the left). The dashed curve on the right corresponds to the deterministic case ($\sigma_{11} = a_1 = b_1 = 0$). The dashed curve in the middle corresponds to the mean frequencies of the stochastic system as obtained from Eq. (4). Finally, the crosses were obtained from simulated mean interspike intervals.

A numerical procedure of Euler type was used in order to solve this set of stochastic equations. For the Brownian part, in the first equation, at each time step of length Δt , a random variable $z = \sigma_{11} \sqrt{\Delta t} u$ was generated where u is a Gaussian variable of zero mean and variance equal to one. In the second equation, a set of exponentially distributed random time intervals between jump instants, with parameters λ_1^+ (resp. λ_1^-), was generated. The process $N_1^+(t)$ (resp. $N_1^-(t)$) was built with jumps of amplitude unity at the jump instants. At each time step of length Δt , at time t , the new value of X_1 , for the Poissonian part, was achieved by adding $a_1[N_1^+(t)(t + \Delta t) - N_1^+(t)(t)]$ and $b_1[N_1^-(t)(t + \Delta t) - N_1^-(t)(t)]$ to the preceding value.

4. Conclusions

The well-known one-point integrate-and-fire neuronal model has been extensively studied in the biophysical literature because of availability of analytical solutions related to it, in the deterministic and stochastic cases. By studying its multidimensional extension, we show that this property for describing spiking neural activity is conveniently preserved. The behavior of the multicompartmental model, being biologically more realistic, because of the introduction of

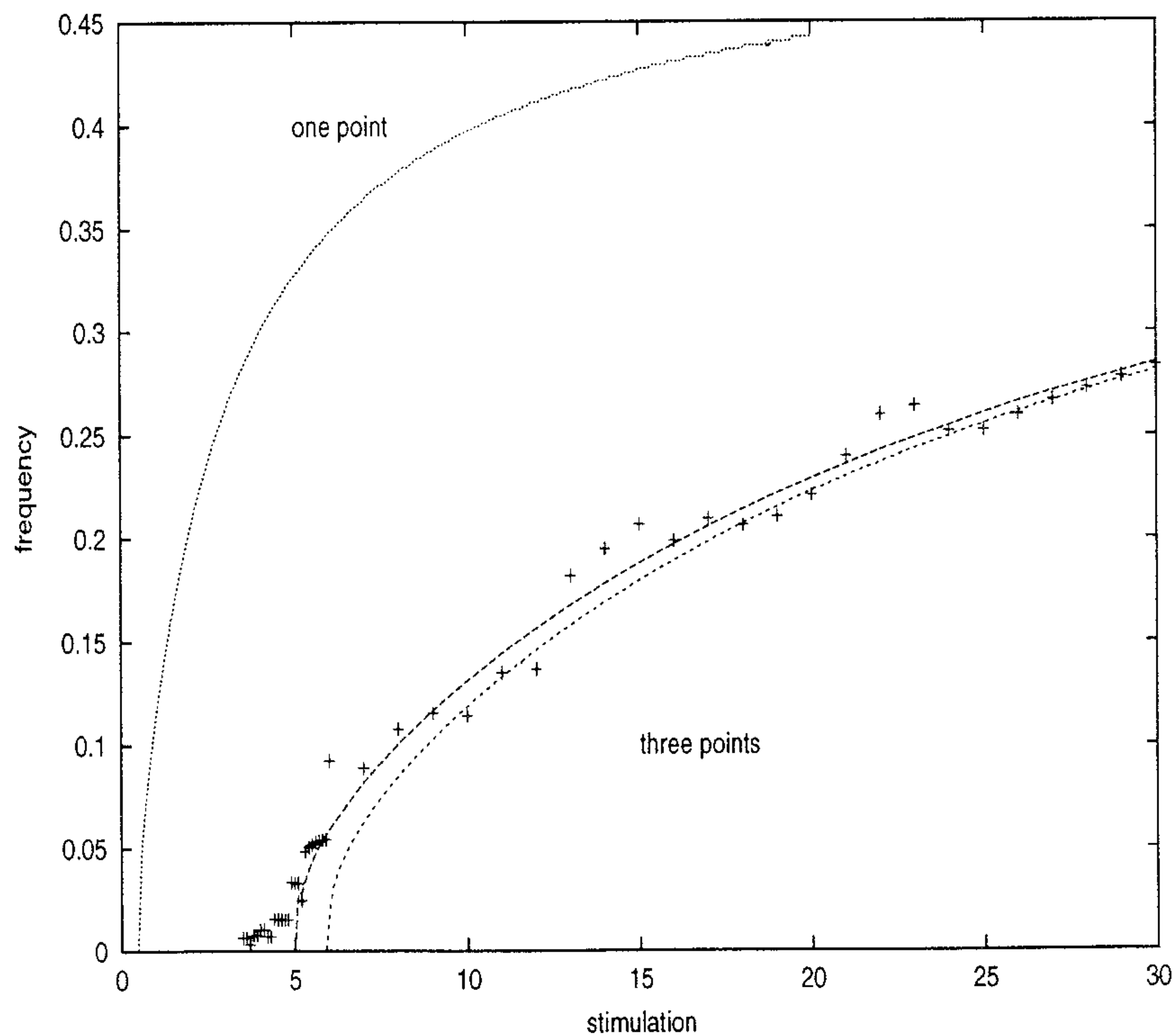


Fig. 5. Transfer functions for stochastic models with Poissonian and white noise stimulations. The parameters are $a_1 = 5$ mV, $b_1 = -2$ mV, $\lambda_1^+ = 0.1$ ms $^{-1}$, $\lambda_1^- = 1/12$ ms $^{-1}$, $\sigma_{11} = 2$ mV/ $\sqrt{\text{ms}}$, $S = 5$ mV, $\alpha = 0.1$ ms $^{-1}$, $\alpha_1 = \alpha_{1,11} = 1/16$ ms $^{-1}$.

possibly complex dendritic structure, can still be analyzed using classical vectorial deterministic and stochastic calculus.

It was generally considered that the coding range of the one-point integrate-and-fire model was too narrow and the threshold input intensity for spike emission was too low as compared with those experimentally observed. The introduction of spatial structure in the model removes, at least partly, these drawbacks. When noise is considered in the input and acts on the dendritic part, a filtering occurs naturally from dendrites to the zone of spike generation. This makes the neuron more robust against fluctuating perturbations. Thus, the multi-compartmental integrate-and-fire models, as compared with more complex and more realistic conductance-based models that can be generally investigated only numerically, may be viewed as convenient prototypes for the analytical study of spiking neurons.

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