Nonlinear Analysis: Hybrid Systems 22 (2016) 178–190

Contents lists available at ScienceDirect

Nonlinear Analysis: Hybrid Systems

journal homepage: www.elsevier.com/locate/nahs

Spatio-temporal averaging for a class of hybrid systems and application to conductance-based neuron models

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ARTICLE INFO

Article history:
Received 25 September 2014
Accepted 18 March 2016

Keywords:
Stochastic averaging
Hybrid systems
Bio-physiological model

ABSTRACT

We obtain a limit theorem endowed with quantitative estimates for a general class of infinite dimensional hybrid processes with intrinsically two different time scales and including a population. As an application, we consider a large class of conductance-based neuron models describing the nerve impulse propagation along a neural cell at the scales of ion channels.

1. Introduction

This article aims to study a class of infinite dimensional hybrid processes $(Z_t^{\varepsilon,N}, t \geq 0)$ with intrinsically two different time scales, this fact being emphasized by the presence of the parameter ε, and including a population whose size's parameter is N. We show the convergence of these models to a limit model when ε and N go to zero and infinity, respectively, and with a certain relative speed. This corresponds to considering an infinite population whose fast component is infinitely accelerated. Our main motivation for studying such a situation comes from mathematical neurosciences and more specifically from conductance-based neuron models describing the generation and propagation of a nerve impulse along a neural cell at the scale of ion channels. Our main result stands in this case a sufficient condition under which the use of reduced (or averaged) conductance-based neuron models is justified.

Hybrid systems, combining discrete and continuous dynamics, have been actively studied in applied mathematics and statistical physics. As highlighted in the recent review [1], they arise in a great variety of applications from bio-physiology through, as already mentioned, the modeling of excitable cells (neural or cardiac cells) [2], the description of molecular motors [3,4], or the study of social networks [5], to the development of cyber–physical systems [6–9], that is systems that interact tightly with the physical world and human operators such as in air traffic control [10]. In this latter line, as mentioned in [11], complex cyber–physical systems must adapt in case of random structural perturbations, such as failures or component degradation. This is why such systems have been the object of numerous development in control and optimization, for which they are particularly well adapted. For instance, advances in the understanding of such complex continuous–discrete models have been performed in the context of piecewise deterministic Markov processes, see [11–14], and in the context of mean field games, see [15–18].

The hybrid processes that we consider can be described as follows. They have two distinct components, $Z^{\varepsilon,N} = (X^{\varepsilon,N}, Y^{\varepsilon,N})$, one continuous $(X^{\varepsilon,N})$ and the other one of pure jumps $(Y^{\varepsilon,N})$. The continuous component is often referred as the macroscopic one in neural modeling whereas the term microscopic stands for the component of pure jumps. Between two jumps of this discrete component, the continuous component evolves according to an abstract evolution equation. When

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http://dx.doi.org/10.1016/j.nahs.2016.03.003

the jump component updates its current value, the parameters of the evolution equation are also updated; and so on. The evolution that we just described is that of a piecewise deterministic process. We will work more specifically in the context of Piecewise Deterministic Markov Process (PDMP). The study of such hybrid processes was carried out comprehensively in the works [19,20] concerning the finite dimension, that is when the evolution equation for the continuous component is an ordinary differential equation (ODE). In the case where the ODE becomes a partial differential equation (PDE), and more generally in our setting an abstract evolution equation, the theory has been established in [21].

