



Neural firing rate model with a steep firing rate function

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ABSTRACT

In this study we justify rigorously the approximation of the steep firing rate functions with a unit step function in a two-population neural firing rate model with steep firing rate functions. We do this justification by exploiting the theory of switching dynamical systems. It has been demonstrated that switching dynamics offer a possibility of simplifying the dynamical system and getting approximations of the solution of the system for any specific choice of parameters. In this approach the phase space of the system is divided into regular and singular domains, where the limit dynamics can be written down explicitly. The advantages of this method are illustrated by a number of numerical examples for different cases of the singular domains (i.e. for black, white and transparent walls) and for specific choices of the parameters involved. General conditions have been formulated on these parameters to give black, white and transparent walls. Further, the existence and stability of regular and singular stationary points have been investigated. It has been shown that the regular stationary points (i.e. stationary points inside the regular domains) are always stable and this property is preserved for smooth and sufficiently steep activation functions. In the most technical part of the paper we have provided conditions on the existence and stability of singular stationary points (i.e. those belonging to the singular domains). For the existence results, the implicit function theorem has been used, whereas the stability of singular stationary points is addressed by applying singular perturbation analysis and the Tikhonov theorem.

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1. Introduction

Neurons carry information from one part of the brain to another, which can be described by various types of mathematical models [1–7]. The firing rate models have the coarsest level of detail. Here the probability for firing action-potential is modeled. Existing firing rate models consist of sets of differential equations, e.g. for synaptic-drive models [8–12] each of the differential equations has the following general form:

$$\tau_j \frac{du_j}{dt} = -u_j + P_j \left(\sum_k \omega_{jk} u_k \right). \quad (1)$$

Here u_j is the synaptic drive from the neuron j , ω_{jk} is the synaptic weight from the presynaptic element k to the post synaptic element j , τ_j is the time constant representing the decay of the synaptic drive u_j following the action potential in the element j . The function P_j represents the firing-rate function converting the net synaptic drive to the firing rate [8,10]. These firing

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rate functions are given as sigmoidal functions i.e. they constitute a one-parameter family of increasing functions in the state variables, parameterized by the steepness of the function, they assume values between 0 and 1 and they approach the unit step function in the limit of infinite steepness.

Rate equation models also occur in other branches of mathematical biology, for example in the study of gene regulatory networks [13–19]. A simple gene regulatory network model is given as

$$\frac{dy_i}{dt} = F_i(Z_1, Z_2, \dots, Z_n) - G_i(Z_1, Z_2, \dots, Z_n)y_i, \quad i = 1, 2, \dots, n, \quad (2)$$

and the functions F_i and G_i are the production and the relative degradation rates of gene i , respectively, and y_i stands for the gene product concentrations. The functions Z_j , which are referred to as the activation functions, are modeled by means of sigmoidal functions, just as the firing rate functions in the model (1). The model (2) has been studied in this limit in [13,14,20]. In this case the right hand side of (2) possesses jump discontinuities along certain surfaces in the phase space. These surfaces are referred to as the singular domains of the dynamical system. In the rest of the phase space (referred to as the regular domains), the dynamical system (2) turns into a system of coupled linear differential equations.

The problem studied in those papers consists in proving uniform convergence of the solutions of (2) when the threshold functions become infinitely steep. This gives, in particular, an algorithm of gluing the limit solutions in the regular domains together with those in the singular domains. The key tool in this analysis is the theory of switching dynamical systems and singular perturbation theory [13,14].

This serves as a background for the present study. Our aim is to justify rigorously the approximation of the steep firing rate functions with a unit step function in the firing rate model (1). We do this justification in a way analogous to [13,14] for the gene regulatory networks of the type (2).

The paper is organized in the following way:

In Section 2, we introduce the two-population (excitatory and inhibitory) firing-rate model and derive an autonomous dynamical system using a linear chain trick [8,21,22]. In Section 3, we establish the platform to investigate the dynamics of the two-population firing rate model using the theory of switching dynamical systems. Some notions from this theory are defined in this section, e.g. regular domains, singular domains and stationary points corresponding to these domains (regular and singular stationary points). We transform the actual dynamical system from the (u_e, u_i) -coordinates to the new net input variables (x, y) in Section 4. This transformation makes it possible to perform the stability analysis of the singular stationary point using singular perturbation theory. Next, in Section 5, the existence of regular stationary points (RSP) and singular stationary points (SSP) is addressed. We explore the existence of regular stationary points for finitely steep activation functions. We also formulate the conditions on the parameters providing the existence of singular stationary points. In Section 6, we investigate the asymptotic stability of regular and singular stationary points. We also study the dynamics along black walls by applying singular perturbation theory and the Tikhonov theorem [23,24]. Section 7 contains the main conclusions and an outlook.

2. Model

The starting point is the simplified two-population synaptic drive model with excitatory and inhibitory activities given by the Volterra equations

$$u_e = \alpha_e * Z_e(\omega_{ee}u_e - \omega_{ei}u_i), \quad (3a)$$

$$u_i = \alpha_i * Z_i(\omega_{ie}u_e - \omega_{ii}u_i), \quad (3b)$$

where

$$(\alpha_m * Z_m(x))(t) = \int_{-\infty}^t \alpha_m(t-s)Z_m(x(s))ds. \quad (4)$$

Here α_m for $m = e, i$ are the temporal kernels showing the impact of past neural firing on the present activity levels in the network [8,11,12]. These kernels are typically parameterized by a single time constant. In this study the temporal kernels are modeled by means of exponentially decaying functions

$$\alpha_e(t) = \exp(-t), \quad \alpha_i(t) = \frac{1}{\tau} \exp\left(-\frac{t}{\tau}\right). \quad (5)$$

The functions u_m for $m = e, i$ in (3) are the average activity levels for excitatory and inhibitory populations. τ is the relative inhibition time, which is given as the ratio between inhibitory to excitatory time constants. The connectivity parameters ω_{mn} ($m = e, i$) model the connection strength (from n to m cells) in the network. In this study, the parameters are assumed to satisfy the following conditions:

$$0 < \omega_{mn} \leq 1, \quad 0 < \theta_m \leq 1, \quad \tau > 0. \quad (6)$$

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