In recent years, these processes have been widely studied in terms of averaging and law of large numbers. That is, we consider either that the microscopic component evolves faster than the macroscopic component, or that the size of the internal population of the model goes to infinity. On the one hand, regarding the class of processes that we consider, limit theorems when N goes to infinity such as the law of large numbers and the central limit theorem have been obtained in [22–25]. On the other hand, the study of the averaging and the associated fluctuations when ε goes to zero was carried out in [26,27]. Our goal in the present paper is to reconcile the two approaches. Considering a general class of PDMP's with intrinsically two time-scale and a size parameter, we obtain a result of law of large numbers type with an explicit rate of convergence, for the joint convergence in (ε, N). The mathematical tools we use in the proof belong to the singular perturbation theory throughout the study of a Poisson equation, and to general probabilities through the study of a martingale problem. Regarding the results previously obtained for this kind of models, and especially the cited averaging results, the main novelty comes from obtaining quantitative bounds for convergence thanks to the use of exponential inequalities for martingales. These quantitative estimates are required to infer a criterion on the relative speed between the time-scale parameter ε and the population size N, allowing joint convergence.

Our main motivation is the study of hybrid models describing the generation and propagation of a nerve impulse along a neuron. Indeed, this action potential evolves along the nerve fiber (or axon) according to a partial differential equation whose parameters are updated based on the current state of the ion channels present all along the axon. These ion channels allow ion exchange between the inside and outside of the cell. They are located all along the axon in discrete sites, forming a population of size N. Their mechanism of opening and closing, depending on the local action potential of the cell membrane, is responsible for the generation and propagation of nerve impulses (on these questions, see the comprehensive book [28]). Note that in the framework of mean field games, the ion channels can be seen as microscopic players behaving rationally with respect to their preferences (permeability to potassium ions for instance) and to the global information of macroscopic nature provided here by the membrane potential. It has been shown that certain ionic channels evolve more rapidly than others, and it is now common to include a small parameter ε in the model to account for this characteristic. Therefore, these neuron models fall naturally into the class of PDMP's that we propose to study. One challenge in the modeling of phenomena including multiple time and space scale, is to obtain reduced models easier to handle, both analytically and numerically. The reduced models are then used as appropriate approximate models. It is then quite important to know when such approximations are valid. Through our study, we obtain a sufficient condition under which the neuron model with the two parameters ε and N converges to a limit as these parameters go respectively to zero and infinity. This condition involves the relative speed of convergence between the two different scales ε and N. Heuristically, the result is as follows: somehow, it is enough that the ion channels evolve faster than the population grows.

The plan of the paper is the following. In Section 2, we define the model of interest and state our main results. Section 3 is devoted to the application of our results to conductance-based neuron models, our first motivation. The proof of our main results is presented in Section 4.

2. Presentation of the model and main results

Let H be a separable Hilbert space and H^* its dual. We denote by $(\cdot,\cdot)$ the inner product on H and by $\|\cdot\|$ the associated norm. The duality bracket between H and H^* is denoted by $\langle\cdot,\cdot\rangle$. We define a sequence $(E_N)_{N\in\mathbb{N}}$ of finite spaces with increasing cardinality such that $E_N \subset E_{N+1}$ according to the canonical injection.[1] For any $x \in H$ we define an intensity matrix $Q^N(x) = (Q^N_{y_1y_2}(x))_{(y_1,y_2)\in E_N\times E_N}$.

Assumption 1. We assume that for each $x \in H$, there is a unique quasi-stationary probability measure $\mu_N(x)$ on E_N associated to $Q^N(x)$ such that

$$\mu_N(x)Q^N(x) = 0.$$

Moreover, we assume that the jump rates are all uniformly bounded:

$$\exists [Q] \in \mathbb{R}_+\ \forall N \in \mathbb{N}\ \forall (y_1, y_2, x) \in E_N \times E_N \times H \quad |Q^N_{y_1y_2}(x)| \le [Q]. \tag{1}$$

The term quasi-stationary refers to the fact that the stationary measure $\mu_N(x)$ actually depends on the external variable x. We will use this intensity matrix to define the jumping component of the studied process. For example, in the neuron

[1] The canonical injection is given by $\iota : i \in E_N \mapsto (i, \mathbf{0}) \in E_{N+1}$ where $\mathbf{0}$ is the zero of $\mathbb{R}^{|E|_{N+1}-|E|_N}$.